BLACK RHINOCEROS (*DICEROS BICORNIS*) HABITAT SELECTION AND MOVEMENT ANALYSIS

BY

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Thesis submitted in fulfillment of the academic requirements for the degree of

DOCTOR OF PHILOSOPHY

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December 2010

As the candidate's Supervisor I agree to the submission of this thesis.

Signed:

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ABSTRACT

Many aspects of habitat selection have been largely ignored in conservation planning of large mammals, including variation between day and night movement patterns, inter-individual niche variation of conspecifics and translocated individual's responses to new environments in relation to the influence of ecogeographical variables. Being a solitary moving animal with a known tendency to move through the night, the black rhino *Diceros bicornis* is a perfect species to test theories about individual spatial and temporal variation in habitat utilisation. I tested the appropriateness of using carrying capacity (CC) estimates as a tool for population conservation planning, and as an indicator of habitat utilisation for black rhino. I found individual selection was not related to the value of the habitat according to modelled CC. I therefore do not recommend the use of a priori calculations of resource quality and abundance of habitats (CC estimates), which do not take into account the factors that influence an animal's selection of a habitat, as indicators of species habitat use. Secondly I tested whether current methods of analyzing mainly diurnal location data of animals result in accurate ecological or conservation conclusions. I found a circadian variation in habitat use for different behaviours, and that excluding nocturnal data from home and browsing range analyses would provide inaccurate results for black rhino habitat use. I then tested for inter-individual niche variation amongst two populations of black rhino at various scales of selection, ranging from habitat through to browse selection. I showed that black rhino, a selective browser, had a significant degree of inter-individual habitat and dietary niche variation. Consequently, pooling habitat location data and diet selection data for black rhino individuals in a population does not reflect the actual selection of any, or many, individuals. To clarify which ecogeographical variables might influence this selection I ran maximum entropy models on individual's diurnal locations across the landscape. I was then able to develop a habitat suitability model which was based on the individual rather than population, providing a more accurate prediction. I repeated the individual models in phases, from the initial post-release phase after the release of individuals onto a new reserve through to their 'settled' phase, allowing me to explore the effect of habitat variables on different settling phases of translocated animals. The results indicate that all the rhinos' acclimation phase lasted no longer than 25 days and that to minimize disturbance to the settling process all individuals in a newly released cohort should be released within this period. This study as a whole provides conservation managers with a better ecological understanding of black rhino in conjunction with a number of management tools. This will enable conservation managers to better understand the way animals utilise and perceive their environment, allowing for better monitoring and analyses of animal movements. This will aid in the development of strategic management plans in the conservation of not only animal species but also the ecosystems that they reside in and the identification of suitable areas for future conservation of animal species.

PREFACE

The work described in this thesis was carried out in the Maputaland region of northern KwaZulu-Natal, South Africa, through the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville, from January 2005 to May 2010, under the supervision of Professor Rob Slotow.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

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DECLARATION 1 - PLAGIARISM

I, Simon Morgan, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other university.

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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, *in press* and published and give details of the contributions of each author to the experimental work and writing of each publication)

Publication 1

Morgan, S., Mackey, R.L. and Slotow, R. (2009). A priori valuation of land use for the conservation of black rhinoceros (*Diceros bicornis*). *Biological Conservation*, 142, 384-393.

Author contributions:

SM conducted all fieldwork, processed and analysed the data, and designed and wrote the paper. RLM contributed to the statistical analyses and provided valuable comments on the manuscript. RS contributed to the design of the paper and provided valuable comments on the manuscript.

Publication 2

Morgan, S., Mackey, R.L. and Slotow, R. *In preparation*. black rhinoceros circadian variation in spatial and behavioural habitat utilisation

Author contributions:

SM conducted all fieldwork, processed and analysed the data, and designed and wrote the paper. RLM contributed to the statistical analyses and provided valuable comments on the manuscript. RS contributed to the design of the paper and provided valuable comments on the manuscript.

Publication 3

Morgan, S., Mackey, R.L., Shaw, J.A. and Slotow, R. *In preparation*. Interindividual niche variation in black rhinoceros.

Author contributions:

SM conducted fieldwork and processed the data on the Mun-ya-Wana population and JAS conducted fieldwork processed the data on the Tswalu population. SM designed, analysed and wrote the paper. JAS contributed to the design of the paper, the analysis of the data and provided valuable comments on the manuscript. RLM contributed to the statistical analyses and provided valuable comments on the manuscript. RS contributed to the design of the paper and provided valuable comments on the manuscript.

Publication 4
Morgan, S., Linklater, W. L. and Slotow, R. *In preparation*. Evaluating the settling response of reintroduced black rhinoceros to ecogeographical variables.

Author contributions:
SM conducted fieldwork, processed and analysed the data, and designed and wrote the paper. WLL conducted some fieldwork, contributed to the design of the paper and provided valuable comments on the manuscript. RS contributed to the design of the paper and provided valuable comments on the manuscript.

Publication 5
Morgan, S. and Slotow, R *In preparation*. The importance of incorporating individual variation in modelling habitat suitability.

Author contributions:
SM conducted all fieldwork, processed and analysed the data, and designed and wrote the paper. RS contributed to the design of the paper and provided valuable comments on the manuscript.

Signed:

Simon Morgan

ACKNOWLEDGEMENTS

I firstly want to acknowledge the population of 15 black rhino which have provided me with the opportunity to learn and to gain utmost respect for wildlife. Thanks Godweni, Paris, Betty, Harriet, Tembe, Ntshonilanga, Amadodamabile, Potty, Stuquza, iMfolozi, Jaluka, Nqogotshane, Dougal, Umkhandi wensimbi and Ngenisa.

This study was made possible by funding by the University of KwaZulu-Natal from National Research Fund Grant GUN No. 2053623; and through my employment by AndBeyond and the support of the landowners of the Mun-ya-Wana Game Reserve and the management of Phinda, especially Kevin Pretorius of Phinda Private Game Reserve.

I am truly indebted to the skilled tracking team of Daniel Tuli, Zama Ncube and Thomas Khumalo, without whom none of the data collection would have been remotely possible. I would like to praise them for their persevering and tenacious attitudes and their willingness to keep teaching me even though they knew it was a hopeless case. I would like to thank them especially for keeping a keen eye out and for literally saving my skin on numerous occasions, you guys rock!

I would like to thank Wayne Linklater and Ron Swaisgood for the use of the VHF transmitters, funded through the Ammerman Foundation, and the US Fish and Wildlife Service (Grant Agreement Nos. 98210-2-G363, 98210-4-G920, and 98210-6-G102). I would also like to thank Wayne for assistance and direction on a number of aspects of the thesis and for providing access to data.

I would like to thank Robin Mackey without whom stats would still be something indecipherable and who provided much needed direction and assistance whenever needed; Tristan Dickerson for his collection of vegetation information; Frank Sokolic for his help with GIS data manipulation; WWF and Ezemvelo KZN Wildlife for establishing the Black Rhino Range Expansion Project; Douglas Morris, Lochran Traill and Abi Vanak for their valuable comments on various chapters; Alain Smith and Tarik Bodasing for office entertainment and support; Chris Kelly and Dale Airton for the early days of rhino tracking; Chris and Jo for their support while I wrapped this up over a year and for all those that supported me through my data collection and the time that I have spent writing this thesis.

I am grateful to Rob Slotow for providing me with the guidance, direction, support and freedom to explore the world of conservation ecology and to get through the task of completing a thesis which I had never dreamed of.

I am for ever grateful to my family, especially Peeps, Mum, Pops & Jon, who have no end of support for the work I do and who are always interested and ultimately sustain me. This is for you.

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CHAPTER 1

General Introduction

When managing or repopulating a conservation area, especially with an endangered species, it is important to have a comprehensive understanding of the suitability of the land as well as the optimal population numbers in order to ensure ecosystem functioning (Bothma *et al.* 2004, Amin *et al.* 2006). A measure of habitat value helps ecologists and managers to better understand the ecosystems that they are dealing with, and to apply the most effective management strategies. If, however, an overestimate of value is made, the ecosystem will be managed incorrectly and overused, resulting in habitat degradation. Various methods have been developed to measure the value of habitats, based either on our perception of value using habitat analyses and carrying capacity (CC) estimates (Fritz & Duncan 1994, McLeod 1997, Luo *et al.* 2001, Adcock 2004, Bothma *et al.* 2004), or according to the species in question by using a measure of habitat utilisation or densities of resident species (e.g. Aebischer *et al.* 1993, Schadt *et al.* 2002, Morris 2003b, Braunisch *et al.* 2008).

Habitat selection, utilisation and suitability modelling are extensively studied topics (e.g. Johnson 1980, Rosenzweig 1981, Aebischer *et al.* 1993, Wintle *et al.* 2005) due to the importance they play in wildlife conservation and management decisions (Ben-Shahar & Skinner 1988, Morris 2003a). Sound management decisions are crucial to the conservation of large mammals, especially where these species are ecologically and economically significant.

1.1. Habitat explained

The base framework for conservation and management planning within an ecosystem is structured around the habitats that comprise it. In the literature the term ‘habitat’ is extensively used in a wide variation of studies, but very few actually go so far as defining what constitutes a habitat. In some descriptions species survival or population growth within the habitat is incorporated as part of the definition (Fabricius & Mentis 1990, Morris 2003a). For example Morris (2003a) defines habitat as ‘a spatially-bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets’. Others go further to include that a habitat needs ‘to provide for the life needs of an organism’ (Melton 1987, Harris & Kangas 1988, Owen-Smith 1988, Fabricius & Mentis 1990). I believe that these definitions are misleading, as in many studies the delineation of the habitats is made before any idea of the density or populations growth in the areas is known (Boyce *et al.* 2003, Osko *et al.* 2004, Calenge *et al.* 2005b, Le Mar & McArthur 2005). Habitats may also exist in an ecosystem that may not be utilised by or provide for a species (unpublished data). It seems that we can simplify this definition to ‘a spatially-bounded area, with a subset of physical and biotic conditions…’ (Morris 2003a). With this definition managers can use existing vegetation mapping units and ecogeographical variables to configure a habitat map for an area. This can be achieved without having to incorporate any animal movements or requirements, which is the process presently being followed by the majority of studies. Following this, a habitat could influence the density and population growth of the species in question and possibly contain some of the resources required for a species survival.

Initially conservation managers may prescribe CC values to specific habitats as an indication of initial stocking densities (Bothma *et al.* 2004). Species and habitat monitoring programs guide the modification of existing management plans and CC values according to cues from ecosystem or population dynamics (McLeod 1997, Bothma *et al.* 2004, del Monte-Luna *et al.* 2004). The availability of essential resources or the CC of an area is used as an indication of habitat value (Verner *et al.* 1986, Fritz & Duncan 1994, Bothma *et al.* 2004), even though CC models have been shown to be misleading in describing plant-herbivore interactions in stochastic environments (see McLeod, 1997 and Del Monte-Luna *et al.*, 2004 for reviews of CC models). They do, however, have a place in describing short-term equilibrium densities as a function of resource-availabilities (McLeod 1997), but ultimately the interconnected number of dynamic biotic and abiotic factors result in a constantly changing CC (del Monte-Luna *et al.* 2004).

Despite ecosystem complexity, the majority of CC models are based on only a few of the essential factors affecting the CC of a habitat (McLeod 1997, Bothma *et al.* 2004, del Monte-Luna *et al.* 2004), which may have been identified using expert knowledge or via regression analyses based on presence-only or presence/absence data of a species (Millspaugh *et al.* 2006). This is where the split in the determination of the CC of an area is made – either only using environmental variables or a relationship between animal species dynamics and habitat factors (McLeod 1997, del Monte-Luna *et al.* 2004). After reviewing seven different models, based on their ability to be objective, to produce quantitative estimates and their ability to consider environmental variation, McLeod (1997) found the interactive model, which related plant biomass to the rate of increase and food intake of herbivores, as the most suitable. This illustrates the importance of incorporating both environmental and animal dynamics into our understanding of habitat value.

So how do we record the value that an animal places on the quality of a habitat? As mentioned previously, animals may exhibit a non-random utilisation of available habitats (Morris 2003a) which we can use as an indication of selection made by the population or an individual. However, empirical studies have shown species density indices may not always indicate habitat quality under all conditions (Van Horne 1983, Greene & Stamps 2001). Environmental factors influencing this include seasonal and other temporal changes in habitat resources and habitat patchiness (Van Horne 1983). We therefore need to ensure that we collect density data over the variety of seasons (Van Horne 1983) and that the correct scale of selection is being analysed (Johnson 1980, Aebischer *et al.* 1993, Boyce *et al.* 2003, Alldredge & Griswold 2006). Thomas and Taylor (1990) identified three study designs at which habitat availability and use can be measured. In design I studies habitat use is calculated at a population level, with no individuals being identified, and the entire study area delineated as available. The next two designs are the more commonly used designs, especially in studies using radio-tracking data (Aebischer *et al.* 1993). Design II studies identify individuals in the population, but still define the area of availability at the population level, while in design III studies both the availability and use is measured at an individual level. The last two designs are the more appropriate as design I studies assume that all individuals in a population are making similar decisions regarding habitat selection, which is often not the case (Alldredge & Griswold 2006). It is important that the issues of scale are taken into account (Johnson 1980, Cumming *et al.* 2006) as a mismatch in scale between actual ecological processes and the management strategies governing them will result in mismanagement of natural resources (Cumming *et al.* 2006). For example, animals may behave at temporal scale that incorporates a full 24 hours, while, from a management perspective, we may only concern ourselves with their daytime movements and habitat utilisation. While it may seem obvious that this will cause a mismatch of scales, there is currently little literature addressing this specific issue.

