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A priori valuation of land use for the conservation of black rhinoceros (*Diceros bicornis*)

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ABSTRACT

The appropriateness of using carrying capacity (CC) estimates to indicate habitat utilisation for a particular species, and thus as a tool for conservation population planning, has been questioned. We argue individual fitness is driven by resource availability, and we therefore assume individuals select habitats with a higher quality, abundance, and availability of key resources. In the past such selection has been related to the CC of a habitat. We tested whether we can use CC estimates to indicate habitat selection by individuals using a selective forager, black rhinoceros *Diceros bicornis*, for which CC approaches underpin species conservation plans. We tested for correlation of individuals' habitat selection with predicted CC values at three spatial scales of selection. Individual selection was not related to the value of the habitat according to our CC estimates for any of the three scales we tested at. We discuss how density-dependence, environmental variables, scale of selection, individual variation and intra- and inter-specific dynamics may have influenced these results. Following this, we question the use of a priori calculations of potential resource quality and abundance of habitats (CC estimates), which do not take into account the various factors that influence an animal's selection of a habitat, as an indicator of species habitat selection. We raise caution regarding the use of such CC models to determine optimal population numbers for an area.

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1. Introduction

When managing or repopulating an area with animals, especially an endangered species, an understanding of habitat selection, habitat quality and the potential of the land, help with determining sizes of population required for optimal population growth (Bothma et al., 2004; Metzger et al., 2007) and how populations will use the space provided (Fagen, 1988; Morris, 2003b). A commonly used management approach has been to calculate a priori estimates of the carrying capacity (hereafter referred to as CC) of the land for a species, based on resource availability and quality, and to plan the future conservation management of the population on this

(Bothma et al., 2004; Hayward et al., 2007). This includes decisions about reintroduction population size, harvesting strategies, the identification of potential high utilisation habitats and a measure of future conservation success. Here we concentrate on the usefulness of CC estimates for determining the quality of habitats as a tool for identifying areas of utilisation by a species for management purposes.

Many variations of calculations, and hence definitions, of CC for herbivores have been used in the past. Due to the stochastic nature of most natural environments, the concept of CC can be unreliable, especially for a herbivore population (for a review see McLeod, 1997). In variable environments, such as African savanna, "... carrying capacity is not a

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measurement of long-term equilibrium density but of short-term potential density as a function of resource availability” (McLeod, 1997). Resource availability therefore drives individual fitness, in this case reproductive productivity, and we would assume individuals will select those habitats with a higher quality, abundance and productivity of key resources (Fretwell and Lucas, 1969; Fagen, 1988) (i.e. higher value of a habitat as indicated by the CC estimates we assign to them). However, resource utilisation may vary depending on population density (Fretwell and Lucas, 1969; Hobbs and Hanley, 1990).

The predictive power of using CCs to estimate habitat selection may differ between individual and population scales. Habitat selection is defined here as the process whereby individuals preferentially use, or occupy, a non-random set of available habitats (Morris, 2003a). At the level of individual selection, a habitat’s CC may be used as an effective indicator of selection by a species (Fagen, 1988; Hobbs and Hanley, 1990) and vice versa. At the population level there has been some discrepancy as to whether one can use CC estimates as an indicator of selection (Van Horne, 1983; Fagen, 1988; Morris, 2003b; for reviews see Hobbs and Hanley (1990), Garshelis (2000) and Chalfoun and Martin (2007)). At the population level, simplified simulation models have shown that habitat use/availability indices were not necessarily good indicators of CC, especially if there was variation in the abundance of resources across habitats (Hobbs and Hanley, 1990). However, one could relate population use/availability ratios directly to habitat values and CC, as long as ideal-free distribution is assumed for the population (Fretwell and Lucas, 1969; Fagen, 1988). This assumption, however, does not take into account the complicated social dynamics and behaviours of many species that do not follow the assumptions of ideal-free distribution, and that show signs of density-dependence (Hobbs and Hanley, 1990; Garshelis, 2000).

Simulation models that make predictions of population habitat selection often cannot take into account the potentially high individual variability within a species’ selection (Aebischer et al., 1993). It is, therefore, imperative that we test these models, because population growth is ultimately a function of individual fitness. However, due to potentially large variations in habitat selection among individuals (Aebischer et al., 1993; Osko et al., 2004), a population-based model may be a flawed approach to understanding habitat selection. Here we test empirically whether we can use habitat CC estimates to indicate habitat utilisation by individuals, using a threatened black rhino (*Diceros bicornis*) population.

The conservation plans for several African countries specify the need for the establishment of new breeding populations and increased meta-population growth rates of the critically endangered black rhino (<http://www.iucnredlist.org>; Emslie, 2001; Metzger et al., 2007), as many population’s growth rates are slowing down due to high densities of rhino (Emslie, 2001; Hall-Martin and Castley, 2003). A better understanding of the ecology and habitat selection of black rhino is required for the successful establishment of new populations, and it is for this reason that we used the black rhino as a study species.

