# Habitat suitability model for black rhinoceros in Augrabies Falls National Park, South Africa

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**To assist with identifying land for reintroduction, a habitat suitability model (HSM) for black rhinoceros (*Diceros bicornis*) was developed in the arid Augrabies Falls National Park, South Africa, from records of sightings, feeding trails and dung middens. Logistic regression and Bayesian Information Criterion were employed to construct and select the best HSM from >35 eco-geographical variables. The modelled and the observed distributions of black rhinos did not differ (*P* = 0.323) and *k*-fold cross-validation confirmed the model's ability to predict the distribution of independent data. The HSM consisted of five variables: availability and equitability of three preferred foods, distance to roads, habitat heterogeneity, slope and shade. The variables 'distance to water' and 'rockiness' were also included in the confidence set of models. Only 50% of the study area had a habitat suitability exceeding 11%, but featured 89% of rhino locations. Of 10 vegetation communities, two with high volumes of favourite foods were preferred. Feeding areas with a high density of preferred food plants were also highly preferred. The riverine vegetation community was not preferred, because its abundant browse was not of the preferred species. The apparent avoidance of roads warrants more research and the attention of park managers.**

**Key words**: *Diceros bicornis,* habitat suitability model, preferred foods, roads, habitat heterogeneity, slope, shade.

## INTRODUCTION

The number of black rhinoceros (*Diceros bicornis*) in Africa plummeted from 65 000 in 1970 to 2410 in 1995 due to intensive poaching and habitat loss (Emslie & Brooks 1999). Increased safety and extensive translocations (Knight & Kerley 2009) have allowed recovery to 4230 animals (Milliken *et al.* 2009). The main aim of the current conservation strategy for the critically endangered black rhino is to ensure a population growth above 5% per annum in southern Africa in order to minimize the loss of genetic diversity and outpace outbreaks of poaching (Emslie 2001). However, growth has fallen short of the target especially in older populations, where growth has levelled off. Limited understanding of black rhino habitat suitability and diet selection has led to rhino removals at levels too low to avoid a density dependent growth impediment (Brooks 2001; du Toit 2001; Emslie 2006; Milliken *et al.* 2009). A better understanding of black rhino habitat suitability is therefore pivotal, both for assessing an appropriate density of the source population at which rhinos can be removed and suitable areas to which to translocate.

This paper presents a habitat suitability model for black rhinos in an arid protected area. The model is not ubiquitously applicable, but is a step towards a better understanding of the requirements of black rhinos under similar conditions. This paper also presents results on the selection of microhabitats for feeding. The study area was the Waterval section of the Augrabies Falls National Park (AFNP), South Africa. Black rhinos were later removed from the park section, but plans exist for the reintroduction into other parts of the park, where the model may be employed.

### Study area

The fieldwork was conducted in the Waterval section of Augrabies Falls National Park (AFNP), South Africa during 1997–1999 (Fig. 1). The park covered 554 km$^2$ along the Orange River (28°25′–28°38′S, 19°53′–20°24′E) and borders Namibia. The 75.3 km$^2$ Waterval section served as

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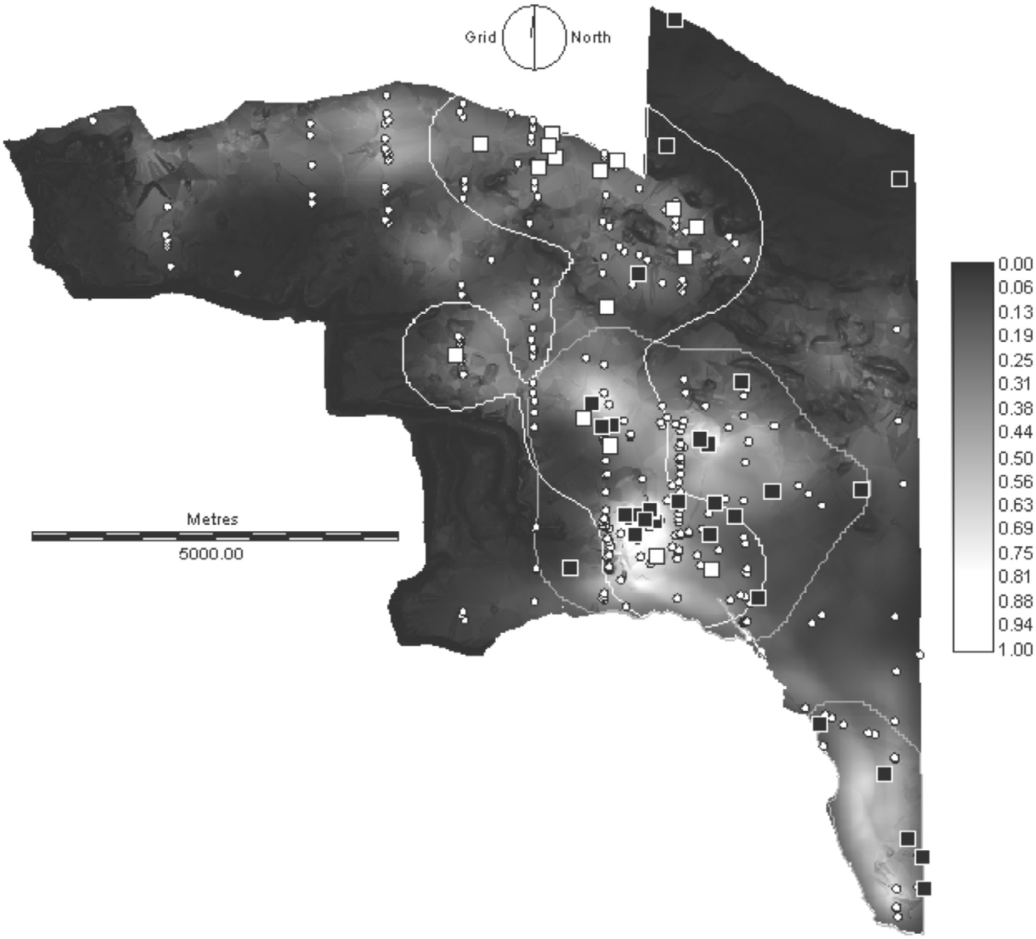

