

JOURNAL 48
 Namibia Wissenschaftliche Gesellschaft / Namibia Scientific Society
 Windhoek, Namibia 2000
 ISSN: 1018 - 7677

THE BLACK RHINOCEROS OF NORTH-WESTERN NAMIBIA (*Diceros bicornis bicornis*): THE ROLE OF DENSITY- DEPENDENCE AND ITS MANAGEMENT IMPLICATIONS.

HEARN, M.E.*, LOUITIT, B.D. AND URI-KHOB, S.

Save the Rhino Trust, P O Box 224, Swakopmund / Namibia, e-mail: srtrhino@iafrica.com.na

ABSTRACT

This paper is adapted from a study done on the black rhinoceros (*Diceros bicornis bicornis*) in the Republic of Namibia, submitted in partial fulfilment of the degree of M.Sc. in Conservation Biology at the University of Kent, Canterbury. The full report is available under the title "Factors Limiting Fecundity and Movement Patterns of The Black Rhinoceros (*Diceros bicornis*) in Kunene Region, Namibia." This gives more detail on the background to the study, the particular characteristics of each of the three study sites and greater detail on the methodology and results of the study. These rhino inhabit the arid rangelands of north-western Namibia (mean rainfall <150mm per year) occurring on communal land boarding the Skeleton Coast Park.

The range patterns of females in three sub-populations of the black rhinoceros were studied in Kunene and Erongo Region to determine the factors limiting spatial movement and fecundity. The population's growth rate across its entire range is estimated at 2% per annum for the last six years, and density is only 0.01 km². Study sites were chosen to reflect the differing and contrasting geology of the range area. The three sites had similar rainfall patterns and variable breeding performance.

Using a geographic information system (GIS), seasonal availability of surface water and landform properties were assigned to each study site. Three habitats were determined from the GIS; slopes, plains, and riverine. The abundance, composition and condition of the perennial woody vegetation was measured in the three habitats across all three sites using a plotless sampling strategy, point centre quarter (PCQ). Using sightings data collected over twenty years the range area and individual home ranges of females in the study sites were plotted and size calculated using minimum convex polygon.

In all three study sites the densest perennial woody vegetation occurred in the riverine habitat. The proportion of preferred perennial woody species, making up the bulk of the rhinoceros diet, was highest in the slopes habitat for the study site with the lowest mean distance to perennial and annual

surface water (Kruskal Wallis, $\chi^2 = 8.708$, $df = 2$, $P = 0.013$). Individual female home range varied across the two focal study sites (Students t-test, $t = 10.346$, $df = 5$, $P = 0.000$: Central study site range 94.37 km² to 114.52 km² (mean = 104 ± 5.8544 km²; $n = 3$), Southern study site range 340.03 km² to 441.20 km² (mean = 385 ± 22.64 km²; $n = 4$)). The smallest home range was recorded for the site with the highest density of female rhinos, best breeding performance and highest proportion of preferred perennial woody species occurring in the slopes habitat. Home range size was found to be positively related to the proportion of slopes habitat occurring in the individual home ranges of females. This suggested that fecundity is limited by the availability of surface water and food resources, which in turn is limited by the variable geology occurring across the three study sites.

This report discusses the findings of the study in the context of the development of conservancies in the communal areas of Kunene and Erongo Region, as part of the Ministry of Environment and Tourism's implementation of Community Based Natural Resource Management (CBNRM). Through this process appropriate management options, that are explored both socially and environmentally, can secure the aims of black rhino conservation, alongside the desires for economic development and self-empowerment of farmers in western Kunene and Erongo Region.

INTRODUCTION

The black rhinoceros (*Diceros bicornis*) of Africa is characterised by large body size and low fecundity, typical of k-selected species, where equilibrium density or carrying capacity will be attained by the population (MacArthur and Wilson, 1967). Long gestation periods for the black rhino stretch the critical periods influencing offspring survival across different periods of the year, so no strong selective pressures favour any particular time for reproduction (Hitchins and Anderson, 1983). Although this makes the species extremely susceptible to over-hunting, characteristics such as late age of first breeding and age-dependent fecundity have also allowed populations of the black rhinoceros to recover from near extinction when successful conservation measures have been implemented.

The desert-dwelling black rhinoceros (*Diceros bicornis bicornis*) of north-western Namibia is one such population. Land tenure is communal and the development of a community-based conservation approach in the early 1980's (Loutit and Owen-Smith, 1989; Owen-Smith, 1996) was balanced by intensive field operations and strong law enforcement carried out by both Ministry and non-governmental organisations (MET, 1997). Intensive monitoring of the population is now co-ordinated by the NGO Save the Rhino Trust (SRT). As the most accurate method of counting rhinos is by individual recognition (Leader-Williams, 1988), SRT operates five teams using vehicles, and in the more mountainous areas camels, to carry out daily monitoring patrols across the range area. These are supplemented by game guard patrols in two of the eight management zones in the newly registered Torra Conservancy, and in the other areas, by patrols from game guards operating through Integrated Rural Development and Nature Conservation (IRDNC) and rangers from the Ministry of Environment and Tourism. A complete census is carried out every five years. This has enabled the collection of valuable data on numbers, movement patterns and breeding performance for more than twenty years.

Studies indicate that the onset and timing of reproduction in the black rhinoceros is a response to the prevailing ecological circumstances. However, only a small proportion of the available browse species and biomass makes up their diet, with the highest densities of black rhinos occurring in scrub-bush and open woodland habitats (Goddard 1968, 1970; Hitchins, 1969; Schenkel and Schenkel-Hulliger, 1969; Joubert and Eloff 1971; Mukinya, 1973, 1977; Frame, 1980; Loutit *et. al.*, 1987; Brett *et. al.*, 1989; Kiwia, 1989a; Oloo *et. al.*, 1993; Emslie and Adcock, 1994). Variations in the home range size of female black rhino appear to be related to food and water requirements (Klingel and Klingel, 1966; Goddard, 1967b; Hitchins, 1969; Frame, 1980; Kiwia, 1989b; Emslie and Adcock, 1994; Conway and Goodman, 1989), with male home range being further governed by social pressures (Owen-Smith, 1992; Adcock, 1994).

In more arid rangelands, such as those seen in north-western Namibia, climatic conditions, elevation, substrate and drainage have a direct effect on height, canopy cover and the composition of woody species (Coughenour and Ellis, 1993). Because breeding is only achieved when females reach 80% of their mature body weight (Georgiades, 1985), in the case of desert-dwelling black rhino, environmental stochasticity would be expected to be the determining factor in the demography, reproductive success and size of home range.

In large bodied mammals with differing life history, population crashes often provide the best way of distinguishing density-dependent cycles from the effects of environmental stochasticity (Clutton-Brook *et. al.*, 1997). Evidence points to sexual maturity among females being the first demographic variable to respond to resource limitation (Fowler, 1987; Owen-Smith, 1990; Langvatin *et. al.*, 1996). Recent studies on other wild ungulate populations have placed further emphasis on the role of density-independence in determining reproduction in mammals. However, little consistency exists between or within species, and we generally have a poor understanding of the direct and indirect impact environmental stochasticity has on population demography and reproduction in large bodied mammals (Langvatin *et. al.*, 1996).

Wildlife management in the communal areas of Namibia has taken a radical change from more "traditional" approaches seen in the past. Ministry of Environment and Tourism policy changes in 1995 sought to give communal farmers similar rights to those of commercial farmers over some wildlife resources as part of a national programme of Community-Based Natural Resource Management (CBNRM) (MET, 1995a and b). Legislative changes, adopted through the Nature Conservation Amendment Act 1996 (Act 5 of 1996), devolve conditional rights over specific wildlife resources and tourism to a community institute, called a conservancy (Blackie, 1999; Blackie and Tarr, 1999). As part of this programme, eight conservancies are proposed, or have been registered, bordering or within the current range area. To realize the goal of sustainable natural resource management and the successful implementation of land use plans currently being drawn up by these conservancies, data on the dynamics of the black rhino population and how the rhino is reacting to its environment in relation to available resources, are urgently required. Hence, the study looked at the factors limiting movement patterns and breeding performance within the current range area of the black rhinoceros in north-western Namibia, in relation to differences in the ecology and habitats.

Aims and objectives

- * Determine the availability of food and water resources in three sub-populations, defined on the basis of variable breeding performance, discrete ranges, differing geology and similar annual rainfall.
- * Relate landform and availability of resources to differences in ranging patterns and reproduction parameters of females in the three sub-populations with a Geographic Information System (GIS).

