

Disturbance and habitat factors in a small reserve: space use by establishing black rhinoceros (*Diceros bicornis*)

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Continued persistence of black rhinoceros (*Diceros bicornis*) will likely depend on the cooperation of many reserves and the application of metapopulation models to manage across reserves. The suitability of any reserve, however, depends on factors that promote and constrain occupancy. Constraining factors, particularly human disturbance, are of concern in small reserves because constraints have potentially greater effects, relative to reserve size, than in large reserves. We investigated landscape use by black rhinos at Zululand Rhino Reserve, South Africa, as a function of elevation, slope, patch type, areas burnt and factors associated with disturbance (distances to nearest water point, human settlement, boundary fence, and roads). Estimated home ranges consistently demonstrated avoidance of human settlements, fragmentation of home ranges and sometimes multi-modal core areas. Resource selection functions confirmed that use of areas increased with greater distance from human settlements (log-odds = 1.3831 ± 0.4623 [95% CI]) and from perennial water points (2.2859 ± 0.8261). Space use was greater for thicket (1.0072 ± 0.5775) and closed savanna (0.8656 ± 0.6153) than for other patch types. Managers who plan reintroductions of black rhinos should consider availability of forage and cover, disturbances that might restrict access to resources, and effects of reserve size on those disturbances.

Key words: black rhinoceros, home range, human disturbance, resource selection.

INTRODUCTION

The black rhinoceros (*Diceros bicornis*) is classified as critically endangered by the IUCN (www.iucnredlist.org, accessed 25 June 2013). Historically, they had an extensive range over eastern, central and southern Africa, with an estimated population of 100 000 in 1960 (Emslie & Brooks 1999). They declined to 2410 by 1995 (Emslie 2008) because of habitat loss, hunting and poaching for horn (Amin *et al.* 2006; Swart & Ferguson 2009). Increased conservation efforts, including translocation to vacant reserves, resulted in an increase to 4200 individuals by 2007, with an estimated 74.3% increase in abundance in the wild over a period of 12 years (Emslie 2008). The Black Rhino Range Expansion Project (BRREP) was established in 2004 with the goal of recovering black rhino populations by repopulating vacant reserves, thus treating those reserves as patches within a metapopulation (Emslie 2004). One of the challenges in applying a metapopulation model to the conservation of any species, however, is to

identify patches that are suitable to support local populations (Thomas 1994; La Morgia *et al.* 2011).

Suitability of an area might be defined partly by environmental factors understood to be important in promoting occupancy of an area by individuals of a particular species or in constraining those promoting factors (Morrison 2001). For black rhinos, promoting factors might be the presence of landscape patches that provide browse for forage and sufficient cover (Göttert *et al.* 2010; Buk & Knight 2012). They might also require sources of free water from which to drink at particular times of day or in particular seasons (Goddard 1967; Joubert & Eloff 1971; Oloo *et al.* 1994). Recently-burnt patches might promote occupancy by stimulating regrowth of forage-producing plants (Coppedge & Shaw 1998; Parrini & Owen-Smith 2009). Individuals might occupy landscapes that allow for ease of movement and conservation of body energetic reserves, of particular importance for animals with an adult body mass of >1000 kg (Wall *et al.* 2006).

Reserve suitability might also be defined by whether environmental factors constrain the use of

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resources in otherwise high-quality habitat patches. For black rhinos constraining factors are usually sources of anthropogenic disturbance (*e.g.* lodges, residences, roads, tourism infrastructure; Mukinya 1973). Moreover, many of the reserves involved in the BRREP are relatively small (<250 km²), and as a consequence, such disturbances might more strongly affect movements, home range establishment, social structure, resource selection, and habitat use by black rhinos, than larger reserves where human presence and infrastructure is more dispersed (Goddard 1967; Mukinya 1973; Berger & Cunningham 1994). Stress caused by human disturbance, for example, is associated with high calf mortality in black rhinos in northwestern Namibia (Hearn 1999; Shaw 2002) and with breeding problems in captive Sumatran rhinos (*Dicerorhinus sumatrensis*; Foose & Strien 1998).

Some landscape features such as water points might sometimes act as promoting factors and at other times as constraining factors. Black rhinos drink from water points when they are available (Joubert & Eloff 1971; Oloo *et al.* 1994), but perennial water is common in many small reserves such that free water to drink would rarely be a limiting factor in black rhino habitat (*e.g.* Odendaal 2011; Buk & Knight 2012). In contrast, animal concentrations around water points are a tourist attraction (Owen-Smith 1996) and a potential source of anthropogenic disturbance that might constrain use of a water point or of nearby areas. Furthermore, water points might be associated with zones of poor-quality or absent resources (Parker & Witkowski 1999) if herbivore foraging has resulted in degradation of surrounding vegetation (*i.e.* a piosphere; Andrews 1988).