**Fig. 1**. Map of the modelled habitat suitability index (min. 0 to max. 1) for black rhinos in Waterval, Augrabies Falls National Park, with 315 known black rhino locations and home ranges of the two adult females (90% kernel). Sightings of female 1 are indicated by black squares, sightings of female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

a fenced black rhino reserve at the time of the study, with one adult male, two adult females, three subadults and two calves.

The Waterval section comprised a narrow flood plain and steep gorges along the Orange River in the south, gravel plains in the centre and mountains in the north. Altitudes ranged from 420 m to 750 m above sea level. The climate is sub-tropical to tropical and arid with an average annual rainfall of 123 mm rain of which 71% falls during October–April. The monthly maximum and minimum temperatures were 37.1°C and 21.6°C in January and 21.3°C and 4.5°C in July. The average annual number of frost nights was 0.9 (South African Weather Service 2001). The park contains the Lower Gariep Broken Veld, Bushmanland Arid Grassland and Lower Gariep Alluvial Vegetation types (Mucina & Rutherford 2006) in the Gariep Centre of Endemism, with 19 of the total of 364 species of flowering plants having not been recorded in other conservation areas (Zietsman & Bezuidenhout 1999). The area includes10 vegetation communities ranging from sparse and open shrublands (61% of area) through open and closed woodlands (38%) to short riverine forest (1%) (Buk 2004). The average total browse availability at 0–200 cm above ground is 1890 $m^3$/ha (range: 597–14 446 $m^3$/ha) (Buk 2004). The park has a number of herbivores potentially competing with black rhino such as giraffe (*Giraffa camelopardalis*), springbok (*Antidorcas marsupialis*), klipspringer (*Oreotragus oreotragus*) and rock hyrax (*Procavia capensis*).

## METHODS

### *Distribution of black rhino*

Geo-referenced locations of black rhinos were sampled in three ways and pooled: sightings, feeding trails and dung middens. Nine sightings came from two systematic aerial surveys, 27 sightings were recorded by trackers and 13 sightings occurred during research. Seventy-four locations were derived from the midpoint of black rhino feeding trails from feeding studies (Buk & Knight 2010) (Fig. 1). All sightings and feeding trails were separated by at least 24 hours, and groups were treated as one sighting or one feeding trail. 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 Idrisi 32.01 (Clark Labs 1999) and ArcView 3.3 (ESRI 2002) geographical information systems (GIS).

The dung transects were placed north–south, spaced by 1 km and had a total length of 72.2 km. The transects were walked along slowly navigating with compass and a GPS receiver during one field trip in June–July. Whenever dung was seen within the transect width of 20 m on either side, its distance from the transect was recorded as were the GPS readings. The programme Distance 4.1 was used to analyse the dung density (Thomas *et al.* 2003).The 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 in dung decomposition rates between substrates. Dung beetles were rare in the study area, so dung remained on the surface of the soil and decomposition was slow in the extreme aridity. Dung density was 1.25 (1.02–1.59; 95% confidence limits) middens per ha. Effective strip width was 10.5 m. The distance from transects to detected dung middens was found not to differ between vegetation communities (one-way ANOVA, $F_{\text{d.f.} = 186} = 1.43$, $P = 0.196$).