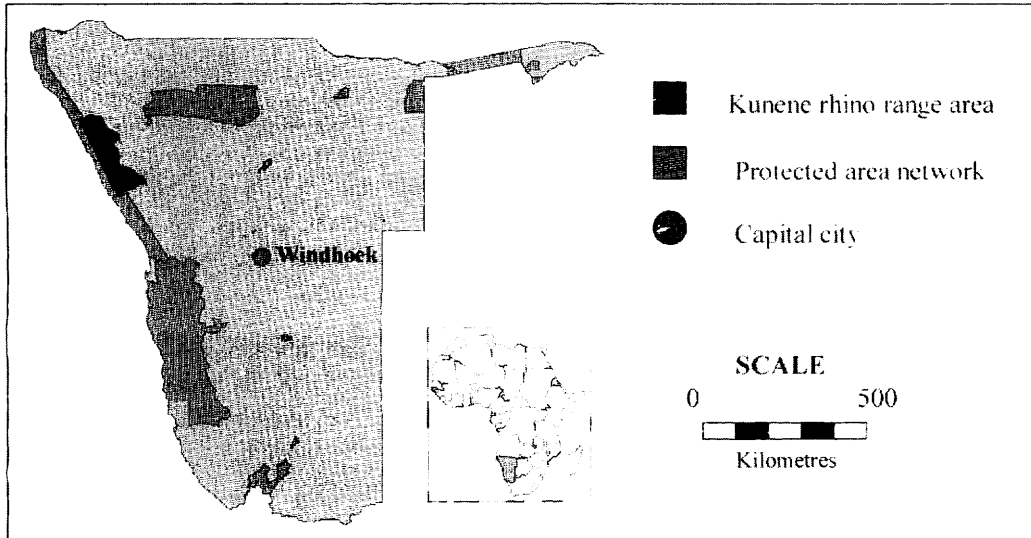


Figure 1. Map of Namibia showing the Kunene rhino range area in relation to the current protected area network. The insert shows Namibia's position on the African continent.

STUDY AREA

The study was carried out in north-western Namibia, namely Kunene and Erongo Region (between 12° 00' and 14° 45' E/18° 45' and 22° 40' S), where the largest population of black rhinos still occurring on communal land are found (Brett, 1997) (Figure 1). The climate is arid with an east-west rainfall gradient ranging from 150mm to 30mm. The area has three defined seasons: the wet season (March to May); the cold dry season (June to August); and the hot dry season (September to February) (Viljoen, 1989b). There is a high inter-seasonal variability in rainfall that in turn accounts for the nomadic behaviour of people, livestock and wildlife in this area (Sullivan, in press). Temperature in the region is similarly variable, ranging from below zero to above 40°C.

In the central parts of the study area, topography consists of a prominent high, volcanic plateau region of flat-topped mountains (Etendeka Group) with steep pediment slopes. In the far north and south, steep slopes are dominated by shists and marble lying in westward-vergent folds and faults. Various other aeolian sandstone formations, volcanic deposits and the Post-Karoo igneous Doros Complex

are dispersed across the southern part of the study area. The southern limit is marked by The Brandberg massif, dominated by granite, with Königstein peak (2573m) forming the highest mountain in Namibia (Diehl, 1990; Swart, 1992). To the west, gently undulating rocky and granite plains, with isolated rock outcrops finally give way to the shifting dunes of the coastal desert.

Drainage is good from areas where rainfall is in the region of 400mm per annum through well defined east-west running ephemeral rivers. Sediment and organic matter are transported westwards from the upper catchments and are laid down to form the deepest soils as the floods subside (Abrams *et al.*, 1997). These alluvial river deposits act as a reservoir for groundwater and support the bulk of the woody vegetation in an area where soil development is generally minimal due to the slow rate of weathering and the impermeable nature of the rock type (Simmonds and Forbs-Irving, 1994).

The area falls in one of three floristic regions partly represented in Namibia, namely the Karoo-Namib regional centre of endemism (Maggs *et al.*, 1998). The study area is further recognised as the Kaokoveld centre of plant diversity within this region and is classified as comprising predominantly “mopane” savannah (Giess, 1971). From east to west along the climatic gradient the dominant vegetation and growth form goes from: *Commiphora spp.*, *Colophospermum mopane* and *Euphorbia damarana* shrubland, and dwarf shrubland to *Calicorema capitata* with *Commiphora spp.* and dwarf shrubland, culminating in the exposed unvegetated plains where succulent species and dwarf shrubs are isolated in drainage lines.

Though the population of Kunene Region stands at 64,017, representing 4.5% of the total Namibian population (UNDP, 1997), most are centred around the major towns or more fertile lands to the east of the study area. Less than 10% live directly next to the eastern border of the range area where subsistence farmers utilise man-made and natural water points. Here a wide variety of wildlife species range freely amongst farming settlements, including predators and elephants.

The economy of the Herero and Damara who dominate the area is mainly confined to semi-nomadic pastoralism or sedentary agriculture, although people’s sources of income/subsistence are extremely diverse. These include: pensions, waged employment with government services, wealthier farmers and the increasing number of tourism ventures in the area and selling products of local industry such as beer and handicrafts (Sullivan, in press).

Choice of intensive study site

Eight rhino management areas have been outlined based on habitat and topography, to allow appropriate grouping for density estimates (Brett, 1997). Three geographically separate areas were chosen as sites for this study, based on the following criteria:

- * Different and contrasting geological characteristics;
- * Similar rainfall patterns, i.e. all falling on the 50mm annual rainfall isohyet;
- * Varying breeding performance in black rhino sub-populations.

The three sites were: the Hoanib/Purros area (northern site: between 12° 30' and 14° 00' E/18° 45' and 19° 35' S), the Axab/Uniab area (central site: between 13° 20' and 14° 00' E/19° 55' and 20° 25' S), and the Doros area (southern site: between 13° 35' and 14° 40' E/20° 28' and 21° 15' S). The choice of these three sites enabled hypotheses on factors determining reproductive performance to be tested without confounding variables of rainfall.

METHODS

Landform classification using a GIS

Two GIS computer software packages, Idrisi version 2.010 (Clark Laboratory Ltd.) and ArcView version 3.0 (ESRI) were used to analyse the attributes of data falling within the home ranges of individual females. These use vector, where information is portrayed as points, lines and polygons; and raster systems, where information is grid-based or pixel-based to capture, store, update, analyse and display all forms of data that are recorded according to geographic location (Johnston, 1998).

For each of the three study sites, habitats were broadly defined as slopes, plains or riverine, following classification of forage habitats in studies on the desert-dwelling elephants (Viljoen, 1989a). This also proves a more suitable form of classification when applied to desert ecosystems (Walter, 1986). Use of the GIS digital data for the rivers, derived from 1:250 000 scale maps of the area held by the Surveyor General, allowed the measurement of riverine habitat. The measurement of slopes and plains habitat was obtained by importing data from a Global Positioning System (GPS) unit where landform properties had been classified at randomised sample plots. This data was then imported into a slope map created from a 1km resolution digital elevation map (DEM) (Figure 2), available from the Eros Data Centre at <http://edcwww.cr.usgs.gov/landdaac/gtopo30/gtopo30.html>.



Figure 2: *Digital Elevation Map of the study area, with the Brandberg in the bottom right corner.*

Cluster analysis of the data, using SPSS version 8.0 for Windows, gave the cut-off between slopes and plains habitats. Sample plots were randomised at five kilometre intervals outside rivers and stratified at 1,3,5,10 and 15 kilometre intervals from focal waterpoints in the riverine habitat. Data for all the water points collected during the last census (Reuter, 1999) was imported into the GIS to calculate the mean distance from permanent and temporary water in each study site.

Vegetation study

At each sample plot a transect was run away from the nearest waterpoint and, using the point-centred quarter (PCQ) method (Mueller-Dembois & Ellenberg, 1974) species contributions to total perennial woody canopy cover in each habitat were calculated from measurements of plant density and mean crown diameters. The results were compared across the study sites in terms of differences in density and plant composition per habitat type using a Kruskal Wallis ANOVA. The condition of available browse across the habitats with perennial woody vegetation was assessed according to the utilisation by all browsers, following Du Plessis and Sannier (in press). This was used as an indication of the condition of available browse. All utilisation, where no regrowth had yet occurred, was taken into account. The results were compared across the study sites in terms of differences in condition per habitat type using a two-way ANOVA.

Home range and distribution area

The area covered by males is greatly influenced by prospective mates, as well as by access to resources (Adcock, 1994). Therefore, only the home range of female rhinos was measured to gauge the quality, quantity and distribution of food and water and how this might influence breeding performance. The location of known female rhinoceros sightings in the three study sites was either pin-pointed on a 1:250 000 scale map from records collected from 1982, then digitised, or plotted using GPS data from more recent sightings. Ten locations were considered the minimum necessary to measure accurately an individual home range (Conway and Goodman, 1989). For the purposes of this study the distribution area for each study site was measured by plotting the peripheral points of all females of breeding age. In Arcview, using minimum convex polygon (Schoener, 1981), the home range of individual females was calculated.