Responses by black rhinos to features within a reserve might also provide an indication of reserve suitability. Reserve configuration, for example, might have to consider that black rhinos range widely during the wet season, but concentrate seasonally around water sources or riparian zones where woody vegetation maintains green foliage for longer into the dry season (Goddard 1967; Joubert & Eloff 1971; Emslie & Adcock 1994; Göttert *et al.* 2010). Moreover, home-range size and configuration can provide a means to assess dispersion of resources or favourable conditions relative to the requirements, mobility, or accessibility by individuals (Nathan *et al.* 2012; Millsaugh *et al.* 2012), which are important aspects of patch suitability as habitat (Morrison 2001). For animals

released into a new environment, exploration of that environment can be expected while individuals look for favourable patches and respond to the presence of other animals in the same environment (Clark & Mangel 1984; Eliassen *et al.* 2007). As a consequence, home ranges and use areas can be expected to be fluid in size and position while individuals habituate to a new environment (Armstrong *et al.* 1997; Lent & Fike 2003; Crook 2004; Göttert *et al.* 2010). This should produce home range estimates that are larger, have more overlaps between individuals and demonstrate more high-use areas (cores, peaks or modes) on the landscape, than would be expected for a long-established population in the same area experiencing the same conditions. For example, adult males maintain home ranges that exclude each other but permit overlap with adult females and subadults (Adcock 1994; Adcock *et al.* 1998; Lent & Fike 2003); thus, the degree of overlap between individuals should be greater among females and subadult males, and between those age-sex groups and adult males, than among adult males.

Given the problem of identifying suitable reserves for black rhino reintroduction, the factors that contribute to suitability, and the potential responses of black rhinos to those factors, our objectives were (1) to investigate home range establishment and overlap following reintroduction, and (2) to estimate how natural landscape (*e.g.* vegetation, elevation) and anthropogenic features (*e.g.* settlements, roads) promoted or constrained occupancy at the Zululand Rhino Reserve (ZRR).

METHODS

Study area

The ZRR is approximately 142 km² and situated in northern Zululand, KwaZulu-Natal, South Africa (S27°42', E31°33'; Fig. 1). The climate is subtropical, with hot and humid summers, and cool dry winters. Mean annual rainfall for years 1987–2006 was 635 mm, with 534 mm falling in the wet season (October–March; Odendaal 2010). The vegetation is classified as Zululand Lowveld and is characterized by *Acacia nigrescens*, *Dichrostachys cinerea*, *Sclerocarya birrea* in open savanna, by *Acacia tortillis*, *Acacia nilotica*, *Spirostachys africanus*, *Berchemia zeyheri* in closed savanna valley bottoms and lowlands, and by *Acacia luederitzii* and *Euclea* spp. in thickets (Odendaal 2010). The range in altitude is 130–437 m. The lowest part

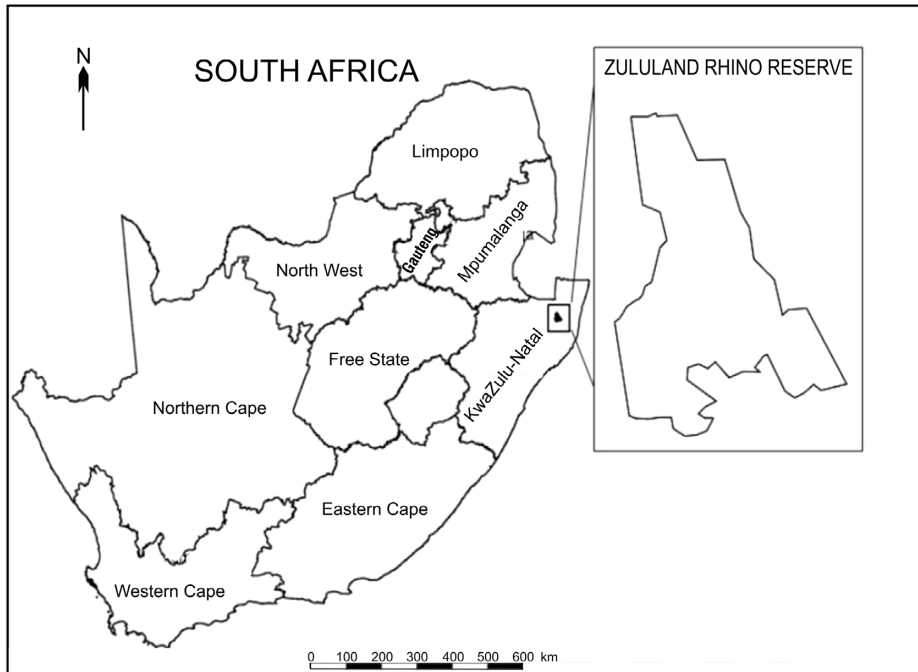


Fig. 1. Location of Zululand Rhino Reserve, KwaZulu-Natal, South Africa.

within the reserve is the Msunduze River, an ephemeral river that forms part of the southern boundary and provides surface water. There are also 52 artificial water points within the reserve, at an average density of one per 0.37 km². The largest distance to perennial water within the reserve is 3.9 km.

Data collection

This study was based on observations of 17 black rhinos (six adult females, two subadult females, five adult males, four subadult males) that originated from Ithala Game Reserve, Mkuze Game Reserve and Hluhluwe-iMfolozi Park. It is not known whether some of the individuals were related or known to other individuals prior to translocation. During capture the animals were ear-notched for field identification, and horn implant VHF transmitters (MOD-80 and MOD-125, Telonics, Mesa, Arizona, U.S.A.) were fitted into the anterior horn (Linklater *et al.* 2006). The animals were tracked by vehicle and on foot with a telemetry receiver and antenna. The rhinos were monitored visually to produce an average of four locations per rhino per month, recorded by hand-held GPS. Visual locations from January 2006 to December 2006 were used in this study. No nocturnal locations were collected.

