Diet selection of and habitat suitability for black rhino in Augrabies Falls National Park, South Africa

M.Sc. thesis by Kenneth G. Buk
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Front page: Female 1 (Shibula) with her calf in the shade of *Acacia mellifera* shrubs and heads in a *Monechma spartioides* with some of Waterval's mountains in the background**.**

Preface

This thesis is presented in partial fulfilment for the award of a M.Sc. in biology at the University of Copenhagen, Denmark. Its main body consists of three self-contained papers, which at the time of writing were unpublished. The papers are preceded by an introduction which lays out the background for and objectives of the study. The papers are followed by brief conclusions to the cluster of papers and a short discussion on further research needs.

The papers presented here form part of a larger study which includes similar research in two other parks in the arid part of South Africa: Karoo and Vaalbos National Park.

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Any statement in this document is purely the responsibility of the author, and not of any other person or any organisation.

This dissertation is dedicated to my late father. He deserves credit for, among other things, building and supporting my interest in wildlife biology.

Introduction

This dissertation deals with diet selection and habitat suitability of the black rhino. However, the dissertation can be read in a wider context. Many of the problems and approaches are common to some or all species of large, wild herbivores, most of which are in need of active conservation. Furthermore, studies of the ecology and conservation biology of today's black rhinos offer a hint of the charismatic keystone species and ecosystem dynamics we lost by eradicating rhinos - and other large mammals - from Europe as well as much of Asia and Africa. It is also a reminder to take much better care of the species of large mammals we have left.

The rise of giants

The oldest rhino fossils are from the middle Oligocene (37-58 million years ago) and fossils of over 60 genera of rhinos are known (Prothero, 1993), especially from the Miocene (24-37 m.y.a.) and Pliocene (5-24 m.y.a.)(Estes, 1990). Rhinos adapted to most herbivore niches and included the largest known terrestrial mammal species 6 metres tall and weighing approximately 20 000 kg (Prothero, 1993). The two surviving species of African rhino, black rhino (*Diceros bicornis*) and white rhino (*Cerathotherium simum*), are sister groups with approximately 2 % DNA sequence divergence (Morales & Melnick, 1994). The white rhino evolved into a specialised grazer and the black rhino into a specialised browser. Black rhino date back 10 m.y. in the fossil record of Africa and the Mediterranean (Prothero, 1993). The black rhino has evolved regional differences and has been divided into 4 subspecies or ecotypes.

- and their fall

Between 10 000 and 30 000 years ago - very recently and suddenly in terms of rhino evolution - all species of rhinos inhabiting Europe and Northern Asia became extinct as a consequence of increased hunting pressure from humans, possibly exacerbated by climate change (Owen-Smith, 1988). In Europe forest rhino (*Dicerorhinus kirchbergensis*) and steppe rhino (*Dicerorhinus hemitoechus*) were eradicated first around the same time as forest elephant (*Elephas antiquus*), followed by the cold-adapted woolly rhino (*Coelodonta antiquititatis*) and woolly mammoth (*Mammuthus primigenius*). Today only five species of rhinos in three genera exist and almost the entire rhino family (Rhinocerotidae) is endangered. The white rhino is the only rhino species not listed as critically endangered by IUCN (The World Conservation Union) because the southern sub-species made a remarkable recovery from a single South African population of about 100 in the 1920's to 8 465 by 1997, thereby offering a ray of hope and inspiration (Groombridge, 1993; Emslie & Brooks, 1999).

The African browsing rhino

The black rhino is a grey, almost hairless perissodactyl ungulate with an adult weight of 900 – 1 362 kg and a shoulder height of 140-170 cm. The brain is relatively small and eyesight is poor, but senses of smell and hearing are very acute. For intra-specific conflict and predator defence it has two – rarely three – solid horns of keratin, which grow continually up to lengths of 132 cm (Estes, 1990). The upper triangular, flexible lip is used for grasping food, which includes a wide range of trees, shrubs and forbs, but almost no grass (Goddard, 1968; Goddard, 1970; Hall-Martin *et al.*, 1982, Jarman, 1971; Joubert & Eloff, 1971; Kotze & Zacharias, 1993; Loutit *et al.*, 1987; Mukinya, 1977; Oloo *et al.*, 1994).

Female black rhinos first conceive around 7 years of age and after 15-16 months of gestation the single young will lactate for 1-2 years. The young can remain with the mother to maturity and they are sometimes joined by unrelated immature rhinos, while bulls may accept company of a submissive male (Estes, 1990). The groups have home ranges of 2-100 km^2 which overlap, but the core areas are defended against intruders of the same species (Estes, 1990). Only in the 1990's it was discovered black rhinos emit infrasound (low frequency sound inaudible to humans), which may be used for long-distance communication (von Muggenthaler et al., 1993).

Weapon for self-defence leads to own mass destruction

In recent times black rhinos were omnipresent in Sub-Saharan Africa except in rain forest, but by 1995 95 % of the population had been confined to conservation areas in South Africa, Namibia, Zimbabwe, Kenya and Tanzania. The world population of black rhino plummeted from about 65 000 in 1970 (Cohn, 1988; Leader-Williams *et al.*, 1990) to 2 410 in 1995 (Emslie & Brooks, 1999).

The drastic reduction in rhino numbers over the past four decades is primarily due to illegal hunting for rhino horn, with habitat loss being a secondary factor. Some horns are used for traditional dagger handles in the Middle East, especially North Yemen (Varisco, 1989), but most horns are ground for use as traditional medicine (mostly as an analgesic of doubtful efficacy) mainly sold in China, South Korea and Taiwan (Cohn, 1988; Martin, 1993; Martin & Martin, 1989; Emslie & Brooks, 1999). The price for African rhino horns reportedly reached 15,000 US $/kg during the 1990's (Berger *et al.*, 1993; Martin & Martin, 1993). An international rhino product trade ban under CITES (Convention on International Trade in Endangered Species) is effect even in the trading countries, but enforcement was initially very poor.

The conservation agencies and landowners in charge of the remaining black rhinos improved their anti-poaching efforts during the 1990's, in some cases by concentrating the rhinos in Intensive Protection Zones. At the same time increasing awareness of the threat to rhinos and improved CITES enforcement resulted in a slow decrease in horn demand and prices. Meanwhile, the price on live black rhinos increased and by 2004 had reached 60 000 US $

per animal. As a consequence black rhino numbers slowly rose from 2 410 in 1995 to 3 100 in 2004 (*Pers.comm.* Dr. R. Emslie, Rhino Management Group)(Figure 1).

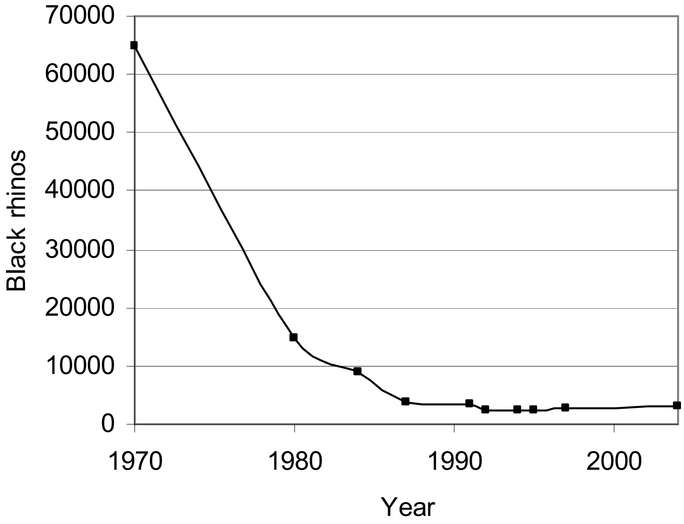

Figure 1

The numbers of black rhinos in Africa from 1970 to 2004.

Why be concerned with one species?

With the current high rates of species extinction and threat to entire biomes why should the endangered status of a single species be cause for so much concern?

- The black rhino is a representative of the largely extinct megafauna and the endangered family of rhinos
- The black rhino is a charismatic flagship species bringing attention to the conservation of natural resources
- The black rhino has outstanding value in tourism and potential value in legal hunting and legal horn sales, which can pay for general conservation efforts
- *In situ* conservation of black rhino leads to protection of other large mammals and the conservation of the habitat they share (not necessarily conservation hotspots)

- The black rhino can play a key role in shaping vegetation structure and diversity, especially in the absence of other megaherbivores

So there are good reasons for conservation, but now that the species is recovering why worry?

Why worry now?

The black rhinos exist in a meta-population of many small and a few larger populations. While this prevents one catastrophic event (such as an epidemic, change in landuse, armed conflict or intensive poaching) from affecting the whole species, it makes each population more prone to extinction due to catastrophic events and also more prone to loss of genetic diversity. The current costs of intensive protection and meta-population management have skewed the distribution towards the relatively rich and stable African countries and wealthy game ranches. Even here the spending is difficult to sustain. Demand for rhino horns persists, and any renewed spree of poaching would still be critical. An alternative to the present ban on sales of rhino products is to flood the market with legal horns from white and black rhinos, which have died naturally or been dehorned (Emslie & Brooks, 1999). Whichever way the situation is analysed the most sustainable solution is for the black rhino population to outgrow the problems as quickly as possible.

Outgrowing the problems: population growth theory

Maximising black rhino population growth is in principle subject to two opposing considerations. One the one hand, the highest natural growth is achieved by spreading the rhinos out relatively thin, free of any intra-specific competition. On the other hand, for protection to be economically viable the rhinos have to be concentrated so the costs of protection (and land) are low and revenue from live sales and game viewing is high.

In large K-selected species population growth rate is unaffected by density during the initial stages of growth until a certain threshold is reached. In black rhinos this threshold appears to be around 75 % of the ecological carrying capacity (ECC)(Emslie, 2001)(Figure 2).

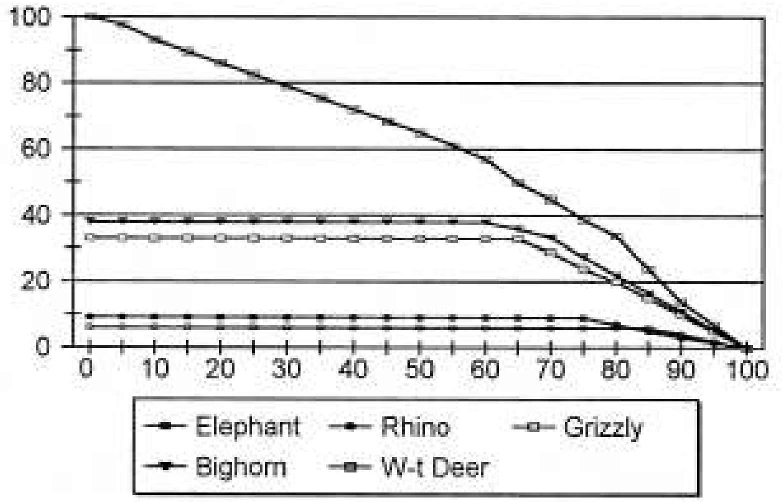

Figure 2.

Growth/population density relationships for a number of species. The X axis shows population density as percentage of estimated long term ecological carrying capacity, and the Y axis shows the maximum rate of reproduction (r_{max}) for a given density (% population increase per year). From Emslie (2001).

This means that the point of maximum local population growth is as high as 80-90 %, rather than 50 % predicted by the logistic growth equation. Therefore, by translocating excess animals into other areas black rhinos can in theory be kept at the relatively high density of 75 % of ECC without compromising growth of the metapopulation. However, it also means that the distance from the point where a slow-down in growth parameters occur (75 % of ECC), to the point with maximum local production (80-90 % of ECC) and through to the point of zero growth (100 % of ECC) and a possible population crash beyond ECC, is very short.

Predicting the ECC is difficult in any species and perhaps more so in a large browsers. Browse varies more in quality than grass or prey, and browse selection and browse production is often inadequately researched. In addition, a large browser can change the structure of the vegetation to a much less productive vegetation structure and condition - or in some cases to a more productive one. One particularly critical scenario documented in black rhino is for the population to overshoot the ECC, eat into the standing capital of browse and cause a sudden drop in browse production and browser numbers (Brett, 2001). This is possible because it takes years for calves to grow up and exert full impact, and because at least some shrub species respond to heavy browsing with rapid and more nutritious growth for some years, followed by reduced growth or death if the browsing does not ease. Monitoring black rhino populations or their habitat is therefore crucial for management of black rhino populations.

Using parameters of population performance (for instance growth rate, mortality and inter-calving interval) to monitor a black rhino population is possible, but only gives a short lead time, as explained above. The nutritional status of individual animals or the state of the vegetation gives more time to react.

- making a real world difference

Taking notice of the issues above and dealing with them translates into real world differences. With a population of 50 animals and poaching of 15 animals every 5 years an annual growth rate of either 3 % or 7 % over 25 years makes the difference between local extinction and more than doubling the population (Emslie, 2001). The maximum natural rate of population growth in black rhino is approximately 9 % per annum. The African Rhino Specialist Group under IUCN promotes a realistic minimum target of 5 % growth per annum (Brooks, 2001). However, many rhino population managers have struggled to successfully monitor the black rhino populations and their habitats, to recognise signs and warnings of slow-down in growth and to keep the populations at or below 75 % of the ECC through translocation. Some populations grew very slowly, some had no growth and a few decreased, primarily due to impact of black rhinos and other browsers on the vegetation (Brett, 2001). As a consequence South Africa produced 250-300 fewer black rhinos in the five years of 1996-2000 than if the growth had reached a modest 5 % (Brooks, 2001).

Bringing back the desert rhino

The subject of this study is the south-western sub-species (*Diceros bicornis bicornis*) or "desert rhino", which occupied the arid south-western Africa in areas with an annual rainfall of less than 500 mm. The south-western sub-species was exterminated from South Africa already in 1853, but in Namibia some 300 animals made it through a bottleneck in 1980 and in 1997 numbered 707 (Emslie & Brooks, 1999). An initial 14 south-western black rhinos were translocated from Namibia into Augrabies, Karoo and Vaalbos National Parks which are all within the original range.

South African National Parks (SANP) manages the populations and are in the process of acquiring land for park expansion. SANP therefore expressed interest in a study of habitat suitability in the three parks.

Study objectives

I decided to set out the following study objectives

I. Develop a simple habitat suitability model for black rhino
II. Quantify the plant species composition of the black rhino diet
III. Compare diet composition to browse availability to determine diet preference
IV. Identify plant species for use as early warning indicators of habitat condition

The study was conducted in the three national parks, but only the study in Augrabies National Park is reported here.

Habitat suitability modelling

The purpose of a habitat suitability model (HSM) is to construct a mathematical tool which can form the basis for habitat/species related management decisions. It is achieved by simplifying the bewildering complexity of the ecosystem without loosing the most important of the system dynamics. HSMs are *not* models of the ecological carrying capacity (ECC), because not all the factors that may affect animal abundance are included. Most HSMs leave out some parameters which are important to ECC, but difficult to measure, model or predict such as disease, competition, predation or fire. Typically, a HSM is simply based on what can be inferred from the distribution of the study animals compared to the distribution of the habitat parameters. However, HSMs *are* intended to predict the *potential* of the included variables to affect ECC (Schamberger & O'Neil, 1986). A HSM can also form part of a model of ECC.

The more detailed a HSM is the better it will mimic the ecosystem, but there is little point in refining a model if it does not significantly alter the output and ease the decision process. For decision making a simple HSM that requires little data input and conveys an understanding of the ecosystem can be better than a more accurate, but data demanding and complex model. A HSM relies on a number of assumptions to simplify ecological complexity into a manageable model. These assumptions are not entirely true, but should be close enough to make for a workable model. For instance, most HSMs assume that the distribution of the study animals is a reflection of the habitat suitability. In reality, dominant animals may lower density in the best habitats through interference competition and displace subordinate animals into marginal habitat, but the aberration is usually small enough for an acceptable HSM output.

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Photos on the following page:

Top left: Koppie with a klipspringer overlooking dense grass cover in vegetation community 6 following good rains

Top right: *Euphorbia rectirama* and rocky hills in central Waterval

Second row, left: Augrabies Falls with Waterval in the background

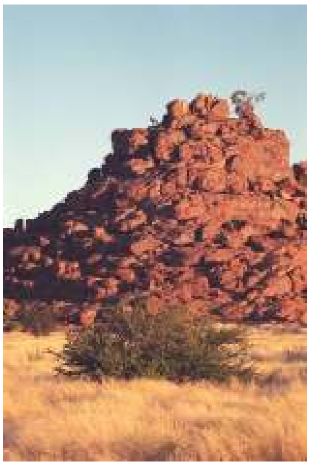
Second row, right: A bull rhino (Ngara) with an unusual third horn

Third row, left: The other mega-browser in Augrabies: Giraffe

Third row, right: Central Waterval viewed towards northeast across a tributary of the Orange River

Bottom row, left: The Orange River at the north-western extreme of Waterval

Bottom row, right: An electrical summer storm at sunset paints the sky and promises rain








Paper 1:

Vegetation, habitats and browse availability in the Waterval section, Augrabies Falls National Park – place of scarcity and diversity.

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Abstract

Factors potentially affecting habitat suitability for large browsers were quantified in 7530 ha of mountainous desert in Waterval, Augrabies Falls National Park, western South Africa. The vegetation was classified and mapped according to plant species associations. In each vegetation community vertical cover, shade, substrate composition as well as canopy volume of each browse species were measured. Furthermore, water availability and steepness of slopes were mapped. The varied topography and soils of Waterval result in a high diversity of browse (D=19.0, H'(ln)=3.45) divided into ten vegetation communities including seven shrublands (61.7 % by area), two woodlands (37.1 %) and a riverine forest (1.1 %). The average browse availability 0-200 cm above ground is 1 096 ±90 m^3/ha, ranging from 597 to 14 446 m^3/ha among vegetation communities. The browse includes *Acacia mellifera* (15.0 %), *Schotia afra* (12.7 %), *Monechma spartioides* (4.5 %), *Acacia karroo* (4.2 %), *Boscia albitrunca* (3.8 %), *Euphorbia rectirama* (2.9 %) and *Indigofera pechuelii* (2.6 %). The riverine forest provides easy access to water, browse, shade and vertical cover. However, some 97 % of Waterval has scarce browse and vertical cover as well as little to no shade. In addition, the northeastern area is steep, 4-6 km from water and bordered by a low-use road. Fortunately, with the exception of community 3, browse is diverse, generally palatable and deciduousness limited to 2-3 months in one major browse species. Research and monitoring is recommended to balance mega-herbivorous black rhino and giraffe with scarce, diverse and endemic vegetation.

Keywords

Augrabies, vegetation communities, browse availability, water, shade, slope, substrate, habitat suitability.

Introduction

Managing arid conservation areas for both biodiversity and large mammals is a complex and potentially conflicting task (Novellie *et al.,* 1991; Lombard *et al.,* 2001; Birkett, 2002). The Orange River Nama Karoo is a species rich desert vegetation type of which only 1.5 % is under formal conservation. Of this two thirds are in the Augrabies Falls National Park (AFNP)(Hoffmann, 1996). AFNP is situated in the Gariep Centre of Endemism, and 54 % of its flowering plant species are not conserved elsewhere (Zietsman & Bezuidenhout, 1999). AFNP aims to conserve 1) a representative sample of the endemic vegetation and the threatened riverine woodland as well as 2) endangered, rare and valuable animal species, including black rhino (*Diceros bicornis*) and Hartmann's mountain zebra (*Equus zebra hartmannae*) and 3) other biodiversity. AFNP encompasses 554 km^2 in which to balance these conservation objectives, but the land is arid, sparsely vegetated and steep or rocky in large parts.

The biggest natural sources of impact on the park's biodiversity are the large mammals, especially the two mega-herbivores: Giraffe (*Giraffa camelopardalis*) and black rhino. Conservation of black rhino is a high priority in the park, because this is a critically endangered species (IUCN, 2003) with only 3100 animals left (*Pers.comm.*: Richard Emslie, Rhino Management Group) and because black rhino is a charismatic species with high tourism potential. Black rhinos were present in the park from 1986 to 1999 and there are plans to reintroduce the species.

To plan and implement the conservation of conflicting components of biodiversity comprised by small, confined populations, it is highly beneficial to map the topographical and ecological variables of the area under protection. Such maps form the basis for understanding the distribution of plant and animal species, as well as for estimating carrying capacities. Habitat suitability modelling for plants and animals as well as interpretation of animal behaviour is also facilitated by resource mapping.

The aim of this study was to describe the Waterval section of AFNP from the perspective of black rhino to acquire data for interpretation of black rhino feeding (Paper 2) and for modelling of black rhino habitat suitability (Paper 3). However, the data may be useful to studies of other browsers or other groups of organisms in the study area.

The specific objectives were 1) to classify and map the vegetation communities (habitats) by their plant species (browse) composition; 2) to describe each habitat by a) the availability of browse of different species, b) the availability of shade, c) the availability of vertical cover and d) the substrate; 3) to map a) steepness of slopes, b) accessible water and c) infrastructure in the study area.

Study area

Location and land use

Augrabies Falls National Park (AFNP) located approximately 120 km west of Upington at 28° 25’ – 28° 38’ S, 19° 53’ – 20° 24’ E was proclaimed in 1966 and gradually expanded to 55 365 ha bisected by the Orange River (Figure 1). Prior to park status the area was used for extensive small stock grazing. This study concerns the 7 530 ha Waterval section of AFNP, which served as a black rhino reserve (Figure 1).

Topography and land types

Waterval can be divided into four land types (Land Type Survey Staff, 1986)(Figure 6): In the extreme south is the gently sloping upper river valley at 610-630 m above sea level which is of land type Ia(1a) consisting of intrusive rocks, mainly granite, overlain with tertiary to recent alluvial silt and fine sand. The lower river valley and incised gorge area at 420-620 m above sea level and the northeastern mountainous area at 610-750 m above sea level are both of land type Ic(3a). This is mostly comprised of exposed red biotite granite gneiss, which is typically orange brown to reddish on weathered surfaces, but the western gorge area is comprised of grey gneiss. The central basin generally sloping south and west at 550-620 m above sea level is of land type Ag(2d), which has the same geology as Ic(3a), but is overlain with sand and gravel. A small plain in the far north at 705-725 m above sea level is of landtype Ae(110b) with gravel and sand underlain by tectonic intrusive rock including Colston granite (Land Type Survey Staff 1986). Outcrops of quartzite occur in the three latter land types.

Climate

AFNP has a hot desert climate (*BWh* in the Köppen system) with summer rainfall. Annual precipitation at Augrabies Waterfall (622 m above sea level) averaged 123 mm for the period 1945-1999 with a coefficient of variation of 59 % (Weather Bureau, 2001). Annual evaporation at Upington (846 m above sea level) averages 3 384 mm. Mean monthly humidity at Augrabies Waterfall ranges from 10 to 40 %. December to April sees 71 % of the rain, peaking in March with 26.7 mm on 2.7 rain days. For the period 1990-2001 the highest and lowest average monthly maximum and minimum temperatures were 37.1 ^{o}C (January), 21.3 ^{o}C (July), 21.6 ^{o}C (January) and 4.5 ^{o}C (July). Absolute maximum and minimum temperatures during 1984-1990 were 46.0 ^{o}C and –2.0 ^{o}C, with an average annual of 0.9 frost nights in July-August (Weather Bureau 2001).