Our aim was to establish whether we can use current a priori estimates of habitat quality, derived from CC approaches,

to predict habitat utilisation by black rhino. Our objectives were therefore (1) to determine values for habitat quality and rank habitats based on population-scale CC estimates; (2) to rank the same habitats according to selection indices by individual black rhino; and (3) to determine whether there is a discrepancy between our a priori estimates of habitat quality and the individual rhinos’ selection of habitats. We then conclude about the value of such population-level CC approaches for conservation management.

2. Materials and methods

2.1. Study site

The 180 km² Mun-ya-Wana Game Reserve (MGR) (27° 40′–27° 55′ S and 32° 12′–32° 26′ E), KwaZulu-Natal, South Africa (Fig. 1), was established in 2004 with the dropping of fences between a group of already existing game reserves. Altitude varies between a low of 4 m a.s.l on the coastal Mzinene floodplain and a high of 340 m a.s.l on the Lebombo Mountains, which run through the south-western section of the reserve (Fig. 1). The region experiences dry warm winters from April to September and hot wet summers from October to March. During the study year the rainfall in the centre of the MGR was just above the last 10 years average rainfall (841 mm versus an average of 764 mm), but was preceded by three years of below average rainfall (427 mm, 354 mm, and 698 mm). The rainfall for the year in the neighbouring Mkhuzi Game Reserve was below the yearly average (473 mm versus an average of 578 mm).

The broad vegetation types across the MGR were Maputaland Coastal Belt, Southern Lebombo Bushveld, Western Maputaland Clay Bushveld, Sand Forest and Zululand Lowveld (Mucina et al., 2005). The high variation in geological formations across the reserve (Anon., 1988) drive a corresponding high variation in the vegetation structure and 16 finer scale habitat types have been identified (Table 1) (van Rooyen and Morgan, 2007; see Electronic Supplementary material (ESM) 1 for a detailed description of the habitat types). Van Rooyen and Morgan (2007) based the classification on the woody layer, which provided a good indication of the vegetation needed to analyse a browsers’ movements and habitat utilisation.

2.2. Study species

Black rhino are locally selective browsers (Oloo et al., 1994; Muya and Oguge, 2000; Ganqa et al., 2005), yet utilise a diverse array of woody species across Africa (Kotze and Zacharias, 1993; Ganqa et al., 2005; Adcock, 2006), and are fairly solitary and sedentary in their movements. Adult bulls spend time socialising with females and on occasion with other males, while females often socialise and sub-adults may associate with females for long periods. Dominant bulls can behave territorially; this behaviour seems to vary across the continent (Goddard, 1967; Adcock, 1994; Adcock et al., 1998). In neighbouring reserves within the study region definite territories are established (Adcock, 1994; pers. obs.) and on the MGR three of the four dominant bulls tolerate sub-ordinate males in their territories.