Home range analysis

Establishment of the home range corresponds to Johnson's (1980) second-order selection. Radio-telemetry data are often auto-correlated in both space and time (Boyce 2006). We used locations with a minimum of one day between observations to reduce temporal autocorrelation. Black rhinos can move up to 25 km in one day (Vanschoenwinkel *et al.* 2011). Movements this large would allow black rhinos at ZRR to reach any part of the reserve, and so an animal's location on one day should not limit the location it could choose the following day. We estimated individual annual home ranges by using adaptive local convex hulls (LoCoH; Getz & Wilmers 2004). This method allows for use of animal locations away from the home-range periphery, to investigate high- and low-density use areas and gaps in home ranges of individuals (Elwen *et al.* 2006). It also accommodates distinct boundaries, home range fragmentation and avoidance of human disturbances, which are poorly managed by alternative methods (Getz *et al.*, 2007). We calculated 50% core and 95% home ranges for animals with 35 observations per individual (Lent & Fike, 2003). We also calculated 100% LoCoH home ranges (*i.e.*, minimum convex polygons; MCP) for comparison to other studies, and for the resource selection function (RSF)

analysis. We compared home range sizes between sex and age classes with the Mann-Whitney U-test (carried out in Microsoft Excel) because we expected that small sample sizes and non-normal distribution of data would make comparison with a parametric test inappropriate. We suspected that the small number of samples and apparent non-normality of data would make it difficult to justify the use of a parametric method to compare sample means. Therefore it was more appropriate to use a non-parametric method.

To determine the degree of home-range overlap between different sex and age classes, we estimated overlap of 95% LoCoH home ranges using $HR_{ij} = A_{ij} / A_i$, where HR_{ij} is the proportion of animal i 's home range that overlaps with animal j 's home range, A_i is the area of animal i 's home range, and A_{ij} is the area of overlap between the two animals' home ranges (Kernohan *et al.* 2001). The results were then expressed as a percentage overlap between neighbouring pairs of individuals.

Resource selection

Selection of components (*i.e.* resources) within the home range corresponds to Johnson's (1980) third-order selection. We developed a habitat model in a geographic information system (GIS; ArcGIS 9.2, Esri, Redlands, California, U.S.A.), which included layers representing factors associated with occupancy by black rhinos such as elevation, slope, patch type described as thicket, closed savanna, open savanna, rocky hills, old agricultural lands, riparian fringe, and areas burnt in 2006. Constraining factors associated with disturbance namely distances to nearest perennial water point, human settlement *i.e.* lodge, residence, camp, boundary fence, high-use district road, and low-use central road were also included in the model. We considered that water points were a constraining factor but assumed that water was not limiting in this reserve and that the larger effects on rhino distribution would be those of disturbance or piospheres. Details about sources and processing of GIS data are in Odendaal (2011).

We estimated a RSF for black rhinos with a mixed-effects logistic regression model (Manly *et al.* 2002). The binary response variable was whether a location was observed use or random use (Keating & Cherry 2004), where random use was represented by a number of random points 10 times that of the observed locations within an individual's MCP home range. Values for the explanatory variables were those associated with

each GIS layer at each observed (used) and random (available) location. We used individual identifier as the random effect (*i.e.* a random intercept model; Gillies *et al.* 2006), thus treating individual rhinos as sample units and locations as a repeated observation within an individual. Because the number of animals and the number of observations per animal were relatively small, we were unable to analyse separately by season or age–sex group.

Where necessary, continuous explanatory variables were converted to categorical variables because of problems with false convergence. This problem occurs when the fitting algorithm for the model does not converge on a maximum likelihood estimate, and it is frequently caused by large divisions in the frequency distribution of an explanatory variable (Allison 2004). Categorizing the variable overcomes this problem if the boundaries between levels are such that each level contains some of the divisions and some of the observations. Thus, we categorized the 'distance-to' variables and elevation into five levels of equal width. The number of levels was arbitrary; however, too few classes would result in the substantial loss of information and too many classes would not solve the convergence problems. As a consequence of categorizing some explanatory variables, interpretation of use or avoidance of a particular level of that variable was relative to a reference level (Godvik *et al.* 2009; Van Beest *et al.* 2010). In cases where the 95% confidence interval (CI) overlapped the reference level, we judged selection of that level to be similar to that of the reference level. If the 95% CI was above or below the reference level, we judged the animal to be using that level more or less, respectively, than the reference level.

To develop the RSF, we began with a full model containing all nine explanatory variables, plus the random effect. We did a one-at-a-time backward elimination of any variable for which there was no evidence of an effect in the model ($P > 0.05$), until all remaining explanatory variables demonstrated some evidence of an effect. This reduced model was compared to the full model with the likelihood ratio test (LRT) to establish that there was no significant difference between models in the variation explained (Ramsey & Schafer 2002). We chose this approach over information-theoretical methods (Burnham & Anderson 2002) because any of the explanatory variables or combinations thereof had a potential to explain variation in resources selection by black rhinos; under such

circumstances, backward-elimination based on P -values does no worse at choosing a model that fits the data than do information-theoretical methods based on an information criterion (Murtaugh 2009). The reduced model became the RSF that we used to interpret habitat use by black rhinos. Unless otherwise stated, 95% CIs accompany estimates throughout. We conducted RSF model-fitting and evaluation in R (R Development Core Team 2008) using the function 'lmer', in the R library 'lme4' (Bates *et al.* 2008).