We can then begin to understand the variation in habitat selection via the identification of specific resource selection functions which will enable to us to forecast habitat utilisation (Boyce & McDonald 1999) using habitat suitability models with correct scaling (Cumming *et al.* 2006). Conservationists and managers use these models to define landscape properties and map the distribution of wildlife habitat. They would be made more efficient if adjusted to incorporate various temporal, behavioural and spatial scales determined by social, ecological and socio-ecological processes (Cumming *et al.* 2006). Within this framework, they will allow us to produce probability maps depicting the likelihood of species occurrence and their response to environmental change, which is vital in planning conservation strategies (Store & Kangas 2001, Wintle *et al.* 2005, Traill & Bigalke 2006).

1.2. Rationale

I aim to address variations in our current perspective of habitat value versus that of animals at various spatial, temporal and behavioural scales, allowing us to better recognise ecological-species interactions at the right scale. I aim to discuss this understanding in a conservation planning framework in the identification and management of habitats for animal species. The objectives were thus 1) to question our knowledge of CC estimates and models and whether there is link between our perception of habitat value and animal habitat utilisation, 2) to question our use of temporally restricted population location data to make assumptions about animal movement and habitat utilisation, 3) to address issues of interindividual niche variation by conspecifics, 4) to determine whether modelling habitat suitability is best done at an individual or population level and 5) finally whether we can understand the influence of ecogeographical variables on a population of reintroduced animals.

I will use the Mun-ya-Wana Game Reserve, located in KwaZulu-Natal, South Africa, and a founder black rhinoceros *Diceros bicornis minor* population to achieve these aims and objectives.

1.3. Overview of the thesis

I have written the data chapters (2 to 6) as independent journal articles (Chapter 2 has been published and the other four are in submission). A full reference list is given at the end of the thesis rather than at the end of each chapter. I completed a black rhino habitat suitability map for the study site, incorporated as a subsection supporting the paper of Chapter 6. I will conclude the thesis in Chapter 7 with a general discussion on the new science learnt from the study and its application in the conservation and management planning for mammals.

1.3.1. Data chapters

In Chapter 2 I address our understanding of habitat utilisation, at various levels, and CC estimates and whether there is any correlation between the two. I did this at an individual selection level after finding that black rhino exhibit no concordance of habitat selection amongst themselves, at any of the selection levels I tested at. Resource availability drives individual productivity and we can assume individuals to select those habitats with a higher quality, abundance and productivity of key resources (i.e. the value of a habitat as indicated by the CC estimates assigned to them). Using a ranking method to display selection and CC estimate values I found that this is not the case. I discuss these findings and question the reliability of habitat CC estimates for species that display either variable individual selection of habitats or patches, or that are selective foragers.

In Chapter 3, I investigate how circadian shifts in a mammal's ecology could make interpretations using only an animal's diurnal activities, habitat selection and ranging behaviour, inaccurate. I also analysed behaviour when analysing the spatial data for habitat selection, as animals may well select specific habitats for particular behaviours. I overlaid day and night habitat movements and selection for various behaviours, and demonstrated variation in spatial use of habitats over time for different black rhino behaviours. I discuss these findings in a conservation management context, especially with regards to monitoring frameworks.

In Chapter 4 I investigate the degree of interindividual habitat and dietary niche variation exhibited by the MGR black rhino population at a broad scale. After finding notable levels of interindividual variation, I sourced fine scale feeding data from another black rhino population and conducted the same analysis. I then analysed the depth of the interindividual dietary variation to see whether the variation was based on their primary or subsidiary diets. Following this I discuss the need to understand the individual before we can make assumptions about populations based on pooled individual information.

In the fifth chapter I will further develop the concept of the individual and test whether we can use a number of individually created habitat suitability models to develop a population level model using a maximum entropy model (Maxent). Currently only complex generalised additive mixed models (e.g. Aarts *et al.* 2008) and eigenanalyses (Calenge *et al.* 2005a) allow for the inclusion of individual variation in sample sizes and niche selection among individuals. I will generate a number of Maxent outputs and establish whether we can generate a more accurate indication of population level habitat suitability using this simpler modelling technique.

In Chapter 6 I investigate our understanding of how ecogeographical variables (EGV) affect newly reintroduced animals and how this knowledge can be used to increase the settling rate of released animals. I again used a novel application of Maxent to assess whether we could generate an indication of changes in suitability over time to answer this question. By doing so I queried whether we are able to incorporate a temporal aspect to Maxent modelling, and how this could benefit us in answering questions related to conservation ecology.

Finally in Chapter 7 I include a general discussion and describe how research in this field could continue into the future. I envisage this study to provide conservation managers with various tools that will enable them to better understand the way animals use and perceive their environment. This will allow for better monitoring and analyses of animal movements and a foundation for sound conservation planning. It will also aid in the development of strategic management plans in the conservation of not only animal species, but also the ecosystems that they reside in and the identification of suitable areas for future conservation of animal species.

I selected the black rhino as a study species as a better understanding of the ecology of this endangered mega-herbivore (Estes 1993) is required. The conservation plans for several African countries specify the need for the establishment of new breeding populations of black rhino (De Alessi 2000, Brooks 2001, Emslie 2001, Mills *et al.* 2003). Populations on state-controlled land in South Africa are already showing signs of density dependence and new private or communal areas that can sustain growing populations need to be identified (Hall-Martin & Castley 2003, Sheriffs 2003). In South Africa the black rhino Range Expansion Project moved 15 black rhino onto the MGR in KwaZulu-Natal (Sheriffs 2003), which provided a known population of black rhino which was easily identifiable and located for study purposes. Being a solitary moving animal with a known tendency to move through the night (Goddard 1967, Owen-Smith 1988, Estes 1993, Brown *et al.* 2003) it was deemed a suitable species to test theories about individual, spatial and temporal variations in habitat utilisation.

1.4. Study Area

1.4.1. Location and land use

The Mun-ya-wana Game Reserve (MGR), located approximately 25 km from Hluhluwe town and 30 km from the coastline between 27^{o} 40‘ – 27^{o} 55’ S and 32^{o} 12’ – 32^{o} 26’ E, was proclaimed in 2004 and encompasses a total of 18 050 ha. This area of Kwa-Zulu Natal lies at the southern end of the East African coastal plain and is between the Lebombo Mountains and the ocean. Forming a link between other conservation areas the MGR forms part of the Greater St. Lucia Wetland Reserve. The reserve runs predominantly in a north-south direction with the longest section at 30 km and the shortest at 3.3 km, with its borders fenced off. The majority of the reserve’s western and southern boundary is adjacent to the Mkhuze Game Reserve and smaller private game reserves, whilst the eastern boundary falls mainly onto rural community areas.

The MGR is a collaboration made up of the following private game reserves: Phinda Private Game Reserve (12 740 ha), Bumbeni (1 530 ha), Zuka (1 390 ha) and Mziki (260 ha), Pumalanga (2 130 ha) and van Rooyens (170 ha) (Fig. 1.1). Before the majority of these reserves were established, they were used for a combination of farming practices, including cotton, cattle and pineapples, while a few were small game farms with limited amounts of wildlife and few large mammals. The farming practices were discontinued with the formation of Phinda in 1991. Currently the Phinda, Bumbeni and Zuka sections of the reserve are being operated as an up-market tourism operation with a total of six lodges. Qualified rangers drive guests on an extensive road network that encompasses the whole of the MGR. Mziki is a housing share block with private home owners who self-drive across the Mziki and Pumalanga sections of the MGR only.

1.4.2. Geology and soils

Due to the high variation in geological formations across the reserve (Fig. 1.2) there is a corresponding high variation in the vegetation structure. The north-eastern half of the reserve is made up of Cretaceous siltstone deposits that have been overlaid with argillaceous sands of the Quartenary System (Hobday 1979). Across the centre of the reserve runs a stretch of conglomerate, siltstone and sandstone and a band of marine glauconitic siltstone with shelly horizons. Across the eastern section of the reserve there is a variation of soils from the higher- to the lower-lying areas made up of red loamy to clayey soils and black vertisols respectively. Rhyodacite and rhyolite dominate the west, while the far southern section of the reserve is dominated by basalt. Moderately fertile clayey but shallow lithosols have been produced across these rhyolite and basalt areas (Hobday 1979).

1.4.3. Land types

Land types are areas with a uniform climate, terrain form and soil pattern. A terrain unit is any part of the land surface with homogeneous form and slope. Terrain unit 1 represents a crest, 2 = scarp, 3 = midslope, 4 = footslope and 5 = valley bottom. There are four groups and seven different land types that fall into the MGR (Idema 1988), namely land types Ae, Ah and Ai; Db and Dc; Ea and Ib (Fig. 1.3). See Appendix 1 for details on the land types on MGR.

1.4.4. Topography

The altitude on the reserve varies between a low of 4 m a.s.l on the Mzinene floodplain to the highest point at 340 m a.s.l on the Lebombo mountains, which run through the southwestern section of the reserve (Hunter 1998, Goodman 2004, van Rooyen & Morgan 2007). Over 88 % of the MGR’s slope profile (Table 1.1) is classified as level to very gentle or gentle (Goodman 2004).

1.4.5. Climate

The Maputaland region experiences dry warm winters from April to September and hot wet summers from October to March. During the study period of January to December 2005, the heavy rains came in April and November, just before the dry season and then slightly into the wet season. Data collected on Phinda Private Game Reserve indicate the years rainfall was 841 mm, which is above the last ten years average of 764 mm at Phinda (MGR weather records) (Fig. 1.4). During the study period the lowest recorded temperature in the neighbouring Mkhuze Game Reserve was 9.6^{o} C in July, with the lowest mean monthly temperature of 18.8^{o} C for the same month. The highest recorded temperature was 41.5^{o} C in November, with the highest mean monthly temperature of 26.8^{o} C for the month of January (Mkhuze Game Reserve weather records, Ezemvelo KZN Wildlife).

1.4.6. Flora

The broad vegetation types on the MGR are the Maputaland Coastal Belt, Southern Lebombo Bushveld, Western Maputaland Clay Bushveld, Sand Forest and Zululand Lowveld (Mucina *et al.*, 2005). The high variation in geological formations across the reserve (Anon., 1988) drive a corresponding high variation in the vegetation structure and 25 fine scale vegetation types were identified on the MGR (van Rooyen & Morgan 2007; see Appendix 1 for a detailed description of the vegetation types). These 25 types were grouped into management units and a total of 16 habitat types were identified (van Rooyen & Morgan 2008; see Appendix 2 for a detailed description of the habitat types). Van Rooyen and Morgan (2007) based the classification on the woody layer, which provided a good indication of the vegetation needed to analyse a browsers' movements and habitat utilization.

1.4.7. Fauna

Well over 300 bird species, 30 frog and nearly 100 butterfly species have been recorded in this diverse area (Butchart & Roche 2002). Noted mammal species in the reserve include the following: African elephant *Loxodonta africana*, Burchell's zebra *Equus burchelli,* white rhinoceros *Ceratotherium simum,* black rhinoceros *Diceros bicornis,* hippopotamus *Hippopotamus amphibious,* bushpig *Potamochoerus porcus,* warthog *Phacochoerus aethiopicus,* giraffe *Giraffa camelopardalis,* blue wildebeest

Connochaetes taurinus, red duiker *Cephalophus natalensis,* common duiker *Sylvicarpa grimmia,* suni *Neotragus moschatus,* impala *Aepyceros malampus,* African buffalo *Syncerus caffer,* kudu *Tragelaphus strepsiceros,* nyala *Tragelaphus angasii*, reedbuck *Redunca arundinum*, mountain reedbuck *Redunca fulvorufula,* waterbuck *Kobus ellipsiprymnus,* brown hyaena *Hyaena brunnea,* spotted hyaena *Crocuta crocuta*, cheetah *Acinonyx jubatus*, leopard *Panthera pardus*, lion *Panthera leo,* black-backed jackal *Canis mesomelas*, honey badger *Mellivora capensis*, large-spotted genet *Genetta tigrina,* white-tailed mongoose *Ichneumia albicuada*, slender mongoose *Galerella spp.,* thick-tailed bushbaby *Otolemur crassicaudatus,* chacma baboon *Papio cynocephalus ursinus,* vervet monkey *Cercopithecus aethiops* and aardvark *Orycteropus afer.*

1.5. Study species

Rhino are large odd-toed ungulates that fall into the Perissodactyla order and the rhinocerotidae family. This order has six representatives left in Africa, namely the two rhino species, three zebra species and the wild ass (Estes 1993). The black rhino is a large grey animal that stands 1.4 - 1.7m and weighs between 996 - 1 362kg. The females weigh in just less than the males, but are not much smaller (Estes 1993). Black rhino have an upper prehensile lip that they use for browsing which is a predominant physiological difference between the two African rhino species. This lip enables them to browse selectively on a diverse array of woody species across their range (Goddard 1968, Estes 1993, Kotze & Zacharias 1993, Rossouw 1998, Buk 2004, Ganqa *et al.* 2005, Van der Heiden 2005). They have poor eyesight, which they compensate for with an acute sense of smell and hearing (Estes 1993; pers. obsv.). Black rhino have two continually growing horns that are variable in shape and size with the front horn normally longer the rear horn. rhino horn is made up of keratin and is used for predator defence, a stave in encounters with other rhino (Estes 1993; pers. obsv.) and a tool for pulling down hard to reach branches for feeding (pers. obsv.). These horns are largely responsible for the demise of the African rhino, due to a demand for their ornamental use and in concoctions of Chinese medicines (IUCN 2008).