### *Habitat suitability modelling*

The underlying assumption of this habitat suitability model (HSM) is that the rhino distribution is an acceptable proxy for habitat suitability (Manly *et al.* 2002). Logistic regression was performed in S-Plus (Insightful Corp 2002) and other statistics in Analyse-it (Analyse-it Software 2003). Logistic regression is suitable for one random sample of available units, which can be categorized as used (1) or unused/undetected use (0) after a single period of selection. However, in this study logistic regression was applied to a large, random sample of pixels in a GIS image of the park section (available pixels) plus all the used pixels, with each GIS layer representing an eco-geographical variable. Thus, in this study there are separate samples of available and used units (pixels). The regression equation can be adapted to circumvent this violation of assumptions of logistic regression, so the resource selection function (RSF) takes the form

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

where $w^*(x)$ is the relative probability of pixel $x$ being used after a single period of selection (Manly *et al.* 2002). Each $b$ represents an eco-geographical variable and each $x$ the corresponding regression coefficient. Subsequently, the equation was scaled (multiplied) such that $w^*(x)$ takes values from 1 down to a theoretical minimum of 0 as is customary for a habitat suitability index.

Eco-geographical variables were removed and added in a stepwise fashion to model candidates by eliminating those variables failing to produce a more parsimonious model based on the Bayesian Information Criterion (BIC). Only one variable from each of nine groups of variables were accepted at a time, because variables in each group were correlated. The only exceptions were for independent food plants (Table 1). We tested for multicollinearity among the variables in the best models and calculated the Variance Inflation Factor, which provides an index that measures how much the variance of an estimated regression coefficient is increased because of collinearity (Kutner *et. al.* 2004). We ranked the models by ascending value of BIC, which considers both fit and parsimony of the model. The more widely used Akaike Information Criterion (AICc) favour models with relatively more variables (Boyce *et. al.* 2002). We ranked models with $\Delta$BIC <10 and calculated their relative BIC weights, which expresses the probability that a model is the best approximation to the truth given the data. The set of best models with $\Delta$BIC < 10 and BIC weights that add up to 0.95 are referred to as the 95% confidence set of models (Burnham & Anderson 2002).The highest ranking model was tested for goodness of fit by computing a Pearson chi-square from observed and expected number of rhino locations in eight habitat suitability intervals.

As an alternative to using independent data for

**Table 1**. The 26 best of the 36 variables tested for improvement of model performance. The change in Bayesian Information Criterion (BIC) when the variable was added to the best base model (most parsimonious model minus one variable) is given as ΔBIC, where a negative value indicates improved performance and the lowest value indicates the largest improvement.

| **Group of variable** Variables | Description | Source | Change in performance ΔBIC |
|---|---|---|---|
| **Fence, distance to:** | | | |
| Fence dist | km to rhino fence | Buk 2004 and Idrisi Distance module | 5.81 |
| Fence dist max 1 km | km to rhino fence, truncated at 1 km | Buk 2004 and Idrisi Distance module | 2.75 |
| **Food** | | | |
| All sppvol | The combined available browse volume of all plant species | Buk 2004 | –1.56 |
| 12 sppvol | The combined available browse volume of 12 food species | Buk 2004 | –14.43 |
| 6 sppvol | The combined available browse volume of 6 food spp. | Buk 2004 | –19.86 |
| 3 sppvol | The combined available browse volume of 3 food spp. | Buk 2004 | –19.86 |
| Species A vol<br>Species B vol<br>Species C vol | Canopy volume of 3 principal food plant species as 3 separate variables | Buk 2004 | –32.53 |
| Species A vol<br>Species B vol | Canopy volume of 2 principal food plant species as 2 separate variables | Buk 2004 | –35.91 |
| Species A vol 500 m<br>Species B vol 500 m<br>Species C vol 500 m | As above averaged over the pixels within a 500 m radius | Buk 2004 with averaging in Biomapper | –73.68 |
| Species A vol 500 m<br>Species B vol 500 m | As above averaged over the pixels within a 500 m radius | Buk 2004 with averaging in Biomapper | –60.25 |
| 3 sppvol 500m | The combined browse volume of 3 species averaged over the pixels within a 500 m radius of the pixel | Buk 2004 with averaging in Biomapper | –32.34 |
| 3 spp × E | The combined browse volume of 3 food species multiplied by their Shannon equitability | Buk 2004 | –45.89 |
| 3 sppvol 500 m × E | The combined browse volume of 3 food species averaged over 500 m multiplied by their Shannon equitability | Buk 2004 with averaging in Biomapper | –80.31 |
| 4 sppvol 500 m × E | As above for 4 species | Buk 2004 with averaging in Biomapper | –42.32 |
| **Habitat heterogeneity** | | | |
| Hab het 500 m | Habitat heterogeneity (Shannon diversity) within a 500 m radius | Buk 2004 with calculation in Biomapper | –23.33 |
| **Hiding cover** | | | |
| All sppvol | Total canopy volume 0–200 cm | Buk 2004 | 5.62 |
| **Roads, distance from:** | | | |
| Road low use max 2 km | km from low use gravel roads (public or mng) truncated at 2 km | Buk 2004 and Idrisi Distance module | –68.89 |
| **Rockiness** | | | |
| Rocks total | % loose rock and bedrock | Buk 2004 | 5.45 |
| Rocks total 500 m | The above averaged over the pixels within a 500 m radius | Buk 2004 with averaging in Biomapper | 0.61 |
| Rocks loose | % loose rock only | Buk 2004 | 5.07 |
| **Shade** | | | |
| Shade | % canopy shade (1 m or wider) | Buk 2004 | 4.99 |
| Shade 500 m | The above averaged over the pixels within a 500 m radius | Buk 2004 with averaging in Biomapper | –0.24 |
| **Slope** | | | |
| Slope deg | Slope in degrees | Idrisi TIN interpolation of 20 m digital contours | –20.37 |
| **Water, distance to:** | | | |
| Water dist | Distance to accessible water in km | GPS and aerial photos plus Idrisi Distance module | 1.35 |