Due to the small sample of sightings per rhino, or rhino *per se*, in the northern study site, fewer than ten, it was not possible to compare the home ranges between all three sites. Therefore analysis of home range and the proportion of each forage habitat within each home range was only carried out between the central and southern study sites. To test for any difference in home range size between study sites, using SPSS version 8.0 for Windows, a Students t-test was carried out. To explore the relationship between home range size and availability of resources within the home ranges, stepwise multiple regression was carried out on the proportion of the three habitats occurring in each female's home range and the number of sightings.

Population characteristics

The study used sightings data collected in Kunene and Erongo Region over the past twenty years and stored by SRT in a Microsoft Access database, adapted by Brett (1997) from the Etosha black rhino database. Depending on the visibility, the identities of individual rhinoceros were confirmed from sex, horn size and shape, notches and marks on the margins of the pinnae of the ears (Goddard, 1967a; Mukinya, 1976; Brett *et. al.*, 1989, Kiwia, 1989a). Photographs are taken, identification forms are filled in and a GPS unit used for positional data at each sighting.

Using updated records from the census in 1998/99 (Reuter, 1999) the structure of each sub-population was determined using age classes after Hitchins (1970). Condition scores were also given to each rhino sighted during the census using criteria outlined in a summary form (Reuter and Horspool, 1996; Reuter and Adcock, 1998). Using the rhino database (Brett, 1997) and historical data (Loutit unpublished data; Gilchrist unpublished data) records were analysed to determine the interval between breeding. To allow data on the age at first calving, adult cows who may not have calved and time since cows last calved to be incorporated into the analysis, breeding performance was also expressed as the cow years per calf. Using this method, accumulated adult years (≥ 7 years) per sub-population are calculated per calf.

RESULTS

Landform classification

Female rhinos ranged over 853.71 km² in the northern study site, of which 134.52 km² was slopes habitat, 676.65 km² plains habitat and 42.00 km² riverine habitat (Figure 3). In the central study site females ranged over 288.71 km², of which 57.96 km² was slopes habitat, 219.10 km² plains habitat and 11.65 km² riverine habitat (Figure 4). Rhinos in the southern study site ranged over 1203.40 km², of which 515.17 km² was slopes habitat, 641.42 km² was plains habitat and 46.81 km² was riverine habitat (Figure 5).

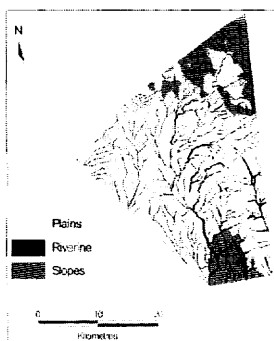


Figure 3: Landform composition of the northern study site, showing the three habitats.

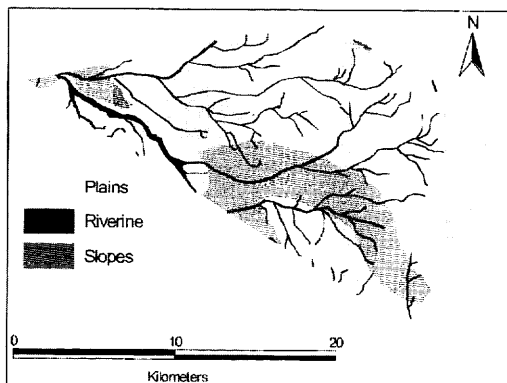


Figure 4: Landform composition of the central study site, showing the three habitats.

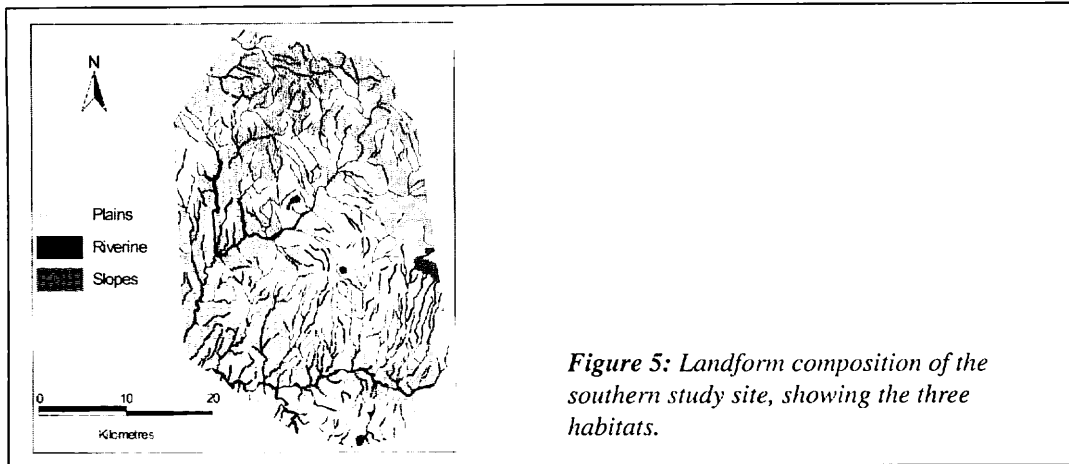


Figure 5: Landform composition of the southern study site, showing the three habitats.

Table 1 summarises the proportion of the three habitats found in each study site, and the mean distance from annual and perennial waterpoints for each study site.

Table 1. Proportion of the three habitats occurring in the range of females and the distance from annual and perennial waterpoints, expressed in metres, for the three study sites.

Study site	% Slopes	% Plains	% Riverine	Distance from Perennial Water	Distance from Annual Water
Northern	20.08	75.90	4.03	16,661	-
Central	15.77	79.31	4.92	3,240	3,240
Southern	42.81	53.30	3.89	5,601	5,601

Figures 6, 7 and 8 represent the distance from annual and perennial waterpoints for each of the three study sites. A mean value was calculated for each study site to determine the access to water in times of stress, when only perennial water is available and after rain, when annual waters are available. This was used to compare access to water across the three study sites and determine its influence on home range and breeding performance. No perennial waterpoint fell inside the northern study site.

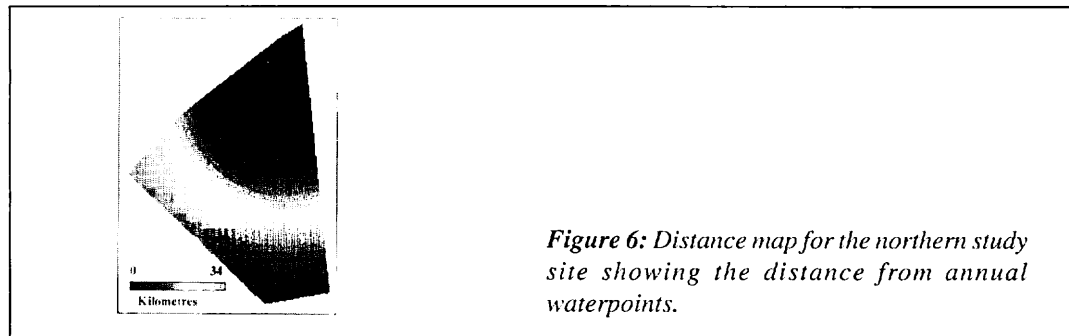


Figure 6: Distance map for the northern study site showing the distance from annual waterpoints.

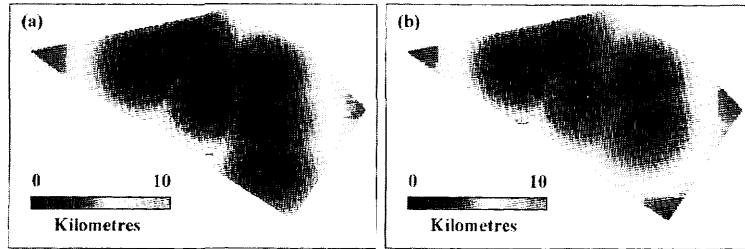


Figure 7: Distance maps for the central study site showing: (a) the distance from annual waterpoints, and (b) the distance from perennial waterpoints.