1.5.1. History

The first proper rhino species appeared in the Oligocene over 37 Ma[a] and peaked into the Miocene and Pliocene (Estes 1993). Then recently, in rhino history, the rhino of Europe and Northern Asia started disappearing between 10 000 and 30 000 years ago, due to climatic changes and hunting pressure by humans (Owen-Smith 1988). There are now only five species of rhino left represented by three genera (Morales & Melnick 1994, Emslie & Brooks 1999). The black rhino and white rhino are the result of a divergence resulting in two sister groups with different specialisations, browsing and grazing respectively, and have an approximate 2% DNA sequence divergence (Morales & Melnick 1994). The black rhino has four sub-species that are recognised, specifically *D. b. minor, D. b. bicornis, D. b. michaeli* and *D. b. longipes* (Emslie & Brooks 1999, Emslie 2004). Historically the black rhino ranged across most of Southern and Eastern Africa and spreading West, below the Sahara, into some reaches of West Africa outside of rainforest areas (Fig. 1.5). In this study the sub-species *D. b. bicornis* is studied, its present day distribution limited to the Eastern sections of Southern and East Africa (Fig. 1.6) (Cumming *et al.* 1990).

1.5.2. Status

Of the three remaining genera of rhino many are critically endangered (IUCN 2008). The three exceptions are all sub-species of the two surviving species of African rhino, the one being the Southern white rhino *C. s. simum,* which is classified as near threatened. The second is the Western black rhino thought to be now extinct (Largot 2007) and the last is the study animal for this dissertation, the South-Eastern black rhino *D. b. bicornis,* which is classified as vulnerable by the IUCN (IUCN 2008). In the early 1970's there was in excess of 60 000 black rhino in Africa (Emslie & Brooks 1999, Emslie 2004). The numbers plummeted to an all time low of ~ 2 400 animals in 1995, and have slowly increased to an estimated 3 610 in 2003. This downfall was largely due to poaching to supply the need for rhino horn in Asia for traditional Chinese medicine and in Northern Yemen for traditional dagger handles (Emslie 2004, IUCN 2008). Nearly 70% of all Africa's black rhino are to be found in Namibia and South Africa and over 25% in

Zimbabwe and Kenya. Of these, 75% are on land owned by state-run conservation agencies and 23% are on private sector land, with a large proportion of these on a custodian basis and still owned by the state (Emslie 2004).

1.5.3. Behaviour

Black rhino are somewhat solitary and sedentary in their movements (Lent & Fike 2003; pers. obsv.). Adult bulls will spend time socialising with females and on occasion with other males, while females socialise often with other females and may have sub-adults which 'attach' themselves to them for long periods (Lent & Fike 2003). Adult bulls can behave territorially and this behaviour seems to vary across the continent (Adcock 1994). In KwaZulu-Natal it seems there are definite territories that are established (Estes 1993, Adcock 1994; pers. obsv.) and within three of the four adult bulls territories in the study site there are sub-ordinate males which are tolerated in the adult bulls territories. The female's movements are within an established home range, which may overlap with one or more bull's ranges (Lent & Fike 2003). The size difference between the sexes' home ranges differs across the continent, with both sexes having the same size range in the Ngorongoro Crater (Goddard 1967) while vast differences were seen in the Serengeti (Frame 1980) and in a Kenyan sanctuary (Tatman *et al.* 2000). On the MGR I noted that the females have a smaller core ranges than the adult bulls, but similar in size to the sub-ordinate males (pers. obs.).

The gestation period is 15-16 months with an inter-calving period of $2^{1}/_{2}$ – 4 years (Estes 1993). After birth the previous calf is driven away, at this stage between $2^{1}/_{2}$ - $3^{1}/_{2}$ years old. At this age the sub-adult will probably accompany other sub-adults or an unrelated cow until reaching adulthood (Estes 1993).

Table 1.1 Slope classes as determined by Goodman (2004).

Slope Class	**Area (ha)**	**% Total Area**
Level to very gentle	12278.7	67.2
Gentle	3834.8	20.9
Moderate	1755.9	9.6
Moderately steep	393.4	2.2
Steep	4.1	0.02

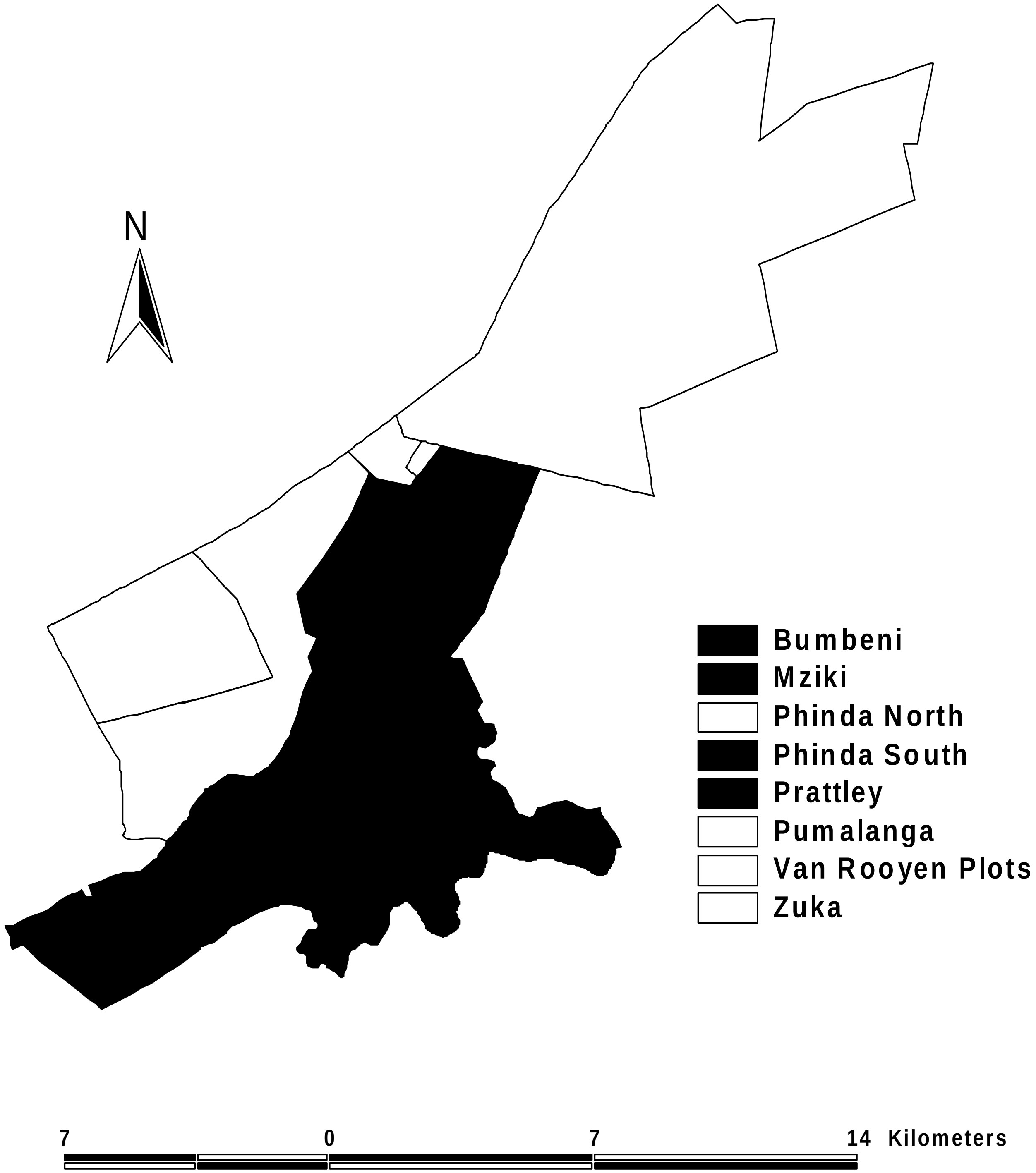

Figure 1.1. The properties comprising the Mun-ya-Wana Game Reserve.

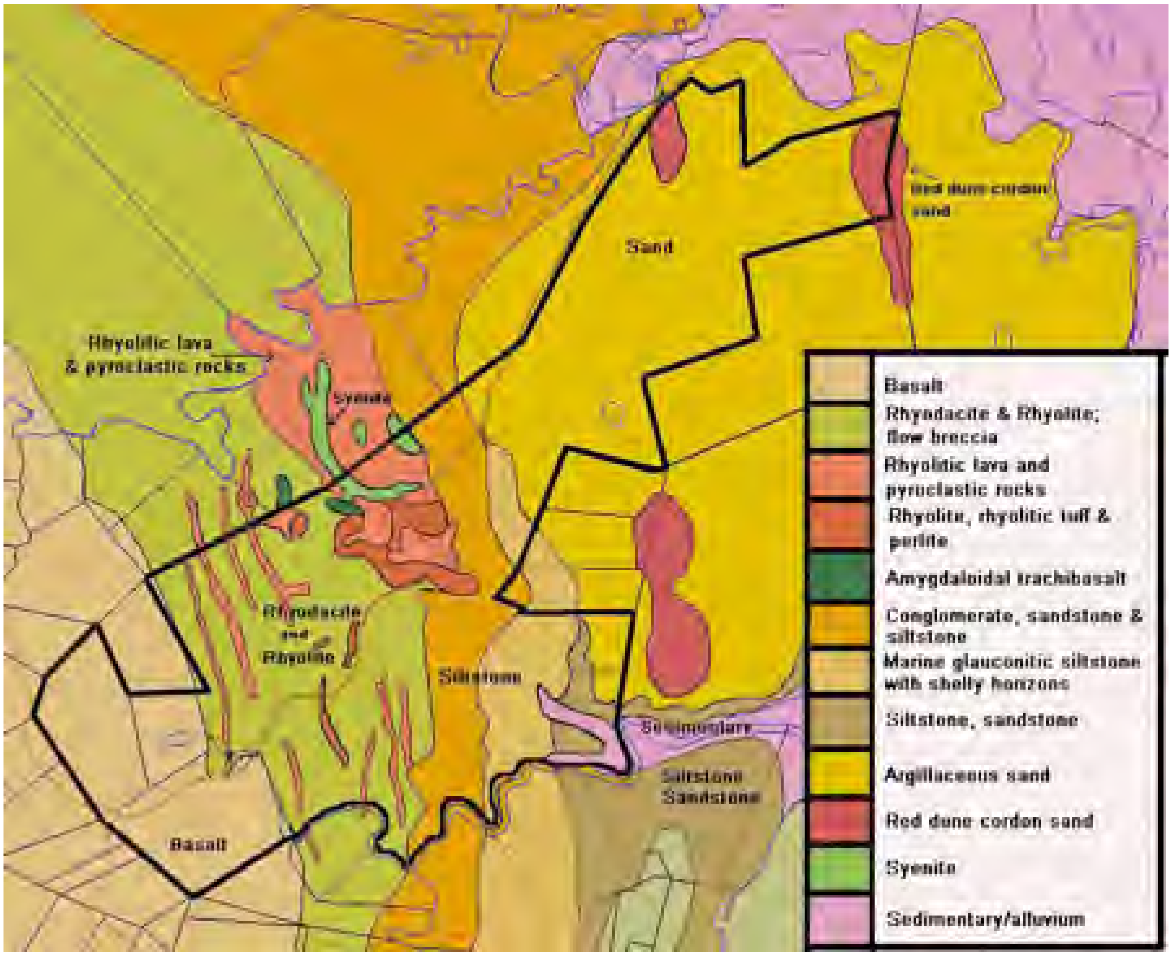

Figure 1.2 Geology of the Mun-ya-Wana Game Reserve, with the reserve boundary indicated by the thick black line (Linström & Wolmarans 1985; adapted from van Rooyen and Morgan, 2007).

