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

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.

Acknowledgements

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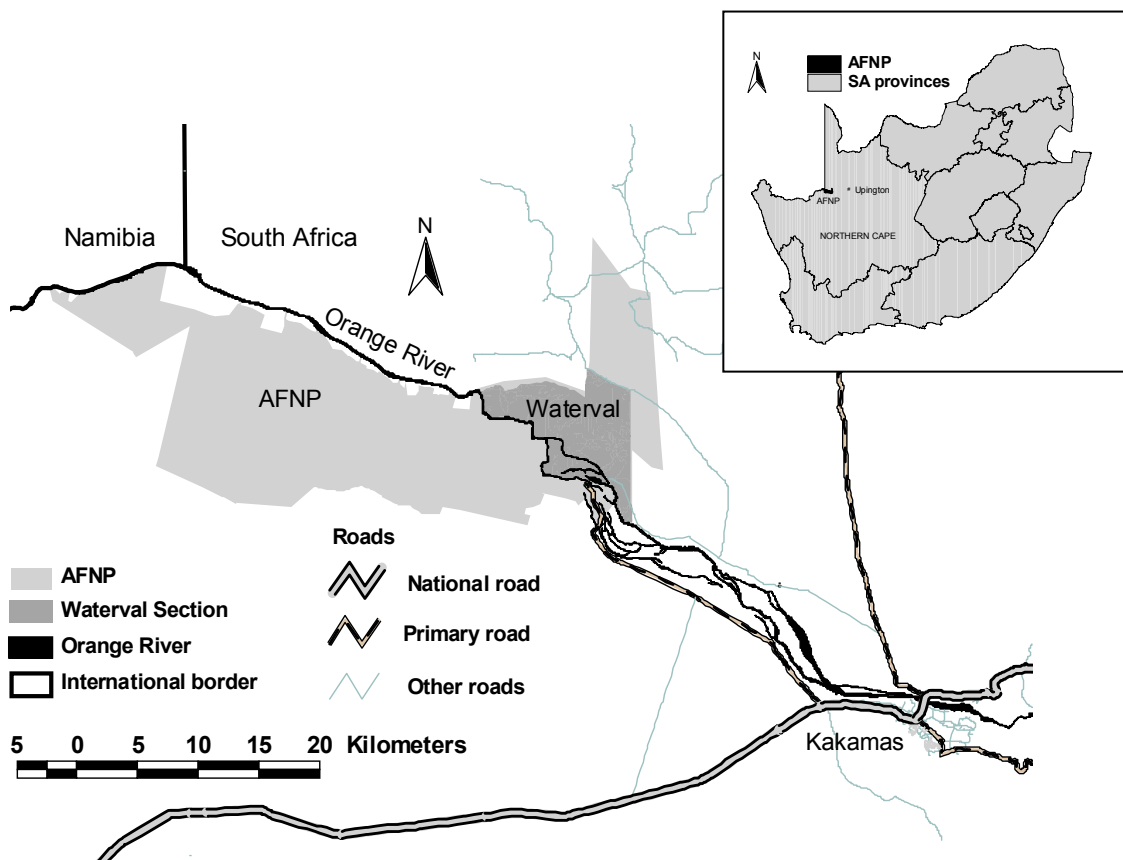
Figure 1.