Vegetation and fauna

AFNP is situated in the Orange River Nama Karoo vegetation type (Hoffman, 1996) in the Gariep Centre of Endemism (Zietsman & Bezuidenhout, 1999). The stocking rate for livestock recommended by the Ministry of Agriculture is 60 ha per large stock unit. Zietsman & Bezuidenhout (1999) listed 364 species of flowering plants recorded in the park, of which 197 were not in the species lists of the three nearest major conservation areas. Bezuidenhout (1996) published a vegetation map of a small section of the park just south of Waterval, while Werger & Coetzee (1977) also included a small part of Waterval (Melkbosrand) in their study without providing a vegetation map.

Preliminary species lists for AFNP include 61 mammalian, 218 avian, 12 amphibian and 53 reptile species (SANParks, 2002). Large, mammalian herbivore species include 1. Medium-long grass feeders: Hartmann's mountain zebra and gemsbok; 2. Mixed feeders: Eland and springbok; 3. Browsers: Black rhino, duiker, giraffe, klipspringer, kudu and steenbok; 4. Selective omnivores: Baboon and vervet monkey. Even the grazers include some browse (5-20 %) in their diet during dry season and droughts (Estes, 1991; Owen-Smith, 1999). The largest predator is caracal and vagrant leopard. Black rhino was introduced into Waterval in 1986 and numbers averaged about six until their removal from AFNP in 1998. The western and eastern parts of the Waterval section had livestock on it until 1974 and 1992, respectively.

Methods

Waterval was classified into vegetation communities according to the composition and availability of browse from 0 to 200 cm above ground, which is the normal approximate height range of browsing in kudu and black rhino (Du Toit, 1990; Smithers, 1983, paper 2). Vertical cover, shade and substrate are closely related with the species composition of the non-grass plants, so vegetation communities were used as stratification for measuring these parameters. Grasses were given a low priority in this study for three reasons. Firstly, in arid areas the quantity and composition of grasses fluctuate strongly with rainfall (Bezuidenhout, 1997), so only long-term monitoring can provide a meaningful quantification. Secondly, the grass layer is extremely limited in Waterval in a year of average rainfall. Thirdly, the main emphasis of this study was on the habitats of black rhinos and other browsers.

Sampling

The study area was stratified into relatively homogenous preliminary phyto-sociological units based on visual classification of 1:50 000 panchromatic aerial photographs and extensive ground-truthing. Sampling plots were placed randomly within each phyto-sociological unit and geo-referenced with a Global Positioning System (GPS) receiver. The proportion of plots in each unit was determined by unit size, browse availability and statistical considerations.

Data collection in the sampling plots took place during November 1999 – May 2000. The plots consisted of an adaptation of belt transects (Mueller-Dombois and Ellenberg, 1974) in which all plants, except grasses, 100 cm or taller were measured. Each adapted belt transect was terminated when 30 plants had been included, and plot length was determined as the equidistance between the 30th and 31st plant. Small, square plots were placed randomly inside the belt transect and all plants less than 100 cm tall were measured, except for grasses. The number of small plots inside each belt transect was increased until they included a minimum of 50 plants. The 58 belt transects thus contained 1740 large plants and the smaller plots more than 2900 small plants. The rationale for employing different plots for different plant sizes was to efficiently acquire just enough data for each size class. The use of transects ensured that sampling cut across clumped distributions of plants, while the randomly placed small plots sampled different microhabitats within the transect.

Each plant was identified to species *in situ* if possible. Alternatively, a specimen was collected for herbarium identification (SANParks, Kimberley; MacGregor Museum Herbarium, Kimberley; National Museum Herbarium, Bloemfontein and National Botanical Institute, Pretoria). Taxon names in this paper are in accordance with Arnold & de Wet (1993). One to three plant canopy heights (top, widest point and bottom) and one or two sets of perpendicular canopy diameters were recorded with measuring tapes as in Smit (1996). For grasses, only the presence of the more dominant species and their estimated canopy cover was noted. For the major browse species presence/absence of leaves, growing shoots, flowers and fruits were recorded.

At 25 regularly spaced points along the western boundary of each plot a pointed metal dropper was dropped from 1 metre with eyes closed. At each point of impact depending on what was struck the following data was recorded: for soil the predominant soil particle size was recorded, for a loose rock two diagonal measurements were recorded, while if dead organic material or bedrock was hit this was simply noted. Substrate classification based on soil particle size (soil texture grades) follows U.S. Department of Agriculture (Strahler 1975).

Data analysis

The percentage projected plant canopy cover was calculated for all species and for each vegetation community, as were canopy volumes using a spreadsheet modification of Smit (1996). Simpson (D) and Shannon diversity (H') were calculated for the study area based on browse volume 0-200 cm above ground. Shannon diversities were compared using Hutcheson's method (Zar, 1999). Simpson equitability (E) was calculated for each vegetation community, but to reduce any bias from small sample sizes, calculations were based on browse volume of the 10 most abundant species only (Begon *et al.,* 1986). Shade for large mammals was calculated as projected canopy cover of plants taller than 2 metres minus the basal area, provided this doughnut shape was minimum 1 metre from inner edge to outer edge. Height of each plant strata (trees, shrubs or herbs) was calculated as the average top height of the plants in each stratum, excluding trees less than 1 metre. No correction was made in cover and shade for overlapping plants.

The projected plant canopy cover and the plant canopy volumes 0-200 cm above ground were entered into two separate TWINSPAN analyses (McCune & Mefford, 1997). For convenience estimated plant canopy cover is usually used for phyto-sociological classification, but three dimensions (canopy volume) better represents what determines vertical cover and availability of food for browsers. The pseudo-species cut off levels (intervals) for plant cover followed the Braun-Blanquet cover classes (Whittaker, 1980), while those for plant canopy volume were 0 m^3/ha (value=0), <1 m^3/ha (1), 1-5 m^3/ha (2), 6-10 m^3/ha (3), 11-30 m^3/ha (4), 31-100 m^3/ha (5), 101-300 m^3/ha (6), 301-1000 m^3/ha (7), 1001-2000 m^3/ha (8) and >2000 m^3/ha (9). The TWINSPAN outputs were refined applying Braun-Blanquet procedures to form phyto-sociological tables (Whittaker, 1980). An ordination (DECORANA)(McCune & Mefford, 1997) was performed to see whether the phyto-sociological units were properly differentiated, or should rather be amalgamated. The initial phyto-sociological classification was changed according to these analyses. The resulting vegetation communities were named by the two most diagnostic or characteristic taxonomic entities in order of prominence. Structural terminology for the communities and vertical plant strata (trees, shrubs, herbs) follows Edwards (1983).

Mapping

The boundaries of the phyto-sociological units were corrected following data analysis and ground-truthing to delineate the final vegetation communities. The aerial photos and the vegetation community boundaries were geo-referenced based on GPS readings entered into a Geographical Information System computer programme (GIS), and the community boundaries digitised on-screen to produce a vegetation map. The size of the area covered by each community was extracted from the GIS file. Points of accessible water were derived from fieldwork.

Results

Vegetation communities cum browser habitats

The vegetation classification yielded 10 vegetation communities in the study area. Using either plant canopy cover or plant canopy volume 0-200 cm above ground resulted in identical classification of plots and communities. Using plant canopy volume in the phyto-sociological table facilitates an overview of available browse and its intra-community variation (Table 1). Below is a brief description of each vegetation community *cum* browser habitat including results on substrate composition and availability of browse, shade and vertical cover.

1*. Schotia afra – Indigofera pechuelii* low, open woodland occurs on red biotite granite gneiss, which is typically orange brown to reddish, and largely falls within the crest, midslope and footslopes of land type Ic3a (Land Type Survey Staff, 1986). This community covers 36 % of the study area (Figure 2, table 2). Bedrock and large rocks make up 58 % of the **substrate** (Table 2) interspersed with 0.3 – 0.6 m deep Hutton soil form (Land Type Survey Staff 1986). **Slope** in this community varies from 0 to 90 degrees, with the median being 7 degrees and 5 % being steeper than 38 degrees (Table 2).

The *Schotia afra – Indigofera pechuelii* low, open woodland community is characterised by species group A (Table 1). The diagnostic species are primarily the tree *Schotia afra* and the herbs *Indigofera pechuelii* and *Hibiscus englerii*. **Browse availability**, expressed as plant canopy volume from 0-200 cm above ground, is 975 m^3/ha, which is 11 % below the average for the study area (Table 4). Simpson equitability (E) among the 10 most abundant browse species is intermediate for the study area at 0.55 (Table 4). This means Simpson's diversity index is 55 % of the potential maximum among 10 species. Simpson's diversity index expresses the inverse of the chance of sampling the same species in two consecutive samples. Thus, the chance of randomly picking the same species twice in a row is 1/(0.55x10)=0.18. *Schotia afra* makes up 28 % of the browse by volume followed by the herb

Forsskaolea candida (10 %), the soft shrub or herb *Indigofera pechuelii* (10 %), the succulent shrub *Euphorbia rectirama* (6 %) and the tall herb *Hibiscus englerii* (5 %).
The tree stratum reaches 5 m (average=270 cm), but its canopy cover is only 3.6 %, while the herbaceous cover is 15.9 % and herbs make up 55 % of the browse volume (Table 3). **Vertical cover** for large mammals is generally low in Waterval, and vegetation community 1 is average in this respect with 596 m^3/ha of browse at 0-100 cm above ground and 379 m^3/ha at 101-200 cm, with another 454 m^3/ha 201-500 above ground (Table 2). In other words, plant canopies occupy 6.0 % of available space from the ground to 1 m and 3.8 % between 1 and 2 metres. **Shade** for large mammals only occurs at 4.4 points per ha (Table 3).

This community is similar to the *Rhus populifolia – Schotia afra* Open Woodland of Bezuidenhout (1996) and resembles the *Schotia afra* community described by Werger & Coetzee (1977).

2. *Adenolobus garipensis – Boscia albitrunca* tall, open shrubland covers 11.7 % of Waterval, occurs on grey granite and largely falls within the crest, midslope and footslopes of land type Ic3a (Land Type Survey Staff 1986)(Figure 2, table 2). The **substrate** is a mixture of gravel (33 %), bedrock (21 %), rocks (21 %) and pebbles (21 %)(Table 2). The terrain varies from level to vertical, with the median **slope** being 8 degrees and 5 % steeper than 40 degrees (Table 2).

The *Adenolobus garipensis – Boscia albitrunca* high, open shrubland community is primarily characterised by the presence of species group B, D, M, R and X and the virtual absence of groups A, F and T (Table 1). The diagnostic species are the shrub *Adenolobus garipensis*, the small tree *Boscia albitrunca* and the succulent shrub *Ceraria namaquensis*. **Browse availability** is 1 076 m^3/ha, which is 2 % below average, and Simpson equitability (E) is high at 0.65 (Table 4). Browse is dominated by the shrub *Adenolobus garipensis* (23 %), the herb

Osteospermum microcarpum (18 %), the herb *Monechma spartiodes* (9 %) and the tree *Boscia albitrunca* (9 %). The tree stratum reaches 5 m (average=274 cm), but its canopy cover is only 1.1 %, while the herbaceous cover is 32.3 % and herbs make up 62 % of the browse volume (Table 3). **Vertical cover** for large mammals is 821 m^3/ha of browse at 0-100 cm above ground and 254 m^3/ha at 101-200 cm (Table 2). **Shade** for large mammals only occurs at 3.4 points per ha (Table 3)

3. *Euphorbia gregaria – Osteospermum microcarpum* tall, sparse shrubland covers 6.7 % (Figure 2, table 2) and occurs exclusively on substrates with a high content of quartz in the form of bedrock (33 %) and large rocks (28 %) interspersed with gravel (11 %) and sand (22 %)(Table 2). Thus, this community is typically found on the crests and slopes of the quartzitic outcrops that occur in any of the non-alluvial land types. Median **slope** is 4 degrees (Table 2).

The *Euphorbia gregaria – Osteospermum microcarpum* tall, sparse shrubland community is characterised by the consistently high presence of the conspicuous succulent shrub-like *Euphorbia gregaria* (Table 5). **Browse availability** is 918 m^3/ha, which is 16 % below average, and Simpson equitability (E) is very low at 0.25 (Table 4). *Euphorbia gregaria* makes up 57 % of the browse followed by the small herb *Tribulus cristatus* (11 %). The tree stratum is virtually absent. Canopy cover of shrubs in the strict sense of woody multi-stemmed plants (Edwards 1983) is only 0.9 %, but *Euphorbia gregaria*, which can be considered a shrub by structure, covers 5.7 % (Table 3). **Vertical cover** is 735 m^3/ha of browse at 0-100 cm above ground and only 183 m^3/ha at 101-200 cm (Table 2). **Shade** for large mammals was not encountered in the five plots (Table 3).

The *Euphorbia gregaria – Osteospermum microcarpum* tall, sparse shrubland is similar to the *Enneapogon scaber-Euphorbia gregaria* community described by Werger & Coetzee (1977).

4. *Acacia mellifera – Euphorbia* spp. tall, open shrubland covers 14.6 % and largely falls within the foot slopes and valley bottoms of land type Ag2d (Land Type Survey Staff 1986)(Figure 2, table 2). The dominant substrate is gravel (48 %) strewn with rocks (9 %) and pebbles (16 %) interrupted by outcropping bedrock (16 %) and sandy (12 %) drainage lines (Table 2). The soil is predominantly of the Hutton form (Land Type Survey Staff 1986). Median **slope** is 3 degrees.

The *Acacia mellifera – Euphorbia* spp. high, open shrubland community is primarily characterised by the presence of species group E, F, H, and T and the limited occurrence of group G (Table 1). The diagnostic species are primarily the large shrub *Acacia mellifera*, the succulent shrubs *Euphorbia rectirama* and *Euphorbia gregaria* as well as the herbs *Blepharis furcata*, *Indigofera pungens*, *Hermannia spinosa* and *Trianthema triquetra*. **Browse availability** is 852 m^3/ha, which is 22 % below average, and Simpson equitability (E) is high at 0.67 (Table 4). Browse consists of *Acacia mellifera* (24 %), *Schotia afra* (10 %), *Indigofera pechuelii* (11 %), *Euphorbia rectirama* (9 %), *Indigofera pungens* (8 %) and *Monechma spartiodes* (8 %)(Table 4). Herbs make the biggest contribution to both canopy volume and cover (Table 3). **Vertical cover** is 608 m^3/ha of browse at 0-100 cm above ground and only 244 m^3/ha at 101-200 cm (Table 2). **Shade** for large mammals only occurs at 1.3 points per ha (Table 3).

This community falls within the *Acacia mellifera* community of Bezuidenhout (1996), but does not match any of the two described sub-communities. The closest community in Werger & Coetzee's (1977) description is the *Monechma spartioides* sub-community of the *Indigofera heterotricha-Zygophyllum suffruticosum* community.

5. *Acacia mellifera – Zygophyllum dregeanum* tall, open shrubland occurs in two variants:

5.1. *Acacia mellifera – Zygophyllum dregeanum – Euphorbia rectirama* tall, open shrubland covering 11.7 % of the study area (Figure 2, table 2) occurs on the foot slopes of land type Ag2d (Land Type Survey Staff 1986) on red biotite gneiss, mostly overlain with gravel (55 %) and pebbles (11 %)(Table 1) of the same material. The gravel in this community features a structure peculiar of arid areas referred to as “schaumboden” in Werger & Coetzee (1977). The top 1-2 mm forms a relatively hard, “polished” crust over 10-20 mm of more porous, compactable material, making this substrate unfavourable for plant establishment. “Schaumboden” gravel (55 %) and pebbles (17 %) dominate the convex surfaces between numerous lightly incised sand (11 %) and gravel filled drainage lines, which are more densely vegetated. Outcrops of red gneiss bedrock (13 %) and rocks (4 %) also occur, with vegetation affiliated with community 1. **Slope** is 1 degree or less in 75 % of the community (Table 2).

The *Acacia mellifera – Zygophyllum dregeanum – Euphorbia rectirama* community is primarily characterised by the high occurrence of the diagnostic species in its name (Table 2). **Browse availability** is only 597 m^3/ha, which is 46 % below average, and Simpson equitability (E) is low at 0.31 (Table 4). Browse consists of *Acacia mellifera* (24 %), *Schotia afra* (10 %), *Indigofera pechuelii* (11 %), *Euphorbia rectirama* (9 %), *Indigofera pungens* (8 %) and *Monechma spartiodes* (8 %)(Table 3). “Schaumboden” impedes herbaceous cover to just 5.4 % and 54 % of browse volume thus consists of shrubs. **Vertical cover** is only 343 m^3/ha of browse at 0-100 cm above ground and only 254 m^3/ha at 101-200 cm (Table 3). **Shade** for large mammals only occurs at 1.3 points per ha (Table 3).

5.2 *Acacia mellifera – Zygophyllum dregeanum – Monechma spartioides* tall, open shrubland differs from the previous sub-community by being dominated by pebbles (57 %) at the expense of “schaumboden”, bedrock and drainage lines (Table 2). This results in higher herbaceous cover (12.4 %) and in higher browse availability (861 m^3/ha) as well as in the virtual absence of *Euphorbia rectirama* and much higher occurrence of *Monechma spartioides* (13 %). *Acacia mellifera* (49 %) and *Zygophyllum dregeanum* (18 %) dominate the sub-community. Vertical **cover** is 495 m^3/ha at 0-100 cm above ground and 366 m^3/ha at 101-200 cm. **Shade** occurs at 6.3 point/ha.

Communities 5.1 and 5.2 are similar to the *Zygophyllum dregeanum* sub-community of the *Indigofera heterotricha*-*Zygophyllum suffruticosum* community described by Werger and Coetzee (1977). Community 5 falls within the *Acacia mellifera* community of Bezuidenhout (1996).

6. *Acacia mellifera – Stipagrostis hochstetteriana* tall, open shrubland covers 12.5 % of the study area in land type Ag2d (Land Type Survey Staff, 1986)(Figure 2, table 2). The dominant substrate is a mixture of 53 % sand and 41 % gravel (Table 2) classified as Hutton soil form (Land Type Survey Staff, 1986). The **slope** is 5 % or less in 75 % of the community (Table 2).

The *Acacia mellifera – Stipagrostis hochstetteriana* tall, open shrubland community is characterised by the combination of the species *Acacia mellifera* (Species group S), *Boscia albitrunca* (group M), *Boscia foetida*, the smallish shrub *Rhigozum trichotomum* (group L), the shrub *Lycium bosciifolium* (group AB), and the herb *Monechma spartioides* (Table 1). None of these are good character species as they show a low degree of community fidelity (Whittaker 1980), but in combination with the virtual absence of species groups A through I (differential species) nevertheless form a set of diagnostic species (Table 1). After good rains the otherwise sparse herbaceous layer becomes completely dominated by the grass *Stipagrostis hochstetteriana*.

Browse availability is 1 078 m^3/ha, which is 2 % below average, and Simpson equitability (E) is low at 0.35 (Table 4). The main browse species are *Acacia mellifera* (44 %), *Monechma spartiodes* (10 %), *Boscia albitrunca and B.foetida* (8 %) and *Rhigozum trichotomum* (5 %) (Table 4). Shrubs account for 61 % of canopy volume and a canopy cover of 9 % . **Vertical cover** is 622 m^3/ha (0-100 cm) and 456 m^3/ha (101-200 cm) (Table 3). **Shade** for large mammals only occurs at 12.6 points per ha (Table 3).

This community resembles the *Stipagrostis hochstetteriana* community described by Werger and Coetzee (1977).

7. *Sisyndite spartea – Forsskaolea candida* tall, open shrubland occurs on wide drainage lines and plains occasionally subject to flooding, which only covers 0.7 % of the study area in one patch (Figure 2, table 2). The **substrate** is 95 % washed gravel (Table 2).

The *Sisyndite spartea – Forsskaolea candida* tall, open shrubland community is characterised by one character species, the shrub *Sisyndite spartea*, plus by high availability of *Acacia mellifera* and *Schotia afra*. **Browse availability** is 1 071 m^3/ha - just 2 % below average - and Simpson equitability (E) is only 0.33 (Table 4). The main browse species are *Sisyndite spartea* (26 %), *Acacia mellifera* (15 %) and clumps of *Schotia afra* (45 %)(Table 4). Trees contribute 50 % of canopy volume and canopy covers for trees (4.5 %) and shrubs (5.8 %) are higher than for herbs (2.6 %). **Vertical cover** is 420 m^3/ha (0-100 cm) and 652 m^3/ha (101-200 cm) (Table 2). **Shade** for large mammals only occurs at 9.4 points per ha (Table 3).

This community resembles the *Sisyndite spartea* communities described by Bezuidenhout (1996) and Werger & Coetzee (1977).

8. *Acacia erioloba* short, closed woodland occurs in two variants:

8.1 *Acacia erioloba – Schmidtia kalahariensis* short, closed woodland is limited to areas where the **substrate** is sand mixed with some gravel (Table 2). It only covers 0.4 % of the study area (Figure 2, table 2).

The *Acacia erioloba – Schmidtia kalahariensis* short, closed woodland community is characterised by the predominance of the species in its name (Table 1). **Browse availability** is around 1 150 m^3/ha (Table 4). The herbaceous layer is poorly developed except for the ubiquitous, opportunistic creeper *Tribulus cristatus* and the annual grass *Schmidtia kalahariensis*, the preponderance of which is highly dependant on summer rainfall. *Acacia erioloba* provides abundant shade (Table 3), but because of its raised canopy reaching eight metres it contributes little to browse availability at 0-200 cm (Table 3 and 4). *Acacia mellifera* and *Monechma spartiodes* also contributes significant amounts of browse.

8.2 *Acacia erioloba – Zygophyllum microcarpum* short, closed woodland is a community variant that differs by occurring on a **substrate** of pure gravel near large drainage lines. Only 0.1 % of the study area falls in this sub-community (Figure 2), and due to its tiny size was pooled with 8.1 for most analyses.

This community variant differs by the high availability of *Zygophyllum microcarpum* (a small shrub) and *Zygophyllum simplex* (a succulent creeper). Otherwise the herbaceous layer is poorly developed. *Acacia mellifera* is also present.

Community 8 is very similar to the *Monechma australe – Acacia erioloba* community of Werger & Coetzee (1977).

9. *Tamarix usneoides - Maytenus linearis* tall, open shrubland occurs on floodplains where the **substrate** is a dusty mixture of pure silt and clay (Table 2). The land type is Ia1a

(Land Type Survey Staff, 1986). The community covers 1.0 % of the study area (Figure 2, table 2). **Slope** is 1 degree or less in the three quartiles (Table 2)

The *Tamarix usneoides - Maytenus linearis* tall, open shrubland community is clearly defined by the diagnostic species of species group U (Table 1). The group comprises the smallish tree *Tamarix usneoides*, the succulent herb *Mesembryanthemum guerichianum* and two succulent *Psilocaulon* herbs. *Maytenus linearis* is also very conspicuous in this community.

Browse availability is 2 581 m^3/ha or more than twice the average. Equitability is intermediate at 0.49. Browse consists of *Tamarix usneoides* (28 %), *Sueda fruticosa* (28 %), which occurs densely on the transition to the riverine community, *Maytenus linearis* (13 %) and *Psilocaulon absimile* (12 %). Shrubs account for 45 % of canopy volume and cover 16 % (Table 3). Large **shade** occurs at 11.6 points/ha and **vertical cover** is 1 747 m^3/ha (0-100 cm) and 834 m^3/ha (101-200 cm)(Table 2).