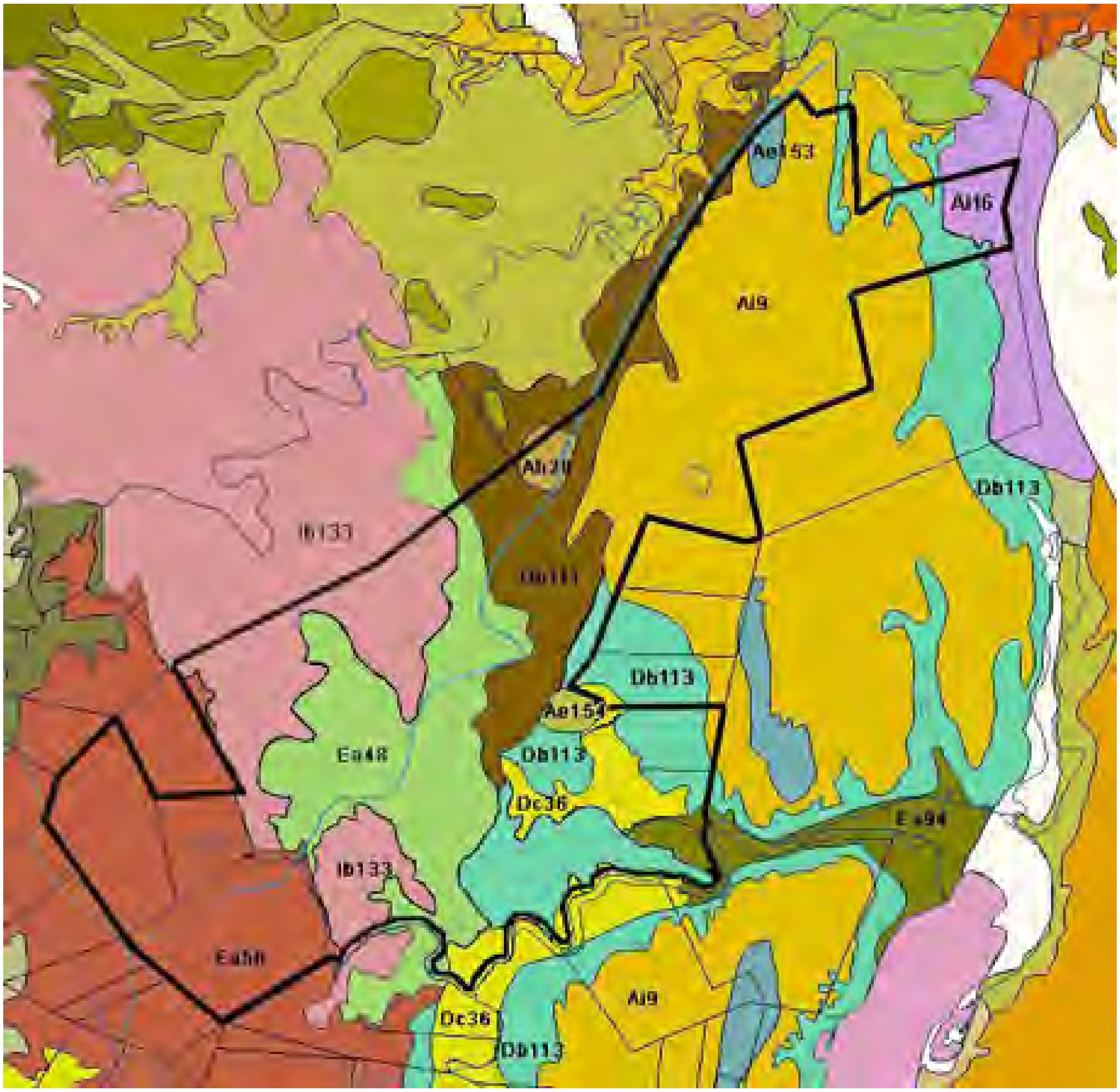

Figure 1.3 Land types of the Mun-ya-Wana Game Reserve, with the reserve boundary indicated by the thick black line (Anon 1988; adapted from van Rooyen and Morgan, 2007).

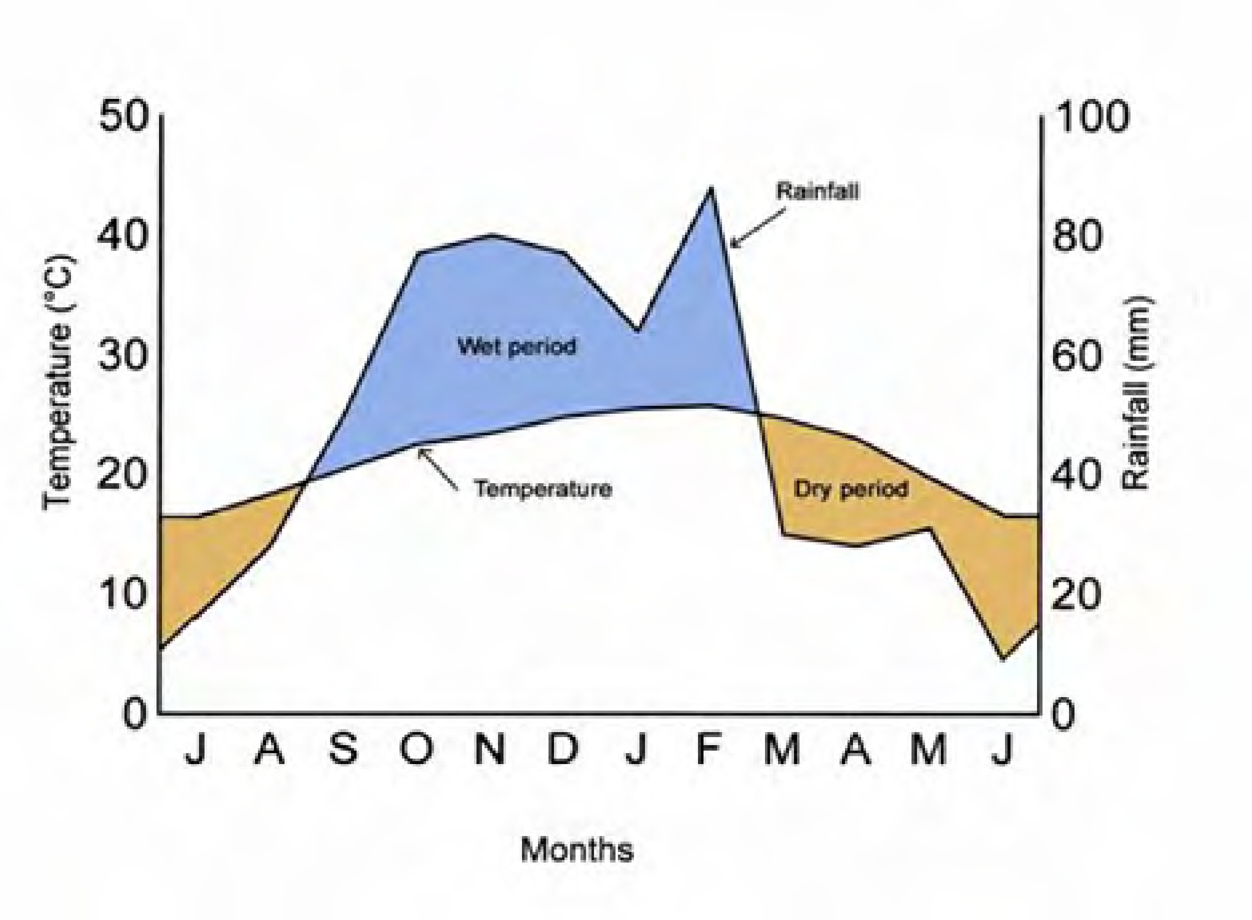

Figure 1.4 Historical rainfall and temperatures in the Mkhuze Game Reserve, which lies to the west of the Mun-ya-Wana Game Reserve (Anon 1998; adapted from van Rooyen and Morgan, 2007).

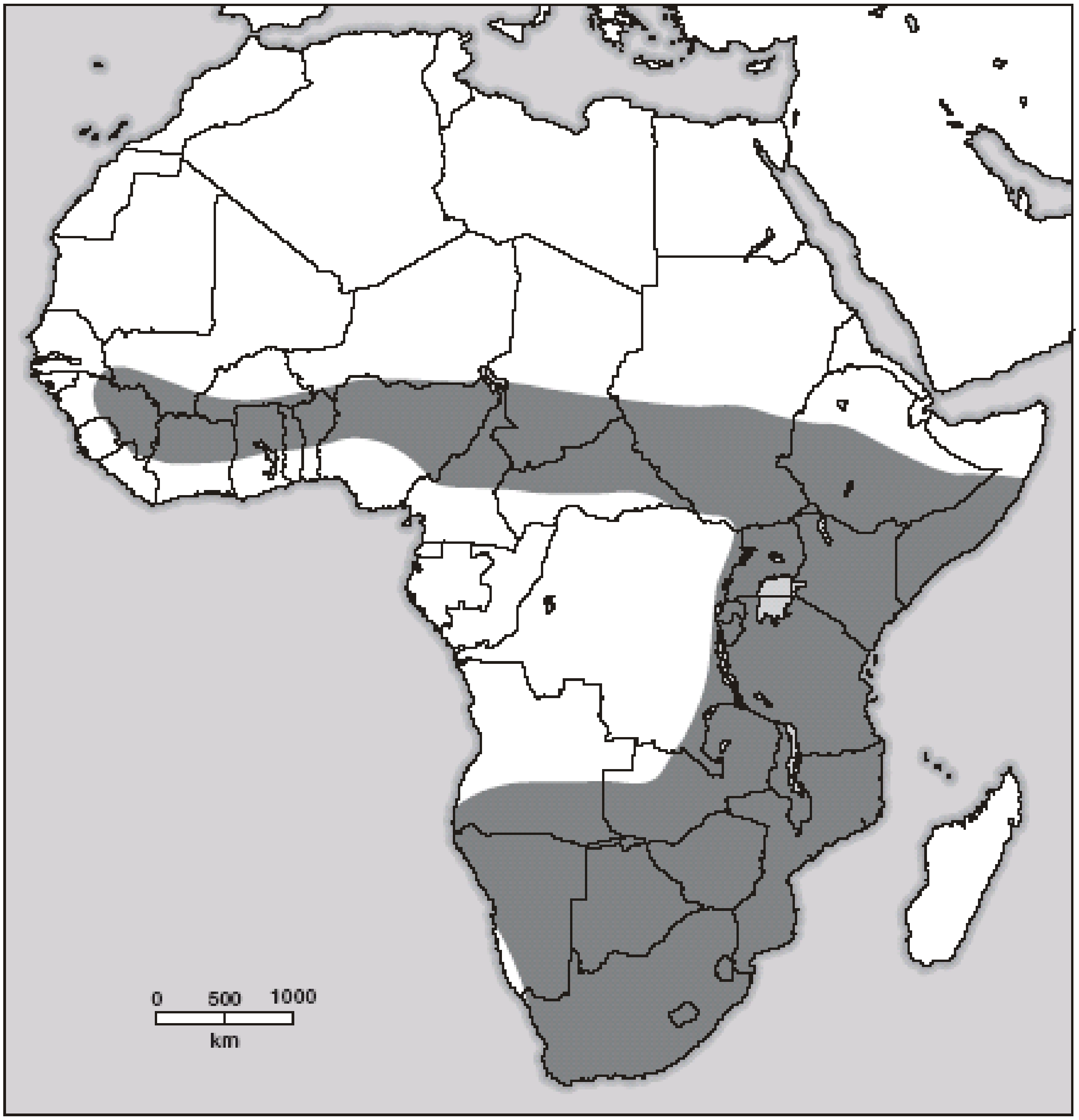

Figure 1.5 Probable historical distribution of black rhino (taken from Emslie and Brooks, 1999)