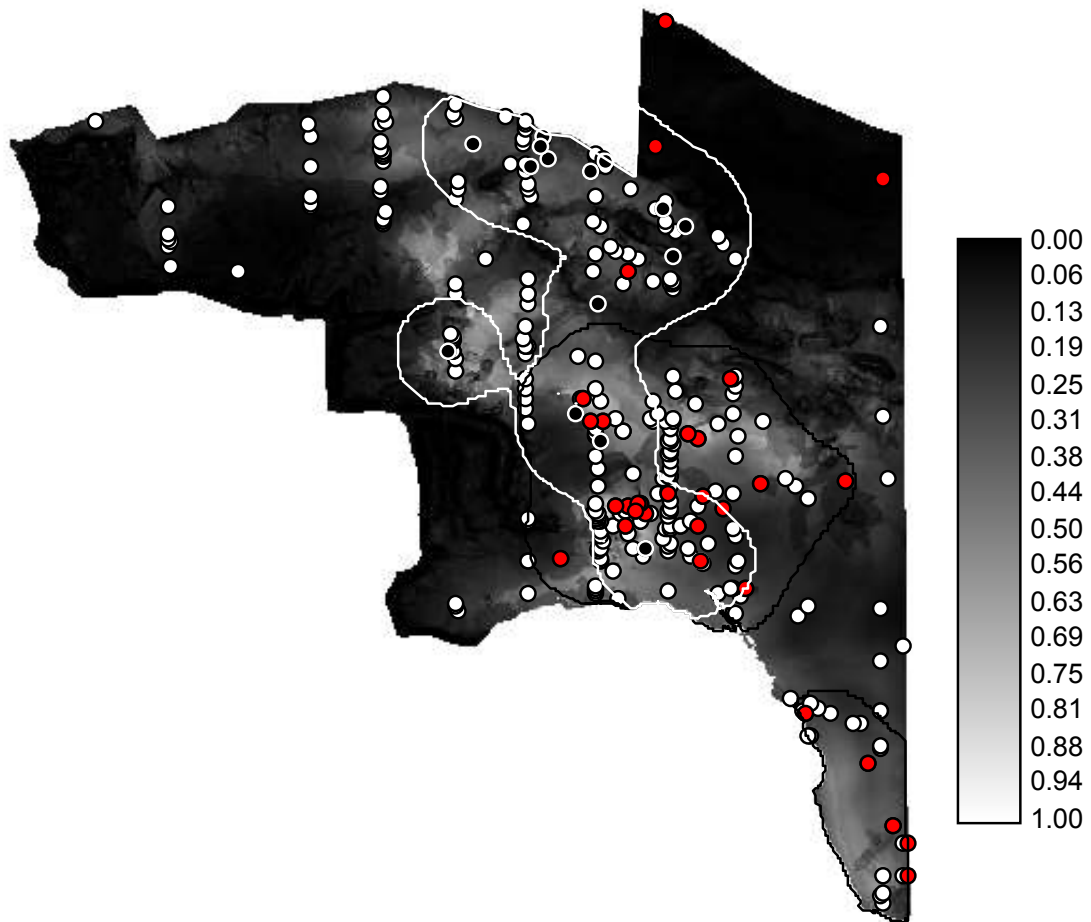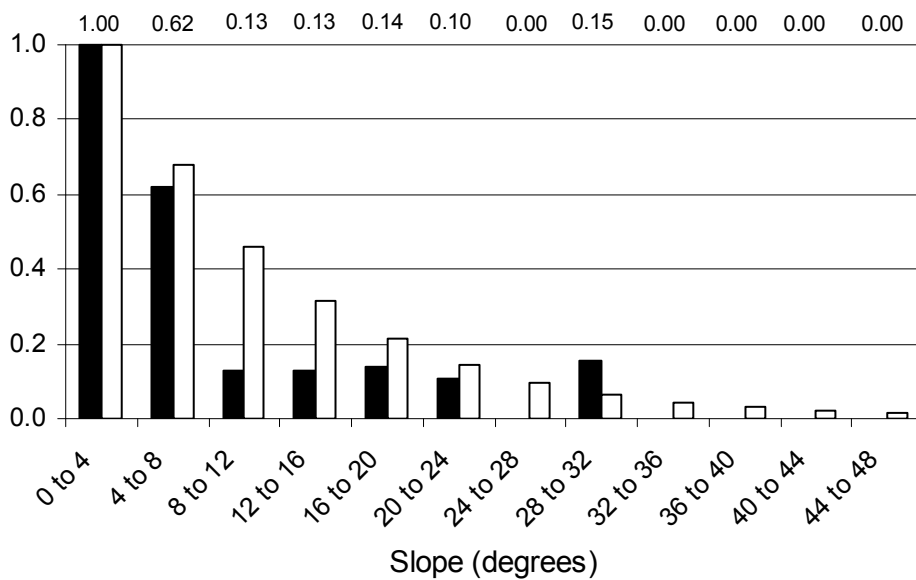