evaluation of the highest-ranking model for its ability to predict independently, we used $k$-fold cross-validation (Boyce *et al.* 2002; Fielding & Bell 1997). The set of known locations ($n = 315$) was randomly subdivided into $k = 3$ equal subsamples: one for validation, and two for training to parameterize the model. This process was repeated three times, with each subsample being used once as validation data. These three models were evaluated with the Spearman rank correlation between the rank of eight intervals (bins) of habitat suitability and the frequencies of rhino locations in each bin, standardized for area. Significant correlations indicate that the model performed well in predicting the distribution of independent locations.

### *Calculation of eco-geographical variables*

The eco-geographical variables were prepared as GIS layers with a pixel size of 10 × 10 m. Aerial photographs (1:50 000 panchromatic) were georeferenced with a GPS receiver and GIS software. Slope was derived from digitized 20-m contours. Distance to accessible water was calculated from aerial photos and GPS readings. In the Orange River Gorge the river is surrounded by slippery rock surfaces with inclines from 45 to 90 degrees, so these waters were regarded as inaccessible. Rockiness was measured as presence/absence of loose rock or bedrock at 25 pinpoints in each of 58 plots (Buk 2004). Percentage rock cover was calculated for each plot and averaged for each of 10 vegetation communities.

Forage was represented by canopy volume from 0 to 200 cm above ground (normal black rhino feeding range; Buk 2004) in each vegetation community, as measured with tape measures on 4640 plants using the BECVol method (Smit 1996). The canopy volumes of three principal food plant species, which were also significantly preferred (Buk & Knight 2010), were used as three separate variables ('Species A–C vol' 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 12 principal plant species were *Zygophyllum* cf. *dregeana, Acacia mellifera, Euphorbia rectirama, Indigofera pechuellii, Hermannia stricta, Rhigozum trichotomum, Monechma spartioides, Indigofera heterotricha, Acacia karroo, Lycium bosciifolium* and *Phaeoptilum spinosum* (Buk & Knight 2010). As a refinement, the combined canopy volumes of these species sets were multiplied by their Simpson equitability ($E$) to factor in any effect of the balance of food species ('3 Spp. vol × E' 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 m of the pixel (*e.g.* '3 Spp. vol. 500 m', etc., in Table 1). The rationale was to factor in movement between nearby habitat patches or resources and to incorporate a more realistic 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 × 10 m) within 500 m using a procedure in Biomapper (Hirzel *et al.* 2002). Vertical hiding cover from terrestrial sources of disturbance was calculated as the total canopy volume from 0 to 200 cm above ground. Shade for black rhinos was calculated as projected canopy cover of plants taller than 2 m minus the basal area, provided the shade exceeded 1 m in width from plant base to the edge of the canopy. The calculated areas of shade were then expressed as a percentage of the area of each vegetation community. Distance from roads was calculated and truncated at 2 km. The roads in question were one public gravel road on the northern boundary of the study area with <100 vehicles per day and one gravel loop within the park with 1–10 vehicles per day as counted during other field work. There were other 4×4 vehicle routes inside the study area, but these were used much less. The distance to the boundary fences was truncated at 1 km.

### *Selection of vegetation communities and feeding areas*

Selection of vegetation communities based on distribution of signs of rhinos was calculated as observed amount of use divided by the amount of use expected based on the community size, or in the case of dung, the length of the dung transect in each community. A selection value <1 indicates avoidance and >1 indicates preference. Selection for feeding areas within vegetation communities was assessed by comparing species composition in 2-m-wide transects around feeding trails with the species composition calculated from 58 belt transects (Buk & Knight 2010; Buk 2004).