This community is very similar to the *Tamarix usneoides-Ziziphus mucronata* sub-community described by Bezuidenhout (1996).

10. *Acacia karroo – Ziziphus mucronata* short forest occupies a 5 – 30 m wide strip along the Orange River and a few tributaries, equal to 1.1 % of the study area, where terrain and hydrology allows soil to build up (Figure 2, table 2). The **substrate** is an alluvial silt-clay combination (48 %) highly enriched with humus (48 %). Three quartiles have a **slope** of 1 degree or less (Table 2).

The *Acacia karroo – Ziziphus mucronata* short riverine forest community is characterised by species group Y (Table 1). Within the study area the trees *Acacia karroo* and *Ziziphus mucronata* are diagnostic for this community, but *Rhus pendulina* and *Salix mucronata* are more typical riverine tree species on a regional scale.

At 14 446 m^3/ha **browse availability** is 13 times the average for the study area, such that this small community (1.1 %) holds 14.6 % of the entire browse up to 2 metres (Table 4). Most abundant is climbing *Asparagus* species (27 %), *Acacia karroo* (25 %), *Salix mucronata* (10 %), *Rhus pendulina* (9 %), *Ziziphus mucronata* (8 %), *Maytenus linearis* (6 %) and the smallish tree *Euclea pseudobenus* (5 %). Equitability is 0.56 (Table 4). Other than *Asparagus* species and *Tribulus cristatus* (2 %) the herbaceous layer contributes relatively little to browse due to the abundance of woody plants. Tree canopies overlap totalling 140 % cover and reach 530 cm on average (Table 3). **Shade** is almost continuous as tree canopy covers overlap by about 40 % (Table 3). **Vertical cover** is extremely dense at 5 878 m^3/ha (0-100 cm), 8 569 m^3/ha (101-200 cm) and 31 221 m^3/ha (201-500 cm), which means plant canopies circumscribe 59, 86 and 104 % of the available space at the respective height intervals (Table 3).

This community is very similar to the *Diospyros lyciodes – Ziziphus mucronata* sub-community of Bezuidenhout (1996) and the *Ziziphus mucronata – Euclea pseudebenus* community of Werger & Coetzee (1977).

Browse availability in Waterval

Average browse availability for the study area is 1 096 ± 90 m^3/ha (±SEM) 0-200 cm above ground. Equitability for the 10 most abundant browse species based on volume is 0.76 while Simpson and Shannon diversity indices for browse in the study area are D=19.0 and H'(ln)=3.45 (Table 4).

Different measurements of availability for 10 of the most important browse species are shown in Figure 3. The average density of these 10 species in Waterval is not correlated with their average canopy cover (Pearson, *p*=.50, n=10) nor canopy volume (*p*=.39, n=10). The average canopy cover of these 10 species is significantly correlated with canopy volume 0-

200 cm above ground (Pearson, r=.83, *p*=0.003, n=10), but some species, including *Indigofera pungens* and *Maytenus linearis*, deviate very much from this correlation (Figure 3).

Browse is vertically distributed with 38 % at 0-100 cm, 24 % at 101-200 cm and 38 % at 201-500 cm above ground (Figure 4, table 2). The riverine community 10, which covers 1.1 % of the study area, contributes 51 % of the canopy volume at 201-500 cm. The lower stratum is more equitable and diverse in species composition than the higher strata (Figure 4).

The most abundant browse species, *Acacia mellifera*, which contributes 15 % of canopy volume at 0-200 cm is subject to annual leaf fall. During this time its preference by black rhino is reduced (Paper 2). However, the time span without leaves is only two to three months (Figure 5).

Water availability, slope and human disturbance.

Due to very steep gorges water is only accessible at certain sections of the Orange River in Waterval in addition to at a natural spring and two artificial waterpoints (Figure 6). Thus, 31 % of Waterval is within 1 km of water, 61.2 % within 2 km, 81.8 % within 3 km, 91.1 % within 4 km, 97.2 % within 5 km and 100.0 % within 6 km. The northwestern area of Waterval is the only area more than 4 km from water. This area also has the largest concentration of steep slopes (Figure 6). In addition, a public high-speed gravel road runs along the northwestern boundary and probably constituted the biggest source of human disturbance. It had less than 100 vehicles per day. Vehicle tracks were present throughout most of the study area, but only in the area just north of the southern "panhandle" (Figure 6) were the tracks used frequently. There was simple accommodation for rangers, visitors and researchers as well as holding pens in this area accessed by 0-15 vehicles a day.

Discussion

Scarcity and diversity

In addition to endemism, scarcity and diversity characterises plant life in Waterval and AFNP. Two other arid South African national parks and rhino reserves can serve as comparison: the Doornhoek section of Karoo National Park which receives 260 mm rain/year and Than-Droogeveld section of Vaalbos National Park which receives 418 mm rain/year. The browse availability of Waterval (1 095 ±90 m^3/ha) is significantly lower than that of the Doornhoek section of Karoo National Park (1 924 ±141 m^3/ha; Mann-Whitney, U=607, p=0.0002) and the Than-Droogeveld section of Vaalbos National Park (1 890 ±174 m^3/ha; Mann-Whitney, U=1447, p<0.0001). The browse diversity of Waterval (D=19.0) is higher than in Doornhoek (D=12.7; Hutcheson, p<0.2) and significantly higher than in Than-Droogeveld (D=5.6; Hutcheson, p<0.001)(Buk, *in prep.a*; Buk, *in prep.b*). In Waterval the three most abundant browse species make up only 31 % of the browse volume, whereas in Doornhoek, and Than-Droogeveld the figures are 38 and 70 % (Buk, *in prep.a*; Buk, *in prep.b*). Waterval also has a high diversity of habitats with a wide range of soils, moisture regimes and topographic conditions as well as browse availabilities varying from 597 to 14 446 m^3/ha.

The regressions between volume and dry leaf mass of Smit (1996) only applies to regular shrubs and trees, but only 40 % of the Waterval browse falls in this category. Hence, dry leaf mass could not be calculated.

Habitat parameters and suitability

The distribution of habitat parameters described by this study was used to analyse food preferences (Paper 2) and habitat use of black rhino in Waterval (Paper 3). While only such detailed studies can reveal how each species of browser respond to habitat parameters, some general expectations can be discussed.

The low browse availability in Waterval will affect suitability of each habitat and the overall carrying capacity, but a favourable combination of plant palatability, species composition, diversity, phenology and canopy height increases the value of the browse. In Waterval no unpalatable plant species makes up a large percentage of the browse, leaf fall is limited to two to three months in one major species (Table 5) and high plant diversity allows a high degree of selectivity and seasonal switching of diet. The only exception is community 3, where *Euphorbia gregaria* dominates. This species has milky latex that makes it unpalatable to many browsers, except klipspringer (Own obs.)

Furthermore, most of the browse is 0-2 metres above the ground within reach of a large browser, except in communities 8 and 10 where large amounts of browse are only available to giraffes and arboreal herbivores (Table 2, figure 4). A large proportion of the browse above 1 metre is comprised of a few species of trees and shrubs, whereas below 1 metre browse is largely composed of a diverse array of herbs (Figure 4).

Community 10 has 14 times higher browse availability (from 0 to 200 cm above ground) than the average for Waterval and may be expected to be highly suitable for browsers. However, black rhino density was hardly affected by total browse availability, but by the availability of a few preferred species (Paper 3).

The north-eastern corner of Waterval (8.9 % of the area) is more than 4 km from water. The north-eastern area also has some steep slopes only exceeded by the near vertical Orange River Gorge. This is expected to make the north-east less utilised and the Orange River Gorge inaccessible to most browsers, with the exception of klipspringer. This held true in the study of black rhinos, which were less than 20 % as frequent on slopes exceeding 8 degrees and only about 5 % as frequent 4 km from water as next to water (Paper 3). Density of giraffe in Amboseli, Kenya was at its maximum 0-2 km from water, 75 % at 2-4 km and 25 % at 4-10 km and 0 % beyond 10 km (Western 1975).

Loose rocks exceeding 20 % in vegetation community 2 and 3 may affect the movement of herbivores and thus the habitat suitability. The high bedrock percentages of communities 1-3 are expected to be less of a problem because bedrock forms a stable substrate, although crevasses can cause injuries. Black rhino density in Waterval was significantly affected by total rock cover (Paper 3).

Disturbance in the form of passing vehicles on the low use public road along the northeastern boundary is expected to affect at least daytime distribution of large mammals. Black rhino density did in fact appear affected by this road as well as one of the park roads (Paper 3).

Vertical cover in the form of plant canopies is low in Waterval, except for community 9 and 10. In some communities topography and bedrock provides some hiding and thermal cover. Several communities, especially 3 and 5.1, have such low shade availability that it must be expected to affect daytime use in the hot summer months. The dense canopy cover of community 10 endows it with a moderated microclimate. Black rhinos were not affected by vertical cover, while shade was only border-line significant (Paper 3).

The riverine forest provides easy access to water, browse, shade and vertical cover. In contrast, the northeastern area is steep, 4-6 km from water and bordered by a public road, while community 3 is rocky, low in palatable browse and lacks shade. Browser habitat utilization is expected to reflect this. However, while black rhino did largely avoid the northeast, they preferred community 4 and 5.1 (Paper 3), which have the lowest browse availability, but are high in the plants rhino prefer (Paper 2).

Vegetation classification and measurements of browse availability

Using measured canopy cover or measured canopy volume 0-200 cm above ground resulted in the same classification into ten vegetation communities. This is because canopy cover and canopy volume are correlated. Thus, the much faster method of an experienced observer visually estimating cover is sufficient for classifying browser habitats. However, cover is not sufficiently correlated with canopy volume across a range a species to be used to estimate available canopy volume through regression. This is unfortunate because rather than the two dimensions of canopy cover, the three dimensions of canopy volume or biomass, are essential measures of browse availability used in measuring browsing preferences, modelling habitat use, estimating stocking rates and more.

Measuring canopy volume using BECvol (Smit, 1996) or similar methods of manual measuring is extremely time-consuming. It would therefore be useful to test whether visual estimation would also work for canopy volume and be sufficiently accurate for most applications. Alternatively, computerised or computer-assisted interpretation of aerial photography may be or become a viable option. In fact, in order to give better answers about browsing there is a need to move from the three dimensional snapshot of browse availability towards acquiring data on the four dimensions of browse growth. There is a big challenge in finding rapid and accurate methods for this purpose.

Conclusions and recommendations

Ten vegetation communities and some of the eco-geographical variables associated with them, including browse availability, were described. Browse availability, slope, water availability, shade, rockiness, vertical cover and disturbance are among the factors potentially affecting habitat suitability for herbivores in Waterval. Their geographical distribution leads to the expectation that utilization is high in and around community 10, while it is low in the northeast. GIS based inventories of habitat parameters, such as this study, should be available in all conservation areas to improve understanding of the area and facilitate research.

Rapid, but accurate methods of estimating browse availability and production are needed for studying aspects of browsing in more depth.

Conservation biology is the science of scarcity and diversity (Soulé 1986), and should be engaged to manage the scarcity and diversity of life in Watervaal and AFNP. To balance conservation of a unique and diverse plant life with that of large and rare herbivores, research on feeding and habitat suitability as well as monitoring of vegetation is recommended. This study provides the eco-geographical variables needed for research on diet preference and key plants to monitor (Paper 2) and habitat suitability (Paper 3) for browsers.

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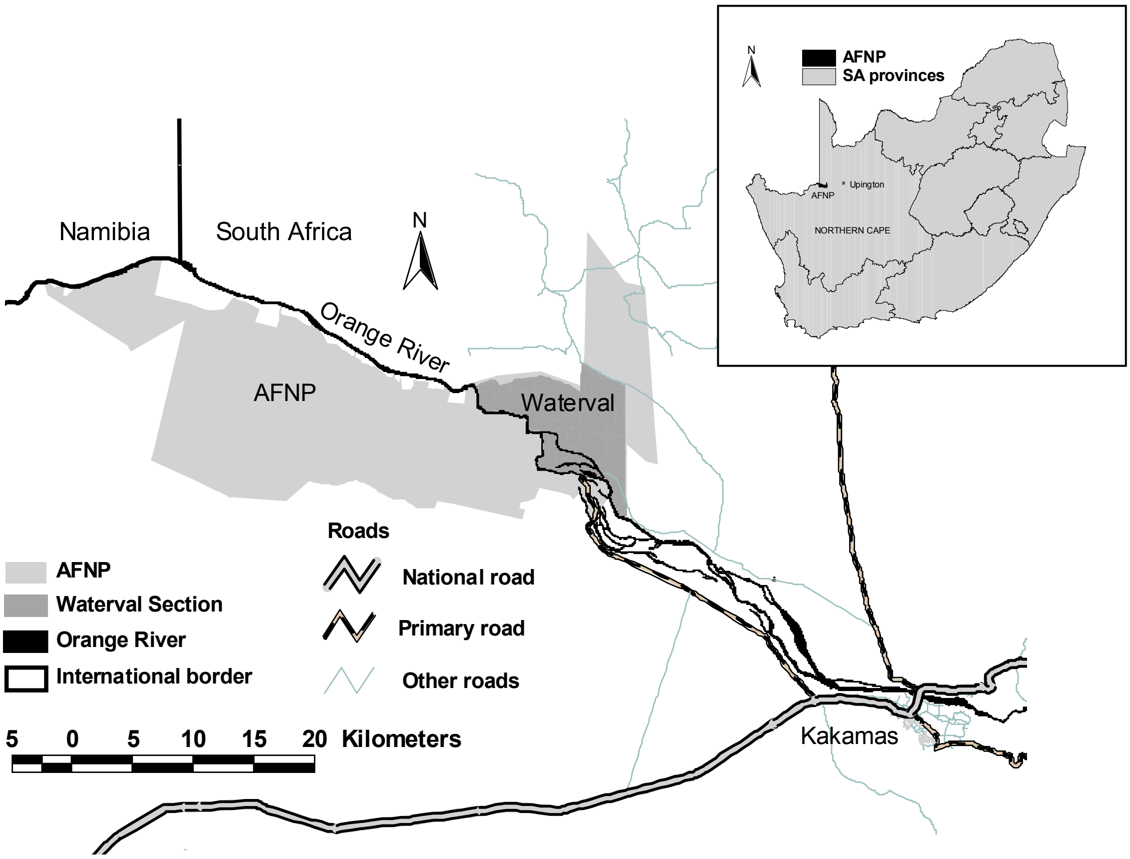


Figure 1.

The location of Waterval and Augrabies Falls National Park (AFNP).

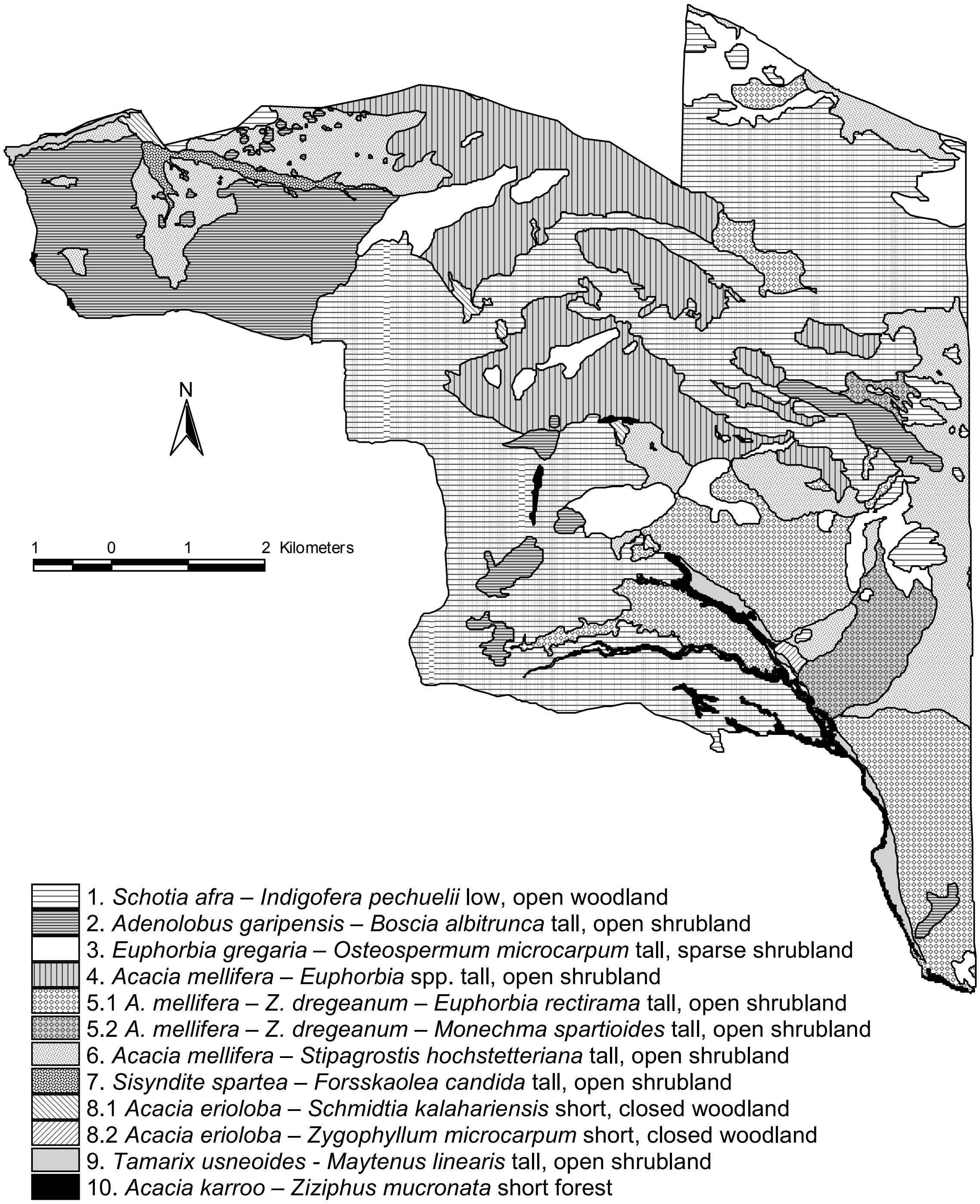


Figure 2.

Vegetation communities in the Waterval section of Augrabies Falls National Park.

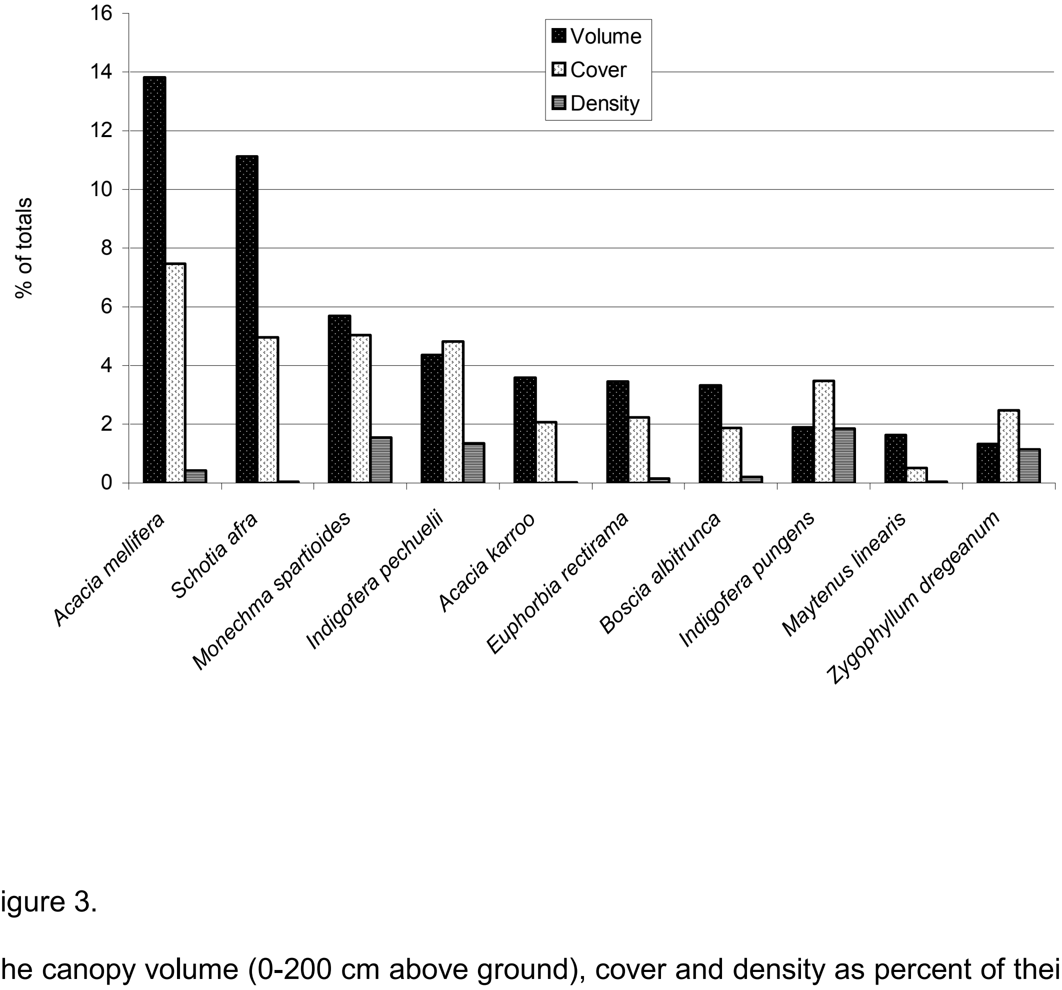


Figure 3.

The canopy volume (0-200 cm above ground), cover and density as percent of their totals for the study area for 10 of the most important browse plant species.