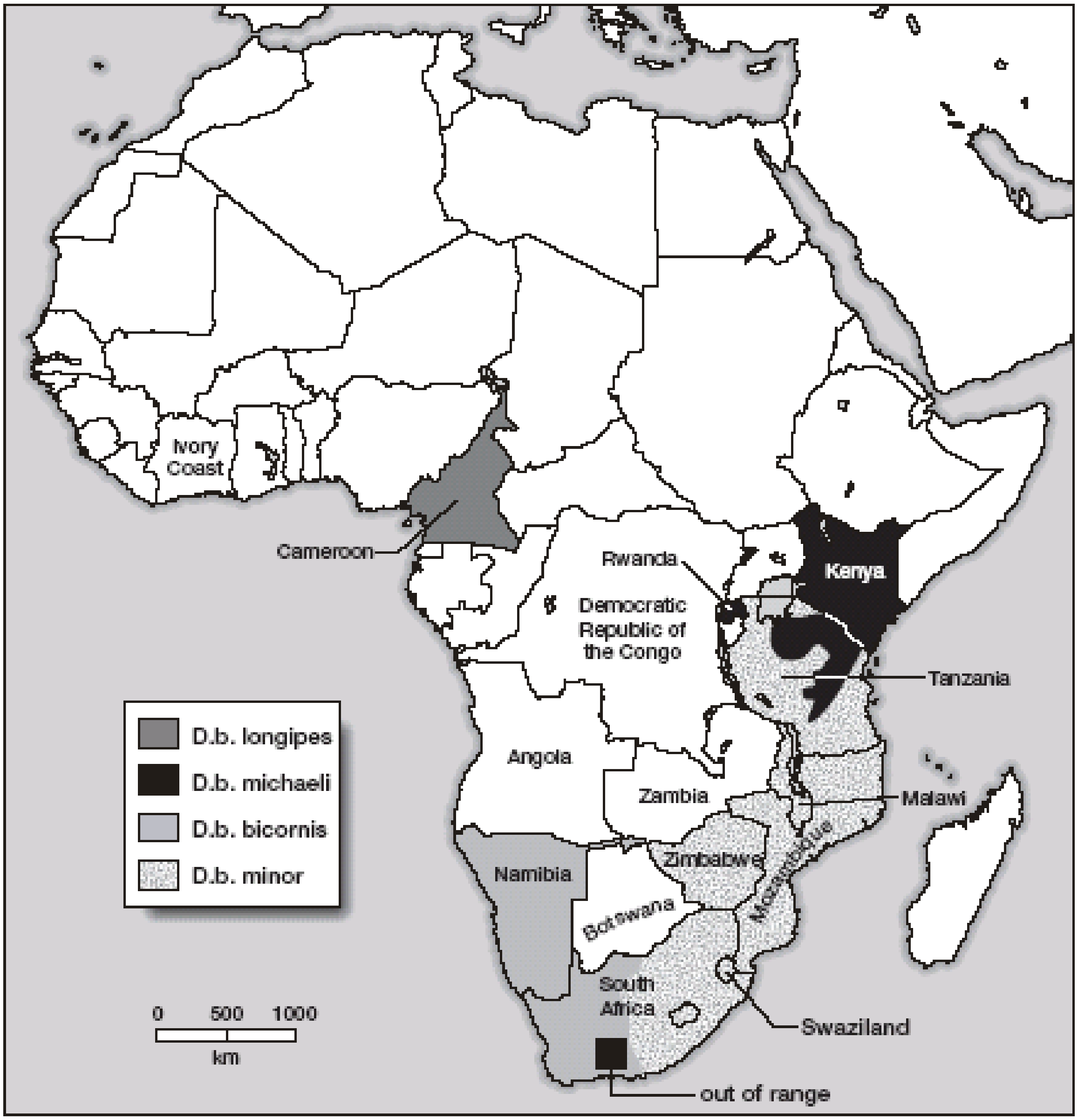

Figure 1.6 Distribution of the four black rhino *Diceros bicornis* sub-species in 1997 (taken from Emslie and Brooks, 1999). It is thought that *D. b. longipes* has since gone extinct (Largot 2007).

CHAPTER 2

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

2.1. Summary

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

2.2. Introduction

When managing or repopulating an area with animals, especially an endangered species, an understanding of habitat selection, habitat quality and the potential of the land, help with determining sizes of population required for optimal population growth (Bothma *et al.* 2004, Metzger *et al.* 2007) and how populations will use the space provided (Fagen 1988, Morris 2003b). A commonly used management approach has been to calculate a priori estimates of the carrying capacity (hereafter referred to as CC) of the land for a species, based on resource availability and quality, and to plan the future conservation management of the population on this (Bothma *et al.* 2004, Hayward *et al.* 2007). This includes decisions about reintroduction population size, harvesting strategies, the identification of potential high utilisation habitats and a measure of future conservation success. Here we concentrate on the usefulness of CC estimates for determining the quality of habitats as a tool for identifying areas of utilisation by a species for management purposes.

Many variations of calculations, and hence definitions, of CC for herbivores have been used in the past. Due to the stochastic nature of most natural environments, the concept of CC can be unreliable, especially for a herbivore population (for a review see McLeod, 1997). In variable environments, such as African savannah, "…carrying capacity is not a measurement of long-term equilibrium density but of short-term potential density as a function of resource availability" (McLeod 1997). Resource availability therefore drives individual fitness, in this case reproductive productivity, and we would assume individuals will select those habitats with a higher quality, abundance and productivity of key resources (Fretwell & Lucas Jr. 1970, Fagen 1988), i.e. higher value of a habitat as indicated by the CC estimates we assign to them. However, resource utilisation may vary depending on population density (Fretwell & Lucas Jr. 1970, Hobbs & Hanley 1990).

The predictive power of using CCs to estimate habitat selection may differ between individual and population scale. Habitat selection is defined here as the process whereby individuals preferentially use, or occupy, a non-random set of available habitats (Morris 2003a). At the level of individual selection, a habitat's CC may be used as an effective indicator of selection by a species (Fagen 1988, Hobbs & Hanley 1990) and vice versa. At the population level there has been some discrepancy as to whether one can use CC estimates as an indicator of selection (Van Horne 1983, Fagen 1988, Morris 2003b). For reviews see Hobbs and Hanley, 1990, Garshelis, 2000 and Chalfoun and Martin,

2007. At the population level, simplified simulation models have shown that habitat use/availability indices were not necessarily good indicators of CC, especially if there was variation in the abundance of resources across habitats (Hobbs & Hanley 1990). However, one could relate population use/availability ratios directly to habitat values and CC, as long as ideal free distribution is assumed for the population (Fretwell & Lucas Jr. 1970, Fagen 1988). This assumption, however, does not take into account the complicated social dynamics and behaviours of many species that do not follow the assumptions of ideal-free distribution and that show signs of density-dependence (Hobbs & Hanley 1990, Garshelis 2000).

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

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

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

2.3. Materials and methods

2.3.1. Study site

The 180 km^2 Mun-ya-Wana Game Reserve (MGR) (27^o 40'– 27^o 55' S and 32^o 12' – 32^o 26' E), KwaZulu-Natal, South Africa (Fig. 2.1), was established in 2004 with the dropping of fences between a group of already existing game reserves. Altitude varies between a low of 4 m a.s.l on the coastal Mzinene floodplain and a high of 340 m a.s.l on the Lebombo Mountains, which run through the south-western section of the reserve (Fig. 2.1). The region experiences dry warm winters from April to September and hot wet summers from October to March. During the study year the rainfall in the centre of the MGR was just above the last 10 years average rainfall (841 mm versus an average of 764 mm), but was preceded by three years of below average rainfall (427mm, 354 mm and 698 mm). The rainfall for the year in the neighbouring Mkhuze Game Reserve was below the yearly average (473 mm versus an average of 578 mm).

The broad vegetation types across the MGR were Maputaland Coastal Belt, Southern Lebombo Bushveld, Western Maputaland Clay Bushveld, Sand Forest and Zululand Lowveld (Mucina *et al.* 2005). The high variation in geological formations across the reserve (Anon 1988) drive a corresponding high variation in the vegetation structure and sixteen finer scale habitat types have been identified (Table 2.1) (van Rooyen and Morgan, 2007; see Appendix 2 for a detailed description of the habitat types used in this chapter). Van Rooyen and Morgan (2007) based the classification on the woody layer, which provided a good indication of the vegetation needed to analyse a browsers' movements and habitat utilization.

2.3.2. Study species

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

Females move within an established home range, which may overlap with the ranges of one or more bulls. The size difference between the home ranges of males and females differs across the continent, with both sexes having the same size range in the Ngorongoro Crater (Goddard 1967) while vast differences were seen in the Serengeti (Frame 1980) and in a Kenyan sanctuary (Tatman *et al.* 2000). On the MGR we observed females to have smaller diurnal core ranges smaller in size than those of the adult bulls, but similar in size to sub-ordinate males (unpublished data). We have noted that there is a significant difference between a black rhino's spatial utilisation during the day versus the night (unpublished results) and for this reason we will differentiate between the day and night movements/ranging patterns of rhino in this paper.

Our study ran from January through December 2005. During this time we located the rhinos at least once every four days with the aid of radio telemetry (see Linklater *et al.*, 2006 for details on horn implant methods). We studied all members of the recently introduced (October, 2004) population: seven adult females and eight males (four adult and four sub-adult) (N = 15). Due to the terrain and habitat occupied by this species, and the typically long distances from the road network to where individuals spent their time, we recorded the majority of locations on foot, using a Garmin 12 GPS (Garmin International Inc., Kansas, USA). This allowed us to approach the rhino (on average within 40 m), decreasing the error associated with triangulating GPS locations (Saltz 1994). We could expect an average GPS error reading of 10 m in a closed canopy habitat type and less than 10 m in more open habitats (Wing *et al.* 2005). The error of our coordinates for rhino movements, home range sizes and habitat patches is minimal and falls within the error of the GPS. We attempted to remain undetected by the rhino, recording their initial behaviour at sighting, the time of day and a GPS location, before leaving the location.

2.3.3. Black rhino habitat carrying capacity scores

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

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

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

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

2.3.4. Individual habitat selection

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

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

i) Habitat selection - We established an individual's preference index for each habitat by dividing the proportion of its area in the rhino's KHR by the proportion available:

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

An index value less than one indicates selection against, a value around one indicates no selection, while a value above one indicates selection for (Manly *et al.* 2002). We therefore split these proportions into three categories for analyses; 0 – 0.75 selection against, 0.76 – 1.25 no selectivity and > 1.25 positive selection. Design 2 studies usually use the area of the habitat types in the home range relative to the area of habitats available in the total study area (Thomas & Taylor 2006). However, we questioned this method for two reasons, firstly the study area is arbitrarily defined and with the largest KHR of a black rhino (32 km^2) on the reserve being less than 20 % the size of the reserve (180 km^2), it did not seem possible that the whole area was available to the rhino to include in a single home range. Secondly, there was an overlap among the KHRs of males that utilised similar areas (a single adult male with one or two sub-adult males), but a lack of overlap, especially of the core 50 % KHR area, among all neighbouring males. Male rhino were probably being excluded from these areas through territorial conflicts (Adcock 1994). The females also seemed to display 'clusters' (sensu Lent & Fike 2003), and either utilised areas similar to the clusters of males already mentioned or to other females. This sharing or utilization of similar home range areas by black rhinos has been noted in other populations (Conway & Goodman 1989, Tatman *et al.* 2000, Lent & Fike 2003).

We therefore decided to redefine the availability of habitats for males and females within these clusters to help us understand population patterns and variation in the response of individuals to changing availabilities of habitat types (Mysterud & Ims 1998, Osko *et al.* 2004). For females we considered a minimum convex polygon (MCP) around all the black rhino KHRs whose core areas overlapped into her KHR, as available. We did the same for males, but excluded those areas that extended into a neighbouring male's KHR (Fig. 2.2). This method would include areas that male and females could potentially shift their KHR to. If there was a relatively small unused area between the fence and MCP it was included in the available area for both the males and females. This variation in our assessments of available habitats for each of the rhinos across the reserve reflects actual conditions. Another option would have been to use virtual species modelling.

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

$$\text{Habitat preference index} = \frac{[\text{\# of locations in habitat type / total \# of locations}]}{[\text{area of habitat type in KHR / total area of KHR}]}$$

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

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

2.3.5. Correlation between individual rhinos' selection and habitat values

We ranked the habitats within each rhino's KHR, in ascending order, according to its CC score; we gave the habitat with the highest CC score a rank of one. The CC scores we used were the absolute values; we did not weight them according to the area they encompassed. We ran Spearman rank correlations between the CC habitat ranks and the habitat preference ranks, at each selection level (i – iii) for each rhino. The use of null-hypothesis testing and p-values (Stephens *et al.* 2005) allowed us to determine whether the rhinos were selecting habitats in relation to the estimated carrying capacity scores of the habitat types at any level. We used an alpha of 0.05 for all statistical analyses, which were performed using SPSS 15.0 (SPSS Inc., Illinois, USA).

2.4. Results

2.4.1. Individual habitat selection

Individual black rhino, on MGR, generally did not select habitats according to their availabilities at the three scales of selection we tested, illustrated by the range of habitat selection indices in Fig. 2.3 (a – c). They were therefore positively selecting some habitats available to them while selecting against others. There is a large amount of variation shown amongst the individuals' selection (Fig. 2.3). This is an interesting result beyond the scope of this manuscript's discussion and we are pursuing this in another study.

2.4.2. Correlation between rhino habitat ranks and CC ranks

The habitat types within individual black rhino KHR’s (habitat selection) were not selected by the rhino according to their value determined by the BrCC-Model v2_1 scores (all individual correlation tests were non-significant, other than one individual (F1)) (Table 2.2). Within their KHR (habitat preference) individual black rhino did not prefer habitats with higher CC scores (all individual correlation tests were non-significant) (Table 2.2). Black rhino did not selectively browse in those habitats with higher CC scores (all individual correlation tests were non-significant, other than one individual (DM3)) (Table 2.2).

2.5. Discussion

An a priori carrying capacity (CC) model, based largely on the quantity of suitable available browse, could not predict black rhino habitat selection at three different scales of selection. We would expect negative density dependent resource utilisation by black rhino, and for this low density population to prefer those habitats within their home ranges, within which we assume ideal-free habitat selection (Fretwell & Lucas Jr. 1970) that have abundant levels of favourable browse. Conversely, these black rhino did not rank their diurnal habitat preference according to the CC value we placed on the habitats, even at this low population density. The diurnal locations included all activities, yet when we based the rhinos’ selection of habitats according to those in which they browsed in more frequently at night, when most browsing takes place (Goddard 1967, Owen-Smith 1988; unpublished results) and canopy cover for bedding sites is not a confounding constraint on selection (Tatman *et al.* 2000; pers. obsv., Rice & Jones 2006), there was still no correlation between their selection and the estimated CC value of the habitat.