### *Home range*

Both 95% minimum convex polygons and 90%

**Table 2**. The most parsimonious model of habitat suitability for black rhinos in Augrabies Falls National Park constructed using logistic regression.

| Variable | *B* | S.E. | Lower 95% CI | Upper 95% CI | BIC* weight |
|---|---|---|---|---|---|
| $B_1$: Volume of three principal food species multiplied by their equitability averaged for pixels within 500 m ($m^3$/ha) | 0.0129 | 0.00151 | 0.00992 | 0.0158 | 1.00 |
| $B_2$: Distance from roads – max. 2 km (km) | 1.01 | 0.135 | 0.750 | 1.28 | 1.00 |
| $B_3$: Habitat heterogeneity (Shannon diversity of habitats within 500 m) | 2.25 | 0.421 | 1.43 | 3.08 | 0.999 |
| $B_4$: Slope (degrees) | –0.0817 | 0.0190 | –0.119 | –0.0444 | 0.999 |
| $B_5$: Shade averaged over 500 m (%) | 0.0540 | 0.0202 | 0.0144 | 0.0934 | 0.530 |
| Constant | –11.6 | 0.461 | –12.5 | –10.7 | |

Differential deviance for the logistic regression was 279.7 with 5 degrees of freedom ($P < 0.0001$)

Output was scaled to a maximum of 1 by multiplying by 0.00282

Habitat suitability index = $0.00282 \times \exp(B_1 \times 0.0129 + B_2 \times 1.01 + B_3 \times 2.25 + B_4 \times -0.0817 + B_5 \times - 0.0540)$

*Bayesian Information Criterion.

kernel methods were used (following Hooge *et al.* 1999) in calculating home range sizes for the rhinos, using sighting data. The smoothing factor (*H*) was calculated using the least square cross validation.

## RESULTS

### The habitat suitability model

The model with the best BIC value included five eco-geographical variables: food (three species combined), distance from roads, habitat heterogeneity, slope and shade (Table 2). The observed and modelled distributions of rhinos along a gradient of habitat suitability did not differ significantly ($\chi^2$ =8.15, d.f. = 7, $P = 0.323$), confirming that the model fits the data. In contrast, the observed distribution of rhinos differed much from the distribution of habitat suitability classes across the study area ($\chi^2 = 323$, d.f. = 7, $P < 0.001$; Fig. 2). Fifty per cent of the study area had a habitat suitability of less than 0.1075, and only 11.1% of rhino locations were found in this half of the study area. The 3-fold cross-validation yielded $r_s$ values of 0.976 ($P$ = 0.010), 0.857 ($P$ = 0.023) and 0.928 ($P$ = 0.014), confirming the ability of the model to predict the distribution of independent data.

Several other models are within the confidence set of candidate models, and the second ranking model performs almost as well as the best (Table 3).

### The eco-geographical variables

Food availability was the variable that contributed the most to model performance, as it resulted in the lowest ΔBIC value (Table 1). Total available browse gave little improvement in model performance (ΔBIC = –1.56), whereas availability of the three most principal food species averaged over a radius of 500 m multiplied by their Shannon equitability gave the most improvement (ΔBIC = –80.31).

The distance from roads gave the second biggest improvement in model performance (ΔBIC = –68.89), followed by habitat heterogeneity (–23.33) and slope (–20.37) (Table 1). Shade provided only a marginal improvement in performance (–0.24) to the base model consisting of the four aforementioned variables (Table 1). Distance to water and rockiness did not contribute towards a more parsimonious model, but models including these variables were still in the confidence set (Table 3). Cover in which to hide and distance from the boundary fence were not included in models in the confidence set.

The five variables included in the best-performing model had Variance Inflation Factors (VIF) ranging from 1.17 (shade) to 1.46 (volume of three food plants), indicating that correlation between the variables was low, and affected the model much less than the generally accepted upper limit of VIF = 10 (Kutner *et al.* 2004).

### Selection of vegetation communities and feeding areas

Almost all direct signs of rhinos (dung middens, sightings and feeding trails) indicated that the rhinos showed avoidance of vegetation communities 1 (*Schotia afra–Indigofera pechuelii* low, open