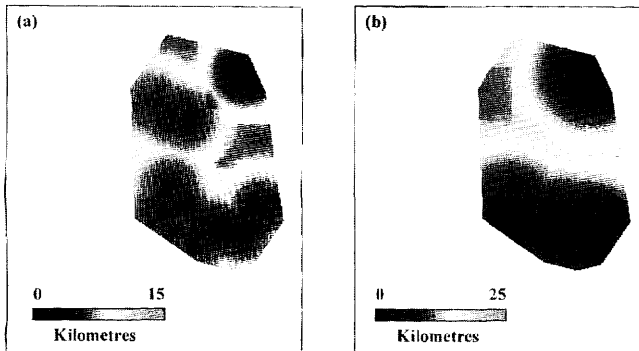


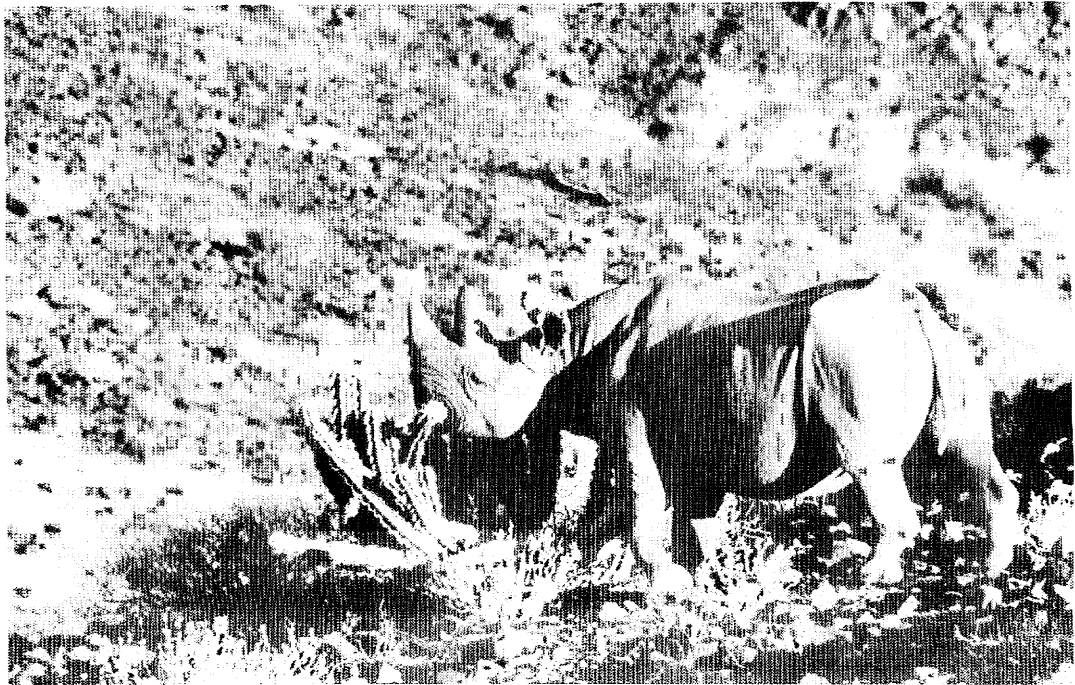
Figure 8: Distance maps for the southern study site showing: (a) the distance from annual waterpoints, and (b) the distance from perennial waterpoints.

Vegetation study

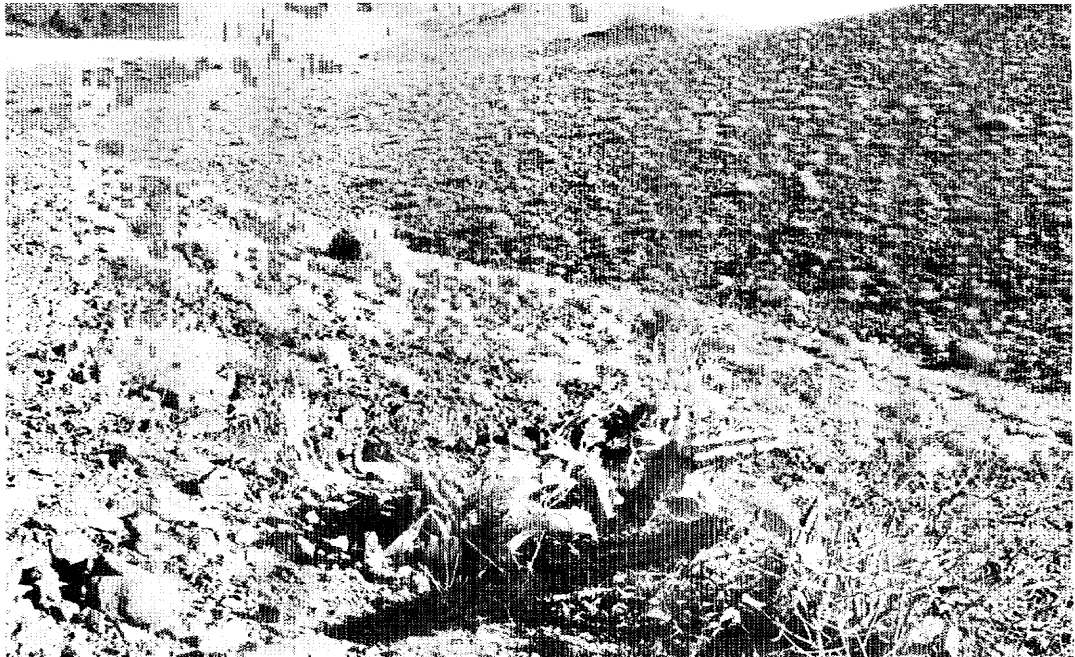
Over 7,000 individual plants across 52 transects within the three habitats were analysed to obtain levels of perennial woody species density and browse condition for the three study sites. Several of these species are known to make up the bulk of the diet of the rhino in these arid areas, based on preference ratios obtained during a feeding study in the southern study site (Loutit *et al.*, 1987), and species identified as “bulk food species” for black rhinos in western Etosha National Park and the eastern parts of the Kunene rhino range (Joubert and Eloff, 1971).

Absolute density

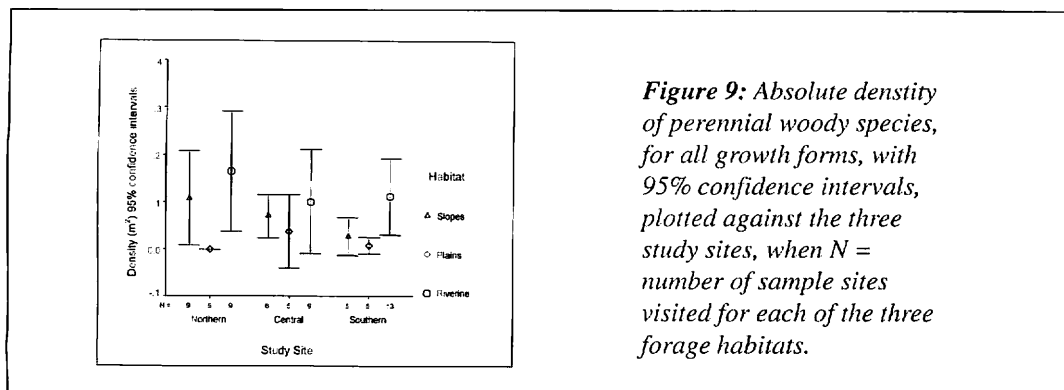
A comparison of the density of perennial woody species showed no differences between the slopes habitat (Kruskal Wallis, $\chi^2 = 1.960$, $df = 2$, $P = 0.375$), plains habitat (Kruskal Wallis, $\chi^2 = 3.963$, $df = 2$, $P = 0.138$) and riverine habitat (Kruskal Wallis, $\chi^2 = 0.790$, $df = 2$, $P = 0.674$) across the three study sites. However, there was a difference in the density of woody species between the three habitats (Kruskal Wallis, $\chi^2 = 11.938$, $df = 2$, $P = 0.003$). Density was generally highest in the riverine habitat and lowest in the plains habitat across the three study sites (Figure 9). Both canopy cover and height were highest in the more dense habitats, with the exception of the central study site, where the height and canopy cover were higher in the plains habitat than the slopes habitat.



Black Rhino feeding on an *Euphorbia Virosa* in the slopes habitat of the central study site.

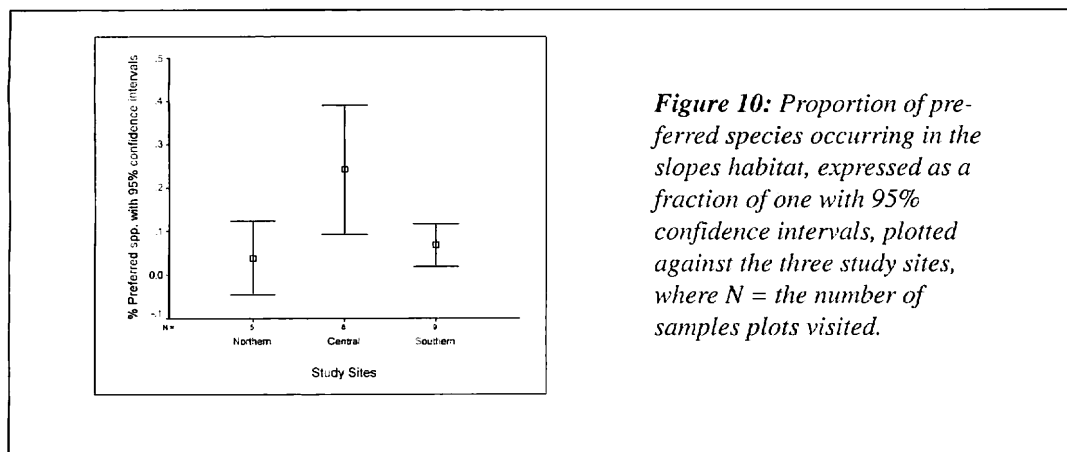


Remainder of the same *Euphorbia Virosa* the following morning.