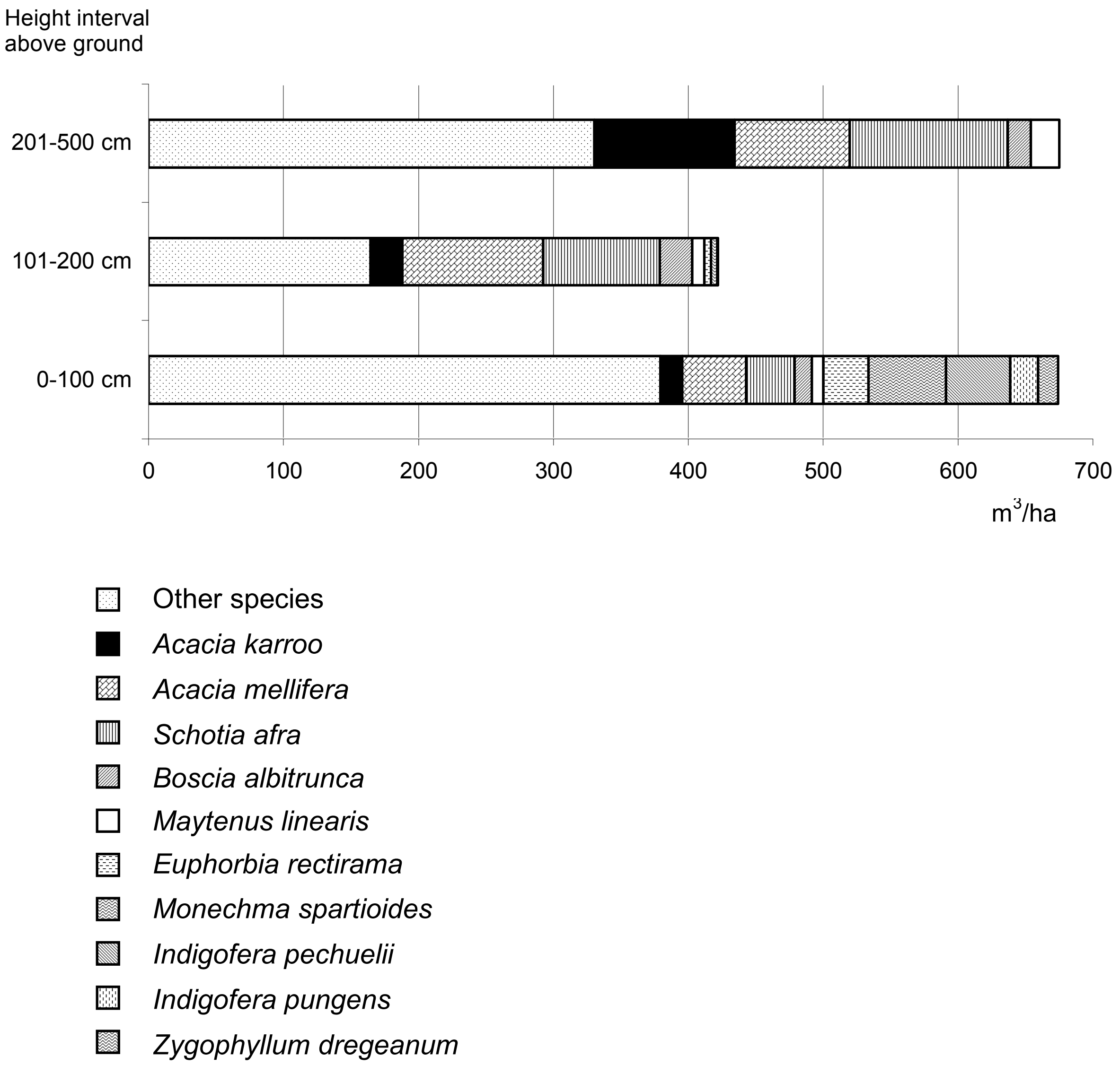


Figure 4.

A vertical profile of the canopy volume for 10 of the most important browse species in the Waterval section of Augrabies Falls National Park.

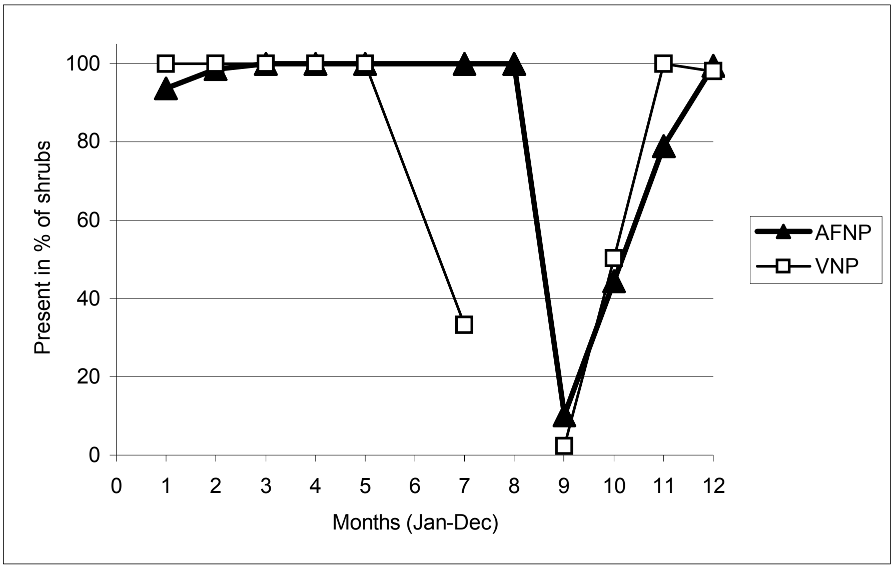


Figure 5.

The monthly presence of leaves on *Acacia mellifera* in Augrabies Falls National Park (n=937) and Vaalbos National Park (n=729).

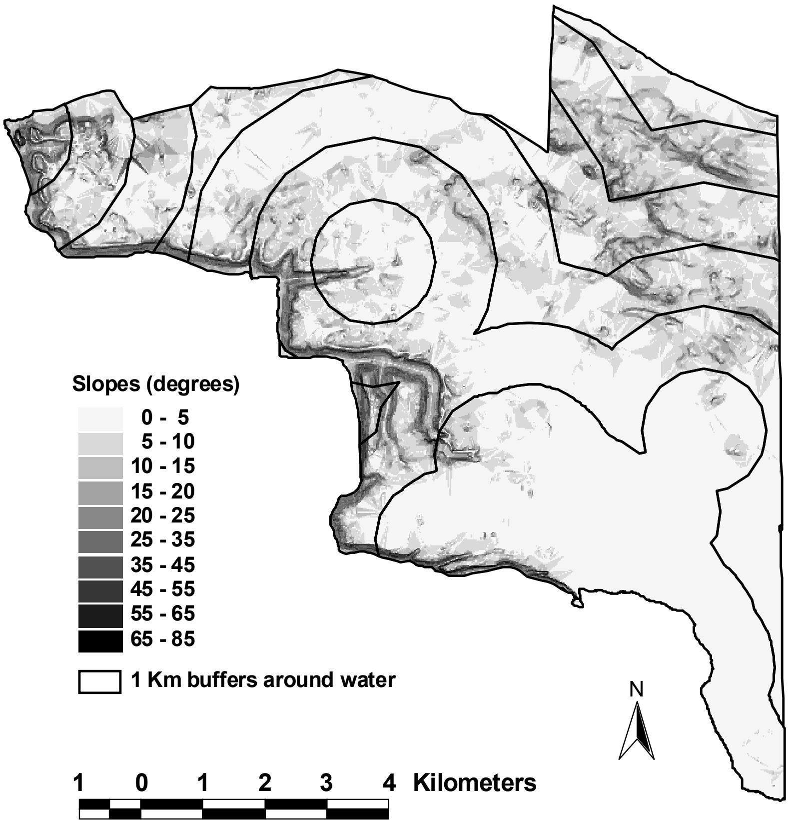


Figure 6.

The distance to accessible water and the slope in the Waterval section of AFNP.

Table 1.

Phytosociological table of the vegetation of the Waterval section of Augrabies Falls National Park based on canopy volume 0-200 cm above ground. The table is continued on the following page.

Species group	Vegetation community number	1									2						3					4										5.1							5.2		6						7			8		9				10			
	Vegetation plot number	44	20	24	45	57	40	19	56	10	54	55	32	34	35	36	25	8	9	49	38	43	18	41	15	16	17	21	23	42	53	12	13	11	14	48	26	22	51	52	37	33	4	5	7	6	1	2	3	39	58	50	27	31	29	47	30	46	28
A	*Schotia afra*	-	6	7	7	6	4	-	7	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	7	-	-	-	-	6	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-	-
	Indigofera pechuelii	7	-	4	3	6	3	-	5	-	5	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Hibiscus englerii	7	-	-	5	5	2	-	2	-	2	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Trichodesma africana	6	1	-	4	-	2	2	-	2	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
	Codon royeni	2	-	1	-	2	3	5	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-
	Euphorbia virosa	6	-	4	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Berkheya spinosisima	-	-	2	-	1	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B	*Adenolobus garipensis*	-	-	-	-	-	7	2	5	-	6	7	7	7	5	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Commiphora gracilifrondosa	-	4	4	-	2	-	4	-	-	-	-	5	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Rhus populifolia	-	5	-	-	4	-	2	-	-	2	-	5	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	*Euphorbia gregaria*	-	-	-	-	-	5	4	6	5	6	4	-	-	-	-	7	7	6	7	7	5	-	-	-	4	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Leucosphaera bainesii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D	*Ceraria namaquensis*	-	-	5	-	-	-	-	5	-	4	6	-	-	3	-	-	-	5	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Nymannia capensis	-	-	-	-	3	4	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E	*Stachys burchelliana*	6	1	4	3	5	3	-	5	-	4	-	-	-	-	-	-	-	-	-	-	5	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Hibiscus elliotiae	-	-	3	3	-	4	2	-	5	-	-	-	-	-	-	2	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Petalidium lucens	-	-	-	-	-	-	-	-	2	-	-	-	-	6	5	-	4	4	-	-	3	5	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Barleria rigida	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Galenia aethiopicum	-	-	-	-	-	-	-	-	-	2	2	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F	*Euphorbia rectirama*	7	-	4	-	-	4	-	5	4	-	-	-	-	2	-	-	-	-	-	-	5	-	7	6	3	5	2	-	5	-	-	4	-	-	-	6	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
G	*Zygophyllum dregeana*	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	4	6	-	-	1	6	5	6	5	4	6	5	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-
H	*Blepharis furcata*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	4	-	-	-	-	-	-	5	4	2	2	4	3	4	3	1	2	-	-	-	3	1	-	2	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Hermannia spinosa	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	1	-	-	1	1	1	-	2	-	3	-	1	1	1	2	1	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Polygala cf. seminuda	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	5	3	3	5	-	-	-	1	-	-	-	-	-	-	-	4	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Aptosimum spinescens	-	-	-	-	-	-	2	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	3	-	-	-	-	1	-	-	1	2	-	-	-	4	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Sarcostemma viminale	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	2	4	-	2	2	4	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
I	*Trianthema triquetra*	-	-	-	2	-	-	-	-	1	-	-	-	-	-	-	4	1	2	3	-	6	1	4	1	1	1	-	-	-	4	1	1	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-
	Rhyncosia totta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	2	-	-	3	3	-	2	-	-	-	-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Peliostomum leucorrhizum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	3	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Indigofera heterotricha	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
J	*Lebeckia spinescens*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
K	*Microloma sagittatum*	-	-	-	-	-	-	2	-	-	-	6	-	-	-	-	-	-	-	-	-	-	2	-	3	2	4	-	1	4	-	2	1	-	1	-	3	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Sericocoma avolans	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	2	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L	*Boscia foetida*	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	5	5	-	-	-	-	-	3	-	-	-	-	2	-	-	5	-	4	-	-	-	4	-	-	-	5	5	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-
	Monechma geneistifolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	1	-	3	-	2	1	-	-	-	-	4	6	-	-	-	-	-	-	-	-	-	-	-	-	-
	Rhigozum trichotomum	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	5	-	-	2	-	3	5	-	-	7	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M	*Boscia albitrunca*	-	4	6	6	-	5	4	-	-	1	-	6	6	6	6	-	-	-	-	5	5	5	4	-	5	6	-	1	-	-	-	-	-	-	-	-	-	-	-	5	6	-	4	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-

N	*Sisyndite spartea*	- 1 - - - - 6 - -	- - 4 - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	6 - - - - -	6 7 6	-	-	6 - - -	- - - -
O	*Hermannia stricta*	- - - - - - - - -	2 - - - - 5	- - - - -	- - - 2 - - - - 4 -	1 - 5 1 5 1 -	- -	2 - - - - -	4 - 5	-	-	- - - -	- - - -
P	*Forsskaolea candida*	4 3 2 - 7 7 1 6 4	2 - 6 - 6 -	2 3 1 - -	- - - - - - 2 - - -	- - - - - - -	- -	7 - - - - -	3 4 2	-	-	- - - -	- - - -
	Indigofera pungens	- - 1 - - - 6 - 7	- - - - 5 5	- - - - -	- 5 7 4 5 4 5 - - -	- 4 - - - - -	- -	- - - - - -	- 4 -	-	-	- - - -	- - - -
	Dyerophytum africanum	- - 5 - - 3 2 5 4	2 - - - - -	4 - - 4 5	- - - - - - - - - -	- - - - - - 3	- -	5 - - - - -	- 2 4	-	-	- - - -	- - - -
	Kohautia cynanchica	- - - - - - - 1 -	2 - - - - -	- 1 - - -	- - - - - - 2 - - -	1 - - 1 5 - -	- -	- - - - 2 1	1 - -	-	-	- - - -	- - - -
Q	*Limeum aethiopicum*	- - - - - - - - -	- - 2 - - 5	- 1 1 - 3	6 2 5 1 1 2 1 3 - -	1 1 - 1 - 1 1	- -	- 2 2 1 1 2	- - 1	5	-	- - - -	- - - -
R	*Monechma spartioides*	6 - - 4 - 6 1 4 2	4 5 4 - 7 4	3 4 5 6 5	5 4 7 4 4 4 5 5 2 6	4 - 5 3 5 3 4	5 6	6 7 4 2 - -	4 5 5	5	-	- - - -	- - - -
	Ostespermum microcarpum	2 - - - - - - - -	- 6 - 2 7 2	2 2 2 6 4	- - 2 - - - - - - -	1 1 - - - - 1	- -	5 - - - 1 -	2 - -	4	-	- - - -	- - - -
	Lotononis platycarpa	- - - - 3 - 1 - -	- 2 - - 2 -	- - - - 2	- - 5 - - - - - - 2	- - - - - - -	- -	2 - - - - -	- - -	4	-	- - - -	- - - -
S	*Acacia erioloba*	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - 4 5	- - -	6	6	- - - -	- - - -
T	*Acacia mellifera*	- - - - - 5 6 - 5	- - - - - -	1 4 - 6 -	6 7 6 5 6 6 5 5 7 6	7 7 7 6 6 5 6	6 7	7 7 6 5 6 7	7 4 5	6	6	4 3 - -	7 - 6 -
U	*Tamarix usneoides*	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	9 5 7 6	- - - -
	Psilocaulon absimile	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- 2 8 -	- - - -
	Mesembryanthemum	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- 2 - 2	- - - -
	Psilocaulon cf. coririum	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- 3 - -	- - - -
V	*Zygophyllum simplex*	- - - - - - - - -	2 - - - - 2	- - - - 3	- - 2 - - - - - 3 -	- - - - - - 1	- -	4 4 - 1 - -	- - -	-	8	5 1 4 -	- - - -
X	*Cleome foliosa*	- - - - - - 1 - 2	- - 6 6 5 4	- - - - 3	- 2 2 - - 1 1 2 - -	1 - - - - - -	- -	6 2 - - - -	1 2 -	5	-	6 - - -	- - - -
Y	*Acacia karroo*	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	9 9 - 9
	Ziziphus mucronata	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- 6 9 8
	Salix mucronata	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	9 8 - -
	Asparagus capensis	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	4 - 2 -
	Asparagus retrofractus	- - - - - - - - -	- - - - - -	- - - - -	- - - 3 - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	4 - 2 2
	Combretum erythrophyllum	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- 7 - -
	Nidorella residifolia	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- 1 - 6
	Gomphostigma virgatum	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- 6 - -
	Maytenus heterophylla	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	6 - - -
	Diospyros lyciodes	- - - - - - - - 3	- - - - - -	- - - - -	- - - - - - - - - -	- - 3 - - - -	- -	- - - - - -	- - -	-	-	- - - -	4 5 - -
Z	*Rhus pendulina*	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	6 - - -	8 9 - 7
	Suaeda fruticosa	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - 9 5	- - - 8
AA	*Maytenus linearis*	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - 5 6 - 4	- - -	-	-	7 5 6 7	8 6 8 5
AB	*Lycium bosciifolium*	- - - - - - - - -	- - - - - -	- - - - -	- - - - - 2 - - - -	5 - - - - - 2	- -	- - - 5 6 5	- - -	-	-	- - - -	- - 6 -
	Euclea pseudobenus	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	2 - 4 2 - - -	- -	- - - - - -	- - 6	-	3	5 - 4 5	7 9 6 3
	Zygophyllum microcarpum	- - 1 - - - - - -	- - - - - -	- - - 2 -	- - - - - - - - - -	- - - - - - 3	- -	- - - 3 5 -	- - -	-	6	- 2 7 -	- - 5 -
AC	*Tribulus cristatus*	- - - - - 5 2 - 1	2 6 - 6 6 4	- 1 2 7 5	7 2 2 1 3 4 - - - 5	1 1 - - - - 1	- -	5 1 4 5 2 5	1 2 1	7	-	- 3 2 7	- - 8 -
	Asparagus sp.	- - - - - - 2 - 2	- 2 - 2 - 2	3 - - - 4	- 4 4 3 2 2 - - 2 2	- 4 4 2 2 2 -	4 4	- 4 - 1 - -	- - -	-	-	- - - -	9 6 9 5
	Thesium lineatum	5 - - - - - - - -	- - - - - -	- - - - -	- 2 - - - - - - - -	- 2 4 - 3 - -	2 -	- - - - - -	- - -	2	-	- - - -	6 - - 5
	Pappea capensis	- 1 - - 1 - 1 - -	- - - - - -	- - - - -	- 1 - - 1 - - 1 - -	- 1 - - 1 - -	- 1	- - - - 1 -	- - -	-	-	- - - -	- - 2 -
	Indigofera argyroides	- - - - - - - - -	- - 2 1 - -	- - - - -	- - 1 - - - - - 1 -	- - - - - - -	- -	2 1 - - - -	- - -	-	-	- - - -	- - - -
	Cadaba aphylla	- - - - - - - - 3	- - 5 - 2 -	- - - - 5	- - 6 - - - - - - -	- - - - - - -	- -	- - - - - 4	3 - -	-	-	- - - -	- - - -
	Cullen obtusifolia	- - 1 - - - - - -	- 3 - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- - - 1
	Hypertelis salsoloides	- - - - - - - - -	- - - - - -	- - - - -	3 - - - - - - - - -	- - - - 1 - -	- -	- - - - - -	- - -	-	-	- - - -	- - - -
	Phyllanthus maderaspatensis	- - - 1 - - - - -	- - - - - -	- - - - -	4 - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- - - -
	Euclea undulata	- - - - 2 - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- - - -
	Ornithoglossum cf. viride	- - - - - - 1 - -	1 - - - - -	- - - - -	- - - - - - - - - -	- - - - - - 1	- -	- - - - - -	- - -	-	-	- - - -	- - - -
	Cleome angustifolia	- - - - - - - - -	- - - - 1 1	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- - - -
	Cucumis dinteri	- - - - - - - - 2	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- - - -
	Abutilon pycnodon	- - - - - - - - -	- 2 - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- - - -
	Portulaca trianthemoides	- - - - - - - - -	- - - - - -	- - - - -	1 - 1 - - - - - - -	- - - - - - -	- -	- - - - - 1	- - -	-	-	- - - -	- - - -
	Curroria decidua	- - - - - - - 4 -	- - - - - -	4 - - - 5	- - - - - - - - - -	- - - - - - -	4 5	- - - - - -	- - -	-	-	- - - -	- - - -
	Ptycholobium biflorum	- - - - - - - - -	2 - - - - -	- - - - -	- - - - - - - 1 - -	- - - - - - 1	- 3	- - - - - -	- - -	-	-	- - - -	- - - -
	Zygophyllum stapfii	- - - - - - - - -	- - - - - -	- - - 3 -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- - - -
	Aizoon asbestinum	- - - - - - - - -	- - - - - -	- - - - -	- - - - 2 1 - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- - - -
	Dicoma capensis	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - 1 - -	- -	- - - - - -	- - -	4	-	- - - -	- - - -
	Geigeria ornativa	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - 2	- - - - - - -	- -	- - 1 - - -	- - -	-	-	- - - -	- - - -
	Aloe dichotoma	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - 2 - - -	- -	- - - - - -	- - -	-	-	- - - -	- - - -
	Pegularia daemia	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - 4	- - -	-	-	- - - -	- - - -
	Maerua gilgii	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - 4 2 -	3 -	- - - - - -	- - -	-	-	- - - 2	- - - -
	Gisekia pharnacioides	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- 2 1	-	-	- - - -	- - - -
	Tetragonia arbuscula	- - - - - - - - -	- - - - - -	- - - - -	- - - 2 - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	- - - -	- - 1 -
	Amaranthus praetermissus	- - - - - - - - -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- 1 -	-	-	- 1 - 1	- - - -
	Phaeoptilum spinosum	- - - - - - - - -	- - - 4 - -	- - - - -	- - - - - 3 - - - -	- 2 - - - - -	- -	- - - - - -	4 - -	-	4	- 6 - -	- - - -
	Solanum nigrum	- - - - - - - 2 -	- - - - - -	- - - - -	- - - - - - - - - -	- - - - - - -	- -	- - - - - -	- - -	-	-	3 - - -	- - - -

Table 2.

Size, sampling intensity, vertical distribution of canopy volume, substrate particle size and slope for each vegetation community.

			Vegetation communities												
Characteristics		Units	1	2	3	4	5.1	5.2	6	7	8.1	8.2	9	10	Study area
Area		ha	2753.5	878.2	507.3	1098.3	879.2	210.0	938.8	51.7	31.5	8.1	76.1	83.4	7529.6
		%	36.6	11.7	6.7	14.6	11.7	2.8	12.5	0.7	0.4	0.1	1.0	1.1	100.0
Veg. plots		#	9	6	5	10	7	2	6	3	2		4	4	58
		%	15.5	10.3	8.6	17.2	12.1	3.4	10.3	5.2	3.4		6.9	6.9	100.0
Canopy Volume	0-1 m	m^3/ha	596	821	738	608	343	495	622	420	863		1747	5878	674
	1-2 m	m^3/ha	379	254	183	244	254	366	456	652	284		834	8569	422
	2-5 m	m^3/ha	454	299	7	112	107	180	520	1043	2581		804	31221	675
Substrate - particle size	Bedrock	%	47	21	33	16	13	4	1	0	0	0	0	3	26
	Rocks	%	11	21	28	9	4	4	0	1	0	0	0	0	10
	Pebbles	%	9	21	6	16	17	57	5	0	0	0	0	0	13
	Gravel	%	18	33	11	48	55	35	41	95	36	100	0	0	32
	Sand	%	13	3	22	12	11	0	53	4	64	0	0	0	17
	Silt & clay	%	0	0	0	0	0	0	0	0	0	0	100	48	2
	Organic material	%	1	1	0	0	0	0	0	0	0	0	0	48	1
	Av. rock diameter	cm	32.3	9.4	17.8	12.5	4.4	5.0	-	5.0	-	-	-	-	-
Slope	25 percentile	Deg.	4	4	2	2	1	1	1	3	1	1	0	0	2
	Median	Deg.	7	8	4	3	1	1	2	4	3	1	1	0	4
	75 percentile	Deg.	15	16	6	5	1	2	5	6	6	1	1	1	9
	95 percentile	Deg.	38	40	13	9	6	6	12	10	9	1	12	12	29

Table 3.

Characteristics of the tree, woody shrub and herbaceous strata of each vegetation community.