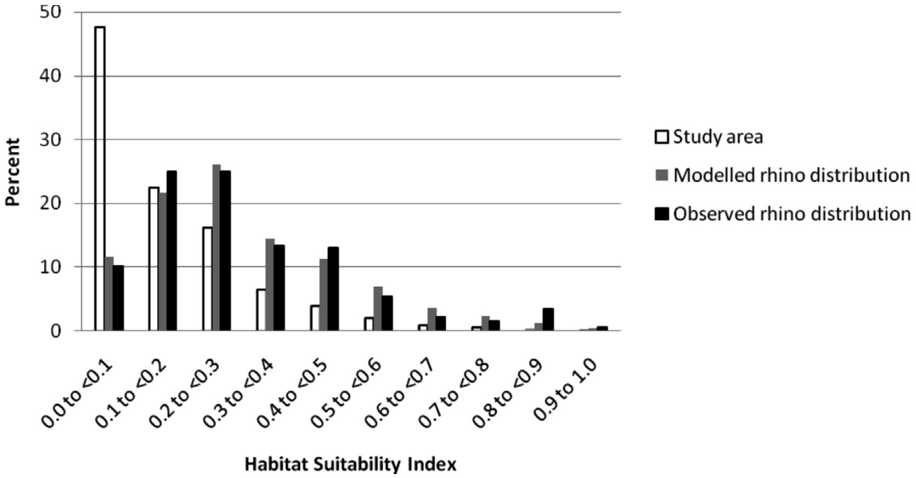

**Fig. 2**. Distribution of the Waterval study area as well as observed and modelled black rhino locations on habitat suitability classes.

**Table 3**. The most parsimonious models according to the Bayesian Information Criterion (BIC) with ΔBIC < 10. The base model includes the variables food, distance to roads, habitat heterogeneity and slope ($B_1$–$B_4$ in Table 2). Models in the BIC 95% confidence set of models are in bold.

| Model | Variables | ΔBIC | BIC model weight | BIC rank |
|---|---|---|---|---|
| **Base model + Shade 500 m** | 5 | 0.00 | 0.365 | 1 |
| **Base model** | 4 | 0.24 | 0.324 | 2 |
| **Base model + Water dist** | 5 | 1.59 | 0.165 | 3 |
| **Base model + Shade 500 m; loose rocks** | 6 | 3.71 | 0.057 | 4 |
| **Base model + Water dist; shade 500 m** | 6 | 4.16 | 0.045 | 5 |
| Base model + Loose rocks | 5 | 5.31 | 0.026 | 6 |
| Base model + Water dist; loose rocks | 6 | 6.87 | 0.012 | 7 |
| Base model + Water dist; shade 500 m; loose rocks | 7 | 8.33 | 0.006 | 8 |

woodland) and 2 (*Adenolobus garipensis–Boscia albitrunca* tall, open shrubland), as well as preference for communities 4 (*Acacia mellifera–Euphorbia* spp. tall, open shrubland) and 5.1 (*A. mellifera–Zygophyllum dregeana–Euphorbia rectirama* tall, open shrubland) (Table 4). No significant selection for other vegetation communities could be detected with the available sample sizes. Preferred browse species were significantly over-represented (Fisher's exact test, Table 5) within 1 m of rhino feeding trails as compared to the species composition in vegetation plots. This was true both when comparing feeding trails and vegetation plots for the whole study area and when comparing within the most preferred vegetation community 5.1 (Table 5). Community 5.1 was used for this analysis to test whether even in the most preferred vegetation community there are preferred microhabitats or feeding areas, and because a large sample size was available for this vegetation community.

## Home range

The two adult females each accompanied by their youngest calf were sighted enough times to estimate their home ranges. Minimum convex polygon estimates (95%) were 20.7 km$^2$ ($n = 31$) and 10.3 km$^2$ ($n = 16$) with 22.0% overlap. Kernel home range estimates (90%) were 18.0 and 18.4 km$^2$, respectively, with a 24.7% overlap (Fig. 1). Applying both methods to all 315 known rhino locations resulted in only 59.6% and 46.5% of the reserve being inside the utilized polygon or kernel, respectively.

**Table 4**. Habitat selection using different signs of rhino distribution. The selection values given are observed value divided by expected value. 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 | Rhino sign distribution | | | |
|---|---|---|---|---|
| | Density of all rhino locations*** | Feeding trail density *** (midpoints) | Sighting density*** | Dung midden density*** |
| 1. *Schotia afra–Indigofera pechuelii* low, open woodland | 0.32*** | 0.16*** | 0.39* | 0.54*** |
| 2. *Adenolobus garipensis–Boscia albitrunca* tall, open shrubland | 0.23*** | 0.00** | 0.00** | 0.46** |
| 3. *Euphorbia gregaria–Ostespermum microcarpum* tall, sparse shrubland | 1.27 | 0.00 | 1.21 | 1.65 |
| 4. *Acacia mellifera–Euphorbia* spp. tall, open shrubland | 1.88*** | 1.39 | 2.37** | 2.78*** |
| 5.1 *A. mellifera–Zygophyllum dregeana–Euphorbia rectirama* tall, open shrubland | 2.58*** | 4.96*** | 2.27** | 2.75*** |
| 5.2. *A. mellifera–Z. dregeana–Monechma spartioides* tall, open shrubland | 0.22 | 0.00 | 0.73 | 0.30 |
| 6. *Acacia mellifera–Stipagrostis hochstetteriana*, tall, open shrubland | 0.88 | 0.81 | 0.65 | 1.17 |
| 7. *Sisyndites partea–Forskaolea candida* tall, open shrubland | 0.00 | 0.00 | 0.00 | 0.00 |
| 8. *Acacia erioloba–Schmidtia kalahariensis* short, open shrubland | 3.46 | 5.50 | 3.87 | 6.48 |
| 9. *Tamarixus neoides–Maytenus linearis* tall, open shrubland | 2.11 | 2.86 | 2.02 | 1.77 |
| 10. *Acacia karroo–Ziziphus mucronata* short (riverine) forest | 1.16 | 0.00 | 1.84 | 0.34 |
| *n* | 315 | 74 | 49 | 192 |