Preferred species

Even though there was no difference between the density of perennial woody species in different study sites (Figure 9), there was a difference in the proportion of preferred perennial woody species in the slopes habitat between study sites (Kruskal Wallis, $\chi^2 = 8.708$, $df = 2$, $P = 0.013$). There was a higher proportion of preferred species in the slopes habitat in the central site than in the northern and southern sites (Figure 10).



There was no difference in the proportion of preferred perennial woody species in either plains habitat (Kruskal Wallis, $\chi^2 = 4.746$, $df = 2$, $P = 0.093$) or riverine habitat (Kruskal Wallis, $\chi^2 = 0.042$, $df = 2$, $P = 0.979$).

Dominance and number of species in each habitat

Table 2 shows the number of different species and the dominant species found in each of the habitats where perennial woody species were recorded. Dominant species represent those that make up over 10% of the canopy cover for all growth forms.

Table 2. Dominant species in each habitat for the three study sites. *N* = the number of different species recorded at each site. Growth form refers to plants occurring as a dwarf shrub (ds), shrub & tree (s/t), only as a shrub (s) or only as a tree (t). A * denotes a preferred woody species that makes up the bulk of the diet for the black rhinoceros in these arid areas.

Area	Habitat	N	Percentage cover	Growth form	Species
Northern	Slopes	41	34.70%	ds	<i>Petalidium cirrhiferum</i>
			28.19%	s/t	<i>Commiphora wildii</i>
Northern	Riverine	51	22.68%	s/t	<i>Tamarix usneoides</i>
			13.14%	ds	<i>Calicorema capitata*</i>
			11.89%	ds	<i>Petalidium cirriferum</i>
Central	Slopes	60	25.80%	ds	<i>Petalidium sp.</i>
			11.50%	s/t	<i>Euphorbia damarana*</i>
Central	Plains	35	77.50%	s/t	<i>Euphorbia damarana*</i>
Central	Riverine	46	25.34%	s/t	<i>Tamarix usneodes</i>
			23.43%	ds	<i>Petalidium sp.</i>
			21.21%	s/t	<i>Salvadora persica</i>
			14.00%	s/t	<i>Colophospermum mopane</i>
Southern	Slopes	25	68.85%	s/t	<i>Commiphora wildii</i>
Southern	Plains	25	27.60%	s/t	<i>Euphorbia damarana*</i>
			24.21%	s	<i>Commiphora kraeuseliana</i>
			10.00%	s/t	<i>Boscia foetida</i>
Southern	Riverine	59	17.63%	ds	<i>Petalidium pilosi-bracteolatum</i>
			15.28%	s/t	<i>Faidherbia albida</i>
			11.60%	s/t	<i>Acacia reficiens*</i>

Condition of available browse

Varying degrees of browse damage were recorded in each habitat for each of the three study sites. There was no difference in browse damage across the three sites in the slopes habitat (two-way ANOVA, $F = 0.885$, $df = 2$, $P = 0.421$), with no difference between growth form (two-way ANOVA, $F = 3.174$, $df = 2$, $P = 0.053$), and no interaction between site and growth form (two-way ANOVA, $F = 0.436$, $df = 4$, $P = 0.781$).

There was no difference in browse damage across the three sites in the plains habitat (two-way ANOVA, $F = 1.950$, $df = 1$, $P = 0.196$), with no difference between growth form (two-way ANOVA, $F = 1.044$, $df = 2$, $P = 0.391$), and no interaction between site and growth form (two-way ANOVA, $F = 0.280$, $df = 2$, $P = 0.760$). The recorded damage to available browse in the riverine habitat (Figure 11) was

highest in the northern study site (two-way ANOVA, $F = 4.388$, $df = 2$, $P = 0.015$). There were no differences between growth (two-way ANOVA, $F = 0.799$, $df = 2$, $P = 0.453$) and no interaction between site and growth form (two-way ANOVA, $F = 0.427$, $df = 4$, $P = 0.789$).

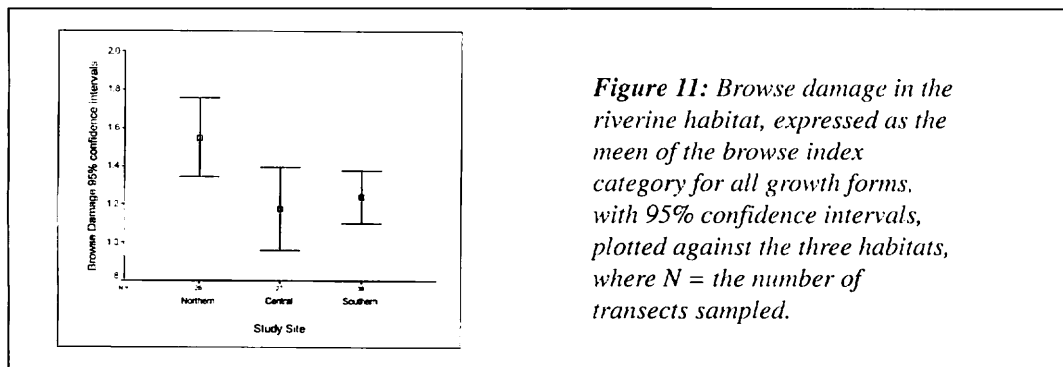


Figure 11: Browse damage in the riverine habitat, expressed as the mean of the browse index category for all growth forms, with 95% confidence intervals, plotted against the three habitats, where N = the number of transects sampled.

Home range

Home range area

In the central study site, two rhinos had fewer than ten sightings and were therefore excluded from the analysis of home range. In the southern study site three rhinos had fewer than ten sightings and were therefore excluded from the analysis of home range. However, all rhinos were included to measure overlap.

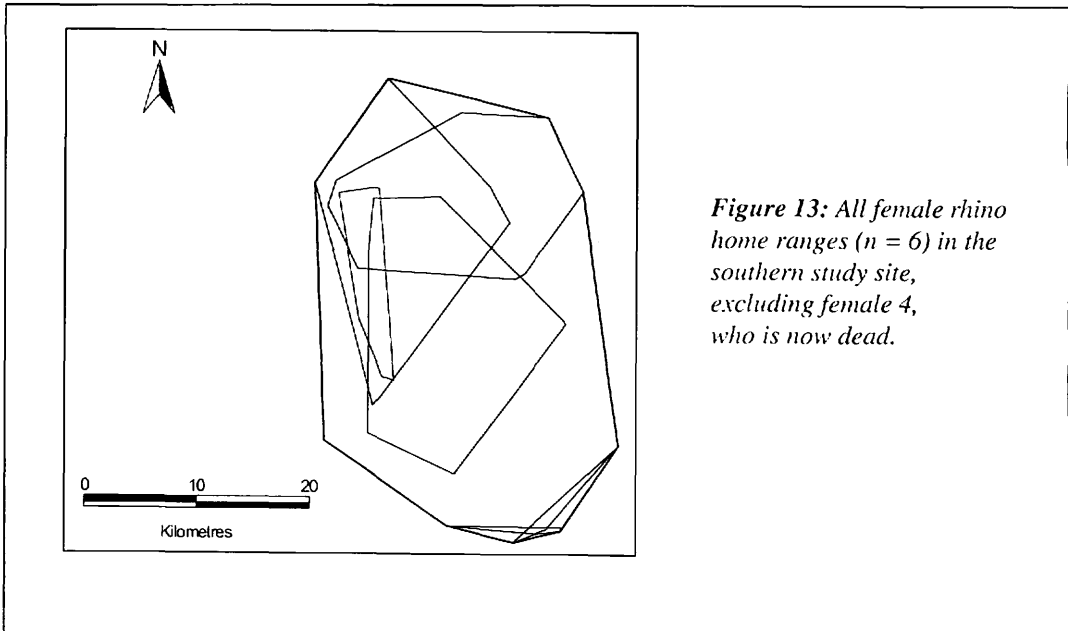
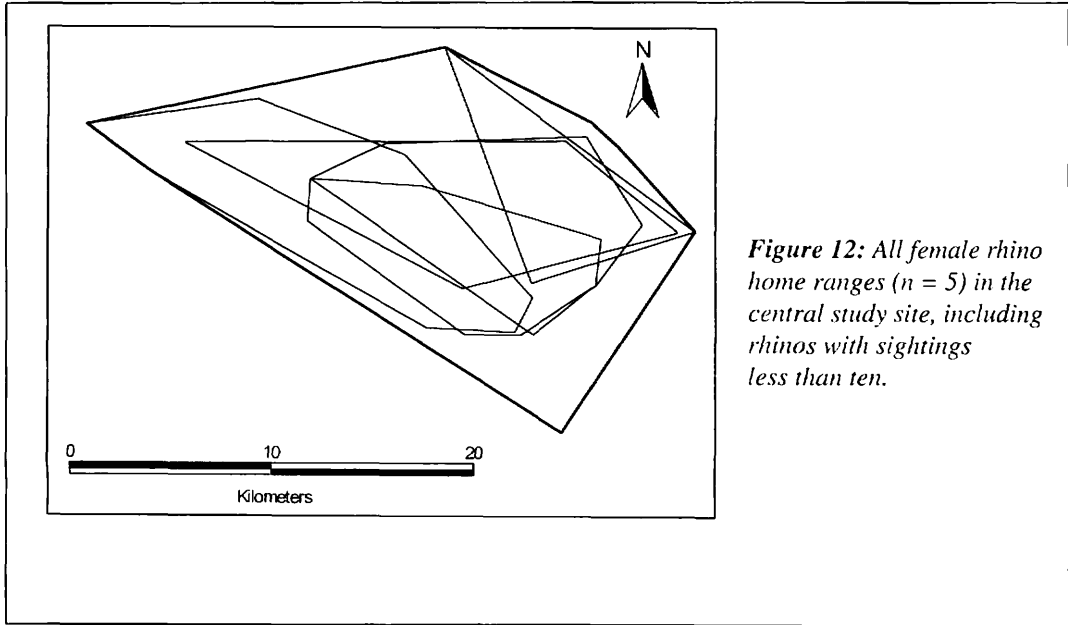
The number of accurately positioned sightings was not sufficient to determine if there was a change in home range size between seasons or if any shifts occurred in spatial movement patterns. Therefore, all data presented here represents the annual home range of females in the central and southern study sites.