Plant community	Stratum											
	Tree			Woody shrubs			Herbaceous			Combined		
	Height (cm)	Cover (%)	Volume (m^3/Ha)	Height (cm)	Cover (%)	Volume (m^3/Ha)	Height (cm)	Cover (%)	Volume (m^3/Ha)	Cover (%)	Shade (%)	Shade (#/Ha)
1	270	3.6	322.6	141	1.3	117.7	26	15.9	535.0	20.8	0.5	4.4
2	274	1.1	112.2	163	2.7	297.0	22	32.3	666.6	36.1	0.5	3.4
3	162	0.4	39.6	201	0.9	87.1	16	22.4	791.1	23.6	0.0	0.0
4	203	1.3	118.7	130	2.9	233.9	15	21.5	499.1	25.7	0.2	1.3
5.1	235	1.0	85.5	132	3.1	322.7	21	5.4	189.0	9.5	0.2	0.5
5.2	151	0.2	12.8	190	5.6	462.2	22	12.6	386.0	18.4	0.7	6.3
6	233	1.2	98.1	107	8.9	641.1	22	13.0	338.7	23.2	2.1	12.6
7	522	4.5	530.5	179	5.8	448.6	42	2.6	92.0	12.9	3.4	9.4
8	590	12.7	232.0	220	4.1	185.0	52	57.2	729.7	71.9	11.4	15.8
9	287	7.0	803.3	122	16.2	1162.6	65	34.6	615.4	57.8	3.0	11.6
10	533	139.2	8364.5	124	9.1	1575.7	42	47.7	5889.6	196.0	98.0	256.2

Table 4.

Available browse for the 10 most abundant species in each community expressed as canopy volume 0-200 cm above ground.

		Vegetation community													
		1	2	3	4	5.1	5.2	6	7	8	9	10	Study area		
Species		m^3/ha	m^3/ha	m^3/ha	m^3/ha	m^3/ha	m^3/ha	m^3/ha	m^3/ha	m^3/ha	m^3/ha	m^3/ha	m^3	m^3/ha±SEM	% ± SEM
Acacia mellifera		27.6		32.5	207.2	293.6	418.2	483.9	159.9	122.7			1143242	151.8 ±21.2	15.00 ±1.70
Schotia afra		270.1			86.0	65.4			484.1				922661	122.5 ±33.0	12.70 ±3.31
Monechma spartioides		42.5	96.4	67.1	71.4	30.4	108.2	109.1	42.3	33.8			469723	62.4 ±16.7	4.50 ±0.94
Forsskaolea candida		100.7	55.5					75.1	7.3				386401	51.3 ±21.6	4.30 ±1.95
Euphorbia gregeria			21.3	520.4									370514	49.2 ± 9.5	5.15 ±0.71
Indigofera pechuelii		92.9			89.0								360920	47.9 ±28.0	2.58 ±1.19
Asparagus sp.							25.0					3903.3	349519	46.4 ±31.3	3.65 ±2.25
Adenolobus garipensis		43.8	243.1			7.5							340611	45.2 ±15.2	4.42 ±1.34
Acacia karroo												3558.4	296769	39.4 ±15.2	4.15 ±1.75
Euphorbia rectirama		59.2			74.0	46.1							285158	37.9 ±17.4	2.87 ±0.93
Boscia albitrunca		40.4	98.5	18.1	31.4			36.5					275781	36.6 ± 8.3	3.75 ±0.87
Tribulus cristatus			80.1	99.7	45.7			29.4		235.5	149.2	285.3	258874	34.4 ± 9.6	2.70 ±0.64
Osteospermum microcarpum			194.7	37.9						14.2			198345	26.2 ±17.2	1.44 ±0.82
Indigofera pungens					63.8				5.2				156940	20.8 ± 9.9	1.90 ±0.75
Hibiscus englerii		50.1											140383	18.6 ±14.1	0.99 ±0.58
Maytenus linearis								39.1	7.6		341.0	881.2	136986	18.2 ± 6.2	1.98 ±0.69
Salix mucronata												1375.5	114717	15.2 ± 9.8	1.38 ±0.90
Rhus pendulina											57.9	1305.6	113295	15.0 ± 8.1	1.41 ±0.70
Cleome foliosa			71.4					44.6		36.7			110266	14.6 ± 6.8	1.13 ±0.48
Zygophyllum dregeanum					24.2	55.5	151.3						109979	14.6 ± 4.9	1.63 ±0.53
Trichodesma africana		35.2											108664	14.4 ±11.4	0.72 ±0.46
Ziziphus mucronata												1189.1	99173	13.2 ± 7.9	1.17 ±0.61
Suaeda fruticosa											723.8	453.9	92936	12.3 ± 8.7	1.02 ±0.72
Ceraria namaquensis			27.0	20.0									87834	11.7 ± 5.0	1.32 ±0.54
Sisyndite spartea									274.1		33.9		83580	11.1 ± 6.4	1.58 ±1.12
Boscia foetida				21.6		10.8	9.2	48.0					81834	10.9 ± 3.8	1.18 ±0.36
Rhigozum trichotomum						8.6	20.2	59.2					70985	9.4 ± 6.9	1.07 ±0.80
Euclea pseudobenus									46.4		36.3	711.1	68586	9.1 ± 6.0	0.78 ±0.54
Dyerophytum africanum									8.1				61533	8.2 ± 3.7	0.83 ±0.43
Tamarix usneoides											708.4		53906	7.2 ± 5.2	0.55 ±0.31
Petalidium lucens			42.2										48583	6.5 ± 3.4	0.66 ±0.34
Lycium bosciifolium								31.1					39258	5.2 ± 2.2	0.73 ±0.39
Limeum aethiopicum										17.1			38840	5.2 ± 2.8	0.53 ±0.33
Cadaba aphylla				13.6									35510	5.7 ± 2.5	0.31 ±0.15
Trianthema triquetra					25.8								32520	4.3 ± 3.3	0.25 ±0.13
Hermannia stricta						16.5			25.7				30150	4.0 ± 2.0	0.47 ±0.31
Indigofera heterotricha						14.7	68.4						28116	3.7 ± 2.6	0.27 ±0.19
Zygophyllum microcarpum										126.6	99.0		27067	3.6 ± 1.9	0.44 ±0.28
Psilocaulon absimile											301.8		22966	3.1 ± 3.0	0.15 ±0.14
Acacia erioloba										253.1			22725	3.0 ± 1.2	0.32 ±0.13
Curroria decidua				14.0			23.1						17667	2.3 ± 1.0	0.29 ±0.13
Combretum erythrophyllum												210.3	17537	2.3 ± 2.3	0.21 ±0.21
Zygophyllum simplex										262.2			19518	2.6 ± 1.5	0.21 ±0.12
Polygala cf. seminuda							7.0						13864	1.8 ± 0.9	0.34 ±0.19
Lotononis platycarpa										7.3			11729	1.6 ± 1.0	0.10 ±0.06
Phaeoptilum spinosum										11.6	54.9		9241	1.2 ± 0.7	0.42 ±0.36
Sarcostemma viminale							7.7						8017	1.1 ± 0.5	0.10 ±0.04
Dicoma capensis										5.2			2160	0.0 ± 0.0	0.00 ±0.00
Browse from top 3 spp.	%	47.5	49.9	74.9	44.9	69.5	78.7	61.1	85.7		68.7	61.2	30.7		
Browse from top 10 spp.	%	78.2	86.5	92.1	84.4	92.1	97.4	87.5	99.0		97.1	96.0	59.8		
Equitability, top 10 spp.	E	0.55	0.65	0.25	0.67	0.31	0.33	0.35	0.33		0.49	0.56	0.76		
Browse diversity	D(H')													18.95 (3.45)	
Total available browse	m^3/ha	975.3	1075.8	917.8	851.7	597.2	861.0	1077.9	1071.1	1146.6	2581.3	14446.2		1095.8	
	±SEM	181.1	259.6	284.1	206.3	116.6	265.7	219.2	488.6	101.5	1083.7	1645.0		89.6	
Total available browse	m^3	2685395	944768	465599	935448	525065	180808	1011955	55375	45407	196435	1204811	8251064		
Total available browse	%	32.5	11.5	5.6	11.3	6.4	2.2	12.3	0.7	0.6	2.4	14.6	100.0		

Photos on the following page:

Top left: Community 1 – *Indigofera pechuellii* shrubs in front, *Schotia afra* trees behind

Top right: Community 2 – *Adenolobus garipensis* shrub at the front, right

Second row, left: Community 3 – *Euphrobia gregaria* shrub-like succulent

Second row, right: Community 4 – *Euphorbia rectirama* shrub-like succulent middle, left and *Acacia mellifera* shrub middle, right

Third row, left: Community 5 (Variant 5.1) – *Zygophyllum cf. dregeana* succulent forb front, right; *Acacia mellifera* shrub top, left and *Euphorbia rectirama* shrub-like succulent top, right

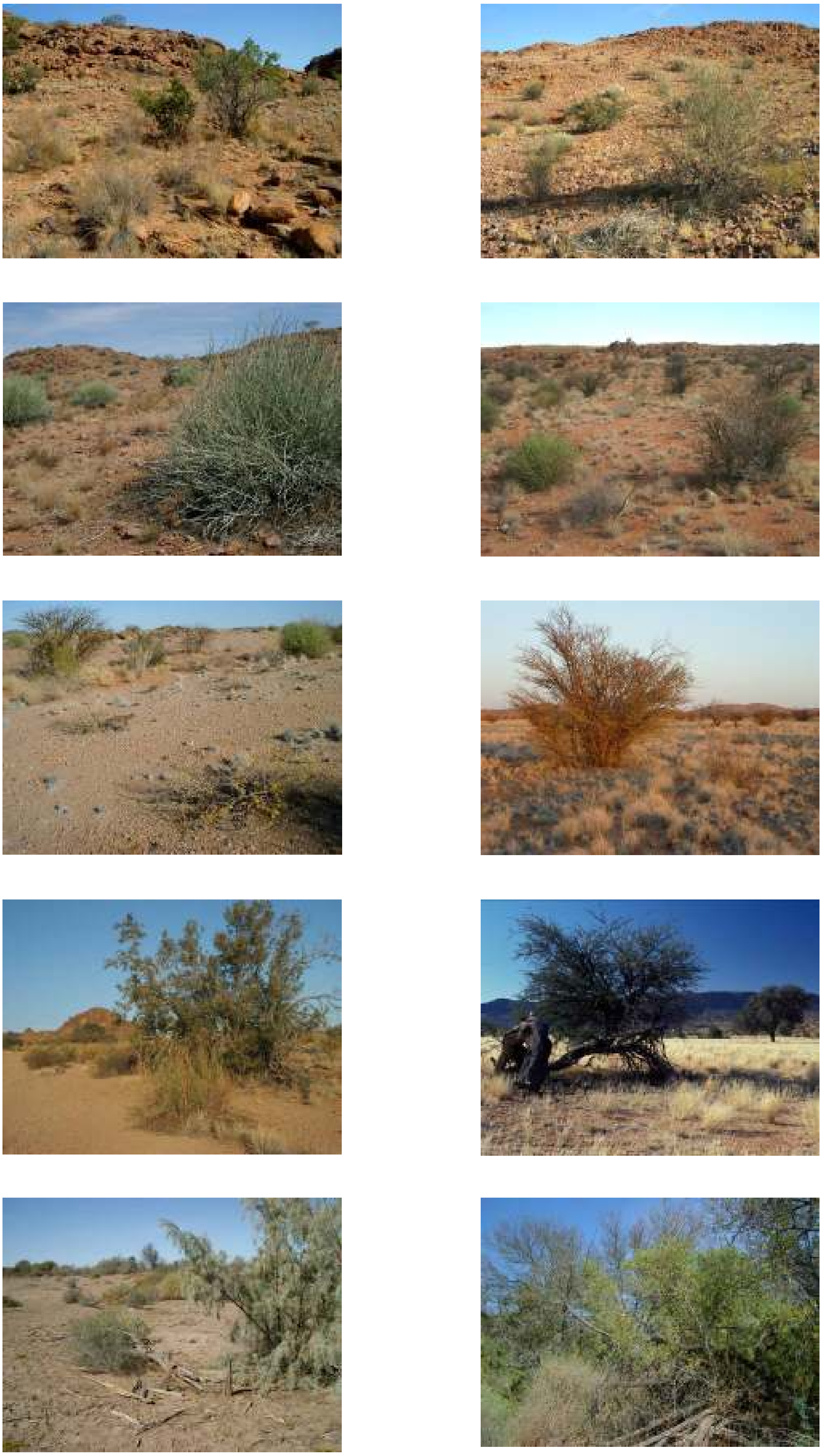
Third row, right: Community 6 - *Acacia mellifera* shrubs

Fourth row, left: Community 7 – *Sisyndite spartea* shrub in front and *Schotia afra* tree behind

Fourth row, right: Community 8 (variant 8.1) – *Schmidtia kalahariensis* grass and *Acacia erioloba* trees

Bottom row, left: Community 9 – *Tamarix usneoides* tree on the right

Bottom row, right: Community 10 – *Ziziphus mucronata* (deciduous tree - front, left); *Rhus pendulina* (bright green – center) and *Acacia karroo* (tall trees – top, left)



Vegetation communities 1 to10 left to right, top to bottom.

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, rs=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 overshot 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 thee 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 been 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 to 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^{o} 25’- 28^{o} 38’S, 19^{o} 53’ – 20^{o} 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, rs=0.37, n=51, *p*=0.0072), for the early dry season (March-May)(Spearman, rs=0.36, n=51, *p*=0.0091) and for the late dry season (June-October)(Spearman, rs=0.40, n=51, *p*=0.0036), but not for the wet season (November-February)(Spearman, rs=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, rs=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, rs=0.24, n=175, *p*<0.0015 and Spearman, rs=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 m^3 (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 m^3 then annual consumption equals 7 300 m^3 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 m^3. The rare, but highly preferred *Tetragonia arbuscula*, occurred with only 82.5 m^3 of total available canopy volume, while annual consumption was 0.33 % of 29 200 m^3, which is 96.4 m^3 or more than 117 % of the available volume. The top principal and highly preferred food, *Zygophyllum cf. dregeana*, occurred with 109 979 m^3 of canopy volume, while annual consumption was 30.55 % of 29 200 m^3, which is 8 921 m^3 or 8.1 % of the available volume. The second ranking principal food, *Acacia mellifera*, occurred with 1 143 242 m^3 of available canopy volume, while annual consumption was 26.16 % of 29 200 m^3, which is 7 639 m^3 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 Oguge, 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 Oguge, 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. dregena* 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. One 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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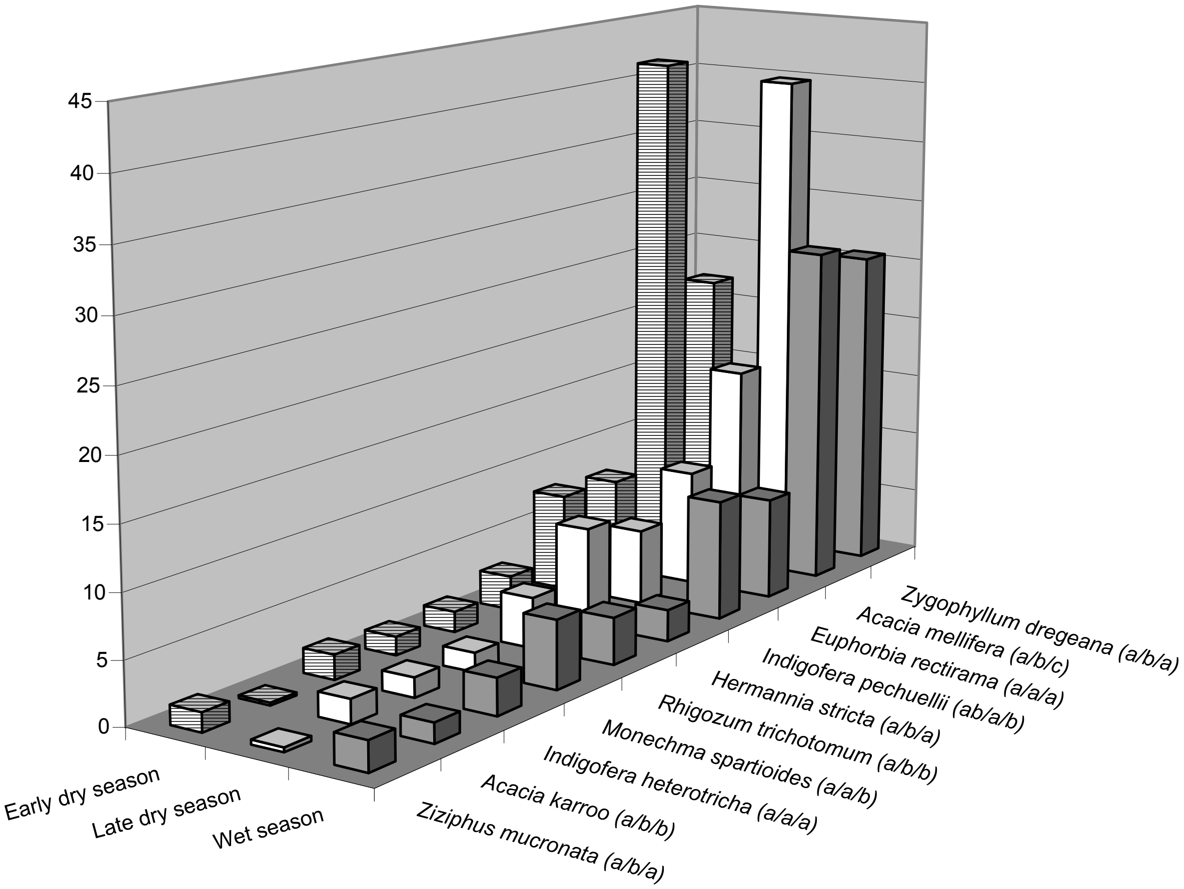

Figure 1.

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).

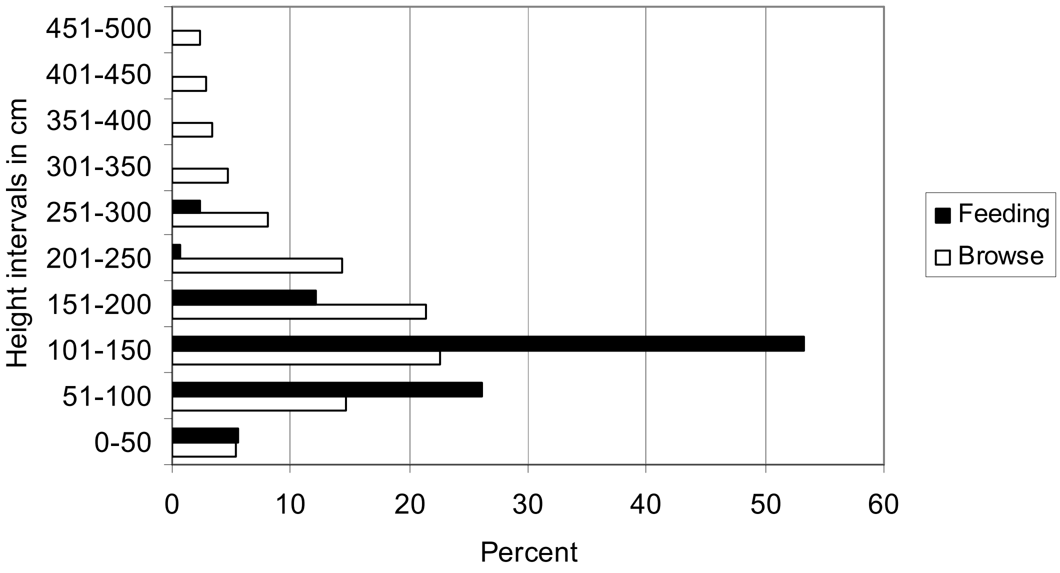

Figure 2.

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

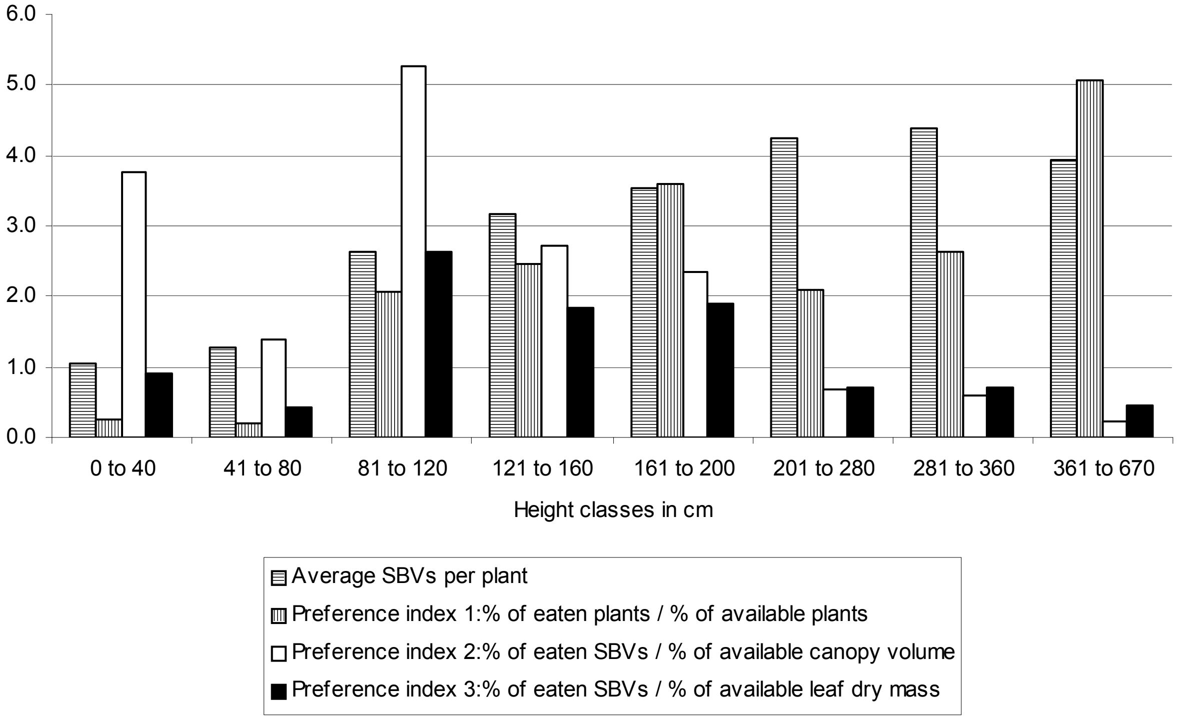

Figure 3.

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.