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

1. Animals base their selection of habitats on a myriad of factors (Aebischer *et al.* 1993, Luck 2002, Morris 2003b, Buk 2004, Van der Heiden 2005, Chalfoun & Martin 2007) and not just the availability and quality of browse. Habitat heterogeneity, slope,

rockiness and the distance to water, roads and fences all play a role in habitat selection by black rhino (Buk 2004, Van der Heiden 2005). As we have demonstrated, using a simple predictive model which assigns value to a habitat without regard to any factors other than those relating to browse quality and abundance would be flawed.

2. Density dependence may influence plant level selection (Kausrud *et al.* 2006) and, hence, the selection of patches/habitats. Being selective browsers (Oloo *et al.* 1994, Muya & Oguge 2000, Ganqa *et al.* 2005) black rhino in the Fish River Game Reserve were able to select only highly preferred plant species due to an abundance of available forage (Ganqa *et al.* 2005). A similar process may be occurring in the low density population of MGR. Here, individual black rhinos are selecting patches/habitats with highly preferred forage, but not necessarily with high abundances of browseable species (Ganqa *et al.* 2005), which is used as the base indicator of habitat quality in most CC estimates (Bothma *et al.* 2004, Adcock 2006). This highlights that we cannot interchange abundance and quality of resources when predicting habitat use of a selective forager. Future research may reveal whether a sliding scale of black rhino browse utilisation based on preference and population density exists. Highly preferred browse may be negatively density-dependent and low-preference browse being positively density-dependent, as noted in domestic sheep *Ovis aries* at a diet level (Kausrud *et al.* 2006).
3. Animals select habitats and resources at various scales (Johnson 1980, Chalfoun & Martin 2007). The scale at which we make assessments of habitat quality may not align with that of the animal's selection. In conjunction with (2) we noted a variation in habitat selection among black rhino on MGR (Fig. 2.3; unpublished results), which would indicate the rhino were potentially making a common selection at a finer scale than the three levels we tested. Being selective foragers (Oloo *et al.* 1994, Muya & Oguge 2000, Ganqa *et al.* 2005) predictions of selection would benefit from analyses at a fine scale, thereby removing the variation amongst individuals that has been noted at larger scales of selection.
4. Access to resources differs amongst individuals (Mysterud & Ims 1998, Garshelis 2000, Osko *et al.* 2004) not only at a home range level, but also within home ranges

(Wittemyer *et al.* 2007). CC estimates of habitat quality are based on the concept of ideal-free distribution, assuming equal access to resources by all members within a population (Fretwell & Lucas Jr. 1970). We factored this into the habitat selection level for black rhino, by assessing their selection of habitats within clusters (see Materials and Methods). However, in a species with a dominance hierarchy, like black rhino (Frame 1980; pers. obsv., Adcock 1994), certain individuals could restrict access and 'hoard' resources from other cluster 'buddies'. Dominant elephant groups have displayed such behaviour during times of resource scarcity (Wittemyer *et al.* 2007). Further insight into the social dynamics within the clusters may yield interesting results in this regard.

5. Interspecific competition can play a role in habitat selection (Garshelis 2000), not only through competition for resources, as seen in black rhino (Birkett 2002) and African elephant (Kerley & Landman 2006), but also by the presence of a physically dominating species (Wasserberg *et al.* 2006). Social interactions between African elephant and rhino can result in conflict, in some incidences even leading to fatalities of rhino (Slotow *et al.* 2000). It is interesting to note there were no combined elephant and black rhino sightings during the study period, indicating black rhino were potentially avoiding areas when elephant were present. There is a relatively dense population of elephant on MGR (~0.6 / km^2) (Slotow *et al.* 2005) that may negatively influence black rhino movement patterns and hence habitat selection. Future research into the influence of interspecific interactions and habitat selection among mega-herbivores may yield interesting insights into competition between these two species.

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

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

Table 2.1 Habitat types of the Mun-ya-Wana Game Reserve according to van Rooyen and Morgan (2007). The un-weighted carrying capacity (CC) score, according to the BrCC-Model v2_1, and its rank are shown for each habitat.

Habitat type		CC score rhino/km2 (rank)
(i)	Old fields	0.590 (1)
(ii)	Acacia borlea shrubland	0.333 (2)
(iii)	Ziziphus mucronata bushland on slopes	0.332 (3)
(iv)	Mixed Acacia broad-leaved shrubland and woodlands	0.262 (4)
(v)	Acacia luderitzii thickets and woodlands	0.229 (5)
(vi)	Acacia tortilis woodlands	0.225 (6)
(vii)	Terminalia sericea woodland on pallid sands	0.210 (7)
(viii)	Riparian woodlands and forests	0.194 (8)
(ix)	Spirostachys africana woodlands	0.191 (9)
(x)	Combretum apiculatum Lebombo open woodlands	0.170 (10)
(xi)	Floodplain grasslands	0.164 (11)
(xii)	Wetlands	0.164 (11)
(xiii)	Pteleopsis myrtifolia closed woodlands	0.115 (13)
(xiv)	Palm veld	0.110 (14)
(xv)	Sand forest	0.056 (15)
(xvi)	Grasslands on clay soils	0.020 (16)

(See ESM 1 for a detailed description of the habitat types)

Table 2.2 Spearman rank correlation (r_s) tests, indicating no correlation between individual black rhino habitat preferences and carrying capacity values, according to the BrCC-Model v2_1, on the Mun-ya-Wana Game Reserve, other than the two results in bold.

	Habitat selection[2]			Habitat preference[5]			Browse level selection[6]		
Rhino[1]	N[3]	r_s	*P*[4]	N	r_s	*P*[4]	N	r_s	*P*[4]
F1	**12**	**0.59**	**0.04**	8	0.62	0.10	7	0.64	0.12
F2	12	0.49	0.10	9	0.44	0.23	7	0.19	0.69
F3	9	-0.52	0.15	8	0.34	0.41	6	0.09	0.87
F4	9	-0.27	0.49	9	-0.14	0.73			
F5	12	0.20	0.52	9	0.15	0.70	7	-0.54	0.22
F6	9	-0.18	0.65	8	0.20	0.64			
F7	12	-0.14	0.67	7	0.38	0.40	5	0.00	1.00
DM1	9	-0.44	0.23	8	-0.05	0.91	8	0.40	0.32
DM2	9	0.37	0.33	9	0.25	0.51	5	0.50	0.39
DM3	11	0.55	0.08	10	0.32	0.36	**10**	**0.66**	**0.04**
DM4	9	0.17	0.67	9	0.07	0.86	7	-0.61	0.15
SM1	9	-0.11	0.78	7	-0.18	0.70			
SM2	11	0.30	0.37	10	0.42	0.23	10	0.59	0.07
SM3	9	-0.23	0.55	9	-0.08	0.83			
SM4	11	0.52	0.11	9	0.70	0.04	5	0.15	0.81

[1] F = female, DM = dominant male and SM = subordinate male, the number identifies individual rhino.

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

[3] N = number of habitat types available.

[4] Significant $P \leq 0.05$

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

[6] The selection of habitats made by a rhino for feeding in at night.

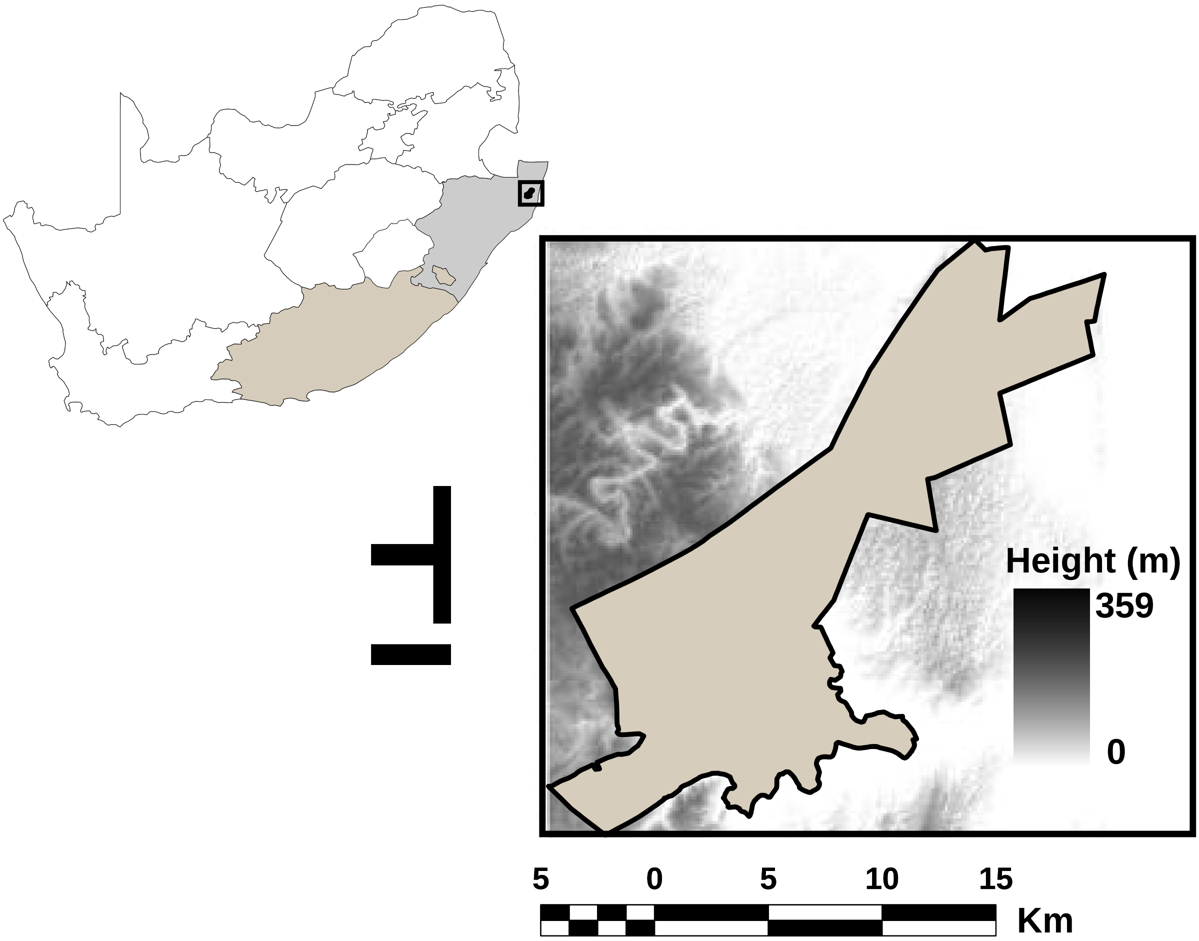

Figure 2.1 A digital elevation map of the Mun-ya-Wana Game Reserve showing its location in KwaZulu-Natal, South Africa.

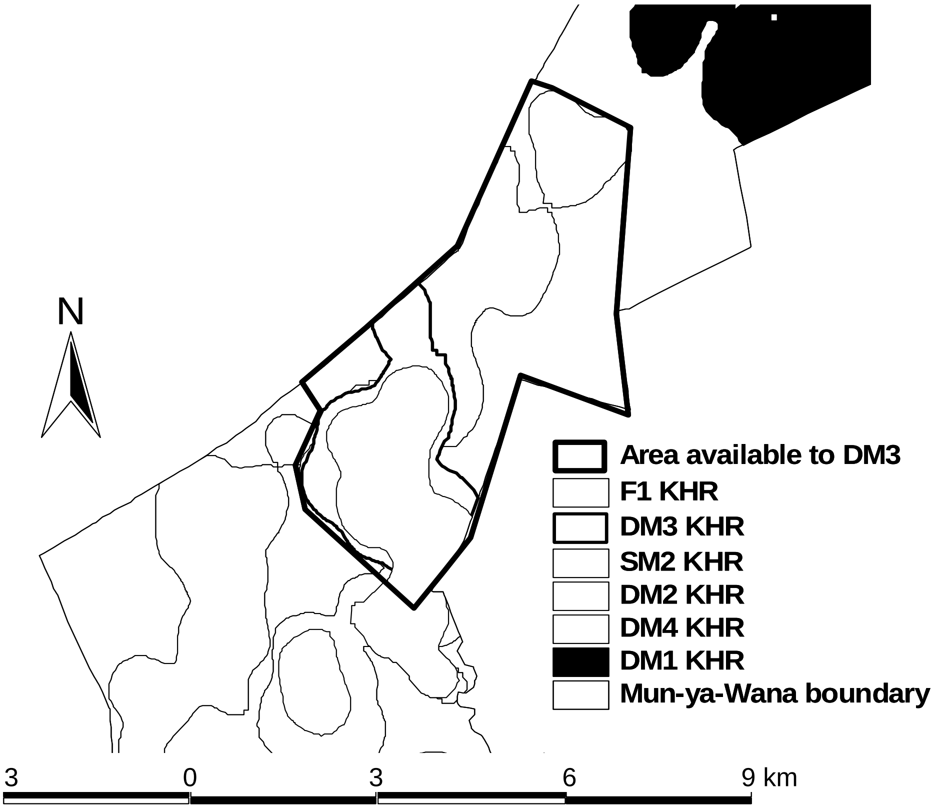

Figure 2.2 The method used to determine the area considered available for habitat selection for a black rhino in the Mun-ya-Wana Game Reserve. A minimum convex polygon was drawn around an individual black rhino's (here DM3) kernel home range (KHR) and that of any other black rhino which had a core range overlapping into its KHR (here F1 and SM2), excluding those areas within a competing males KHR (here DM1, DM2 and DM4). We used our discretion in allocating unused areas to the availability polygon between KHR's and the fence line. Rhino are designated by their sex class (F = female, DM = dominant male, SM = subordinate male) and identity number.