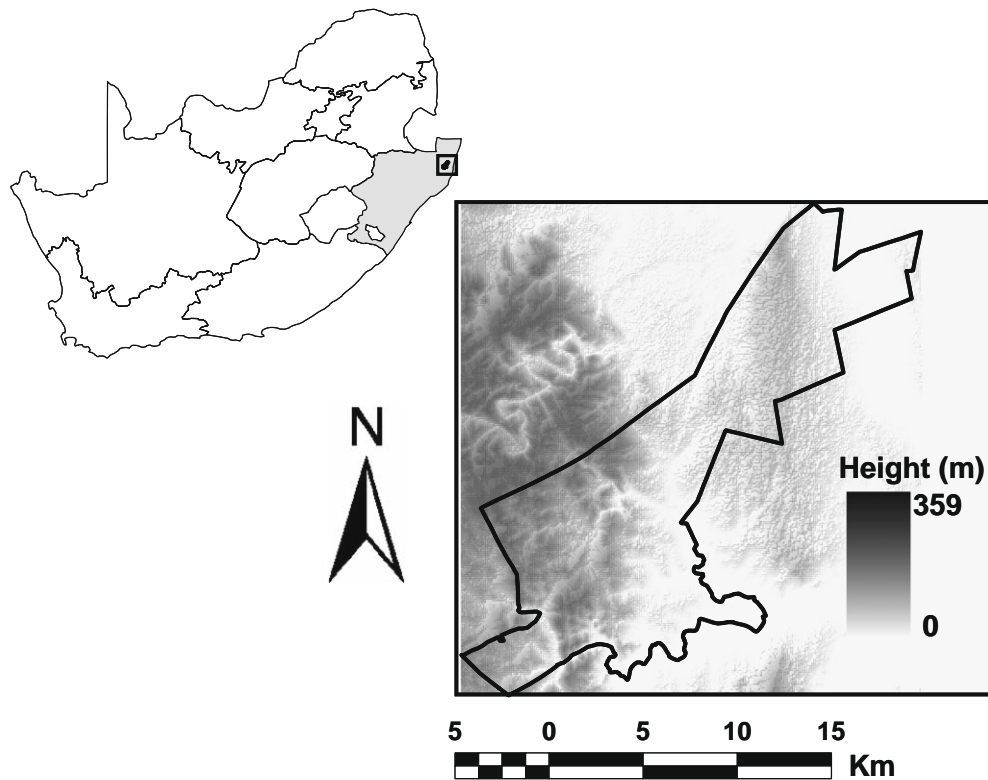


Fig. 1 – A digital elevation map of the Mun-ya-Wana Game Reserve showing its location in KwaZulu-Natal, South Africa.

Table 1 – Habitat types of the Mun-ya-Wana Game Reserve according to van Rooyen and Morgan (2007). The un-weighted carrying capacity (CC) score, according to the BrCC-Model v2_1, and its rank are shown for each habitat.

Habitat type	CC score rhino/km ² (rank)
(i) Old fields	0.590 (1)
(ii) <i>Acacia borlea</i> shrubland	0.333 (2)
(iii) <i>Ziziphus mucronata</i> bushland on slopes	0.332 (3)
(iv) Mixed <i>Acacia</i> broad-leaved shrubland and woodlands	0.262 (4)
(v) <i>Acacia luderitzii</i> thickets and woodlands	0.229 (5)
(vi) <i>Acacia tortilis</i> woodlands	0.225 (6)
(vii) <i>Terminalia sericea</i> woodland on pallid sands	0.210 (7)
(viii) Riparian woodlands and forests	0.194 (8)
(ix) <i>Spirostachys africana</i> woodlands	0.191 (9)
(x) <i>Combretum apiculatum</i> Lebombo open woodlands	0.170 (10)
(xi) Floodplain grasslands	0.164 (11)
(xii) Wetlands	0.164 (11)
(xiii) <i>Pteleopsis myrtifolia</i> closed woodlands	0.115 (13)
(xiv) Palm veld	0.110 (14)
(xv) Sand forest	0.056 (15)
(xvi) Grasslands on clay soils	0.020 (16)

See [ESM 1](#) for a detailed description of the habitat types.

Females move within an established home range, which may overlap with the ranges of one or more bulls. The size difference between the home ranges of males and females differs across the continent, with both sexes having the same size range in the Ngorongoro Crater (Goddard, 1967) while vast differences were seen in the Serengeti (Frame, 1980) and in a Kenyan sanctuary (Tatman et al., 2000). On the MGR we observed females to have smaller diurnal core ranges than those of the dominant bulls, but similar in size to sub-

ordinate males (unpublished data). We have noted that there is a significant difference between a black rhino's spatial utilisation during the day versus the night (unpublished results) and for this reason we will differentiate between the day and night movements/ranging patterns of rhino in this paper.

Our study ran from January through December 2005. During this time we located the rhinos at least once every four days with the aid of radio telemetry (see Linklater et al., 2006 for details on horn implant methods). We studied all

members of the recently introduced (October, 2004) population: seven adult females and eight adult males (four dominant and four subordinate) ($N = 15$). Due to the terrain and habitat occupied by this species, and the typically long distances from the road network to where individuals spent their time, we recorded the majority of locations on foot, using a Garmin 12 GPS (Garmin International Inc., Kansas, USA). This allowed us to approach the rhino (on average within 40 m), decreasing the error associated with triangulating GPS locations (for a review on triangulation errors see Saltz (1994)). We could expect an average GPS error reading of 10 m in a closed canopy habitat type and less than 10 m in more open habitats (Wing et al., 2005). The error of our coordinates for rhino movements, home range sizes and habitat patches is minimal and falls within the error of the GPS. We attempted to remain undetected by the rhino, recording their initial behaviour at sighting, the time of day and a GPS location, before leaving the location.

2.3. Black rhino habitat carrying capacity scores

There is a visual method for determining black rhino browse availability (Black Rhino Browse Availability Assessment v2.0; Adcock, 2004) (BAA) that is combined with a model determining the estimated black rhino CC of the land (BrCC-Model v2_1; Adcock, 2006). This model has recently been developed and, as yet, has not been used prior to black rhino introductions, but rather as a follow up procedure to monitor the land and to establish future harvesting (live-removals) of rhino.

We completed black rhino browse availability assessments (BAA) for all plants available to rhino, according to the guidelines set out by Adcock (2004). This entailed a calibrated visual assessment of the actual biomass of browse, based on the cover and volume of each plant species available to a black rhino, within a number of cylindrical plots (10 m diameter and 2 m in height) in each of the vegetation types across the reserve. Adcock (2004) tested the visual estimate technique for variability in estimates amongst researchers and for discrepancies between actual and estimated values, both of which showed an insignificant variability (Adcock, 2004), making this technique robust and easily replicated. The final score for each habitat type was the average BAA score of the plots within that habitat.