	Diet				Available browse	Diet preference			
	Mar-May	Jun-Oct	Nov-Feb	Full year	Waterval	Mar-May	Jun-Oct	Nov-Feb	Full year
Browse species	% of volume consumed				% vol	Diet / browse availability			
Zygophyllum cf. dregeana	21.90^{a3}	39.71^{b3}	25.57^{a3}	30.55^{3}	1.63	**13.44**	**24.36**	**15.69**	**18.74**
Acacia mellifera	41.47^{a3}	16.25^{b}	27.06^{c3}	26.16^{3}	15.00	**2.76**	1.08	**1.80**	**1.74**
Euphorbia rectirama	7.40^{a3}	9.19^{a3}	8.05^{a3}	8.36^{3}	2.87	**2.58**	**3.20**	**2.81**	**2.91**
Indigofera pechuellii	7.73^{ab3}	5.97^{a2}	9.51^{b3}	7.59^{3}	2.58	**2.99**	**2.31**	**3.69**	**2.94**
Hermannia stricta	2.73^{a3}	7.80^{b3}	2.47^{a3}	4.76^{3}	0.47	**5.82**	**16.59**	**5.26**	**10.12**
Rhigozum trichotomum	1.64^{a}	4.01^{b2}	3.72^{b3}	3.32^{2}	1.07	1.53	**3.75**	**3.47**	**3.10**
Monechma spartioides	1.49^{a3}	1.55^{a2}	5.41^{b}	2.83^{3}	4.50	**0.33**	**0.35**	1.20	**0.63**
Indigofera heterotricha	1.97^{a3}	1.57^{a1}	2.90^{a3}	2.11^{3}	0.27	**7.29**	**5.81**	**10.73**	**7.82**
Acacia karroo	0.22^{a3}	1.91^{b1}	1.58^{b3}	1.38^{3}	4.15	**0.05**	**0.46**	**0.38**	**0.33**
Ziziphus mucronata	1.53^{a}	0.37^{b}	2.36^{a2}	1.32	1.17	1.31	0.31	**2.02**	1.13
Lycium bosciifolium	0.77^{a}	1.83^{a}	0.53^{a}	1.13^{1}	0.73	1.05	2.50	0.73	**1.55**
Phaeoptilum spinosum	0.58^{a}	1.75^{b1}	0.15^{a}	0.93^{1}	0.42	1.39	**4.16**	0.37	**2.20**
Petalidium lucens	2.33^{a2}	0.24^{b}	0.60^{b}	0.88	0.66	**3.53**	0.37	0.91	1.34
Indigofera pungens	1.49^{a}	0.00^{b2}	1.07^{a1}	0.73^{3}	1.90	0.79	**0.00**	**0.56**	**0.38**
Schotia afra	0.69^{a3}	0.00^{b3}	1.60^{a3}	0.71^{3}	12.70	**0.05**	**0.00**	**0.13**	**0.06**
Hermannia spinosa	0.73^{a1}	0.63^{a}	0.61^{a2}	0.65^{3}	0.05	**13.50**	11.60	**11.26**	**11.96**
Maytenus linearis	0.07^{a3}	1.46^{b}	0.04^{a3}	0.64^{3}	1.98	**0.04**	0.74	**0.02**	**0.32**
Dyerophytum africanum	0.66^{ab}	0.94^{a}	0.07^{b3}	0.58	0.83	0.79	1.13	**0.09**	0.70
Monechma genistifolium	1.49^{a1}	0.12^{b}	0.18^{b}	0.48	0.42	**3.53**	0.29	0.42	1.14
Polygala cf. seminuda	0.22^{a}	0.24^{a}	0.96^{b1}	0.48	0.34	0.64	0.72	**2.83**	1.40
Zygophyllum microcarpum	0.33	0.85	0.07^{1}	0.46	0.44	0.75	1.94	**0.16**	1.05
Sericocoma avolans	0.51	0.37	0.33	0.39	0.34	1.49	1.07	0.96	1.13
Rhus pendulina	0.00^{a3}	0.73^{b}	0.21^{ab3}	0.38^{3}	1.41	**0.00**	0.52	**0.15**	**0.27**
Euclea psedobenus	0.15^{1}	0.65	0.12^{2}	0.35^{2}	0.78	**0.19**	0.83	**0.15**	**0.44**
Tetragonia arbuscula	0.69^{1}	0.12	0.32^{1}	0.33^{2}	0.01	**98.92**	17.41	**45.80**	**47.25**
Grewia flava	0.00	0.00	0.89^{3}	0.30^{2}	0.00	NA	NA	NA	NA
Blepharis furcata	0.00^{a}	0.49^{b}	0.11^{ab}	0.24	0.24	0.00	2.03	0.45	0.99
Barleria rigida	0.22	0.00	0.53^{1}	0.23^{1}	0.02	12.86	0.00	**31.43**	**13.69**
Acacia erioloba	0.29	0.00	0.43	0.22	0.32	0.91	0.00	1.34	0.67
Boscia foetida	0.00^{a2}	0.49^{b}	0.00^{3a}	0.20^{3}	1.18	**0.00**	0.41	**0.00**	**0.17**
Tamarix usneoides	0.04^{1}	0.27	0.14^{1}	0.17^{1}	0.55	**0.07**	0.50	**0.26**	**0.31**
Asparagus sp.	0.07^{3}	0.12^{3}	0.18^{3}	0.13^{3}	3.65	**0.02**	**0.03**	**0.05**	**0.04**
Aptosimum spinescens	0.07	0.00	0.32^{1}	0.13	0.04	2.08	0.00	**9.16**	3.57
Euphorbia gregaria	0.22^{3}	0.00^{3}	0.20^{3}	0.12^{3}	5.15	**0.04**	**0.00**	**0.04**	**0.02**
Nicotiana glauca	0.00	0.00	0.36^{1}	0.12	0.00	0.00	0.00	**445.28**	148.43
Psilocaulon absimile	0.00	0.12	0.11	0.09	0.15	0.00	0.81	0.71	0.58
Cleome foliosa	0.07^{2}	0.00^{1}	0.18^{3}	0.08^{3}	1.13	**0.06**	**0.00**	**0.16**	**0.07**
Plexipus garipensis	0.00	0.00	0.18	0.06	0.00	NA	NA	NA	NA
Ceraria namaquensis	0.00^{3}	0.12^{1}	0.00^{3}	0.05^{3}	1.32	**0.00**	**0.09**	**0.00**	**0.04**
Ehretia rigida	0.00	0.12	0.00	0.05	0.00	NA	NA	NA	NA
Suaeda fruticosa	0.00^{2}	0.00^{1}	0.14^{3}	0.05^{3}	1.02	**0.00**	**0.00**	**0.14**	**0.05**
Hermannia minutiflora	0.00	0.00	0.14	0.05	0.00	0.00	0.00	142.49	47.50
Adenolobus garipensis	0.00^{3}	0.00^{3}	0.14^{3}	0.05^{3}	4.42	**0.00**	**0.00**	**0.03**	**0.01**
Thesium lineatum	0.07	0.00	0.07	0.04	0.14	0.52	0.00	0.51	0.30
Unindentified	0.07	0.00	0.07	0.04	0.00	NA	NA	NA	NA
Salsola sp.	0.00	0.00	0.11	0.04	0.00	0.00	0.00	53.43	17.81
Commiphora erythrophyllum	0.00	0.00	0.11	0.04^{1}	0.21	0.00	0.00	**0.51**	**0.17**
Osteospermum microcarpum	0.07^{3}	0.00^{1}	0.00^{3}	0.02^{3}	1.44	**0.05**	**0.00**	**0.00**	**0.01**
Sisyndite spartea	0.00^{3}	0.00^{2}	0.04^{3}	0.01^{3}	1.58	**0.00**	**0.00**	**0.02**	**0.01**
Boscia albitrunca	0.00^{3}	0.00^{3}	0.04^{3}	0.01^{3}	2.70	**0.00**	**0.00**	**0.01**	**0.00**
Euclea undulata	0.00	0.00	0.04	0.01	0.00	0.00	0.00	8.91	2.97
Forsskaolea candida	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			
% consumed browse volumes/ % canopy volume in reserve			% browse volumes/ % of plants along feeding trail			% mass eaten / % mass presented			
Species		*p*	Species		*p*	Species		*p*	Rank
Tetragonia arbuscula	47.25	<0.001	*Acacia karroo*	3.86	0.3991	*Zygophyllum dregeana*	2.57	<0.0001	1
Zygophyllum dregeana	18.74	<0.0001	*Tetragonia arbuscula*	3.31	0.7018	*Ziziphus mucronata*	1.71	0.0304	2
Barleria rigida	13.69	<0.05	*Lycium bosciifolium*	3.31	0.6201	*Euphorbia rectirama*	1.70	<0.0001	3
Hermannia spinosa	11.96	<0.0001	*Barleria rigida*	2.48	0.8360	*Monechma spartioides*	1.69	0.1350	4
Hermannia stricta	10.12	<0.0001	*Euphorbia rectirama.*	2.21	0.0002	*Acacia mellifera*	1.13	0.2499	5
Indigofera heterotricha	7.82	<0.0001	*Acacia mellifera*	2.02	<0.0001	*Rhus pendulina*	1.07	0.0942	6
Aptosimum spinescens	3.57	>0.05	*Indigofera pechuellii*	1.89	0.0046	*Diospyros lycioides*	0.75	0.0968	7
Rhigozum trichotomum	3.10	<0.001	*Hermannia stricta*	1.79	0.0196	*Acacia karroo*	0.58	<0.0001	8
Indigofera pechuellii	2.94	<0.0001	*Petalidium lucens*	1.71	0.4077	*Schotia afra*	0.33	<0.0001	9
Euphorbia rectirama	2.91	<0.0001	*Plexipus garipensis*	1.65	0.8529				10
Phaeoptilum spinosum	2.20	<0.05	*Phaeoptilum spinosum*	1.24	0.9287				11
Acacia mellifera	1.74	<0.0001	*Rhigozum trichotomum*	1.17	0.7997				12
Lycium bosciifolium	1.55	<0.05	*Zygophyllum dregeana*	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
Indigofera pungens	354.0	0.06	1.12	14.9
Zygophyllum dregeana	219.5	0.07	1.13	12.9
Indigofera pechuellii	257.2	0.19	1.34	5.6
Monechma spartioides	295.1	0.21	1.40	5.3
Euphorbia rectirama	27.0	1.40	2.05	1.2
Acacia mellifera	80.7	1.88	3.31	1.4
Maytenus linearis	5.4	3.33	1.14	0.27
Schotia afra	8.4	14.56	4.54	0.25
Acacia karroo	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 less 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 less 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

Paper 3:

A habitat suitability model for black rhino in Augrabies Falls National Park, South Africa – how to humour a species on the edge.

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Abstract

A habitat suitability model (HSM) for black rhino (*Diceros bicornis bicornis*) in the very arid (123 mm rain/year) Augrabies Falls National Park, South Africa was constructed based on the distribution of 315 sightings, feeding trails and dung middens. These three sources of rhino locations did not differ significantly from their combined locations in their distribution along gradients of slope and distance to water. Logistic regression was employed to construct the HSM from 36 eco-geographical variables from nine groups of variables. The HSM was highly significant ($p<0.0001$) and there was no difference between the modelled and the observed distribution of black rhinos ($p=0.1996$). The six variables of the HSM in order of significance are: availability of preferred foods, distance to roads, habitat heterogeneity, slope, distance to water and rockiness. Shade was borderline significant. Habitat preference among 10 vegetation communities showed significant preference for two and against two. The riverine vegetation featuring water, shade, level ground and almost no rocks in addition to 14 times more browse than the average for the study area was *not* preferred, which emphasizes the importance of preferred browse rather than total browse. Rhinos also selected micro-habitats with over-representation of preferred browse species. Minimum convex polygon home ranges of two adult females were 35.5 and 14.2 km^2, which is lower than expected considering the low rainfall. Just 50 % of the study area had a habitat suitability exceeding 13 %, but featured 88 % of all rhino locations.

Keywords

Black rhino, habitat suitability, home range, preferred foods, water, slope, habitat heterogeneity, roads

Introduction

The black rhino (*Diceros bicornis*) population plummeted from 65 000 in 1970 to 2 410 in 1995 due to intensive poaching and habitat loss (Emslie and Brooks, 1999). Partly by design and partly by default black rhinos have primarily endured in small reserves where effective antipoaching is feasible. This allowed black rhinos to move back from the edge of extinction to reach 3100 animals by 2004 (*Pers. comm.:* Richard Emslie, Rhino Management Group). However, even with poaching under relative control the targeted 5 % annual population growth has proven rather difficult to achieve (Emslie, 2001).

Habitat suitability has become pivotal both for the expanding populations in the small reserves and for fragile reintroduced populations. Incomplete understanding of the parameters of black rhino habitat suitability has led to cases of overestimation and overshooting of carrying capacity or to degrading of habitat. The consequences have been slowed population growth and even rhino deaths (Brooks, 2001; du Toit, 2001, *Pers. comm.:* Keryn Adcock, Rhino Management Group).

This study aims at producing a first habitat suitability model for black rhino. The purpose is not to deliver a universal equation for black rhino habitat suitability, but to take a step towards a better understanding of the requirements of black rhinos. The study area was the Watervaal section of the Augrabies Falls National Park (AFNP). Field work was terminated when the black rhinos were removed due to a partial degazetting of the Watervaal Section, but opportunities exist for reintroduction in other parts of the park, where the model may be employed. The study is part of a larger study of the diet (Paper 2) and habitat selection of

Diceros bicornis bicornis, which is the black rhino ecotype inhabiting the arid west of Southern Africa. Of several study sites AFNP constitutes the arid extreme, with the least productive, but perhaps most nutritious browse.

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

Distribution of black rhino

Global Positioning System (GPS) geo-referenced locations of black rhinos were sampled in three ways. Feeding trails, dung middens and sightings are all direct evidence of presence of a rhino at a location, so each of these three indicators were pooled as rhino locations. Nine sightings were sourced from two systematic aerial surveys by South African National Parks, 27 sightings from tracking by rangers during patrol or guided tourist tours and 13 sightings from chance encounters during research. Seventy-four locations were derived from the midpoint of black rhino feeding trails tracked in connection with feeding studies (Paper 2). All sightings and feeding trails were separated by at least 24 hours. One-hundred-ninety-two locations were obtained by recording black rhino dung middens along transects. All the recorded black rhino locations were entered into the Geographical Information Systems (GIS) Idrisi 32.01 (Clark Labs, 1999) and ArcView 3.3 (ESRI, 2002). The Animal Movement Program (Hooge *et al.*, 1999) was used for mapping home ranges from sightings as well as the range of utilization from all rhino locations.

The dung transects were placed north-south spaced by 1 km and had a total length of 72.2 km. The transects were walked slowly navigating with compass and a GPS receiver. Whenever dung was seen within the transect width of 20 metres on either side, its distance from the transect was recorded as were the GPS readings. The dung was separated into fresh (retaining intestinal fluids inside), unbleached and sun-bleached. Then it was weighed with spring scales and the volume estimated by compacting it under human weight into a bucket with a litre scale. The dung was then left where it was found. Volumes of moist dung were converted into dry weight using the established volume-weight conversion for dry dung. The PC programme “Distance 4.1” was used to analyse the dung density (Thomas *et al.*, 2003).

A more indirect indicator of black rhino distribution was the number of browsed twigs on the shrub *Acacia mellifera*. This was recorded on 273 shrubs in the 37 of 58 vegetation plots, in which the shrub occurred, and averaged for each plot (Paper 1).

Preferences for habitats based on distribution of signs of rhinos were calculated as observed value divided by the value expected from the habitat size - or in the case of dung the length of the dung transect in each habitat. Micro-habitat selection was assessed by comparing species composition in 2 metre wide transects around feeding trails (Paper 2) with species composition calculated from 58 belt transects (Paper 1). Statistics were calculated using Analyse-it (Analyse-it Software, 2003) and S-Plus (Insightful Corp, 2002) computer programmes.

Habitat suitability modelling

The underlying assumption of this habitat suitability model (and most other habitat suitability models) is that distribution is an acceptable proxy for habitat suitability. Logistic regression was employed to model habitat suitability. This type of regression is suitable for a population or a random sample of available units for which it is known whether each unit is used or unused after a single period of selection. In this context “unused” means either no use or undetected use. In this study logistic regression was applied to a large, random sample of available pixels plus all the used pixels obtained from a layered raster GIS image, with each layer representing an eco-geographical variable. Thus, in this study there are separate samples of available and used units. This violation of assumptions of logistic regression can be circumvented by adapting the regression equation accordingly (Manly *et al*., 2002). The calculations remain almost the same as for a conventional logistic regression, but the resource selection probability function instead takes the form

$$w^*(x) = \exp(a + b_1x_1 + b_2x_2 + \ldots + b_px_p)$$

in which w*(x) states the probability of pixel x being used after a single period of selection. The only other necessary correction is on the constant a (Manly *et al*., 2002). Each b represents an eco-geographical variable and each x the corresponding regression coefficient. Subsequently, the equation was scaled such that w*(x) takes values from 1 down to a theoretical minimum of 0 as is customary for a habitat suitability index.

A stepwise approach was used for adding and removing eco-geographical variables eliminating those underperforming at the 5 % significance level. Only one variable from each of nine groups of variables were accepted at a time, except for independent food plants (Table 1). Models were evaluated on the basis of their level of significance as well as making biological sense. Due to the relative small number of known locations (n=315) it was decided to use all of them for modelling rather than reserving some for model validation.

Calculation of eco-geographical variables

The eco-geographical variables tested for significance in the model are summarised in table 1. The study area was delineated from 1:50 000 panchromatic aerial photographs, which were geo-referenced by use of a GPS and the Project module in the GIS Idrisi. Each variable was derived from paper 1 and 2, and were prepared as layers in the GIS Idrisi with a pixel size of 10 x 10 m. Slope was derived from digitised 20 m contours interpolated with the TIN module in Idrisi. Distance to accessible water was calculated in Idrisi from aerial photos and GPS readings at springs and artificial water points. In the Orange River Gorge the river is surrounded by slippery rock surfaces with inclines from 45 to 90 degrees, so these waters were considered inaccessible. Rockiness was measured as presence/absence of loose rock or bedrock at 25 pinpoints in each of 58 plots. Percentage rock cover was calculated for each plot and averaged for each of 10 vegetation communities (Paper 1). The variable “Rockiness, loose” represented percentage cover of loose rocks only, while the “Rockiness, total” included both loose rock and bedrock.

Food was represented by canopy volume from 0 to 200 cm above ground (Normal black rhino feeding range, paper 2) in each vegetation community measured by the BECVol method (Smit, 1996) as explained in paper 1. The canopy volumes of four principal food plant species, which were also significantly preferred (Paper 2), were used as four separate variables (“Species A-D volume” in table 1). Alternatively, the canopy volume of three, four, six or 12 species of principal food plant species were added to make four mutually exclusive variables (“3/4/6/12 spp vol.” in table 1). The first four species in question are *Zygophyllum cf. dregeana*, *Acacia mellifera*, *Euphorbia rectirama* and *Indigofera pechuellii*, while the remaining eight principal and preferred species are listed in paper 2. In a refinement these summed volumes were multiplied by their Simpson equitability (E) to factor in any effect of the balance of food species (“3/4/6/12 spp vol x E” in table 1). In another refinement the volume of each of four principal food species were multiplied by their value of preference (consumption/availability) by black rhino (Paper 2) and then summed to make one variable (“4 spp vol x pref.” in table 1). Each of these food variables were also tested in a variant in which the pixel value was replaced by the mean of all pixel values within 500 metres (for instance “Species A-D vol. 500m” etc. in table 1). The intention was to factor in movement between nearby food patches as well as the gradual change from one vegetation community to another. This averaging variant was also applied to rockiness and shade. Biomapper (Hirzel *et al.*, 2002) was used for averaging.

Habitat heterogeneity was calculated as the Shannon diversity of vegetation communities among all pixels (10 x 10 m) within 500 metres using a procedure in Biomapper. Hiding cover was calculated as the total canopy volume from 0 to 200 cm above ground. Shade for black rhinos was calculated as projected canopy cover minus the basal area of plants taller than 2 metres, provided the shade exceeded 1 metre in width from plant base to the edge of the canopy. The calculated areas of shade were then expressed as percentage of the area of each vegetation community. Distance to roads in kilometres was calculated in Idrisi and truncated at 2 km. The roads in question were one public gravel road just outside the northern boundary of the study area with less than 100 vehicles per day and one gravel loop with 0-15 vehicles per day giving access to simple accommodation in the study area for rangers, visitors and researchers. There were other 4x4 vehicle routes inside the study area, but these were used infrequently. Distance to the wildlife fence was calculated in Idrisi and truncated at 1 km.

Results

Selecting a model

A number of models showed similar levels of significance. However, some of the most significant models were eliminated because they did not make biological sense. In some models availability of one or more of the preferred food plants were negatively correlated with habitat suitability. In other models distance to water was not incorporated despite distance to water showing a strong linear correlation (Pearson, r= -0.83, n=15, *p*=0.0001) with density of rhino locations (Figure 3), and despite a reasonable expectation of water playing a significant role in an arid environment.

The habitat suitability model

The selected model is highly significant (*p*<0.0001) and incorporates six significant eco-geographical variables: food, distance to roads, habitat heterogeneity, slope, distance to water and rockiness (Table 2). Modelled habitat suitability and known rhino locations are mapped in figure 2. The observed and modelled distributions of rhinos along a gradient of habitat suitability did not differ (Chi square=12.2, df=9, *p*=0.1996), whereas the observed distribution of rhinos did differ from the expected distribution based on the area of each class of habitat suitability (Chi square=344.2, df=9, *p*<0.0001)(Figure 4). Fifty % of the study area has a habitat suitability of less than 0.13, but less than 12 % of rhino locations were found in this half of the study area. When modelling was subsequently attempted with a randomly selected half of the sample (Half of 315 locations) distance to water and rockiness did not reach the 5 % significance level.

The eco-geographical variables

Hiding cover (Total canopy volume 0-200 cm above ground) was not significant in any of the models. Distance to fence was close to a significant positive coefficient of regression in several models. If added to the selected model its regression coefficient reached *p*=0.0702 (t=1.81). Shade reached significance or nearly so in some of the better models when smoothed out by calculating the mean of all pixels within 500 m. Added to the selected model Shade 500m was border-line significant (t=1.954, *p*=0.0507). Shade 500m was not linearly correlated with density of known rhino locations (Pearson, r=0.46, n=8, *p*=0.2420). Total rock cover reached significance in many of the better models, although total rock cover was not linearly correlated with density of known rhino locations (Pearson, r= -0.45, n=6, *p*=0.3753). Other measurements of rockiness were not significant in the best models. Distance to water was not significant in all the models, although convincingly linearly correlated with density of rhino locations (Pearson, r= -0.83, n=15, *p*=0.0001)(Figure 3). Distance to low use roads (truncated at 2 km) was significant in all the models, although linear correlation with density of known rhino locations was relatively weak (Pearson, r= 0.67, n=11, *p*=0.0230). Slope was significant in all the models, and linearly correlated with rhino location density (Pearson, r= -0.76, n=11, *p*=0.0072)(Figure 3). Habitat heterogeneity was significant in all models and the variable most linearly correlated with density of rhino locations (Pearson, r= 0.96, n=9, *p*<0.0001).

Various indicators of food availability were the most significant variable in almost all the models, even if linear correlation with density of rhino locations were not the highest (Pearson, r= 0.76, n=11, *p*=0.0067 for “4 spp. vol x E 500m”)(Figure 3). The food variables averaged over all pixels within 500 m were invariably the most significant. Including more than four food species usually only increased significance marginally, in which case the most parsimonious model was chosen. Adding the canopy volume of several principal and preferred food species made for the least significant food variable, while treating the volume of each food species as separate variables gave much higher significance. Adding food volume multiplied by Simpson equitability (E) of several food species into one variable also resulted in high levels of significance. The highest significance level was achieved by multiplying food plant volume with preference index by black rhino (Paper 2) and summing over four species. However, this type of food variable made distance to water non-significant, so it is not used in the selected model. Model variables and their significance are summarised in table 1.

Indicators of black rhino distribution

The rhino locations used for modelling were comprised of sightings, feeding trails and dung middens. There was no significant difference between all locations combined and any of its three components in their distribution along gradients of slope and distance to water (Table 3). All three indicators were correlated with slope and two of them with distance to water (Table 4). However, feeding trails did differ from the other two indicators in distribution along a gradient of slope (Table 3), by being more concentrated on flat inclines. Similarly, dung middens were concentrated closer to water than the other two indicators. Dung weight and browsing intensity were not included in the habitat suitability model. Dung weight was generally more concentrated and browsing intensity more dispersed than the other three indicators of habitat use (Table 3 and 4).