RESULTS

Home range analysis

The average 95% LoCoH home range ranged between $2.69 \pm 1.59 \text{ km}^2$ for adult females and $5.43 \pm 10.76 \text{ km}^2$ for subadult females, with the average for all 17 rhinos being $3.77 \pm 0.93 \text{ km}^2$ (Table 1). The average 50% LoCoH core area ranged between $0.58 \pm 0.61 \text{ km}^2$ for subadult males and $1.35 \pm 3.53 \text{ km}^2$ for subadult females, with the overall average being $0.90 \pm 0.36 \text{ km}^2$ (Table 1). Small sample sizes, however, led to imprecise estimates and relatively wide CIs for subadult males and subadult females (2.83 ± 2.25 and $5.43 \pm 10.76 \text{ km}^2$, respectively). These estimates compared to a much larger average MCP home range of $12.30 \pm 4.87 \text{ km}^2$. The average ratio of their 50% to 95% LoCoH home range areas was $0.23 \pm 0.05 \text{ km}^2$. Despite the variation in home range sizes, we detected no differences in 95% LoCoH home range sizes between adult males and adult females, subadult males and subadult females, or all adults and all subadults (Mann-Whitney U -test, $P > 0.05$ for all comparisons).

We identified three different configurations based on fragmentation of 95% LoCoH home ranges (Fig. 2): (1) a single area with unimodal core (one

core range); (2) a home range split into spatially separate areas each with a unimodal core; and (3) a home range split into spatially separate areas with a multimodal core (more than one core range). Twelve of the 17 rhinos exhibited the first type of home range, and four rhinos had the second type. One adult male showed the third home range pattern with a multimodal home range and core area. In the cases with the multiple home ranges the gap or hole tended to coincide with a source of human disturbance (*e.g.* residence, lodge, camp; Fig. 2). In these cases, individuals initially used one range and then shifted to concurrent use of multiple home ranges and core areas. Average overlap in home range for all rhinos was 32% (range: <1–98), based on a total of 48 instances of overlapping 95% LoCoH home ranges (Table 2). The degree of overlap depended on the age-sex groups involved. For adult females, average overlap was relatively large with subadult females (61%), but somewhat smaller with adult males (31%), other adult females (22%), and with subadult males (8%; Table 2). Interestingly, the home ranges of two adult males (>10 years of age) overlapped by 1.37 km^2 (29%; 40% and 18% for each animal). Average overlap between male adults and subadults was 28% (Table 2).

Resource selection

Starting with the full resource selection function model, we reduced the number of explanatory variable from nine to six. There was no evidence that distances to central road, district road, or the boundary fence influenced space use by black rhinos (LRT = 14, d.f. = 10, $P = 0.173$). The occupancy variables that remained in the RSF were slope, elevation, patch type, and burn status (Table 3). Not surprisingly, use of areas by rhinos decreased as they became steeper (log-odds = -0.0998 ; -0.0496 , -0.1500). With the exception of

Table 1. Average home range estimates and 95% confidence intervals for establishing black rhinoceros in the Zululand Rhino Reserve, South Africa, January–December 2006, including 50% and 95% local convex hulls (LoCoH) and minimum convex polygons (MCP).

	Mean and range of the number of locations	Home range (km^2)		
		95% LoCoH	50% LoCoH	MCP
All rhinos ($n = 17$)	47 (38–54)	3.77 ± 0.93	0.90 ± 0.36	12.30 ± 4.87
Adult males ($n = 5$)	44 (38–46)	5.18 ± 1.85	1.17 ± 0.80	16.03 ± 16.17
Adult females ($n = 6$)	48 (39–54)	2.69 ± 1.59	0.73 ± 0.88	9.70 ± 5.31
Subadult males ($n = 4$)	49 (45–51)	2.83 ± 2.58	0.58 ± 0.61	11.46 ± 1.33
Subadult females ($n = 2$)	50 (50)	5.43 ± 10.76	1.35 ± 3.53	12.46 ± 5.08