From the survey of feeding trails we completed on the Mun-ya-wana GR (see methods below) we identified and recorded all those plants browsed by black rhino. Black rhino browse is very recognizable from other browsers; as the characteristic 45° clean cut from the proximal molars gives the branch a 'pruned' look. We then established a preference list of species by calculating the frequency that rhinos browsed each species relative to the total number of browse points along all the feeding trails. We used our list in conjunction with suitability scores calculated from other black rhino populations in Southern Africa (Adcock, 2006) to identify those species non-browsed by, or deemed unsuitable for, black rhino from the BAA. We then weighted each habitat's black rhino browse availability score according to the percentage of suitable plants present for black rhino (see Adcock, 2004 for detailed methods).

We calculated the black rhino CC score for each habitat using the BrCC-Model v2_1 designed by Adcock (2006), which is based largely on the BAA scores. We deemed this model the most representative and up to date CC model available for a single species. Adcock continues to develop the model over time and has incorporated baseline data from at least 15 other reserves. The model includes numerous factors, including the quantity of suitable browse available for black rhino, monthly growth rate of plants, monthly rainfall data and each habitat's soil fertility and fire regime. So, although the analyses are done on a yearly basis, monthly variation is taken into account. These additional characteristics help with determining the quality and potential growth of the available browse to black rhino. By doing so we based the value assigned to each habitat on its quantity and quality of available resources, giving resource quantity and quality equal weights to one another.

2.4. Individual habitat selection

We imported the diurnal GPS locations of the rhino into Arcview® 3.2 (ESRI, California, USA) and established a 95% kernel home range (KHR) to indicate the greatest range extent (Worton, 1989) for each rhino, using the animal movement extension (Hooge et al., 1999). We could produce accurate home ranges as we had an average of 90 sightings (min. of 49) per individual over a 12-month period (Lent and Fike, 2003) and these locations were unaffected by autocorrelation, as they were each recorded on separate days.

Different selection processes may operate at different scales (Luck, 2002) making it important for us to test selection at various scales, which we categorise here and explain below. Thomas and Taylor (1990) identified three study designs for the design and analysis of resource selection studies, which were subsequently generalised by Manly et al. (2002) and again expanded on by Thomas and Taylor (2006). We used a variation of the design 2 study, using the proportion of habitats within each rhino's KHR relative to the available habitats, and we labelled this as the rhino's habitat selection. At a slightly finer scale we labelled the utilisation of habitats within the KHR, a design 3 study (Thomas and Taylor, 2006), as the rhino's habitat preference (Johnson, 1980; Thomas and Taylor, 2006). Finally we assessed the selection of habitats at a foraging scale, based on those areas utilised for browsing by the rhino at night, labelled as the browse-level selection of habitats.

2.4.1. Habitat selection

We established an individual's preference index for each habitat by dividing the proportion of its area in the rhino's KHR by the proportion available

$$\text{Habitat selection index} = \frac{[\text{area of habitat/total area of KHR}]}{[\text{area of habitat type available/total area available}]}$$

An index value less than one indicates selection against, a value around one indicates no selection, while a value above one indicates selection for (Manly et al., 2002). We therefore split these proportions into three categories for analyses; 0–0.75 selection against, 0.76–1.25 no selectivity and >1.25

positive selection. Design 2 studies usually use the area of the habitat types in the home range relative to the area of habitats available in the total study area (Thomas and Taylor, 2006). However, we questioned this method for two reasons, firstly the study area is arbitrarily defined and with the largest KHR of a black rhino (32 km²) on the reserve being less than 20% the size of the reserve (180 km²), it did not seem possible that the whole area was available to the rhino to include in a single home range. Secondly, there was an overlap among the KHRs of males that utilised similar areas (a single dominant male with one or two sub-ordinate males), but a lack of overlap, especially of the core 50% KHR area, among all neighbouring males. Male rhino were probably being excluded from these areas through territorial conflicts (Adcock, 1994). The females also seemed to display ‘clusters’ (*sensu* Lent and Fike, 2003), and either utilised areas similar to the clusters of males already mentioned or to other females. This sharing or utilisation of similar home range areas by black rhinos has been noted in other populations (Conway and Goodman, 1989; Tattman et al., 2000; Lent and Fike, 2003).