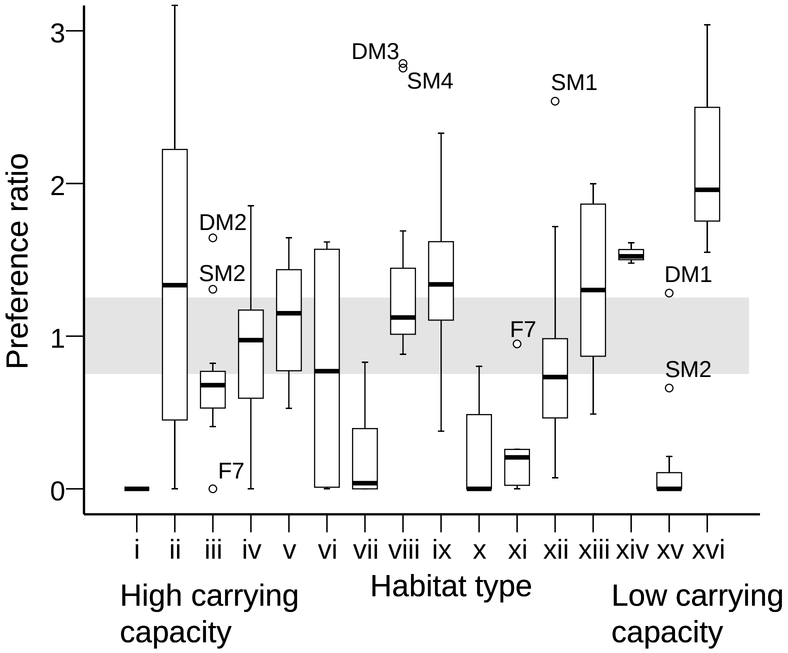
Preference ratio
3
2
1
0
DM3
SM4
SM1
DM2
SM2
F7
DM1
F7
SM2
i
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
xiii
xiv
xv
xvi
Habitat type
High carrying capacity
Low carrying capacity

Figure 2.3 (a)

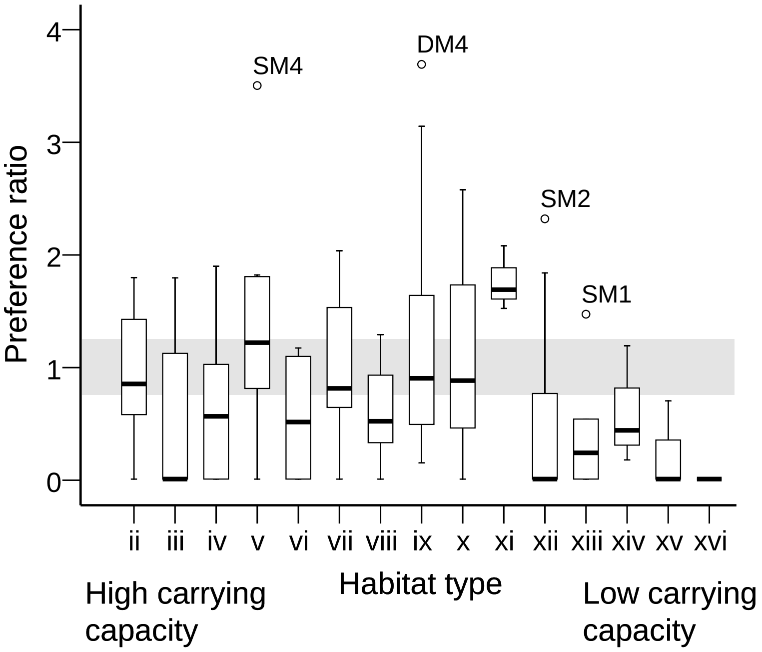
4
3
2
1
0
Preference ratio
SM4
DM4
SM2
SM1
ii
iii
iv
v
vi
vii
viii
ix
x
xi
xii
xiii
xiv
xv
xvi
High carrying capacity
Habitat type
Low carrying capacity

Figure 2.3 (b)

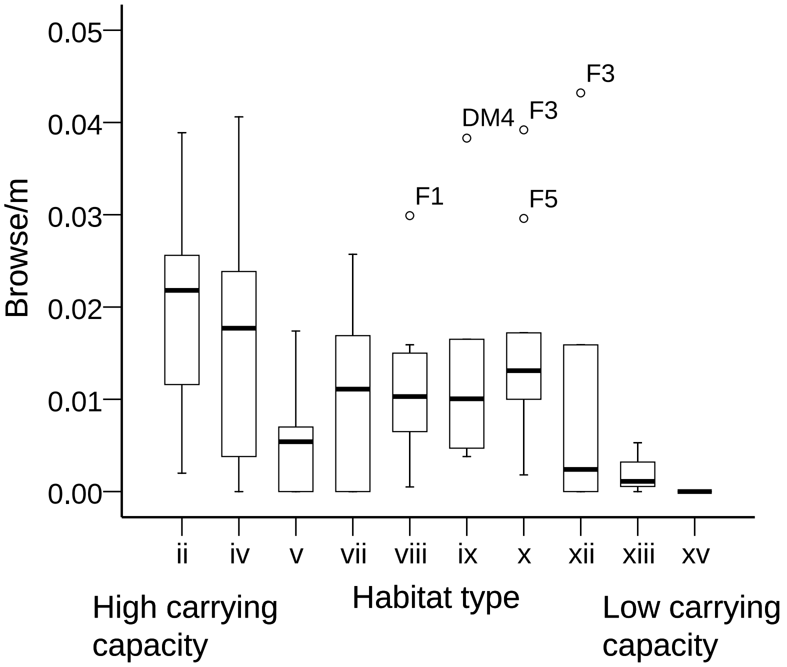

Figure 2.3 (c)

Figure 2.3 The black rhino habitat selection on Mun-ya-Wana Game Reserve. Variation in (a) habitat selection relative to habitat availability for their kernel home ranges, (b) preferences according to habitat utilization within their kernel home ranges and (c) their preference of habitats for browsing in at night are illustrated. In graphs (a) and (b) the three selection groups (against, none and positive) are differentiated by the shaded area. We ordered the habitat groups from the highest to lowest carrying capacity score, ranked according to the BrCC-Model v2_1, and omitted those habitats which were not available. Data are box plots: thick line within box is the median preference ratio; box represents the 25th and 75th percentiles; and the whiskers indicate the 5th and 95th percentiles. The minimum number of rhinos using each habitat type presented is three. Outliers are designated by their sex class (F = female, DM =

dominant male, SM = subordinate male) and identity number. In (c) we removed the extreme outliers, SM2 (Habitat v; 0.137) and F3 (Habitat ix; 0.080), from the graph.

CHAPTER 3

Black Rhino circadian variation in spatial and behavioural habitat utilisation

3.1. Summary

We question whether current methods of analysing mainly diurnal location data of animals provide accurate ecological or conservation conclusions. We determined the diurnal home ranges of black rhino *Diceros bicornis* to assess whether there was any habitat preference for two important different behaviours, browsing and resting. We followed the tracks of black rhino nocturnal movements to assess whether they selected or avoided habitats for browsing in at night. We then determined whether there were significant nocturnal movements of rhino outside of their diurnal ranging areas. During the day some black rhino selected habitats based on browsing or resting requirements, while other rhino did not base their selection of habitats for these activities. However, at night all the rhino exhibited a similar behaviour, by all selecting habitats to browse in. Black rhino moved significantly outside of their diurnal core and home ranges at night, and some of the areas the rhinos browsed in during the night were spatially distinct from those used during the day for browsing. This study highlights a circadian variation in habitat use for different behaviours. Excluding nocturnal data from home and browsing range analyses would provide inaccurate results for black rhino habitat use. We encourage the continued use of backtracking techniques to incorporate nocturnal ranging and browsing habits of black rhino. We suggest that before informed management decisions can be made that there is a need for adequate knowledge of the variation in a species' habitat utilisation and movements during both the day and night.

3.2. Introduction

Circadian shifts in a mammal's ecology potentially make interpretations using only diurnal activities, habitat selection and ranging behaviour inaccurate. Factors such as predator-prey relationships, luminosity, temperature, rainfall patterns and access to resources (Erkert & Kappeler 2004, Donati & Borgognini-Tarli 2006) drive the majority of species' circadian patterns (Halle & Stenseth 2000). For example, temperature changes across the day and into the night affects the movement patterns and habitat selection of large-bodied species such as *Loxondonta africana* African elephant (Kinahan *et al.* 2007). Assessing whether there is any circadian variation in the movement patterns and selection of species is the first step in fully understanding species ecology. Following this, sound management-orientated research on how these factors affect animals, and the decisions they make, will aid in the conservation and management planning of ecologically significant species.

Black rhinoceros *Diceros bicornis* spend a large portion of the day inactive (Schenkel & Schenkel 1969, Rice & Jones 2006), which means it is possible that they utilise areas outside of their diurnal home ranges at night (Conway & Goodman 1989), when they spend most of their time browsing (Goddard 1967, Brown *et al.* 2003). Since black rhino are not only a critically endangered species (IUCN 2008) but also an ecologically important species we need to establish whether current monitoring and habitat studies based on diurnal movements of black rhino are accurate.

In South Africa the Black Rhino Range Expansion Project moved 15 black rhino onto the Mun-ya-Wana Game Reserve (MGR) in KwaZulu-Natal (Sheriffs 2003). This provided a known population of black rhino, which was easily identifiable and located. It is important that the scale and set of resources being analysed are classified (Orians & Wittenberger 1991, Bowyer & Kie 2006), because animals have different orders and scales of resource selection (Johnson 1980, Bowyer & Kie 2006). We previously noted individual black rhino on the MGR to select specific habitats within their home ranges during the day (Morgan *et al.* 2009). We therefore decided to analyse the highest order of habitat selection, which within small reserves is third order selection, pertaining “to the usage made of various habitat components within the home range” (Johnson 1980). Our objectives in this study were to (1) gain a better understanding of behavioural habitat selection of the black rhino population on MGR during the day and during the night and (2) to establish whether there are any variations in black rhino movements during the day and night. We interpret the conservation implications of such variation.

3.3. Materials and methods

3.3.1. Study area

The South African Mun-ya-Wana Game Reserve (MGR) (27^o 40‘– 27^o 55’ S and 32^o 12’ – 32^o 26’ E, 180 km^2), was established in 2004 with the dropping of fences between a group of already existing game reserves (Fig. 3.1). The MGR is situated at the southern end of the East African coastal plain, between the Lebombo Mountains and the vegetated sand dunes abutting the ocean. The altitude on the reserve varies between 4 – 340 m a.s.l. The region experiences dry warm winters from April to September and hot wet summers from October to March. During 2005 the rainfall was 841 mm, which falls just above the ten year mean (± standard error) annual rainfall of 758 ± 65 mm (MGR, unpublished data). The climate is typified by hot/wet summers and dry/warm winters. A detailed vegetation map of the MGR was developed, based primarily on the woody layer (N. van Rooyen and S. Morgan, Mun-ya-Wana Game Reserve, unpublished report; Appendix 2).

3.3.2. Study species

Black rhino are odd-toed ungulate browsers, with adult weights reaching up to 1 600 kg (Morkel & Kennedy-Benson 2007). They utilise a wide variety of woody forage across Africa (Kotze & Zacharias 1993, Ganqa *et al.* 2005, Adcock 2006) while being locally selective in their choice of species (Oloo *et al.* 1994, Muya & Oguge 2000, Ganqa *et al.* 2005). Both sexes of black rhino are solitary in their movements and establish individual home ranges, although they will socialise often with other black rhino that have overlapping home ranges (Lent & Fike 2003). Adult bulls can behave territorially, with evidence suggesting a variation in this behaviour across the continent (Goddard 1967, Emslie & Adcock 1994, Adcock *et al.* 1998).

3.3.3. Data Collection

We collected location data of the rhinos (n = 15) from January to December 2005. There were seven females, four adult males and four sub-adult males, all of which we located with the aid of VHF radio telemetry (see Linklater *et al.*, 2006); as satellite technology has yet to be developed for black rhino. Due to the terrain and habitat utilised by this species, and the typically long distances of their locations from the road network, we made the majority of sightings on foot. This also helped with accurate activity readings, because it was easier to view the rhinos without disturbing them while on foot. We were limited to small numbers of rhino to study due to the time involved in locating and the difficulty of tracking black rhino.