Dung density was 1.25 middens per ha with upper and lower 95 % confidence limits of 1.02 and 1.59. Effective strip width was 10.5 m. The distance between detected dung middens and the transects did not differ between vegetation communities (one-way ANOVA, F=1.43, df=186, *p*=0.1957).

Habitat preferences and home range

All direct signs of rhinos (Dung middens, dung weight, sightings and feeding trails) consistently indicated that the rhinos have a negative preference (avoidance) towards vegetation communities 1 and 2 as well as positive preference for communities 4 and 5.1 (Table 6). Communities 7-10 and sub-community 5.2 are small, so any preference would be difficult to confirm due to relative small sample size. The amount of rhino browsing on *Acacia mellifera* was also highest in vegetation community 4 and 5, but there was also high utilization of *A. mellifera* in community 1 (Table 6).

Preferred browse species were significantly over-represented within 1 metre of trails of feeding rhinos as compared to the species composition in vegetation plots (Table 7). This was true when comparing feeding trail and vegetations plots for the whole study area of the preferred habitat 5.1.

Only the two adult females accompanied by their youngest calf were sighted enough times to estimate their home ranges. Home ranges were 20.7 km^2 (n=31) and 10.3 km^2 (n=16) with 22.0 % overlap when estimated with 95 % minimum convex polygons (Table 5). With the 90 % kernel method home ranges were 18.0 and 18.4 km^2 with 24.7 % overlap (Table 5 and figure 2). The same two methods applied to all 315 known rhino locations revealed that only 59.6 and 46.5 % of the study area appeared to be really utilized by rhinos (Table 5).

Discussion

Model validation and variables

Ideally, a habitat suitability model should be tested with a data set other than that used for model development, but this is rarely practised because limited data is usually a constraint on model development in the first place (U.S. Fish and Wildlife Service, 1981). Instead, fit of the model as well as significance and consistency of its variables can be tested. Fit between modelled and observed distribution of rhino locations in this study was such that there was 20 % likelihood that the two were in fact two samples of the same distribution (Figure 4). By comparison, the likelihood that the observed rhino locations were a sample of random distribution was <0.0001. Five of the six variables were highly significant (p<0.0001), and four of them remained significant when sample size was halved. Thus, model performance was highly satisfactory, despite the relative simplicity of the model.

Food availability was the most significant variable. This was partly expected (Hearn, 2000), but it may be a surprise that available canopy volume of just four species of principal and preferred species performed so well, despite that they only represent 22 % of available browse (Paper 1). Adding more species did tend to improve the model marginally, but for practical application this has to be weighed against data collection efforts, so it was decided to show that a parsimonious model with just four species functions well. The highest significance was achieved when canopy volumes were multiplied by preference values by rhino for the food plant species. This indicates that the food preferences are real, and emphasizes preferred foods rather than total food abundance co-determines habitat suitability. However, using preference values made distance to water non-significant, plus it requires detailed data on rhino feeding and browse availability to apply. Therefore, browse volume of the four species multiplied by their equitability was employed instead. This calculation also increases the importance of relatively sparse, preferred plants, but requires less data collection.

All the food variables improved in significance when original values were changed to the mean of all pixels within 500 metres. The intention was to factor in commuting between nearby food patches as well as the gradual change from one vegetation community to another. Simply averaging seems to do both with some success, but more sophisticated and realistic modelling of movements could be devised.

That slope was a significant variable was also to be expected. Modelling could perhaps be improved by separating slope into two components: energetic cost of going up or down a slope and the risk of injury on steep slopes. For instance, walking along a contour is energetically neutral, but may carry a risk of injury. Distance to water was a significant variable too, although not quite as significant as expected. This was perhaps due to the relatively short distances to water in the study area. Additional natural water points during the rainy season were extremely short-lived and unpredictable, and would have little influence on habitat selection. Browsers are generally less dependent on drinking water than other herbivores due to comparatively higher water contents in their dry season food (Owen-Smith, 1999). Black rhinos usually drink once every 24 to 48 hours, but perhaps less frequently when feeding on succulents (Mukinya, 1977; Joubert & Eloff, 1971). Density of giraffe – another mega-browser - in Amboseli, Kenya was at its maximum 0-2 km from water, 75 % at 2-4 km and 25 % at 4-10 km and 0 % beyond 10 km (Western, 1975).

Habitat heterogeneity was a surprisingly significant variable. It is unclear what the rhinos are attracted to in areas of high habitat heterogeneity. Perhaps it is a wider choice of food plants (Edge effect (Holmes, 1986)) or perhaps the apparent attraction is an artefact of rhino movement between small patches of suitable habitat.

Distance to roads was perhaps a more significant variable than anticipated for such low use roads. It is possible that some of the animals were a little edgy, not from poaching but from translocations. However, when rhino locations were plotted against distance to roads the variable did not appear so convincing. Caribou or reindeer (*Rangifer tarandus*) show avoidance of areas closer than 250-5000 m to roads, oil wells, power lines and tourist resorts, but the magnitude of the avoidance seems highly dependent on previous individual and collective experience (Dyer *et al.*, 2001; Nelleman *et al.*, 2001). This variable would benefit from more data under different situations to clarify how sensitive black rhinos are to disturbance. As a precaution managers should place even low use park infrastructure, including rhino holding pens away from highly suitable black rhino habitat, although game viewing will require some compromises.

Rockiness was significant in the selected model, but rockiness ranged as wide as 0 - 61 % in the study area, and the variable is probably not significant in less rocky areas. In sunny, arid and/or hot climates access to shade can be a very important requirement for maintaining a balanced heat and water budget (Eckert *et al.* 1988, Baharav 1982). In this study shade was borderline significant. When plotting rhino density against shade it appeared that only shade cover below 4 % had any clear effect on habitat selection. Rhino density was almost significantly positively correlated with distance to the boundary fence, the reason presumably being that rhinos followed the fence on exploratory movements. This would explain the sightings in the unsuitable far north of the study area, which all occur along the fence (Figure 2).

Indicators of rhino distribution

In this study rhino locations from sightings, feeding trails and dung were pooled to augment sample size. The pooled distribution did not differ from the distribution of sightings, feeding trails and dung. Yet, feeding trails tended to be more concentrated on low inclines. Perhaps rhinos prefer to feed on level ground, or food quality is higher there or trails were more likely to be detected there. Sightings tended to be more geographically spread out, perhaps because the rhinos tended to drink and forage at night and then finally rest at the furthest end of the feeding grounds during the day when sightings would occur (Own obs.; Mukinya, 1977).

Dung midden density was more concentrated close to water, perhaps because drinking and defecation is physiologically associated or because dung serves as communication at water points. Dung weight density, which was not used for modelling, was far more concentrated both around water sources and on lower inclines. It is unclear whether this reflects true rhino distribution or increased defecation in preferred areas where 2-way communication is more likely to occur. Differential rate of breakdown of dung was not formally examined, but a small pilot study weighing and periodically re-weighing fresh dung deposited on sand, mixed substrate and rocky substrate did not reveal any obvious differences. Dung beetles were rare in the study area, so dung remained on the surface of the soil and decomposition was slow in the arid climate.

The distribution of feeding signs per *Acacia mellifera* shrub (not used in modelling) was also negatively correlated with slope (Table 4), but otherwise differed from the other habitat use indicators (Table 3). Feeding intensity variations in one species is a complex product of habitat selection and food availability. The data indicated that *A. mellifera* utilization was very high in both the two preferred vegetation communities (4 and 5.1), but also quite high in the significantly avoided vegetation community 1 (Table 6), where *A. mellifera* is relatively rare (Paper 1). In short, the three selected indicators of rhino distribution corresponded sufficiently, but also complemented each other well.

Model limitations

Habitat suitability models (HSM) are not models of ecological carrying capacity (ECC) because not all the factors that may affect animal abundance are included. In this model, for instance there is no measure of food production (only availability), interspecific competition, social interactions or disease. However, HSM *are* intended to predict the *potential* of the included habitat variables to affect ECC (Schamberger & O'Neil, 1986).

Limitations of this habitat suitability model include the low number of independent rhinos in the study population, the relatively low number of rhino locations as well as the lack of stratification of the model into time of day, time of year, different behaviours and demographic groups.

Immobilization and fitting of telemetry equipment was not possible in this study because it is expensive, potentially harmful and may interfere with photo-tourism - particularly in this large, endangered and charismatic species. With supporting data Alibhai *et al.* (2001) argue that immobilization affects rate of reproduction negatively, and they supply guidelines for minimizing impacts of immobilizations. Telemetry could give much bigger sample sizes with useful demographic, temporal and behavioural stratification. Improved safety is an additional advantage. This has to be weighed against the risks of immobilization (Boyd, 2002).

The model may be employed to evaluate the habitat suitability of other parts of Augrabies Falls National Park before black rhinos are reintroduced there. The model also throws light on which variables may significantly affect habitat suitability in other areas, but general conclusions would be greatly increased by modelling other study areas.

Habitat preferences and home range

The importance of food quality, rather than quantity is emphasized by the riverine habitat in the study area not being preferred, although it contains 14 times more browse than the study area on average in addition to being level, next to water, shady and almost free of rocks. Only sightings suggest positive preference for riverine vegetation (Table 6), but sightings represent day time use, which usually means resting in the shade, rather than feeding. The two preferred habitats are the ones that score highest on availability of preferred foods and their equitability. The availability of quality foods is a result of complicated interactions between microclimate, soils, plant chemistry, competition and rhino physiology.

The importance of understanding what constitutes good black rhino habitat is highlighted by the observation that some 40 to 55 % of the study area is virtually unused (Table 3).

Feeding rhinos also selected microhabitats within the habitats which had a species composition higher in eaten and especially in preferred browse species than the habitat in general (Table 7). The feeding trails were also higher in *Acacia karroo* and *Maytenus linearis* although they have low preference values. These large shrub species occur close to water where they are encountered by rhinos feeding on their way to and from drinking water. Their large size also means that although they are not preferred by available browse volume they are preferred by number. From observation it was evident that in some habitats the rhinos also clearly preferred drainage lines, which have higher total plant densities. However, the preference for feeding in patches of higher plant densities could not be documented because zigzagging and backtracking of feeding rhinos made it difficult to measure the size of the 2 metre wide transects surrounding the feeding trails.

Female black rhino home range size is believed to be related to food and water availability (Hearn, 2000) or even directly correlated with ecological carrying capacity (Adcock, 2001), whereas male home range size is also strongly affected by territoriality (Adcock 1994).

Calculation of home range size is affected by the number of observations (locations). One of the only two home ranges in this study did not fulfil the minimum requirement of 30 observations suggested by Seaman *et al.* (1999) for kernel estimates. This small sample size precludes any conclusive discussion.

The average Minimum Convex Polygon Home Range (MCPHR) of adult females in Augrabies Fall National Park of 25 km^2 (n=2) is at level with MCPHRs of areas with much higher rainfall and longer growing seasons such as Ngorongoro, Tanzania (31.5 km^2 ,n=2) and Mkuzi on the east coast of South Africa (27.5 km^2)(Kiwia, 1989; Huggins, 1996). It could be viewed as another indication that availability of quality food, rather than simply food production, is a major determinant of black rhino habitat suitability.

Conclusions for research and management

Habitat suitability models are revealing and thought-provoking. They actually test the habitat evaluation often left to so-called expert opinion. Studies of habitat suitability for black rhino should be performed in a range of different climates and landscapes on a large number of animals, preferably with use of telemetry while observing immobilization guidelines. The usefulness of dung, sightings and feeding trails as indicators of habitat use depend on local conditions, and they have limitations and differences which should be recognised. Feeding signs on woody vegetation can give useful information on browsing intensity on selected species, but are less suitable indicators of habitat use due to switching between feeding on various species of woody plants and feeding on non-woody plants, which is practically undetectable unless following a fresh feeding trail.

In selecting sites for black rhino reintroductions and trying to assign their stocking rates one should keep in mind the variables in this model: Available canopy volume and equitability of preferred foods distance to roads or human disturbance, habitat heterogeneity, slope, distance to water and high levels of rock cover.

Managers of existing and future rhino reserves should note the significance of roads and distance to water. Disturbance and water are two variables managers can partly manipulate either to increase carrying capacity, distribute browse impact more evenly or even reduce impact in some areas. Also the mounting evidence that a few preferred foods, rather than total browse availability are of paramount importance should be noted. What the implications are under the range of conditions in each reserve requires further research.

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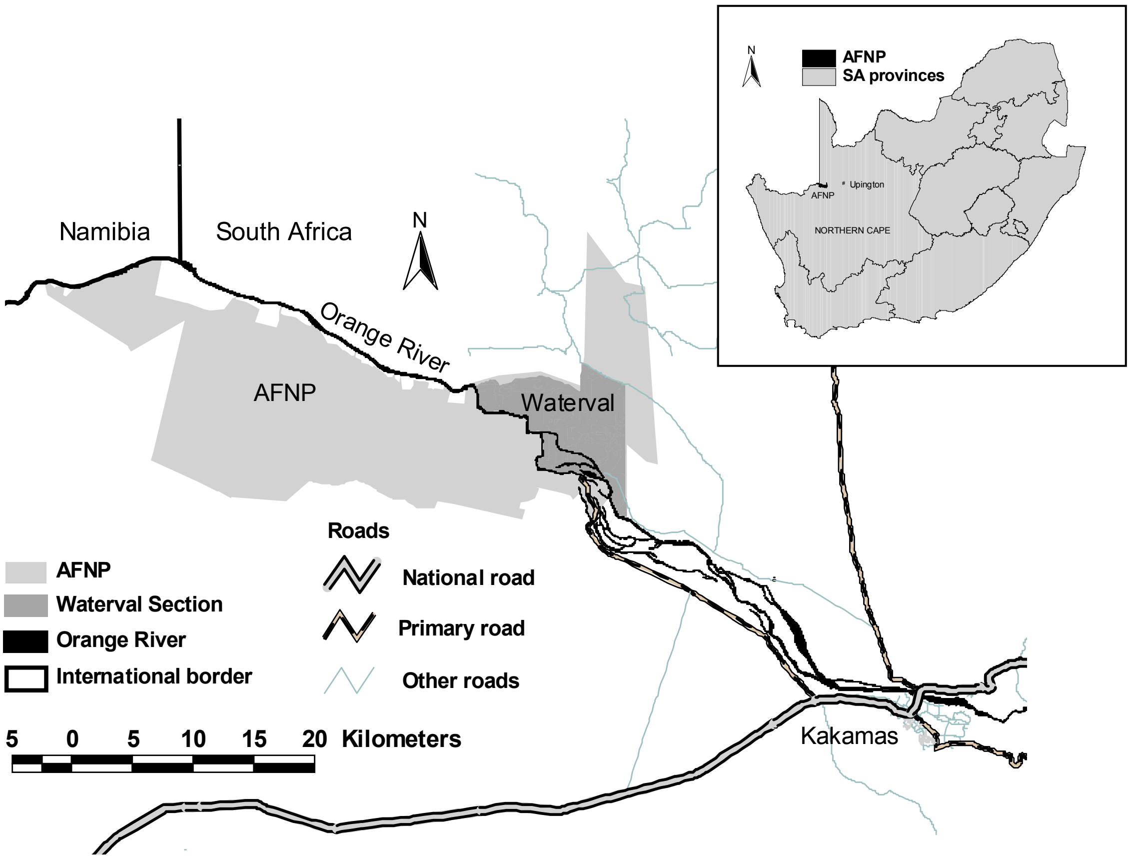


Figure 1.

The location of Waterval and Augrabies Falls National Park (AFNP).

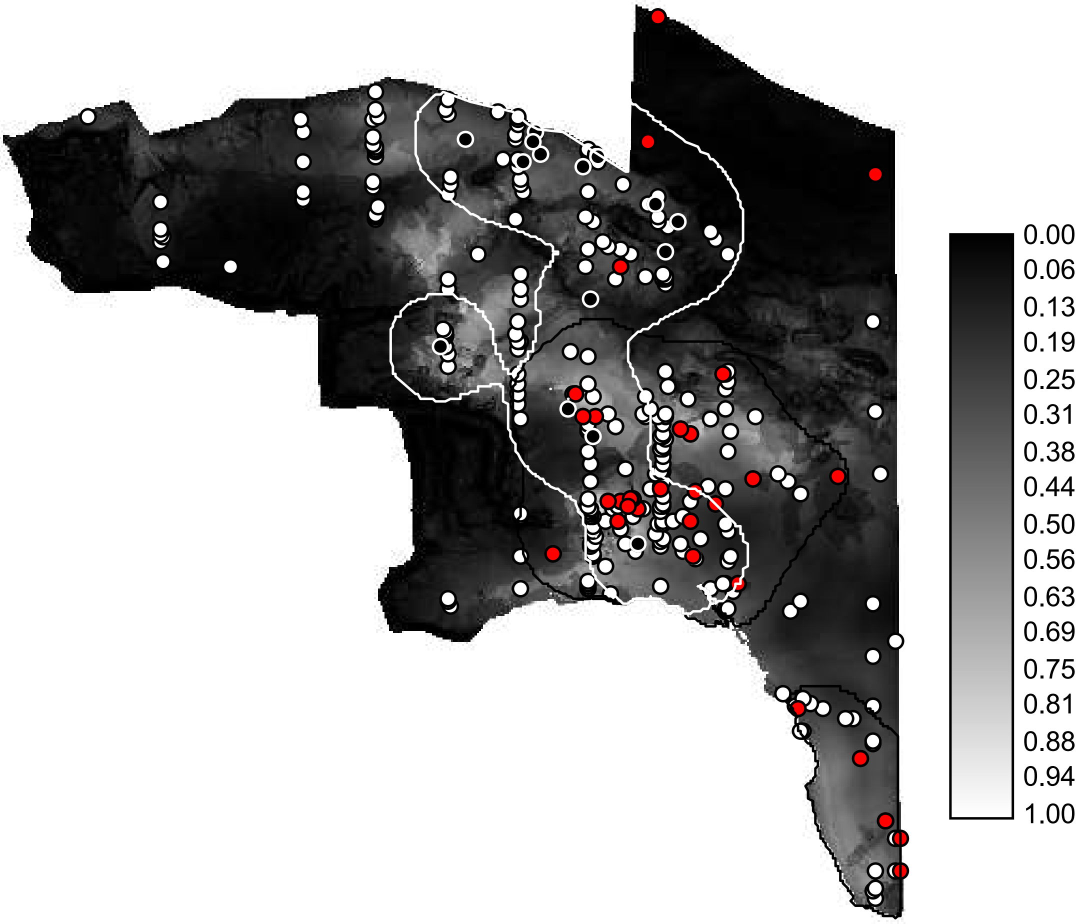
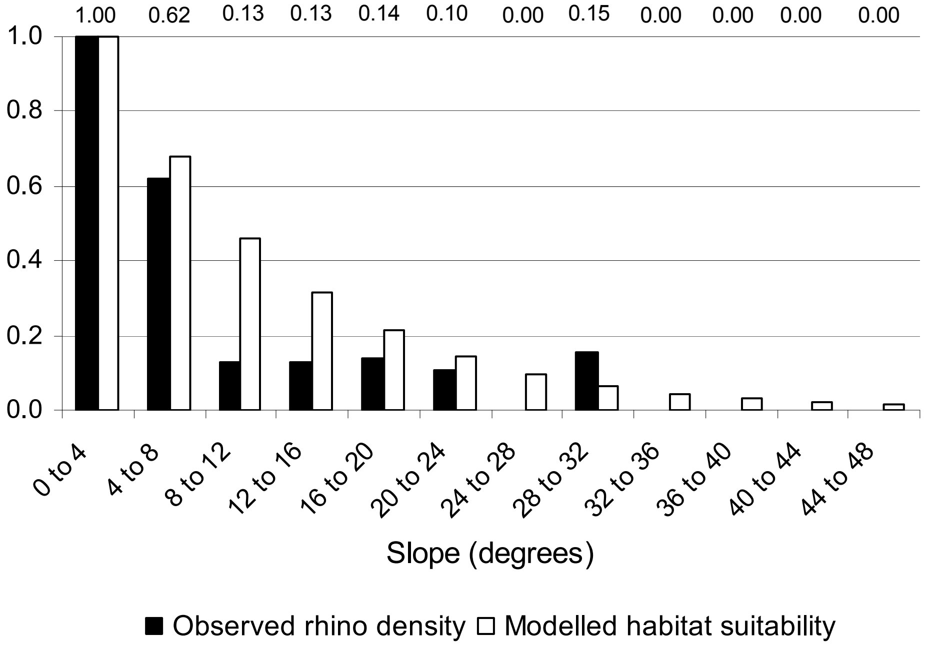


Figure 2.

Map of the modelled habitat suitability index (min. 0 to max. 1) for black rhino in Watervaal, Augrabies Falls National Park according to the model with 315 known black rhino locations and home ranges of the two adult females (90 % kernel). Sightings of female 1 are indicated by grey dots with black outlines, sightings of female 2 by black dots with white outlines and other rhino locations by white dots with black outlines.