We therefore decided to redefine the availability of habitats for males and females within these clusters to help us understand population patterns and variation in the response of individuals to changing availabilities of habitat types (Mysterud and Ims, 1998; Osko et al., 2004). For females we considered

a minimum convex polygon (MCP) around all the black rhino KHRs whose core areas overlapped into her KHR, as available. We did the same for males, but excluded those areas that extended into a neighbouring male’s KHR (Fig. 2). This method would include areas that male and females could potentially shift their KHR to. If there was a relatively small unused area between the fence and MCP it was included in the available area for both the males and females. This variation in our assessments of available habitats for each of the rhinos across the reserve reflects actual conditions. Another option would have been to use virtual species modelling.

2.4.2. Habitat preference

We calculated a preference index for each habitat by dividing the proportion of a rhino’s locations (the diurnal sightings of the rhino) in a habitat by the proportion of the habitat available within a rhino’s KHR

Habitat preference index =

$$\frac{[\# \text{ of location habitat type} / \text{total} \# \text{ of location}]}{[\text{area of habitat type in KHR} / \text{total area of KHR}]}$$

If a habitat type was not present within a rhino’s KHR we excluded it from that individual’s analysis. We ranked the habitats in ascending order, giving the highest preference index a rank of one.

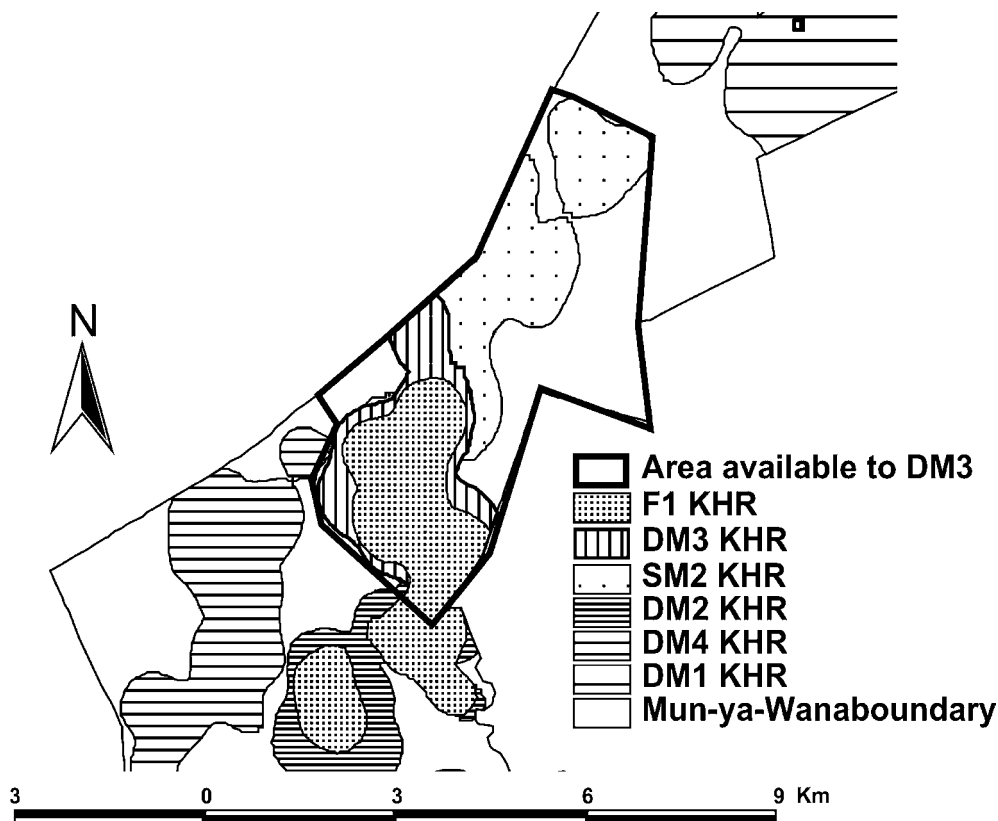


Fig. 2 – The method used to determine the area considered available for habitat selection for a black rhino in the Mun-ya-Wana Game Reserve. A minimum convex polygon was drawn around an individual black rhino’s (here DM3) kernel home range (KHR) and that of any other black rhino which had a core range overlapping into its KHR (here F1 and SM3), excluding those areas within a competing males KHR (here DM1, DM2, and DM4). We used our discretion in allocating unused areas to the availability polygon between KHR’s and the fence line. Rhino are designated by their sex class (F = female, DM = dominant male, SM = sub-ordinate male) and identity number.