The home range of females in the central study site ranged from 94.37 km² to 114.52 km² (mean = 104 ± 5.8544 km²; $n = 3$) (Figure 12). The home range of females in the southern study site ranged from 340.03 km² to 441.20 km² (mean = 385 ± 22.64 km²; $n = 4$) (Figure 13). The mean home range of females in the two study sites differed significantly (Students t-test, $t = 10.346$, $df = 5$, $P = 0.000$) (Table 3).

Table 3. Mean and range of home range for adult females, calculated using minimum convex polygon, for the central and southern study sites.

Area	N	Mean	Range
Central	3	104.1	94.37 - 114.52
Southern	4	385.9	340.03 - 441.2

The proportion of overlap between all females in central study site ($n = 5$) was 45% (Figure 12) and 25% for all females in the southern study site ($n = 6$) (Figure 13). Female number 4 (Table 4) is now dead so was excluded from the analysis of overlap.



Influences on home range

Table 4 shows the size of each landform occurring in the home range of females in the central and southern study.

Table 4. Size, expressed in kilometres squared, of each habitat occurring in the home range of females in the central and southern study sites. A (+) indicates a breeding female.

Rhino	Area	Slopes	Plains	Riverine	Total
Female 1 +	Central	22.96	68.49	2.92	94.37
Female 2 +	Central	21.42	76.98	3.03	101.43
Female 3 +	Central	40.06	66.81	7.65	114.52
Female 4 +	Southern	222.24	197.60	21.31	441.15
Female 5 +	Southern	155.54	175.19	9.30	340.03
Female 6 +	Southern	144.69	242.69	14.49	401.87
Female 7	Southern	177.78	165.48	15.36	358.62

The slopes habitat showed a positive correlation to home range size, following a linear stepwise multiple regression (Table 5)

Table 5. Results of the multiple regression showing slopes habitat to be significant.

Variable	Unstandardised		Standardised		Sig.
	B	Std. Error	Beta	T	
Slopes	623.080	111.553	5.586	.003	
(Constant)	823.355	243.121	0.835	3.387	.020

Population characteristics*Population structure*

The population structure of rhinos in the three study sites is summarised in Table 6. Rhino condition scores for a small sample of rhinos seen during the 1997/98 census showed that adult males' and females' scores combined in the northern study site were in worse condition than those in the central and southern study sites (Kruskal Wallis, $x^2 = 12.042$, $df = 2$, $P = 0.002$).

Table 6. The age and sex composition of the rhinos in the three study sites following the census in 1997/98 (Reuter, 1999) and updated records. The figures in brackets refer to the mean condition scores obtained during the census in 1997/98.

Area	Adult		Sub-Adult		Dependent		Unsure
	Male	Female	Male	Female	Male	Female	
Northern	4 (2.5)	3 (2.3)	-	-	-	-	-
Central	3 (4)	5 (3.6)	2(4)	-	2(3.5)	-	1(3)
Southern	4 (3.3)	6 (3.8)	-	-	-	1(4)	1(3)

Breeding performance

A small sample of intercalf intervals collected from the three sub-populations varied from 23 to 77 months (Table 7). However, there was no difference in the mean intercalf interval between populations (one-way ANOVA, $F = 1.586$, $df = 2$, $P = 0.252$). When breeding is expressed as cow years per calf to include the age at first calving, adult cows who may not have calved, and time since cows last calved, a clear difference is seen. The shortest cow years per calf was found in the central study site, where female densities were highest and calf mortality was low (Table 7). Breeding performance has also been expressed as calves per female per year, to make subsequent comparisons with other populations across Africa (see discussion).

Table 7. Breeding performance across the three study sites expressed as cow years per calf and calving intervals, with recorded calf mortalities and density of females.

Study Site	Total Cows	Female Density	Calf Mortality	Calf interval			Breeding Performance		
				Mean	Range	<i>n</i>	Calves Calf	cow years/ Calf	calves/ female/ year
Northern	3	0.004	0	41	36 - 46	2	3	12.2	0.063
Central	5	0.017	0	33.1	23 - 39	7	11	4	0.12
Southern	6	0.005	3	47.0	34 - 77	6	9	6.2	0.089

DISCUSSION

Differences in the geology and topography of each study site led to variations in the height, canopy cover, frequency and composition of the perennial woody species recorded in each habitat, and access to water. The hypothesis that the movement patterns of desert-dwelling black rhino are related to the availability of resources, notably water and food, appears to hold. The home range size of females in the southern study site was larger than in the central study site (Figure 14c) and the main influence on home range appears to be related to the proportion of the slopes habitat (Figure 14a) occurring in the home range of females and the distance from water (Figure 14b). Although there is no difference in the density of perennial woody species in the slopes habitat across the sites, more preferred perennial woody species occur in the slopes habitat of the central study site.

Commiphora wildii dominated the slopes habitat in the northern and southern study sites, whilst the more favoured *Euphorbia damarana* was a dominant species in the slopes habitat of the central study site (Table 2). This explains the significantly higher proportion of bulk food species found in the central study site. *E. damarana* dominated the plains habitat of the southern and central sites, whilst cover in the plains of the northern study site did not warrant analysis of the density and abundance of perennial woody species. Loutit et. al. (1987) identified the gravel plains north of the Doros complex as important feeding grounds in the early mornings for black rhinos in the southern study site. The dominance of *E. damarana* suggests these plains form an important source of fodder in this study site.

In both the northern and southern study sites bulk food species were dominant species in the riverine vegetation. In the central study site no bulk food species were recorded as dominant species in the riverine habitat. However, a *Petalidium sp.* (an important food species following rains (Loutit et. al.,