**Table 5**. The species composition within 1 m of rhino feeding trails compared to expected composition as calculated from availability in randomly placed vegetation plots. Figures are based on number of plants observed along the trails. 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) | | | | Vegetation community 5.1 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Expected | | Feeding trails | | Expected | | Feeding trails | |
| | | Plants | % | Plants | % | Plants | % | Plants | % |
| *Zygophyllum* cf. *dregeana* | 18.8 | 41 | 1.2 | 1494*** | 42.3 | 578 | 23.8 | 1207*** | 49.7 |
| *Indigofera pechuelli* | 2.94 | 48 | 1.4 | 149*** | 4.2 | 0 | 0.0 | 57*** | 2.3 |
| *Euphorbia rectirama* | 2.91 | 5 | 0.1 | 148*** | 4.2 | 15 | 0.6 | 140*** | 5.8 |
| *Acacia mellifera* | 1.74 | 15 | 0.4 | 258*** | 7.3 | 54 | 2.2 | 166*** | 6.8 |
| *Monechma spartioides* | 0.63 | 55 | 1.6 | 111*** | 3.1 | 93 | 3.8 | 148** | 6.1 |
| *Indigofera pungens* | 0.38 | 66 | 1.9 | 47 | 1.3 | 1 | 0.0 | 0 | 0.0 |
| *Acacia karroo* | 0.33 | 0 | 0.0 | 6* | 0.2 | 0 | 0.0 | 0 | 0.0 |
| *Maytenus linearis* | 0.32 | 1 | 0.0 | 19*** | 0.5 | 0 | 0.0 | 1 | 0.0 |
| *Schotia afra* | 0.06 | 2 | 0.1 | 4 | 0.1 | 2 | 0.1 | 2 | 0.1 |
| *Boscia albitrunca* | 0.00 | 7 | 0.2 | 3 | 0.1 | 0 | 0.0 | 3 | 0.1 |
| Other species | | 3288 | 93.2 | 1289 | 36.5 | 1685 | 69.4 | 704 | 29.0 |
| Total | | 3528 | 100.0 | 3528 | 100.0 | 2428 | 100.0 | 2428 | 100.0 |

[1] From Buk (2004) and Buk & Knight (2010).

## DISCUSSION

### Model validation and variables

The model achieved a significant fit and ability to predict distribution of black rhinos in the park section. Food availability was the most important variable in the model. The three principal species of browse were sufficient to achieve the most parsimonious model. Those species represented 65% of the diet in AFNP, Karoo and Vaalbos National Parks (Buk

& Knight 2010). In other study areas where three species comprised 30–50% of the diet (Ganqa *et al.* 2005; Kotze & Zacharias 1993; Muya & Oguge 2000; Mukinya 1977; Oloo *et al.* 1994), the addition of more forage species could improve the predictive ability of similar models.

Distance from roads was the second most important variable. The roads included low-use gravel roads, so tourist activity could have a negative impact on black rhino habitat and range use. This warrants further research, and in the interim suggests managers should be cautious of the negative impact roads may have on black rhino habitat use. Large herbivores typically avoid roads (Fahrig & Rytwinski 2009), but the degree and distance of avoidance varies with local circumstances, as shown for instance in caribou (*Rangiferta randus*) (Dyer *et al.* 2001; Nelleman *etal.* 2001; Dahle *et al.* 2007), and elk (*Cervus canadensis*) (Schultz & Bailey 1978).

Habitat heterogeneity was the third most important variable. It is unclear whether the rhinos were attracted to a wider choice of food plants in heterogeneous areas, or whether this result was an artefact of rhino movement between small patches of highly suitable habitat.

Slope was the fourth most important variable in this study area, where slopes exceeded 9° on 25% of the area and 29° on 5% of the area (Buk 2004). Slope could be much less significant in a flatter reserve. Shade was the fifth most important variable, although distance to water and rockiness (loose rocks) were almost equally important variables. In hot, arid climates with little tree cover, access to shade can be a very important requirement for maintaining a balanced heat and water budget (Eckert *et al.* 1988; Cain *et al.* 2008). When plotting rhino density against shade it appeared that only shade cover below 4% had any clear effect on habitat selection, so in rhino reserves with more tree cover shade distribution may not impact much on habitat selection. Excluding shade from the best model only reduced its performance slightly (Table 3).