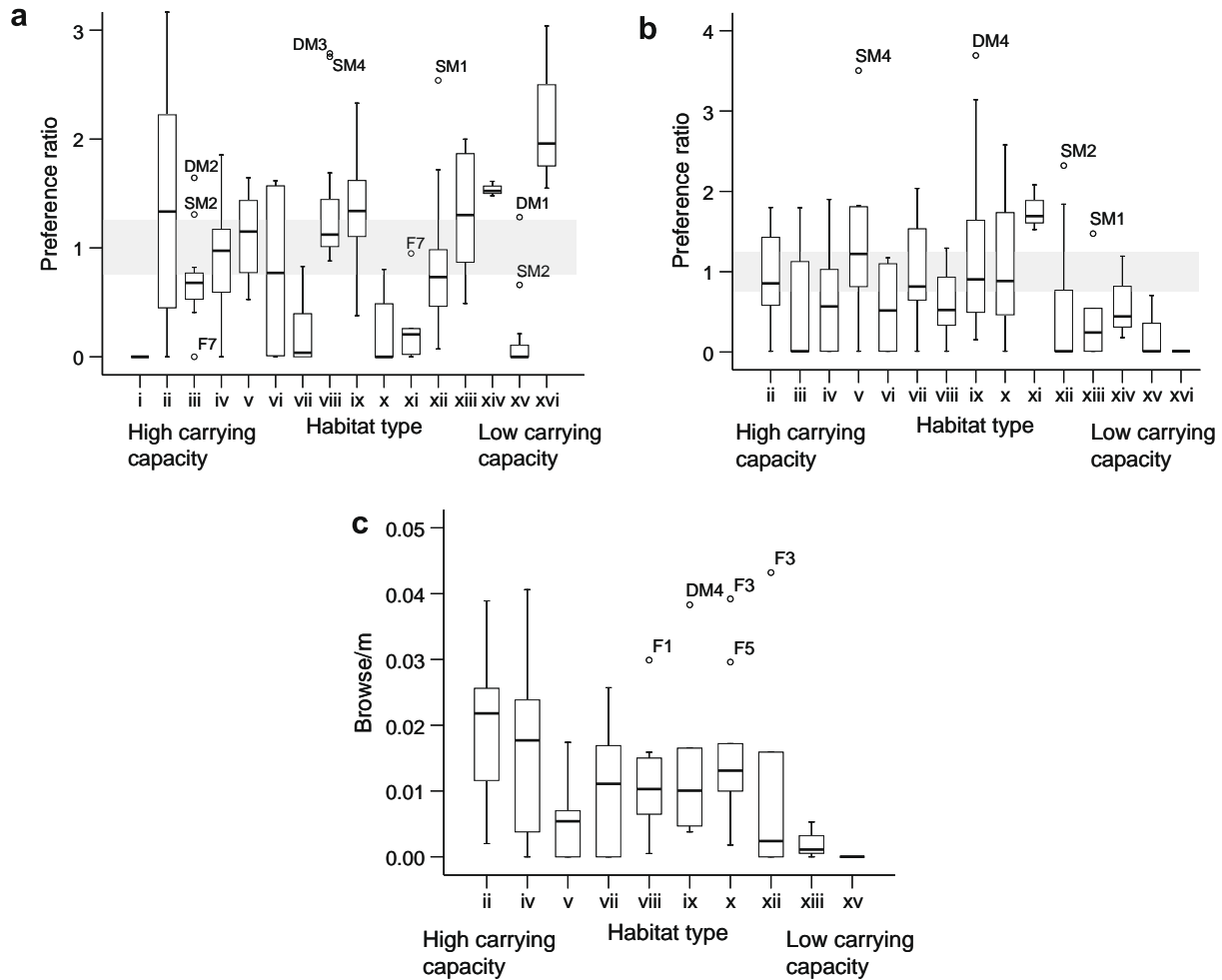


Fig. 3 – The black rhino habitat selection on Mun-ya-Wana Game Reserve. Variation in (a) habitat selection relative to habitat availability for their kernel home ranges, (b) preferences according to habitat utilisation within their kernel home ranges, and (c) their preference of habitats for browsing in at night are illustrated. In graphs (a) and (b) the three selection groups (against, none and positive) are differentiated by the shaded area. We ordered the habitat groups from the highest to lowest carrying capacity score, ranked according to the BrCC-Model v2_1, and omitted those habitats which were not available. Data are box plots: thick line within box is the median preference ratio; box represents the 25th and 75th percentiles; and the whiskers indicate the 5th and 95th percentiles. The minimum number of rhinos using each habitat type presented is three. Outliers are designated by their sex class (F = female, DM = dominant male, SM = sub-ordinate male) and identity number. In (c) we removed the extreme outliers, SM2 (Habitat v; 0.137) and F3 (Habitat ix; 0.080), from the graph.

2.4.3. Browse-level selection

We evaluated the rhino’s selection based on the browsing regime of the rhinos at night. We selected 11 individuals, which we deemed to be the easiest to track (six males and five females), and backtracked their trails, using their spoor, from a sighted location of the animal at sunrise. We attempted to complete the track to the previous evening’s sunset location of the same animal, but this proved difficult due to the terrain we were tracking on. We completed 102 backtracks, covering a total track length of over 150 km. We recorded each separate plant that the rhino browsed along the track, identified due to its greenness (an indication that it was freshly browsed) and the spoor of the rhino near the browse point. The average number of browsed plants per meter walked (br/m) in each habitat type was used as an indication of preference. We ranked the habitats in ascending order with the highest num-

ber of br/m being the most preferred habitat and given a rank of one.