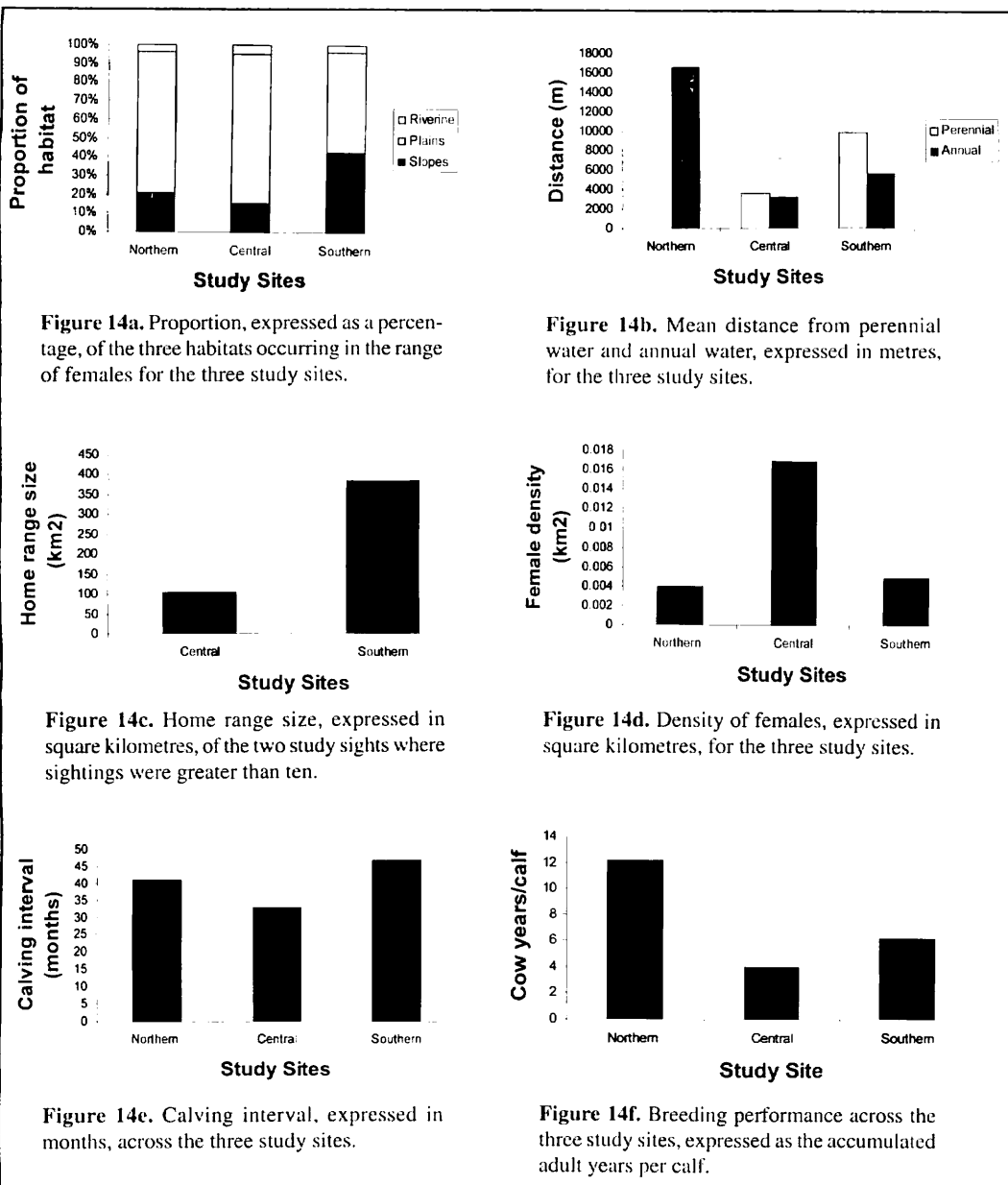


Figure 14. Summary of the physical characteristics and the demographic properties of the three study sites (all data are derived from table and figures in the results section).

1987)) contributed a higher proportion of canopy cover than the dominant species in the riverine habitat for the northern and southern study sites. The longer persistence of palatable herbs in the riverine habitat (not accounted for in this study) would also account for the importance of this habitat for black rhino in the arid rangelands of north-western Namibia. Studies in Hluhluwe (Adcock and Emslie, 1994) and the dense bushland of Ol Ari Nyiro Ranch in eastern Africa (Oloo *et al.*, 1993) found that riverine habitat was important for black rhinos especially in the dry season. Though Mukinya (1973) found riverine and slopes habitats not to be highly favoured as a forage habitat, this reflects the high density of herbs occurring on the rich volcanic soils of the more open country in eastern Africa.

The high level of browse damage in the riverine habitat of the northern study site reflects the poor condition of perennial woody species in this habitat. Browse damage in the slopes habitat across sites showed no difference, even though *C. wildii* dominated this habitat in the northern and southern sites (Table 2). This supports the hypothesis that *Commiphora spp.* are favoured by black rhinos in the less vegetated areas (Loutit *et al.*, 1987).

The relative abundance and high browse category of *E. damarana* across all three study sites emphasises its importance as a bulk food species. Other studies on the diet of the black rhino also stress the importance, or preference, of this family in arid climates (Lydekker, 1926; Van Rensburg, 1963; Joubert and Eloff, 1971; Loutit *et al.*, 1987; Emslie and Adcock, 1994; Doka Marjan, 1998). Even in the rich soils of eastern Africa, plants in the family *Euphorbiaceae* were highly favoured (Mukinya, 1977; Oloo *et al.*, 1993). Goddard (1968) found *Euphorbia spp.* in Olduvai (typically a habitat rich in leguminous forbs), though not dominant, makes up 25% of diet in the gorge habitat in the wet season and 70% in the dry season. Although Goddard suggests its importance may be as a result of the high water content, Loutit *et al.* (1987) found that water content did not appear markedly to influence selection. Studies on baboon troops in the Kazinga Channel, Queen Elizabeth National Park (where water is not a limiting factor) further support this, as extensive damage to *Euphorbia candelabrum* was recorded and the distribution of baboons reflected the distribution of *E. candelabrum* (Lock, 1972). Alternative suggestions for the “euphorbia bingeing” behaviour observed by both sexes of black rhino suggest it may be to boost steroids, so improving fecundity (Moll and Witt, 1995).

Table 8. Mean and range of home range for adult females, expressed in square kilometres, for other populations that have used minimum convex polygon.

Area	N	Mean	Range	Reference
Ngorongoro	6	31.5	12.5 - 47.3	Kiwiia, 1989a
Olduvai	19	36	3.6 - 91	Goddard, 1967b
Serengeti	4	75.5	43 - 99	Frame, 1980
Masai Mara	7	13.8	5.6 - 22.7	Mukinya, 1973
Hluhluwe	39	6.7	5.8 - 7.7	Hitchins, 1969
Mkuzi	-	27.5	7.2 - 51.8	Huggins, 1996
Ndumu	2	11.05	8.3 - 13.8	Conway and Goodman, 1989
Central	3	104.1	94.37 - 114.52	This study
Southern	4	385.9	340.03 - 441.2	This study

Compared to other studies where minimum convex polygon was used to measure home range, even the lowest recorded home range of a female in the central study site was almost twice the size of the largest home range recorded elsewhere. Home range of females in the central study site was lower than measures of home range recorded by Berger (1997) for the Kunene rhino population, using an adaptation to the minimum convex polygon. For females Berger found a mean of 538 km² (\pm 161 km²; $n = 13$; range 101 km² - 2067 km²). This is most likely due to the home range being calculated for the entire range and not broken down by management areas as was done in this study. Loutit *et. al.*, (1987) found similar home range sizes in the southern study site (approximately 500km², for males and females). Home range has also been recorded to vary in differing habitats, with savanna habitats having the largest home range (Fame, 1980). Other studies (Goddard, 1967b; Mukinya, 1973; Conway and Goodman, 1989; Kiwia, 1989b) have found home range to vary according to the proportion of thickets and the density of woody plants, hence presumably the availability of food (Table 8).

Other studies have indicated that rhinos have defined home ranges with no evidence of territoriality (Hitchins, 1969; Klingel and Klingel, 1966; Goddard 1967b). The high proportion of overlap amongst the females in this study supports this, though tolerance levels are more likely to be higher in females (Adcock, 1994). The greater proportion of overlap between females in the central study site, 45%, compared to only 25% in the southern study site, is most likely a consequence of the increased individual home range of females. If overlap is used as a measure of utilisation (Goddard, 1967b), the findings suggest the central study site can support a higher level of utilisation, hence density is higher (Figure 14d) and therefore home range is smaller (Figure 14c) and the rate of fecundity higher (Figure 14f).

Joubert and Eloff (1971) refer to the exploits of rhinos down the linear oasis of the desert margins and the “vertical dimension” to the home range of a black rhino in the Kunene population. This suggests that riverine habitat would be expected to also have a positive relationship to an increase in the home range. However, this was not the case, even though the riverine habitat has a higher density of perennial woody species, a greater proportion of “bulk” food species in some areas, and a longer persistence of palatable herbs. This can be explained by the limitations of the method used to measure home range, which gave no level of utilisation.

The structure of the sub-populations showed a marginally higher ratio of females in both the southern and northern study sites. The sex ratio of neonates born in the central study site over the last six years shows a bias towards males. A bias towards males is now proving to be a serious issue in management of smaller populations following the establishment of breeding nuclei with disparate sex ratios (Hitchins 1983; MET, 1997; Adcock *et al.*, 1998; Brett, 1998).

Calf intervals were not significantly different across the three study sites (Figure 14e). However, the number of cow years per calf was greater in the northern and southern study sites compared to the central study site, indicating lower recruitment levels (Figure 14f). This suggests that in sites where female home range is increased relative to the availability of resources and lower female density (Figure 14d), recruitment rates are lower. The calf mortality in the southern study site, where two calves have been lost to unexplained causes, further support this. The poor condition of females in the northern study site and high level of browse damage in the riverine habitat suggests the condition of browse species, and therefore the variable environmental conditions, could impinge on fecundity.

Comparing the calving with other populations indicates that breeding performance is lower in all sites. This might be linked to the limited resources, or equally that these populations have reached carrying capacity, although lower fecundity rates occurred in sites with a lower density. Hitchins and Anderson (1983) found that the lower fecundity rate in the more densely populated Hluhluwe population, when compared to the Corridor/Umfolozu populations, suggested these rhino were close to carrying capacity (Table 9).

Table 9. Data on the breeding performance of other black rhino populations.