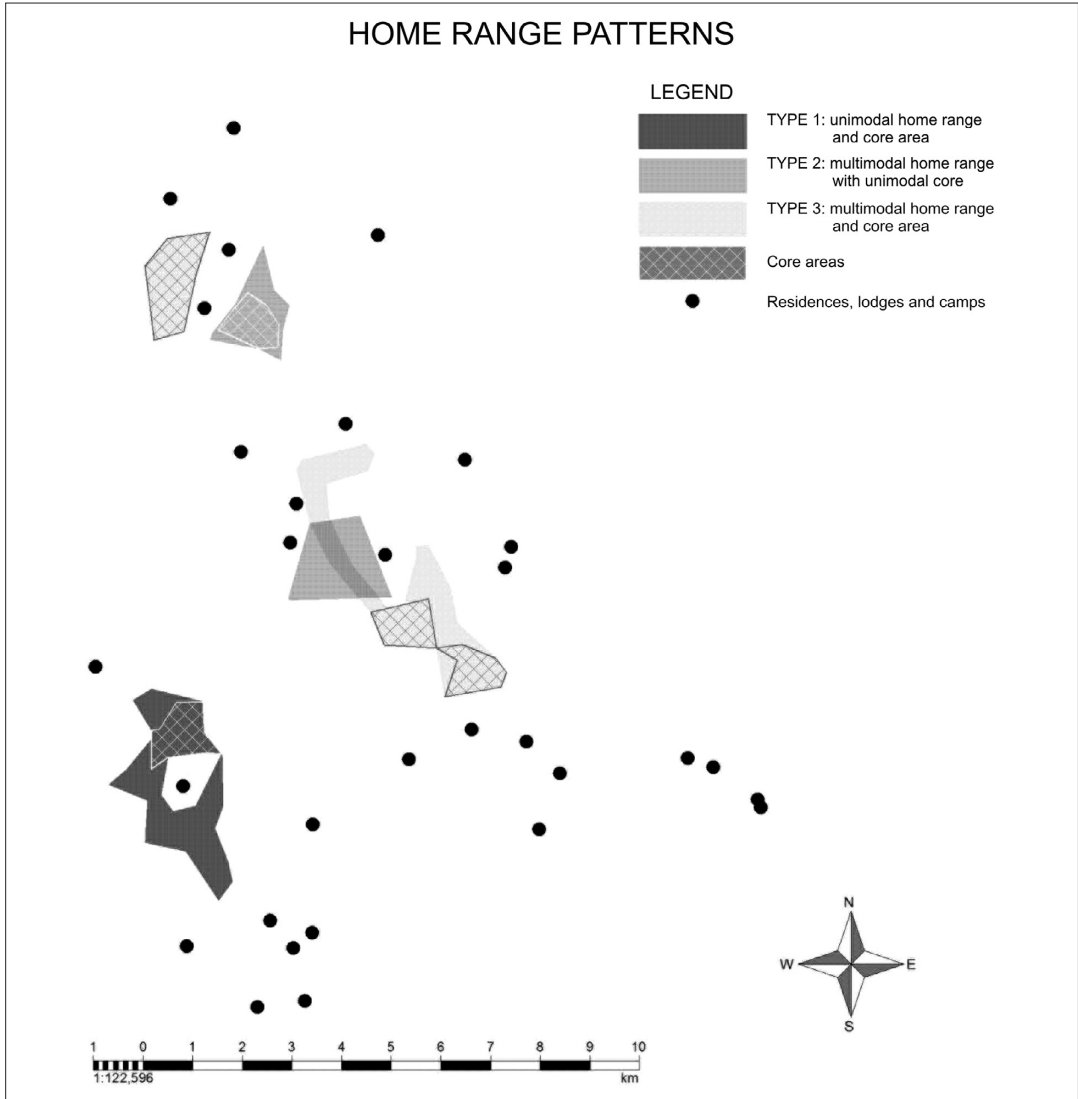


Fig. 2. Ninety-five per cent local convex hull home ranges for three black rhinoceroses, Zululand Rhino Reserve, South Africa, January–December 2006, exemplifying the three home range patterns exhibited by black rhinos in the reserve.

the 314–376 m elevation category, which was used less than other categories (log-odds = -0.7806 ; -1.4370 , -0.1241), there was no strong evidence that use of an area was influenced by elevation (Fig. 3A). Thicket (log-odds = 1.0072 ; 0.4294 , 1.5850) and closed savanna (log-odds = 0.8656 ; 0.2503 , 1.4809) were used more than the other patch types (Table 3; Fig. 3B). Moreover, black rhinos appeared to avoid areas that were burnt during the study period (log-odds = -0.6377 ; -1.1896 , -0.0859 ; Table 3).

The constraining variables that remained in the

RSF were distances to nearest perennial water point and to settlements (Table 3). For areas 1097 m away from water points, use of an area by rhinos increased with increasing distance from water points (Table 3; Fig. 3C); indeed, the difference in use increased by a factor of 2.2859 (1.4598, 3.1120) over the closest distance category. In addition, use of areas increased overall with greater distance from human settlements (Fig. 3D); use of the furthest category increased by a factor of 1.3831 (0.9209, 1.8454) over that of the closest distance category.

Table 2. Average overlap and 95% confidence intervals in 95% local convex hull home ranges between establishing black rhinoceros individuals by age and sex group, Zululand Rhino Reserve, South Africa, January–December 2006.

Sex or age group	No. overlap	Amount of overlap (%)
All rhinos	48	32 ± 8
Adult females with adult males	16	36 ± 15
Adult females with adult females	4	22 ± 40
Adult females with subadult males	8	8 ± 12
Adult females with subadult females	4	61 ± 39
Adult males with adult males	2	29 ± 47
Adult males with subadult males	4	28 ± 38

DISCUSSION

For rhinos at ZRR, occupancy factors included presence of patch types that provide browse and cover (thickets and closed savannas), but use of those areas by rhinos appeared to be affected by whether they experienced frequent disturbance by humans. These findings demonstrate an important role of factors that both support wild

animals, in terms of providing the resources and conditions that indicate a suitable environment to black rhinos, as well as factors that constrain access to those favourable resources or conditions. It is these latter factors that might have a heightened effect for rhinos that are reintroduced to areas to which they were previously extirpated.

Table 3. Resource selection function for establishing black rhinoceros at Zululand Rhino Reserve, South Africa, January–December 2006.