Distance to water was only included in two models in 95% confidence set. 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; Western 1975). Black rhinos usually drink once every 24–48 hours, but perhaps less frequently when feeding on succulents (Mukinya 1977; Joubert & Eloff 1971) as in AFNP (Buk & Knight 2010). Equally important, nowhere in the study area was water more than 6 km away, which is within easy reach for a black rhino. Rockiness was only included in one model in the 95% confidence set. Rockiness ranged as wide as 0–61% in the study area, but in less rocky study areas this variable is probably not an important model component.

All the food, shade and rockiness variables improved in fit when original values were changed to the mean of all pixels within 500 m. The reason for this could be that it accommodates commuting between nearby highly suitable patches and the gradual change from one vegetation community to another.

A black rhino habitat suitability study in high-rainfall Liwonde National Park based on 430 GPS points yielded a linear regression model with water hole density, permanent water holes, road density, occurrence of riverine vegetation, and a crude vegetation classification all having positive regression coefficients (van der Heiden 2005). However, the positive relation with road density was thought to be incidental. Browse availability multiplied by a preference index was not a significant variable, perhaps because it included all browse species, rather than the most eaten.

## Model limitations

Habitat suitability models analyses the relative selection for various resource variables, but does not measure the absolute capacity of the area to sustain black rhino. Limitations of this model include the low number of independent rhinos in the study population, the relatively low number of rhino locations, and the lack of stratification of the model into time of day, time of year, different behaviours and demographic groups. An absolutely free distribution cannot be achieved in a fenced-in, territorial species, but the observations that about half the reserve was not used by rhinos and that there was 20–25% overlap in home range of the two adult females both indicate that the distribution was probably an acceptable proxy for habitat suitability.

The model was developed in a relatively small study area, and specific qualities of the study area such as topography and availability of food plants, shade and water affects the model. This must be kept in mind, if the model is employed to evaluate the habitat suitability of other parts of AFNP before black rhinos are reintroduced there. The model is not directly applicable to other parks, but may give an indication of some variables affecting habitat suitability, especially in arid, rocky areas. Modelling several different types of study areas would allow for useful generalizations and an understanding of important variables in each park type.

### Selection of vegetation communities and feeding areas

The riverine vegetation contained 14 times more browse than the study area on average in addition to being level, next to water, shady and almost free of rocks. Yet, the riverine vegetation is not preferred, emphasizing the importance of food quality, rather than quantity. Although the rhino sighting data showed a non-significant positive association with the riverine vegetation, this relates more to their day time use of the habitat for shade rather than feeding (Table 4). Similarly, the higher density of feeding trails than other signs in vegetation community 5.1 probably reflects this community's importance for feeding rather than general occupancy. The non-significant preference for vegetation community 8 and 9 most likely results from their location between preferred feeding habitats and drinking water. The two significantly preferred vegetation communities are the ones that scored the highest on availability of preferred foods and their equitability. Similarly, in Mun-Ya-Wana Game Reserve (800 mm rain/year) night-time browsing intensity in each vegetation type corresponded better with estimated black rhino carrying capacity than diurnal sightings did (Morgan *et al.* 2009).

Feeding rhinos selected microhabitats or feeding areas within the vegetation communities, which had a species composition higher in preferred browse species, than the vegetation community in general (Table 5). In other words, the rhinos make selections at both the vegetation community and at the feeding area or microhabitat levels in accordance with selection for preferred browse species (Buk & Knight 2010). The feeding trails also had a higher proportion of *A. karroo* and *Maytenus linearis* although these species have preference values <1. In AFNP 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. Although not documented here, it was evident that in some vegetation communities the rhinos also clearly preferred drainage lines, which have higher total plant densities.

### Home range

The average minimum convex polygon home range of two adult females in AFNP of 25 km$^2$ is similar to those noted in areas with much higher rainfall and longer growing seasons such as Ngorongoro, Tanzania (31.5 km$^2$, $n = 2$) and Mkuze on the east coast of South Africa (27.5 km$^2$) (Kiwia 1989; Huggins 1996).

## CONCLUSIONS

In a very arid park black rhino distribution was affected by preferred foods, presence of roads, vegetation heterogeneity, slope and shade. The importance of understanding what constitutes good black rhino habitat was highlighted by the observation that 50% of the study area was virtually unused by rhinos. Modelling habitat suitability in different rhino parks could provide important guidance for translocations, stocking rates and infrastructure development. The selection at both the vegetation community and feeding area levels was in accordance with the selection for the three principal and preferred browse species. Low-use gravel roads impacted negatively on habitat suitability, and this should be an issue of concern for both black rhino managers and researchers.

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