Area	Calves/females/year	Reference
Ngorogoro, 1967	0.25	Goddard (1967b)
Ngorongoro, 1981	0.24	Kiwi (1989a)
Olduvai, 1967	0.26	Goddard (1967b)
Tsavo, 1970	0.30	Goddard (1970)
Amboseli, 1972	0.25	Western and Sindiyo (1972)
Addo, 1977	0.46	Hall-Martin and Penzhorn (1977)
Hluhluwe, 1983	0.19	Hitchins and Anderson (1983)
Corridor, 1983	0.28	Hitchins and Anderson (1983)
Umfolozi, 1983	0.33	Hitchins and Anderson (1983)
Luangwa, 1985	0.17	N. Leader-Williams (in Milner-Gulland, 1999)
Northern Study Site	0.089	This study
Central Study Site	0.12	This study
Southern Study Site	0.063	This study

Assessing the reproductive performance in this population, where there is a high percentage of inaccessible terrain and sightings of matings are limited as most of these occur at night (Goddard 1967), is very difficult. The results must therefore be treated with caution as they might only reflect the variable access to the rugged terrain. Non-invasive means of assessing reproductive status offer useful alternatives (Brett *et. al.*, 1989).

Management implications

Considering the existing habitat conditions, this study suggests the northern and southern sites have a lower carrying capacity, though another factor, such as poaching, may have had a greater impact in areas where resources are limited. The provision of permanent water points in these and similar resource limited areas may provide the rhino with access to key feeding grounds during critical times of stress, notably the dry season. Since this study was carried out two more calves, and possibly a third, have died in the southern study site. Following the installation of a waterpoint in 1999 in the southern study site close to the feeding grounds identified by Loutit *et. al.* (1987), the long term effects on the high calf mortality, lower density, poor breeding and the large home range sizes of females in this site needs monitoring. This may form an appropriate form of management for the northern study site and other areas where there is an increase in the range area of females relative to the abundance of water and food resources.

Studies by Loutit *et. al.* (1987) in the southern study site indicate a change in the diet of desert-dwelling black rhino between seasons. Compounded further by the high interseasonal variability in rainfall, this suggests that shifts in ranging patterns would occur throughout the year. This needs further research to gain a better understanding of the carrying capacity of the area and the role of density dependence in regulating population size across the entire range area. The population can then be

managed at maximum sustainable yield, thereby allowing satellite populations to be set up elsewhere within communal areas and benefits to be derived from the sale of live rhinos. These studies can also improve current management strategies, such as whether the provision of waterpoints in other areas is necessary and to determine if seasonal movement patterns place rhinos in more vulnerable areas where the threat of poaching is increased. Oloo *et. al.* (1993) describes the poaching of as many as twenty rhino in 1984 after they moved off Ol Ari Nyiro Ranch during drought.

Without any restrictions on the movement of livestock and increased tourism traffic in the range area, disturbance could be another factor (not accounted for in this study) that may have serious limiting effects on the movement patterns and fecundity of the Kunene black rhino population. The influx of cattle into the southern study site during drought may have been a contributing factor to the death of a rhino in the Ugab river (Morkel, 1992). Also, studies in Mukuzi National Park in South Africa by Huggins (1996) indicate that tourist roads through the park have a negative impact on the movement of black rhino. These issues press home the need for appropriate land use practices, across the range area, incorporating zoning strategies that limit and in some cases restrict access to areas and ensure the sustainability of CBNRM initiatives.

At the time of going to press, three conservancies have now been registered in Kunene Region, #Khoadi Hôas, Torra and Purros. All have either/both transient or resident rhinos falling within their boundaries. The southern study site has four conservancies, still to be registered, falling within some part of the range. Also, with its unique geological land forms, scenic landscape and close proximity to the major town of Swakopmund, it is a highly popular destination for both tour operators and self-drive tourists. It is vital that conservancies, especially in areas where resources are limited, draw up land use plans that consider the needs of the rhino within their entire range and not each conservancy in isolation.

Currently rhino management in Kunene and Erongo Region occurs at three distinct levels: The conservancy, where land use plans are drawn up; regionally, where monitoring is co-ordinated by the NGO Save the Rhino Trust, with the support of the MET and assistance from conservancy field staff; and nationally, where proposals are discussed on rhino management and research by the Rhino Advisory Committee for approval by the Minister. The demise of black rhino across Africa (Leader-Williams, 1992; Martin and Vigne, 1997) means this population is of vital importance not only to the sustainability of CBNRM programmes locally but to the international community at large. Collaboration across all these levels needs formalising to ensure efficiency and that informed decisions are made regarding management of black rhino in Kunene and Erongo Region.

Securing land tenure in communal lands and therefore making provision for a community to have legal rights to restrict access from outsiders to communally shared resources is a crucial next step. This will give legal backing to existing traditional systems of common property resource management and will strengthen the means of controlling access in the range area of the black rhino.

Conservancy development, as with other community-based natural resource management programmes, is based on the assumption that local populations have a greater interest in the sustainable use of resources than does the state (Brosius *et. al.*, 1998). Sullivan (1999) argues that constructing the framework for conservancy development in north-western Namibia purely on the large huntable game species cannot claim that it “empowers peoples’ diverse interests in land and natural resources”. This leads to the question of whether the current framework can ultimately lead to habitat protection, crucial for the black rhino, and the sustainability of such programmes.

Gorilla tourism in central Africa provides an example where the over emphasis on generating revenues, with little attention to long-term sustainability, is now putting the gorilla at threat from the practice its advocates hailed as essential to the continued existence of the species (Butynski and Kalina, 1998). By focusing on huntable game conservancy development must consider what future there is for social development and conservation of biological resources in areas of north-western Namibia which can make only a low relative potential net contribution to the economy. Studies by Barnes (1995) indicate that areas such as the Brandberg massif and the southern study site are examples of just such a case, when compared to areas supporting higher densities of game species. Yet these areas also contribute significantly to the country’s endemic taxa, notably; plants, reptiles, anuran amphibians and birds (Simmons *et. al.*, 1998).

These issues must be prioritised during the evolutionary process of conservancy development. The responsibility to ensure this and that the right environment for its growth is created rests with the implementing agencies, both government and NGOs. Already #Khoadi Hôas conservancy in Kunene Region offers hope. It has shown how the creation of a Forum for Integrated Resource Management can diversify the responsibilities of a conservancy committee. These stretch across four programmes of the Ministry of Agriculture, Water and Rural Development and the MET (Blackie, 1999).

The emerging conservancies in north-western Namibia still face many challenges that unless resolved, could jeopardize the long term sustainability of these programmes. However, the initial steps they have made towards recognizing the role of communities in the management of natural resources on communal land and creating additional opportunities for income generation in rural areas can only be seen as a positive step towards the conservation of biotic diversity and habitat protection.

CONCLUSION

The information presented here has identified the key habitat requirements of the Kunene black rhino population and limiting factors on fecundity. The use of a GIS to identify spatially explicit landform categories within the home range of individual females could be clearly related to differences in female home range and breeding performance across the study sites. Using a more detailed and up to date satellite image, thereby avoiding the fact that data used in the analysis of landform was from differing sources and at varying degrees of quality, might improve the process of landform classification and resource availability. However, despite these limitations, the study gave a good insight into the role of density-dependence in controlling population numbers in the desert-dwelling black rhino

of north-western Namibia. It is hoped that the information gained here will be of use to land use planning, in future black rhinoceros research, habitat suitability analysis and ultimately the continued high standard of conservation seen in Kunene and Erongo Region.

ACKNOWLEDGEMENTS

Field-work and equipment for the original study were funded with the kind support of The Friends of Port Lympne and Howletts Zoo and The Peoples Trust for Endangered Species. For their assistance with other costs I would like to thank Orebi Futures, The Durrell Trust, The Linbury Trust, Air Namibia and Save the Rhino International. Permission for the study was granted by the Ministry of Environment and Tourism (MET) and greatly appreciated. A big thank you to Peter Erb, Wynand du Plessis, Martin Hipondoka, Bob Smith and Nigel Leader-Williams for their assistance with the design of the study.

Thanks to Sebulon Hoeb and Martin !Nawaseb for their help during the vegetation study, and the trackers from Save the Rhino Trust, rangers from the MET, community game guards and all the other people who have been involved in the ceaseless monitoring work carried out in the area.

A thank you also to Betsy Fox, Sharon Montgomery and Jojo Walker for their comments on the drafts of this paper.

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Michael Hearn is the research and monitoring officer for the Save the Rhino Trust. He has been working for SRT since 1993, during which most of his time has been spent operating with tracking teams in Kunene Region. In 1996, together with local community game guards, he set up the camel patrols now operating in the mountainous parts of the rhino area. In 1998 he returned to the UK to study for his MSc in Conservation Biology. Since his return late last year he has been focusing on the assessment of the black rhino population date in Kunene and Erongo Region to contribute to conservancy development on communal land.