2.5. Correlation between individual rhinos’ selection and habitat values

We ranked the habitats within each rhino’s KHR, in ascending order, according to its CC score; we gave the habitat with the highest CC score a rank of one. The CC scores we used were the absolute values; we did not weight them according to the area they encompassed. We ran Spearman rank correlations between the CC habitat ranks and the habitat preference ranks, at each selection level (i-iii) for each rhino. The use of null-hypothesis testing and *p*-values (Stephens et al., 2005) allowed us to determine whether the rhinos were selecting habitats in relation to the estimated carrying capac-

Table 2 – Spearman rank correlation (r_s) tests, indicating no correlation between individual black rhino habitat preferences and carrying capacity values, according to the BrCC-Model v2_1, on the Mun-ya-Wana Game Reserve, other than the two results in bold.

Rhino ^a	Habitat selection ^b			Habitat preference ^e			Plant level selection ^f		
	N ^c	r_s	P ^d	N	r_s	P ^d	N	r_s	P ^d
F1	12	0.59	0.04	8	0.62	0.10	7	0.64	0.12
F2	12	0.49	0.10	9	0.44	0.23	7	0.19	0.69
F3	9	-0.52	0.15	8	0.34	0.41	6	0.09	0.87
F4	9	-0.27	0.49	9	-0.14	0.73			
F5	12	0.20	0.52	9	0.15	0.70	7	-0.54	0.22
F6	9	-0.18	0.65	8	0.20	0.64			
F7	12	-0.14	0.67	7	0.38	0.40	5	0.00	1.00
DM1	9	-0.44	0.23	8	-0.05	0.91	8	0.40	0.32
DM2	9	0.37	0.33	9	0.25	0.51	5	0.50	0.39
DM3	11	0.55	0.08	10	0.32	0.36	10	0.66	0.04
DM4	9	0.17	0.67	9	0.07	0.86	7	-0.61	0.15
SM1	9	-0.11	0.78	7	-0.18	0.70			
SM2	11	0.30	0.37	10	0.42	0.23	10	0.59	0.07
SM3	9	-0.23	0.55	9	-0.08	0.83			
SM4	11	0.52	0.11	9	0.70	0.04	5	0.15	0.81

a F = female, DM = dominant male and SM = sub-ordinate male, the number identifies individual rhino.

b The selection of habitats within a rhino's home range relative to those available within the local cluster of ranges (see text).

c N = number of habitat types available.

d Significant $P \leq 0.05$

e The preference of habitats by a rhino relative to the available habitats within its home range.

f The selection of habitats made by a rhino for feeding in at night.

ity scores of the habitat types at any level. We used an alpha of 0.05 for all statistical analyses, which were performed using SPSS 15.0 (SPSS Inc., Illinois, USA).

3. Results

3.1. Individual habitat selection

Individual black rhino, on MGR, generally did not select habitats according to their availabilities at the three scales of selection we tested, illustrated by the range of habitat selection indices in Fig. 3a–c. They were therefore positively selecting some habitats available to them while selecting against others. There is a large amount of variation shown amongst the individuals' selection, as seen in Fig. 3. This is an interesting result beyond the scope of this manuscript's discussion and we are pursuing this in another study.

3.2. Correlation between rhino habitat ranks and CC ranks

The habitat types within individual black rhino KHR's (habitat selection) were not selected by the rhino according to their value determined by the BrCC-Model v2_1 scores (all individual correlation tests were non-significant, other than one individual (F1); Table 2). Within their KHR (habitat preference) individual black rhino did not prefer habitats with higher CC scores (all individual correlation tests were non-significant; Table 2). Black rhino did not selectively browse in those habitats with higher CC scores (all individual correlation tests were non-significant, other than one individual (DM3); Table 2).

4. Discussion

An a priori carrying capacity (CC) model, based largely on the quantity of suitable available browse, could not predict black rhino habitat selection at three different scales of selection. We would expect negative density dependent resource utilisation by black rhino, and for this low density population to prefer those habitats within their home ranges (within which we assume ideal-free habitat selection (Fretwell and Lucas, 1969)) that have abundant levels of favourable browse. Conversely, these black rhino did not rank their diurnal habitat preference according to the CC value we placed on the habitats, even at this low population density. The diurnal locations included all activities, yet when we based the rhinos' selection of habitats according to those in which they browsed in more frequently at night, when most browsing takes place (Goddard, 1967; Owen-Smith, 1988; unpublished results) and canopy cover for bedding sites is not a confounding constraint on selection (Tatman et al., 2000; Rice and Jones, 2006; pers. obs.), there was still no correlation between their selection and the estimated CC value of the habitat.