Explanatory Variable	Coefficient ^b	95% LCL ^a	95% UCL ^a
Intercept	-3.3513	-3.9621	-2.7404
Promoting variables			
Slope	-0.0998	-0.1500	-0.0496
Elevation [191–253]	0.1284	-0.0768	0.3335
Elevation [253–314]	0.0373	-0.2472	0.3217
Elevation [314–376]	-0.7806	-1.4370	-0.1241
Elevation [376–438]	-1.1011	-2.6375	0.4853
Patch type [Old agricultural lands]	-0.9209	-1.9780	0.1362
Patch type [Open savanna]	0.2481	-0.3409	0.8371
Patch type [Rocky hills]	0.6056	-0.0586	1.2697
Patch type [Closed savanna]	0.8656	0.2503	1.4809
Patch type [Thicket]	1.0072	0.4294	1.5850
Burnt in 2006 [Yes]	-0.6377	-1.1896	-0.0859
Constraining variables			
Distance to perennial water [548–1097]	-0.0460	-0.2332	0.1411
Distance to perennial water [1097–1645]	0.5960	0.3724	0.8196
Distance to perennial water [1645–2194]	0.8091	0.4059	1.2124
Distance to perennial water [2194–2742]	2.2859	1.4598	3.1120
Distance to human settlements [566–1132]	0.7262	0.4482	1.0042
Distance to human settlements [1132–1698]	0.6234	0.3334	0.9133
Distance to human settlements [1698–2264]	0.4909	0.1393	0.8424
Distance to human settlements [2264–2830]	1.3831	0.9209	1.8454

^aLCL = lower confidence limit; UCL = upper confidence limit.

^bFor categorical variables, the coefficients for each level represent the estimated difference in the log-odds between that level and the lowest level (*i.e.* reference class).

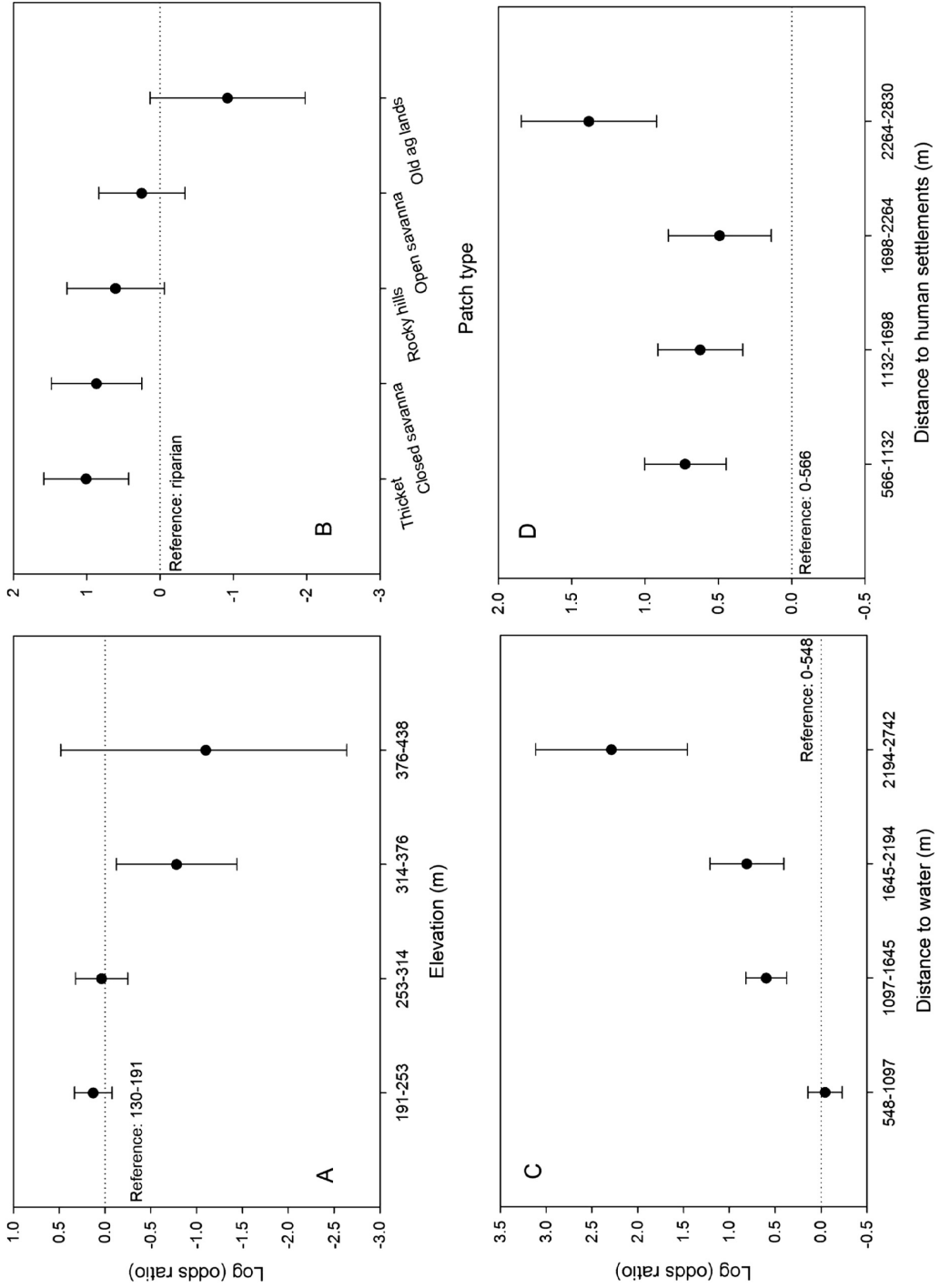


Fig. 3. Resource selection function for establishing black rhinoceros in the Zululand Rhino Reserve, South Africa, January–December 2006.