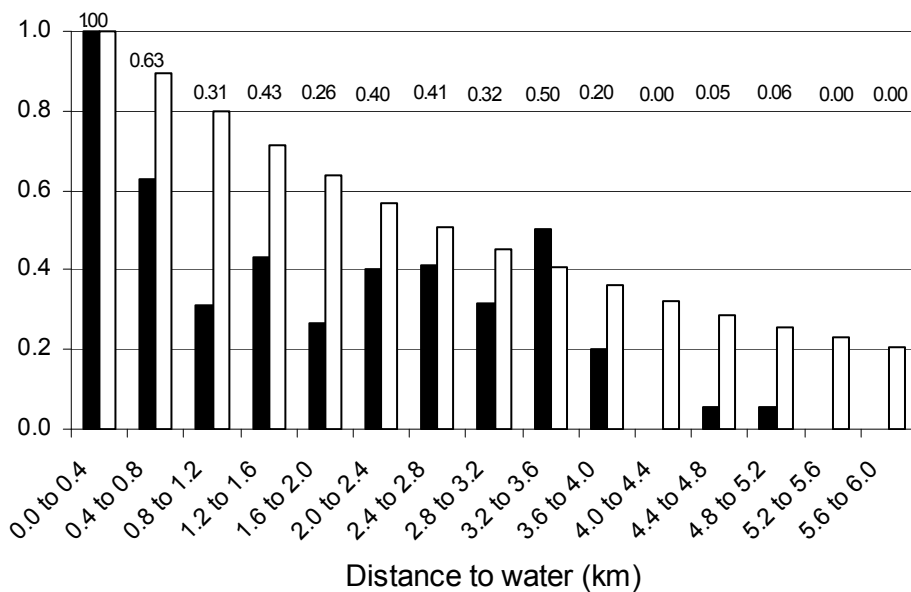The location of Waterval and Augrabies Falls National Park (AFNP).