There are several potential reasons for why these rhino did not select the more productive, browseable habitats:

1. Animals base their selection of habitats on a myriad of factors (Aebischer et al., 1993; Luck, 2002; Morris, 2003b; Buk, 2004; van der Heiden, 2005; Chalfoun and Martin, 2007) and not just the availability and quality of browse. Habitat heterogeneity, slope, rockiness and the distance to water, roads and fences all play a role in habitat selection by black rhino (Buk, 2004; van der Heiden, 2005). As we have

demonstrated, using a simple predictive model which assigns value to a habitat without regard to any factors other than those relating to browse quality and abundance would be flawed.

2. Density dependence may influence plant level selection (Kausrud et al., 2006) and, hence, the selection of patches/habitats. Being selective browsers (Oloo et al., 1994; Muya and Ouge, 2000; Ganqa et al., 2005) black rhino in the Fish River Game Reserve were able to select only highly preferred plant species due to an abundance of available forage (Ganqa et al., 2005). A similar process may be occurring in the low density population of MGR. Here, individual black rhinos are selecting patches/habitats with highly preferred forage, but not necessarily with high abundances of browseable species (Ganqa et al., 2005), which is used as the base indicator of habitat quality in most CC estimates (Bothma et al., 2004; Adcock, 2006). This highlights that we cannot interchange abundance and quality of resources when predicting habitat use of a selective forager. Future research may reveal whether a sliding scale of black rhino browse utilisation based on preference and population density exists. Highly preferred browse may be negatively density-dependent and low-preference browse being positively density-dependent (as noted in domestic sheep *Ovis aries* at a diet level (Kausrud et al., 2006)).
3. Animals select habitats and resources at various scales (Johnson, 1980; Chalfoun and Martin, 2007). The scale at which we make assessments of habitat quality may not align with that of the animal's selection. In conjunction with (2) we noted a variation in habitat selection among black rhino on MGR (Fig. 3; unpublished results), which would indicate the rhino were potentially making a common selection at a finer scale than the three levels we tested. Black rhino, being selective foragers (Oloo et al., 1994; Muya and Ouge, 2000; Ganqa et al., 2005), predictions of selection would benefit from analyses at a fine scale, thereby removing the variation amongst individuals that has been noted at larger scales of selection.
4. Access to resources differs amongst individuals (Mysterud and Ims, 1998; Garshelis, 2000; Osko et al., 2004) not only at a home range level, but also within home ranges (Wittemyer et al., 2007). CC estimates of habitat quality are based on the concept of ideal-free distribution, assuming equal access to resources by all members within a population (Fretwell and Lucas, 1969). We factored this into the habitat selection level for black rhino, by assessing their selection of habitats within clusters (see Section 2). However, in a species with a dominance hierarchy, like black rhino (Frame, 1980; Adcock, 1994; pers. obs.), certain individuals could restrict access and 'hoard' resources from other cluster 'buddies'. Dominant elephant *Loxodonta africana* groups have displayed such behaviour during times of resource scarcity (Wittemyer et al., 2007). Further insight into the social dynamics within the clusters may yield interesting results in this regard.
5. Interspecific competition can play a role in habitat selection (Garshelis, 2000), not only through competition for resources, as seen in black rhino (Birkett, 2002) and African elephant (Kerley and Landman, 2006), but also by the

presence of a physically dominating species (Wasserberg et al., 2006). Social interactions between African elephant and rhino can result in conflict, in some incidences even leading to fatalities of rhino (Slotow et al., 2000). It is interesting to note there were no combined elephant and black rhino sightings during the study period, indicating black rhino were potentially avoiding areas when elephant were present. There is a relatively dense population of elephant on MGR ($\sim 0.6/\text{km}^2$; Slotow et al., 2005) that may negatively influence black rhino movement patterns and hence habitat selection. Future research into the influence of interspecific interactions and habitat selection among mega-herbivores may yield interesting results.

It is clear we would not be able to rely on the BrCC-Model v2_1 to estimate areas of utilisation by black rhino, especially in low density populations, as would be the case for all founder populations. Managers should rather rely on the use of established resource selection functions (Manly et al., 2002) or predictive distribution models (Carter et al., 2006; Elith et al., 2006; Klar et al., 2008), integrated with a species' behavioural ecology, to make accurate predictions of utilisation. Creation of such integrated decision-making tools warrants further attention.

Here we have highlighted various reasons why the habitat selection of a species cannot be predicted by a priori calculations of potential resource quality and abundance of habitats. This leads us to raise caution to the use of such CC models which aim to determine optimal population numbers for an area and yet do not take into account the various factors which influence an animal's utilisation and selection of a habitat.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2008.10.033](https://doi.org/10.1016/j.biocon.2008.10.033).

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