Home range

Comparison of home-range dynamics to other studies can be problematic. Although degree of establishment can be expected to affect the picture of home-range dynamics, so too can social interactions, number of intra- or interspecific competitors, habitat or resource conditions, reserve size and boundary permeability, methods of data collection, number of sightings, or methods of home-range estimation (Linklater 2010; Millsaugh *et al.* 2012). For example, Lent & Fike (2003) reported on a dataset of black rhino locations spanning 14 years at the Great Fish River Nature Reserve (440 km²), South Africa. Average home-range estimate for that study was 11.7 km² (95% MCP). Apparently, 95% adaptive kernel home ranges were also estimated, but they only appear by way of ratios between the 50% and 95% home-range areas (*e.g.* Lent & Fike 2003); based on the average ratio (0.21), the average home-range size would be 32.4 km². Based on those data the average 95% kernel home range estimate (fixed or adaptive not specified) was 23.0 km². These compare to average estimates of 12.3 km² (100% MCP) and 3.77 km² (95% LoCoh) for ZRR rhinos, based on one year of observations. Similar comparisons are possible for core home ranges, but with the same limitations. We observed an average 50% LoCoH home range of 0.9 km², compared to the 6.8 km² for the Great Fish River Nature Reserve (50% adaptive kernel; Lent & Fike 2003). In comparison, Tatman *et al.* (2000) reported a mean of 7.7 km² in home-range sizes (for both 100% MCP and harmonic mean 95 % isopleth) for black rhinos at Sweetwater Rhino Sanctuary (93 km²), Kenya, but they based their estimates on one 3-month period of observation.

Thus, the numbers are available to permit comparisons among black rhino studies, but differences in areas and methods as well as the accuracy of home range estimates which are affected by few locations, disjointed observations and detection bias (Linklater 2010) likely preclude useful conclusions about the degree to which home ranges reflect the settlement of translocated individuals. Estimates from kernel-based methods, for example, are strongly influenced by choice of smoothing or bandwidth parameter, and they use fundamentally different algorithms to linkage or cluster-based methods (MCP, LoCoH) to estimate utilization distributions (Millsaugh *et al.* 2012). Relatively small home range estimates at ZRR might also reflect differences in estimation methods;

kernel methods smooth across holes, corners, and sharp boundaries, depending on the smoothing parameter used for the method (Getz *et al.* 2007), which might result in a larger estimate of home range size.

Configuration of the home range and overlaps between individuals should provide further indications of the degree to which individuals are habituating to a new environment and locating favourable patches on the landscape. Gaps in the home ranges of ZRR rhinos appeared to coincide with human dwelling and other sources of human disturbance. Because ZRR was recently formed from lands of 15 different landowners, land use before the conservancy formed likely resulted in higher levels of human disturbance than protected areas without such recent land use change (*e.g.* Great Fish River Nature Reserve). That disturbance, primarily in the form of permanent human settlements, might have contributed to discontinuities in home ranges and core areas.

Degree of home-range overlap between individual black rhinos varies according to the age and sex of neighbouring individuals (Adcock *et al.* 1998; Lent & Fike 2003). Based on established populations, we expected that home ranges of adult males would overlap little with each other, but that their home ranges would overlap more with those of adult females and subadults; plus, there would be more overlap among females and subadults (Adcock 1994; Adcock *et al.* 1998; Lent & Fike 2003). With establishment of home ranges and reduction in exploratory movements, mutually exclusive home ranges for adult males, and clusters (*i.e.* predictable associations of 2 individuals; Lent & Fike 2003) containing other age–sex groups, might be expected to emerge. By the end of our study, there was one cluster of four rhinos (adult female, subadult male and females) that shared 10.5 km². The range of home-range overlaps for ZRR black rhinos was <1–98%. Lowest mean overlap was between adult females and subadult males (8%), but this was likely influenced by the greater presence of adult males in female home ranges (36% overlap). By comparison, a group of seven black rhinos at Ndumo Reserve, South Africa, shared 4.3 km², and the range in overlaps was 12.4–79.5% (Conway & Goodman 1989).

Home ranges of adult males generally do not overlap (Kes Hillman-Smith & Groves 1994; Tatman *et al.* 2000; Lent & Fike 2003), and core areas are more strongly defended than the broader home range (Adcock 1994). Contrary to

this general pattern, however, home ranges of two adult males (>10 years) at ZRR overlapped by 1.37 km² (40% and 18% for each animal), but their core areas did not overlap. Overlaps between adult and subadult males can be more common (Adcock 1994; Kes Hillman-Smith & Groves 1994). For example, the core area of one adult male rhino overlapped with that of a subadult male by 0.46 km² (c. 50% of the core area for each animal). The results from this study show similar overlaps in comparison to other studies with the exception of the higher overlaps between males. Such patterns would be consistent for animals that had not become fully established in a new environment and were still exhibiting large exploratory movements (Armstrong *et al.* 1997; Lent & Fike 2003; Crook 2004; Göttert *et al.* 2010).