1.00
0.62
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0.00
0.00
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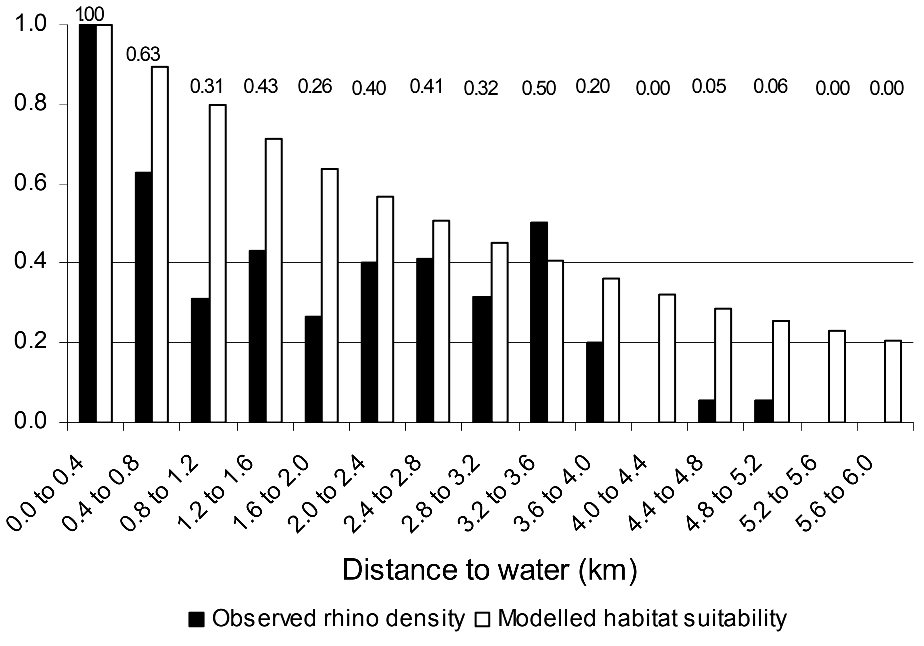
1.0
0.8
0.6
0.4
0.2
0.0
0 to 4
4 to 8
8 to 12
12 to 16
16 to 20
20 to 24
24 to 28
28 to 32
32 to 36
36 to 40
40 to 44
44 to 48
Slope (degrees)
■ Observed rhino density
□ Modelled habitat suitability


100
0.63
0.31
0.43
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0.40
0.41
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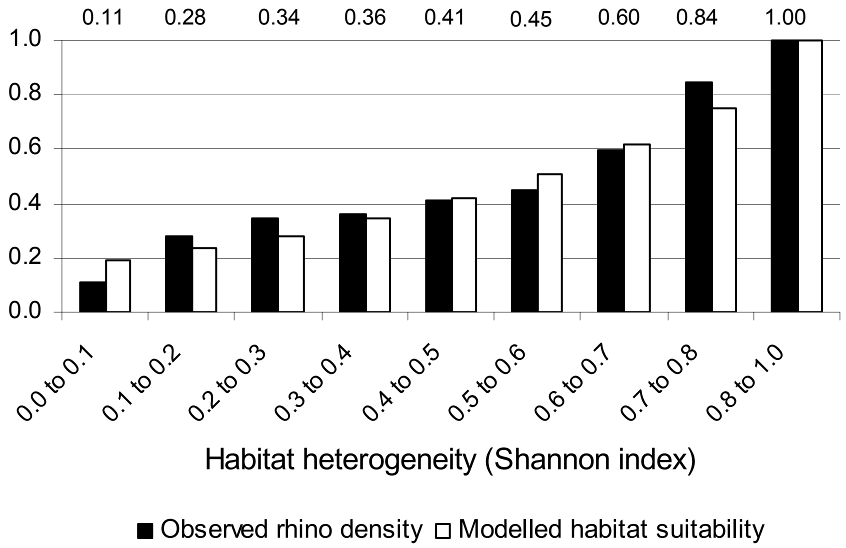
0.8
0.6
0.4
0.2
0.0
0.0 to 0.4
0.4 to 0.8
0.8 to 1.2
1.2 to 1.6
1.6 to 2.0
2.0 to 2.4
2.4 to 2.8
2.8 to 3.2
3.2 to 3.6
3.6 to 4.0
4.0 to 4.4
4.4 to 4.8
4.8 to 5.2
5.2 to 5.6
5.6 to 6.0
Distance to water (km)
■ Observed rhino density
□ Modelled habitat suitability



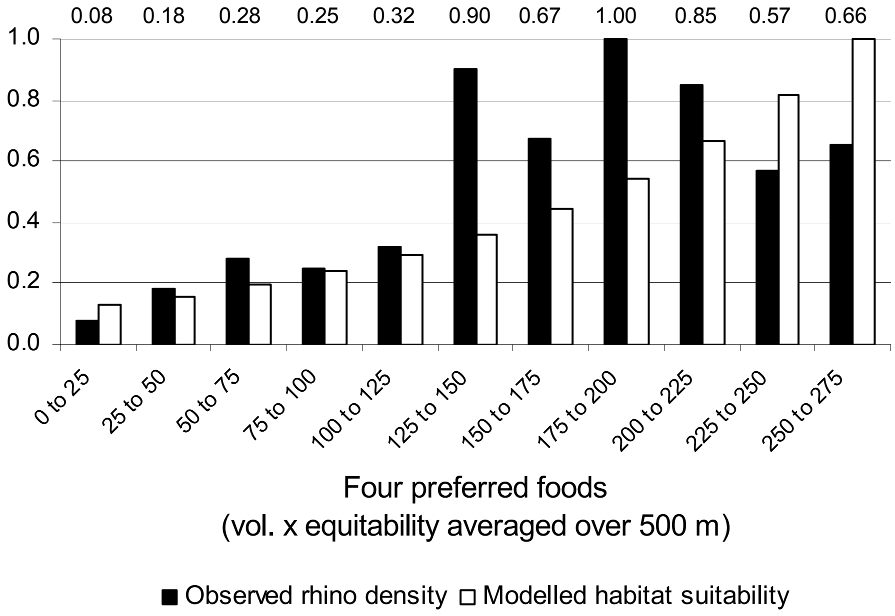


Figure 3

Relative density of known black rhino locations as a function of slope, distance to water, habitat heterogeneity and food availability compared to the modelled habitat suitability.

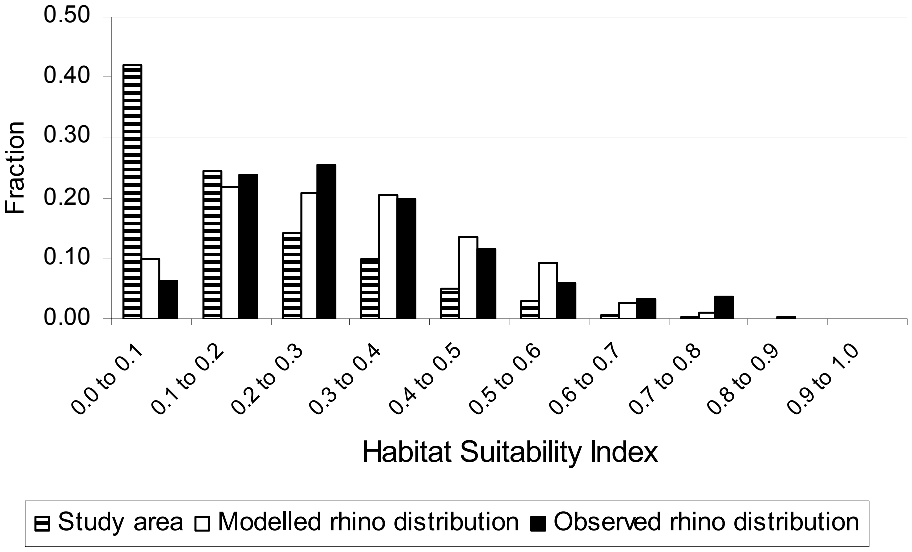


Figure 4

The distribution of the study area, the known black rhino locations and the expected distribution of black rhinos on classes of habitat suitability.

Table 1

Variables tested for significance in the habitat suitability model for black rhinos in Augrabies Falls National Park. Relative significance across the best models is indicated.

Group of variable Variables	**Description**	**Source**	**Significance**
Slope	Slope in degrees	Idrisi TIN interpolation of 20 m digital contours	High
Distance to water	Distance to accessible water in km	GPS and aerial photos plus Idrisi Distance module	Medium
Rockiness			
Total	% loose rock and bedrock	Habitat study (paper 1)	Medium
Total 500m	The above averaged over the pixels within a 500 m radius	Habitat study (paper 1) with averaging in Biomapper	Low
Loose	% loose rock only	Habitat study (paper 1)	Low
Loose 500m	The above averaged over the pixels within a 500 m radius	Habitat study (paper 1) with averaging in Biomapper	Low
Food			
Species A-D volume	Browse volume of food species (four principal species tested)	Habitat study (paper 1)	Medium
Species A-D vol 500m	The above averaged over the pixels within a 500 m radius	Habitat study (paper 1) with averaging in Biomapper	High
3/4/6/12 spp vol	The combined browse volume of 3, 4, 6 or 12 food species	Habitat study (paper 1)	Low
3/4/6/12 spp vol 500m	The above averaged over the pixels within a 500 m radius	Habitat study (paper 1) with averaging in Biomapper	Medium
3/4/6/12 spp vol x E	The combined browse volume of 3, 4, 6 or 12 food species multiplied by their Shannon equitability	Habitat study (paper 1)	Medium
3/4/6/12 spp vol x E 500m	The above averaged over the pixels within a 500 m radius	Habitat study (paper 1) with averaging in Biomapper	High
4 spp vol x pref. 500m	The volume multiplied by preference of four food species averaged over 500 m radius	Habitat study and feeding studies (paper 1 & 2) with averaging in Biomapper	High
Habitat heterogeneity	Habitat heterogeneity (Shannon diversity) within a 500 m radius	Habitat study (paper 1) with calculation in Biomapper	High
Hiding cover	Total canopy volume 0-200 cm	Habitat study (paper 1)	Low
Shade			
Shade	% canopy shade (1 m or wider)	Habitat study (paper 1)	Low
Shade 500m	The above averaged over the pixels within a 500 m radius	Habitat study (paper 1) with averaging in Biomapper	Medium
Distance to roads			
Low use gravel max 2 km	Kms to low use gravel roads (public or mng.) truncated at 2 km	Habitat study (paper 1) and Idrisi Distance module	Medium
Distance to fence	Kms to rhino fence, truncated at 1 km	Habitat study (paper 1) and Idrisi Distance module	Medium

Table 2

Results of logistic regression for the habitat suitability model for black rhino in Augrabies Falls National Park.

Variable	Regr.coefficient	SE	95 % conf. int.	ltl	*p*
Food 4 spp Vol x E 500m	$8.1710 \cdot 10^{-3}$	$1.2404 \cdot 10^{-3}$	$2.4311 \cdot 10^{-3}$	6.588	<0.0001
Distance to roads	$6.4441 \cdot 10^{-1}$	$1.2434 \cdot 10^{-1}$	$2.437 \cdot 10^{-1}$	5.182	<0.0001
Habitat heterogeneity	1.9500	0.4004	0.7847	4.870	<0.0001
Slope	$-9.6720 \cdot 10^{-2}$	$2.0439 \cdot 10^{-2}$	$4.0060 \cdot 10^{-2}$	4.732	<0.0001
Distance to water	$-2.8242 \cdot 10^{-1}$	$0.6771 \cdot 10^{-1}$	$1.3271 \cdot 10^{-1}$	4.171	<0.0001
Total rockiness	$-9.9444 \cdot 10^{-3}$	$3.1024 \cdot 10^{-3}$	$6.0807 \cdot 10^{-3}$	3.205	0.0012
Constant	9.5442				
Differential deviance 257.49 with 6 df (*p*<0.0001)					
Output was scaled to a maximum of 1 by multiplying by 390.39625					

Table 3

Significance levels when using chi square to test whether distributions of indicators of habitat use differ in their distribution along gradients of slope (numbers in upper triangle) and distance to water (lower triangle).

		Slope					
		Dung middens	Dung weight	Sightings	Feeding trails	All locations	Browsing intensity
Distance to water	Dung middens		0.1417	0.8561	**0.0037**	0.1624	**0.0018**
	Dung weight	0.2305		0.7861	**<0.0001**	**<0.0001**	**<0.0001**
	Sightings	**0.0047**	**<0.0001**		**0.0071**	0.7463	**0.0046**
	Feeding trails	**0.0210**	**<0.0001**	0.1620		0.1915	**0.0005**
	All locations	0.8853	**0.0008**	0.1408	0.4500		**0.0008**
	Browsing intensity	**<0.0001**	**<0.0001**	0.2469	**<0.0001**	**<0.0001**	

Table 4

Correlation coefficients (rs) and significance levels when using Spearman to test whether different indicators of habitat use are correlated with slope and distance to water.

	Density of dung middens	Dung weight	Density of rhino sightings	Density of feeding trails	Density of all rhino locations (Dung, feeding and sightings)	*Acacia mellifera* browsing intensity
Slope	**-0.76 (0.0040)**	**-0.88 (0.0001)**	**-0.65 (0.0220)**	**-0.76 (0.0040)**	**-0.83 (0.0009)**	**-0.61 (0.0035)**
Distance to water	**-0.84 (0.0002)**	**-0.93 (<0.0001)**	-0.38 (0.1625)	**-0.88 (<0.0001)**	**-0.83 (0.0001)**	-0.38 (0.4026)
Sample size	192 middens	767.2 kg	49 sightings	74 trails	315 locations	37 plots

Table 5

Home ranges sizes of two adult females, the overlap of home ranges as well as the size and percentage of the study area under use by black rhino.

	Female 1 (n=31)	Female 2 (n=16)	Overlap	All rhino locations (n=315)
MCP 100 %	35.5 km^2	14.2 km^2	5.6 km^2 (12.7 %)	65.3 km^2 (90.6 %)
MCP 95 %	20.7 km^2	10.3 km^2	5.6 km^2 (22.0 %)	43.0 km^2 (59.6 %)
Kernel 95 %	30.9 km^2	23.5 km^2	13.7 km^2 (33.7 %)	48.4 km^2 (67.1 %)
Kernel 90 %	18.0 km^2	18.4 km^2	7.2 km^2 (24.7 %)	33.5 km^2 (46.5 %)

Table 6

Habitat preferences using different signs of rhino distribution and browse utilization. The numbers given are observed value divided by expected value, such that value <1 indicate avoidance and >1 indicates preference. Four of the distributions were tested (Chi square and Fisher's Exact Test) for significance (*=*p*<0.05, **=*p*<0.001 and ***=*p*<0.0001).

		Vegetation communities											Sample size
		1. *Schotia afra* - *Indigofera pechuelii* low, open woodland	2. Adenolobus garipensis – Boscia albitrunca tall, open shrubland	3. Euphorbia gregaria – Ostespermum microcarpum tall, sparse shrubland	4. *Acacia mellifera* – *Euphorbia* spp. tall, open shrubland	5.1 *A.mellifera – Zygophyllum dregeanum – Euphorbia rectirama* tall, open shrubland	5.2. *A.mellifera – Z.dregeanum – Monechma spartioides* tall, open shrubland	6. Acacia mellifera – Stipagrostis hochstetteriana tall, open shrubland	7. Sisyndite spartea – Forskaolea candida tall, open shrubland	8. Acacia erioloba – Schmidtia kalahariensis short, open shrubland	9. Tamarix usneoides – Maytenus linearis tall, open shrubland	10. Acacia karroo – Ziziphus mucronata short forest	
Rhino sign distribution	Dung midden density***	0.54***	0.46**	1.65	2.78***	2.75***	0.30	1.17	0.00	6.48	1.77	0.34	192 middens
	Dung weight density	0.52	0.12	1.43	2.38	1.95	0.01	0.26	0.00	4.62	1.68	0.01	767.2 kg
	Sighting density***	0.39*	0.00**	1.21	2.37**	2.27**	0.73	0.65	0.00	3.87	2.02	1.84	49 sightings
	Feeding trail density*** (midpoints)	0.16***	0.00**	0.00	1.39	4.96***	0.00	0.81	0.00	5.50	2.86	0.00	74 trails
	Feeding trail length	0.20	0.00	0.62	1.39	4.59	0.00	0.80	0.00	1.04	3.53	0.45	42.0 km
	Density of all rhino locations* **	**0.32*** **	**0.23*** **	**1.27**	**1.88*** **	**2.58*** **	**0.22**	**0.88**	**0.00**	**3.46**	**2.11**	**1.16**	315 locations
Browse utilization	Feeding signs per *A.mellifera*	7.7	1.3	NA	14.6	11.7	5.4	4.5	0.0	NA	5.0	NA	37 plots

Table 7

The species composition in the study area and habitat 5.1 compared to the species composition within 1 metre of feeding rhinos expressed as numbers of plants of each species. Significant differences (Fisher's Exact Test) are indicated by *=*p*<0.05, **=*p*<0.001 and ***=*p*<0.0001

Plant species	Preference value based on browse volume[1]	Waterval (study area)		Habitat 5.1	
		Availability	Feeding trails	Availability	Feeding trails
Zygophyllum cf. dregeana	18.8	41	1494***	578	1207***
Indigofera pechuelli	2.94	48	149***	0	57***
Euphorbia rectirama	2.91	5	148***	15	140***
Acacia mellifera	1.74	15	258***	54	166***
Monechma spartioides	0.63	55	111***	93	148**
Indigofera pungens	0.38	66	47	1	0
Acacia karroo	0.33	0	6*	0	0
Maytenus linearis	0.32	1	19***	0	1
Schotia afra	0.06	2	4	2	2
Boscia albitrunca	0.00	7	3	0	3
Other species		3288	1289	1685	704

[1] From paper 2

Photos on the following page:

Top, left: Female 1 (Shibula) with her calf behind

Top, right: The Orange River is inaccessible to the black rhinos in most of the gorge

Second row, left: Central Waterval viewed towards southwest

Second row, right: A defecating black rhino spreading its dung by kicking backwards

Third row, left: Female 2 (Blompot) with two of her offspring

Third row, center: Weighing and measuring volume of black rhino dung along a transect

Third row, right: Print of a large male (Ngara)

Bottom row, left: A piece of black rhino horn naturally broken off a live animal. Note the structure.

Bottom row, right: A favourite drinking point along a tributary of the Orange River

What have we learned?

Let us review the most salient points of what we have learned from the three preceding papers, in terms of

1) Findings specifically applicable to the Waterval and Augrabies Falls National Park

2) Implications for black rhino management in general

3) Lessons applicable to problems and approaches in plant-herbivore studies

- about rhino management in Augrabies Falls N.P.

Paper 1 estimated the browse availability used to analyse diet selection in paper 2 and laid out the habitat parameters for the habitat suitability model (HSM) in paper 3. Waterval is characterised by browse which is scarce, but diverse and of good palatability. The exceptions are the riverine habitats, which are extremely high in woody browse. Access to water is limited by steep gorges along the river, but is nowhere more than 6 km away. Access to browse may be limited in places by distance to water, steep slopes and perhaps rockiness. This is also likely to be true of other potential black rhino reintroduction sites within Augrabies Falls National Park (AFNP).

Paper 2 analysed various aspects of diet selection (objectives II and III in the introduction). The diet of black rhino in Waterval is dominated by *Zygophyllum cf. dregeana*, *Acacia mellifera*, *Euphorbia rectirama, Indigofera pechuellii, Hermannia stricta, Rhigozum trichotomum, Monechma spartiodes* and *Indigofera heterotricha*. This partly reflects availability, but all these plants are significantly preferred except *M.spartiodes*. Indeed, *Z. dregeana, H. stricta* and *I. heterotricha* are highly preferred. The abundant riverine vegetation was browsed remarkably little. When *A. mellifera* drops its leaves during the dry season, *Z. dregeana* and other species become even more important and preferred. It is therefore important for the conservation of both the vegetation and the rhinos to monitor certain of the plant species in the diet (specified in paper 2), so that they can act as early warning indicators (objective IV in the introduction). Variations in browse availability within AFNP will affect the diet composition in each park section - if black rhinos were to be reintroduced - , but the trends are likely to be similar.

In paper 3 a model was developed of how various habitat parameters contribute to habitat suitability for black rhino (objective I in the introduction). In Waterval the significant parameters in order of importance were availability of preferred foods, distance to roads, habitat heterogeneity, slope, distance to water and rockiness. The most preferred habitats were actually very low in total browse availability, but high in availability of preferred foods. Although the model is very simple, subject to assumptions and based on limited data specifically from Waterval it would be a valuable tool helping to evaluate the suitability of new introduction sites within AFNP. The exact values of the logistic regression are not to be taken too literally, especially when applied outside the study area, but in its vicinity the relative weighting of each habitat parameter is likely to be about right.

Implications for black rhino management in general

In this study, as well as in several others, a few preferred plant species make up the bulk of the black rhino diet (Paper 2). It means that to estimate ecological carrying capacity (ECC) one cannot simply consider the total amount of browse, but must identify the principal and preferred diet species and then estimate the availability of these species. These species tend to belong to certain families, which include *Acacia*, *Hermannia*, *Indigofera*, *Rhigozum* and *Zygophyllum* where available. It also means that monitoring key plant species as early warning indicators of the rhino population approaching ECC only requires sampling a few species, making it a manageable task.

This study showed that some plant species were so highly preferred that the concept of ice cream species certainly applies to black rhino feeding and that some plant species may even be locally threatened. It also showed that the black rhinos feeding on *Acacia mellifera* shrubs prefer feeding at 100-150 cm above ground, prefer shrubs with leaves and fresh shoots and prefer shrubs with high density of leaves and twigs. The black rhinos browsed lightly, but frequently on *Acacia mellifera* supporting the notion that acacias may function as the browsing equivalent of grazing lawns. The acacias provide fast, nutritious regrowth, as long as they are not browsed too hard – perhaps a case of co-adapted strategies.

The habitat suitability model (HSM) is constructed specifically for Waterval, Augrabies Falls National Park. However, while the regression equation is not transferable several of the habitat parameters that turned out significant (previous page) may very well be the most important in other areas too.

Lessons for plant-herbivore studies

The most striking observation of studying plant-herbivore relations, perhaps particularly where browsing is concerned is that it turns out to be an extremely complex network of interactions between species and individuals at two trophic levels capable of changing behaviour and responses, making it difficult to identify the negative and positive feedbacks for certain.

One of the complexities revealed in this study is how rhinos and presumably other herbivores select their food by selecting at many levels: habitat, microhabitat, feeding height, species, season in combination with species phenology, densities of leaves and twigs as well as previous browsing. This is important to consider when designing a study, as one can estimate selectivity erroneously if only focussing at one level.

The construction of a Habitat Suitability Model (HSM) is relatively simple and fails to take in all the ecological complexity, so its output should not be taken too literally. On the other hand, structured simplicity is the strength of a HSM (and other models) because its ranks and quantifies correlations, conveys basic understanding and leaves out the confounding complexity. In constructing a HSM it is important to also test habitat variables perceived to be less important in order not to prejudice the model. For instance, in this study habitat heterogeneity was unexpectedly significant.

The method of estimating browse availability applied in this study (adaptation of Smit, 1996 – paper 1) provides data of good quality, but is very time consuming. At the moment no better alternative appears to have been described in the literature. However, the real interest is the browse production rather than the standing browse capital, and methods to assess this are even more time consuming.

Reintroduction into their natural habitat has become an important part and means of the conservation of large herbivores. Upon reintroduction in many cases the population cannot be allowed to increase unchecked because it conflicts with other interests, including those of other herbivores or plants in need of conservation or with a desire for maximum production. In such cases it is important not to rely entirely on early "expert opinion" about and guesstimates of the ECC or desired stocking rate. It is best to follow a procedure of clearly stating a desired management effect (for instance maximum production, ECC or a specific availability of certain plants important to conservation) and then adopt an adaptive approach to reach that effect, such as this one:

1. State the desired management effect (preferably as a clear target)
2. Evaluate the intended area of reintroduction prior to the reintroduction using HSM and ECC estimates from similar areas where the species occurs
3. Introduce the species in numbers which are very conservative in comparison to the preliminary estimates of desired stocking rate and be prepared to regulate the population
4. Study the diet selection of the large herbivore in the area of reintroduction
5. Identify early warning indicators (for instance key plants or dung nutrients) and monitor them

6. Study the local distribution of the large herbivore
7. Develop a local HSM
8. Use the early warning indicators and the HSM to re-estimate the stocking rate that best meets the desired management effect
9. Regulate the population if and when necessary by translocation or hunting/culling (or reintroduction of predators if a feasible option)
10. Keep monitoring the early warning indicators as well as refining HSM and desired stocking density estimates

How do we improve our understanding?

What research is most needed to improve our management and understanding of the black rhinos, co-existing browsers and their environment?

Firstly, to quickly improve our monitoring and management of black rhinos and their environment we need to:

- Test key plant species as early warning indicators of population performance of black rhinos and compare this to other monitoring systems such as dung nutrient contents, body condition scores and population growth parameters (% population growth, mortality and inter-calving interval)

Secondly, if we could upgrade Habitat Suitability Models (HSM), such as this one to models of Ecological Carrying Capacity (ECC) it would have a wide range of applications for management and research of black rhinos and the rest of their ecosystem. For this purpose we need to:

- Develop a rapid, yet accurate method of estimating standing browse availability and especially browse production under different conditions. This will help estimating food preferences and ECC
- Study the competition of black rhino with other browsers and mixed feeders to evaluate how they affect ECC for black rhino

Thirdly, to refine our understanding and modelling of black rhino-plant relations we need to:

- Measure the digestibility, nutrient contents and plant toxins of a range of preferred and avoided plants in several different rhino reserves. This will help reveal requirements and preferences of the black rhino and the quality of the available browse