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 | 0.13 | 0.13 | 0.14 | 0.10 | 0.00 | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 |

Slope (degrees)

■ Observed rhino density □ Modelled habitat suitability

| | 100 | 0.63 | 0.31 | 0.43 | 0.26 | 0.40 | 0.41 | 0.32 | 0.50 | 0.20 | 0.00 | 0.05 | 0.06 | 0.00 | 0.00 |

Distance to water (km)

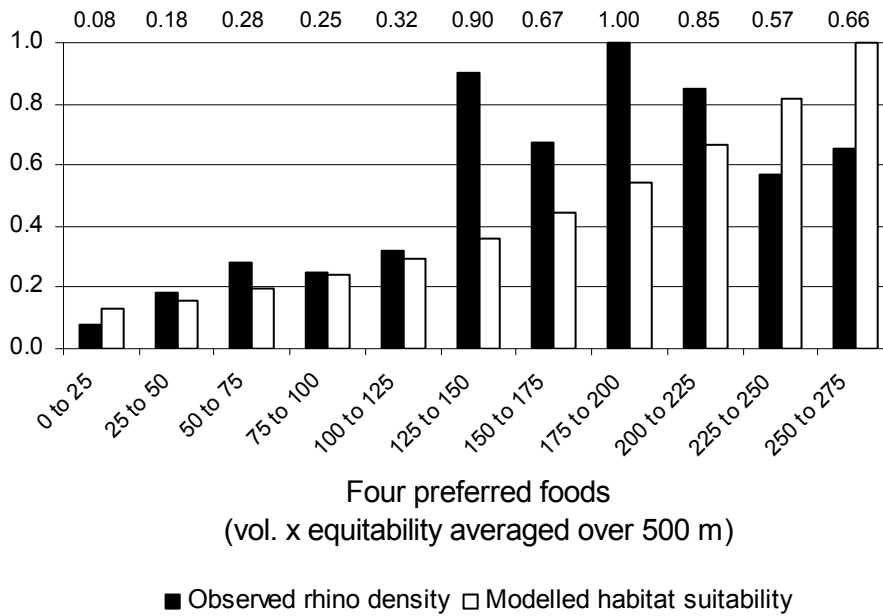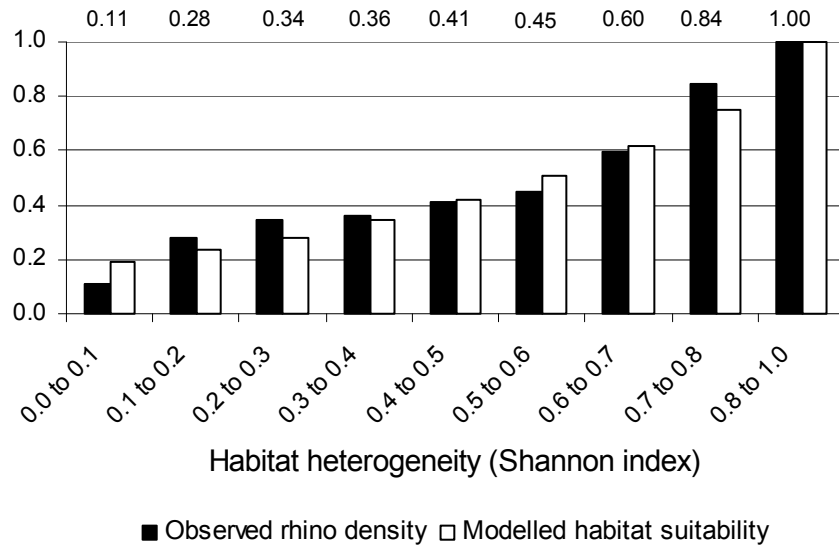■ Observed rhino density □ Modelled habitat suitability

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.
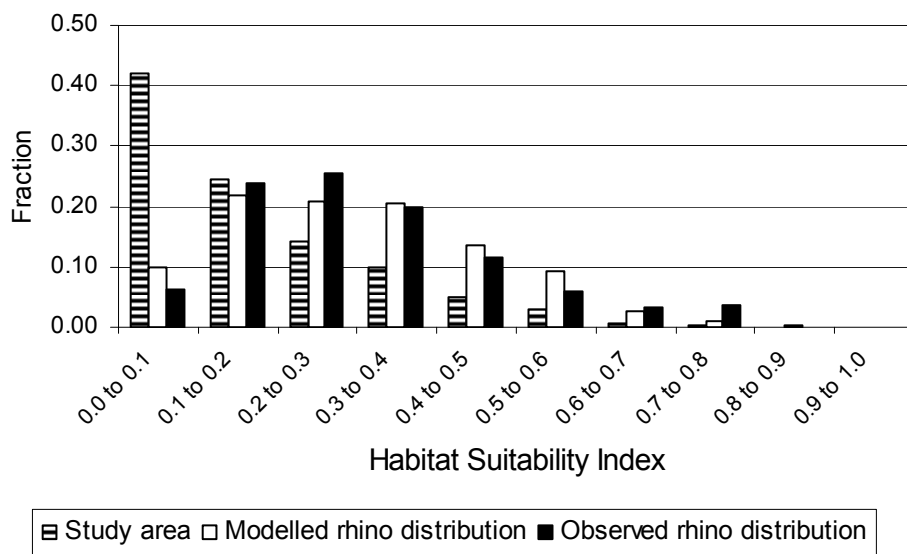
Figure 4

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											
		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* – *Zziphus mucronata* short forest	Sample size
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