Resource selection

Wildlife managers commonly assess selection based on patch categorization of the landscape (Goddard 1967; Tatman *et al.* 2000; Reid *et al.* 2007) or availability of key resources using estimates of browse species and abundance (Kotze & Zacharias 1993; Ganqa *et al.* 2005; Buk & Knight 2010). More recent efforts have attempted to quantify resources and conditions explicitly (*e.g.* Buk & Knight 2012), an approach consistent with estimating the important niche dimensions for an animal (Morrison 2001). Our analysis follows this final approach.

Promoting factors

Black rhinos at ZRR tended to use areas that were relatively flat. Areas with slopes 30° are considered inaccessible to black rhinos (Adcock 2001), and steep slopes can affect accessibility and use of areas containing browse (*e.g.* Ithala Game Reserve, South Africa; Kotze & Zacharias 1993). Although the evidence was not compelling, black rhinos also appeared to prefer areas of altitude <314 m. Given their large body size and the energetic expenditure of moving through topographically challenging environments, adherence to environments that facilitate movement was to be expected. Moreover, degree of fine-scale rockiness in ZRR, although not considered explicitly in this analysis, increases with elevation and is greatest in areas >300 m elevation (K. Odendaal-Holmes, pers. obs.). This rockiness might have affected accessibility at higher elevations (Buk & Knight 2012; van der Heiden 2005).

Black rhinos at ZRR were associated more with

thicket and closed savanna than with the other patch types. Patch selection, in general, is driven by availability of forage and cover (Mukinya 1973; Reid *et al.* 2007). Forage species such as *Acacia* spp. (Adcock 2001; Buk & Knight 2012; Ganqa *et al.* 2005), *Spirostachys africana*, *Dicrostachys cinerea* (Adcock 2001), *Euphorbia* spp. (Adcock 2001; Buk & Knight 2012; Ganqa *et al.* 2005) and *Maytenus senegalensis* (Muya & Oguge 2000; Adcock 2001) are common at ZRR (Odendaal 2011). Thicket patches at ZRR are dominated by *Euclea* spp., and they are commonly used as shelter by females with calves. *Euclea* spp. are considered less palatable than other browse plants (Adcock 2001), but thickets also contain palatable species such as *Acacia* spp., *Ziziphus mucronata* and *Spirostachys africana* (Odendaal 2011). Deciduous acacias (*e.g.* *A. nilotica*, *A. karroo*) are important forage species for black rhinos at Ithala Game Reserve (Kotze & Zacharias 1993) and other deciduous species (*e.g.* *Spirostachys africana*) are important at Hluhluwe-iMfolozi Park (Emslie & Brooks 1999). *Euclea* spp. is also common within black rhino home ranges at the Sweetwaters Rhinoceros Sanctuary, and more common than grassland and *Acacia* spp. patches (Tatman *et al.* 2000). A shortcoming of our study was a reliance on patch categorizations to infer forage availability; a more robust analysis would have involved measures of browse to estimate forage abundance directly (*e.g.* biomass estimates from canopy volume; Smit 1996).

Burnt areas are commonly used by many large herbivore species (Coppedge & Shaw 1998; Biondini *et al.* 1999; Shrader *et al.* 2006; Parrini & Owen-Smith 2009) because of forage regrowth stimulated by fire. Rhinos at ZRR, however, appeared to use areas with recent burns less than other areas in the reserve, a pattern inconsistent with the prediction that they would preferentially use areas likely to have an abundance of charcoal. Two blocks with a total area of 8.2 km² (5.7% of the study area) in the southern part of the reserve burnt in August 2006 and thus were only available to rhinos for the last four months of the study period.

Constraining factors

Use of areas by black rhinos increased with distance from water points, with greatest use occurring for areas 2194–2742 m away. Given the abundance of water points at ZRR, water is unlikely to be in short supply. Avoidance, however,

could be related to habitat conditions near water points. Point resources such as a water source focus use by many herbivore species near perennial water (Parker & Witkowski 1999) and might lead to degradation of nearby forage and reduced browse availability for black rhinos. We found that areas <1097 m from water were used less than other distance categories. Such avoidance might be the consequence of piospheres or of humans in search of wildlife for tourism purposes.

Sources of human disturbance played a large role in affecting locations of black rhinos at ZRR. Rhinos avoided areas close to human settlements; however, there was no evidence that roads or the boundary fence had an effect on habitat use. Absence of human disturbances is considered important for patch suitability for black rhinos (Goddard 1967; Mukinya 1973; Conway & Goodman 1989; Tatman, *et al.* 2000; Buk & Knight 2012). In northwestern Namibia, for example, human-caused disturbances were linked to high calf mortality (Hearn 1999; Shaw 2002).

In applying a metapopulation model to the range expansion of the black rhinoceros, a critical part of recognizing the suitability of potential patches for local populations will continue to be, whether a reserve contains sufficient forage and cover to support a viable number of individuals. Just as important, however, will be recognition of factors that might prevent use of otherwise favourable patches. It is this latter problem that might limit the suitability of many reserves, particularly small ones, to contribute to the expansion of black rhinoceros range in southern Africa.

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