For diurnal sightings we attempted to make sightings of each rhino once every four days. The rhino were located sequentially until we had found each one, where upon the list was started again. In some cases rhino were located incidentally, following which we recorded their locations and added them to the dataset. The majority of these sightings were made from midday till sunset, because the nocturnal tracks were being recorded in the morning. We also used the morning locations of the rhino before we started tracking them as a diurnal sighting. Due to the temperament of the rhinos, the density of the bush, and the frequency of sightings, we would try to remain undetected, and record only the initial behaviour observed, time of day and GPS location.

To record nocturnal movements a single rhino was located as close to sunrise as possible and backtracked from that location along the tracks it made in the ground. We selected eleven individuals to track: five females, four adult males and two sub-adult males. We chose rhino based on sex and the ease with which we could track them. Again, we tracked the rhino sequentially and we attempted to locate and track each rhino’s nocturnal movements equally. However, due to environmental conditions and faulty transmitters not all individuals were tracked with equal frequency, in total we managed to complete over 180 km of backtracks (Table 3.1). This method allowed us to determine where the rhino moved through the night and its activities along the way.

Coordinates were recorded every 8 seconds along the rhino track, to represent the path that the animal took, using a Garmin 12 GPS. We found this period gave us the optimum number of points along a track for the time we were walking, due to a limit of memory on the GPS unit. We made a further GPS waypoint for each browsing event; black rhino browse is recognisable as a 45° cut in the twig (Joubert & Eloff 1971) and we could discern fresh browse from day old or older browse by the colour and wetness. We made cut samples of the various species to establish what fresh browse would look like and how it changed as it dried. There is a probability we underestimated the consumption of grasses and certain annuals using the backtracking method (van Lieverloo *et al.* 2009), but we believe for the purposes of this study we managed to collect a large enough sample and that our error would have been spread equally across habitat types. We also recorded a waypoint for resting, indicated by any point on the track where the rhino had lain down.

3.3.4. Data Analysis

For the purpose of this study we used the 16 habitat types identified by van Rooyen and Morgan across the reserve. Due to the high heterogeneity of habitats across the reserve and degrees of interindividual variation in habitat (Morgan *et al.* 2009) and browse selection (Chapter 5) by black rhino, we analysed all the data at an individual level and made no comparisons between individual rhino and the specific habitats they selected in this study. We were interested in whether black rhino were utilising habitats indiscriminately during the day and night for browsing and resting in (irrespective of the actual habitat selected). We did not analyse any of the data seasonally because of the small numbers of tracks completed in each season.

We have previously shown that black rhino on MGR preferred certain habitats over others during the day (Morgan *et al.* 2009). We based our previous analysis on preference indices that calculated the proportional utilisation of a habitat relative to the proportional area available to the rhino (Morgan *et al.* 2009). Here, we go into more detail and establish whether individual rhino favoured habitats for browsing or resting in during the day. At each sighting of a rhino we recorded whether it was socialising, mobile, drinking, standing, browsing or resting. There were, however, incidences when we either disturbed the rhino or were unable to see it, and therefore could not take a behavioural record. We relocated disturbed rhino 3 to 4 days after disturbance, during which time we felt the impact of the disturbance had no bearing on their location or behaviour. We removed rhino F3 from the diurnal habitat selection analysis due to her large number of unknown behavioural sightings, which was largely due to her temperament and tendency to occupy dense thicket patches during the day.

To determine whether any one habitat type's terrain or structure biased our ability to record an activity reading for the rhino we ran a Pearson correlation test between the total and the number of unknown behavioural sightings for each individual across the habitats. There was a significant correlation, meaning we could analyse the data without concern for biases resulting from unknown behavioural sightings in certain habitats. The exception was rhino SM1 which had a bias in the distribution of its unknown sightings (Pearson $r = 0.535$ and $P = 0.216$), meaning we could not analyse its data using the methods outlined below.

If black rhino favour certain habitats for either browsing or resting, we would expect a non-significant correlation in the frequency of observations of behaviours across the habitats relative to the total number of locations in a habitat. We ran a Pearson correlation test for each rhino between the distribution of sightings across the habitats and the distribution of (1) their browsing locations and (2) their resting locations. Using this method we steered away from needing to incorporate sometimes arbitrary measures of availability and rather looked at the spatial distribution of the rhino and whether an individual's decision to select a habitat was governed by its need to browse or rest. and interindividual variation in selection (Chapter 5) we do not go into the specifics of the habitat types selected, but rather whether decisions by these rhino to occupy specific habitats was based on their browsing or resting requirements.

From tracks we completed of rhino movements from sunset to sunrise the following day (n = 8) we were able to determine an average movement rate (± standard error) for the rhino of 0.26±0.04 km/hr (maximum of 0.47 km/hr). This is a conservative calculation because we removed one hour for potential resting stops, although we only located two resting spots along the eight tracks completed. Using the maximum movement rate as a conservative guide we removed tracks covering less than 500 m and the first 500 m of each backtrack from this analysis, effectively the last hour of rhino movement, to ensure we encapsulated nocturnal rather than crepuscular activities. The average distance (± standard error) of each track was 2.23±0.27 km, which effectively would translate to over 8 hours of nocturnal rhino movement. To calculate whether the rhinos preferred certain habitat types for nocturnal browsing we compared the expected and actual number of browse points per m (br/m) walked by each rhino in every habitat. We calculated the expected values by the proportion of overall track length in a habitat type multiplied by the total number of browse points. We performed a Log-likelihood G-test (Zar 1999) to establish whether there were significant differences between the actual and expected number of br/m walked. To overcome the problem of dividing by 0 we used a value of 0.1 browse points in those habitats with no recorded browsing (Aebischer *et al.* 1993). Due to the infrequency of the tracked rhino resting at night we could not make statistical inferences as to whether the rhino were selecting specific habitats to rest in at night.

To establish the variation in the day and night ranging movements of the rhino we first calculated diurnal home ranges for each of the 15 rhino from their the diurnal location data, using the Animal Movement extension (Hooge *et al.* 1999) in Arcview ® 3.2. To illustrate the diurnal spatial utilisation by the rhino we established a core range which is commonly estimated to be a 50 % probability kernel (Jácomo *et al.* 2009, Weston *et al.* 2009, William *et al.* 2009) and home range (95 % probability kernel). We used this technique so probability of occurrence could be made with nocturnal locations and for comparison to recent studies of black rhino (Tatman *et al.* 2000, Lent & Fike 2003, Reid *et al.* 2007). The mean number of locations per individual for this study was 90 (min of 49), which is greater than the recommended 30 locations needed to establish an annual home range that will be comparable to other studies (Lent & Fike 2003). Using the same method we established a 95 % probability kernel for each rhino using only the diurnal browse sightings of a rhino (diurnal browse range).

To determine variations between black rhino diurnal and nocturnal movements we selected a single track point and a single browse point from each individual's night-tracks. We selected a point located as far from the centre of its range as possible. Since the numbers of nocturnal tracks were far fewer than the diurnal locations, we felt justified in selecting those locations far from the centre, as they are probable locations had we searched for the rhino at night. We used a Log-likelihood G-test to establish whether there were significant differences between the numbers of an individual's selected nocturnal points outside the diurnal home and browse ranges against an expected value of 50 % of the number of points for the core home range and 95 % of the number of points for the home and browse ranges. Since the nocturnal data are limited the results from this analysis would only suffice as an indication of nocturnal and diurnal variation.

3.3.5. Statistical analyses

We performed all statistical tests in SPSS 15 (SPSS Inc., Illinois, USA).We used an alpha of 0.05 for all analyses and the assumptions of parametric tests were tested and satisfied.

3.4. Results

We studied the rhino's habitat use during the day and night and compared this selection spatially. We tested each rhino individually and did not test whether they were selecting similar habitats to one another due to the high heterogeneity of available habitats and noted levels of interindividual habitat selection (results shown here and Chapter 5).

Some rhino strongly selected habitats to browse or rest in during the day, while others showed no preference for habitats to browse or rest in (Table 3.2). To help us understand these results we eliminated the effect of different habitat availabilities on selection (Osko *et al.* 2004) by grouping rhino into clusters of individuals with overlapping core home ranges, as discussed in a previous study of this population (Morgan *et al.* 2009). It seems the difference in selection was not specific for males or females, or for clusters of rhino utilising the same areas (Table 3.2). At night rhino browsed more frequently along their route in certain habitats while traversing through others (G-Test, all $P < 0.001$). Since we were interested in decisions governing habitat utilisation we will not detail the specifics of the habitat types selected here.

Black rhino had a significant number of nocturnal locations outside of their diurnal core range ($G_8 = -34.67$, $P < 0.001$) and home range ($G_8 = -28.32$, $P < 0.001$) (Table 3.1). The rhino also had a significant number of nocturnal browse locations outside of their diurnal browse ranges ($G_8 = -31.59$, $P < 0.001$) (Table 3.1).

The entire population was released four months prior to the study period and it could be argued that the variation shown in the circadian patterns of these rhino was due to the rhino still settling into the reserve. We, however, believe that the differences noted here are biologically significant because:

1. Black rhino show marked decreases in displacement patterns within 15 days of being released and by day 25 are past the initial settlement phase (Linklater & Swaisgood 2008).
2. Following the initial settlement phase any sporadic lengthy travels of the rhino outside of their home range during the settling phase (Linklater & Swaisgood 2008) are accounted for by using a testing value of 95 %, thereby excluding occasional sporadic events.
3. We analysed their movement patterns across the full year, not taking into account potential range shifts (Lent & Fike 2003) or settling range shifts, thereby maximising their diurnal ranging areas over the year, meaning any difference we noted between the day and night would have been biologically significant.
4. The daily time frames for resting and browsing (SM, unpublished data) and the diurnal home ranges (Table 3.2) for the MGR black rhino population are similar to those of black rhino in other areas (Ritchie 1963, Goddard 1967, Owen-Smith 1988, Conway & Goodman 1989, Lent & Fike 2003, Van der Heiden 2005), indicating the rhino were following similar ranging behaviour, albeit diurnally.

3.5. Discussion

We now have an idea of black rhino movements across an entire 24 hr period and that during the night, black rhinos often make movements out of their diurnal core and home ranges. This is in support of Conway and Goodman (1989), who suggested that black rhino day and night ranges could vary, and they included known nocturnal drinking points that were not recorded in diurnal sightings of certain individuals to give ‘logical limits’ to the ranges (Conway & Goodman 1989). We may, therefore, underestimate or skew home and core ranges without the inclusion of nocturnal data. These differences would have potential management implications because wildlife managers may use adult male home ranges as an indication of carrying capacity (Emslie & Adcock 1994) and core ranges as indicators of habitat use patterns (Tatman *et al.* 2000, Lent & Fike 2003, Reid *et al.* 2007).

There are a range of factors that could potentially influence an individual animal’s circadian patterns and habitat utilisation, with some affecting diurnal movements, and others nocturnal movements of the same animal (Metcalfe *et al.* 1999, Donati & Borgognini-Tarli 2006, Hill 2006, Tattersall 2006). Here we were unable to address the various factors causing these variations due to differences in the way we collected nocturnal and diurnal data and the limited nocturnal data we had for individuals. We found that all black rhino selected habitats during the day (Morgan *et al.* 2009). However, we expected them to all select habitats specifically for diurnal resting or browsing (Tatman *et al.* 2000, Van der Heiden 2005), while in fact only half of them did so. We believe that some black rhino were optimising their movements, and thereby selected habitats that suited both their browsing and resting requirements during the day, hence the lack of a specific selection within their diurnal home range area for either of these activities. We did not take into account all factors affecting black rhino movement, for example water points and distances to road systems (Buk 2004, Van der Heiden 2005), which may have had an effect on their selection. From the results in this study it is unclear why there is a variation in this selection amongst individuals, even amongst those exposed to the same habitat types.

In contrast, and although the data were collected and analysed in different manners, we suggest black rhino make a specific selection of habitats to browse in at night and may exhibit a degree of variation in diurnal and nocturnal browse areas. The individuals in the MGR black rhino population had long rest periods during the day (SM, unpublished data), while we observed only evidence of short resting spots along their nocturnal tracks while recording extensive browsing sessions throughout the night. This, coupled with evidence from other studies that have shown that black rhino browse predominantly at night (Schenkel & Schenkel 1969, Tatman *et al.* 2000, Rice

& Jones 2006) and the potential variation in day and night resting requirements (for example shade cover) means they could be more selective of habitats based on their browsing requirements. It is likely that these factors drive the variation in their selection of areas to browse in during the day and night. We would be able to confirm this by being able to collect data similarly during the day and night. However, following rhino through-out the course of the day is difficult without disturbing them and back-tracking their entire day's movement is not possible. We are also currently restricted in our abilities to record behavioural data from a number of rhino in one night. Hopefully future developments in satellite and GPS technology will allow us to gather consistent data through the day and night.

Using only diurnal foraging browse points as an indication of specific browse selection will yield inaccurate results of a rhino's complete utilisation. Backtracking techniques to collect foraging data are commonplace (Ganqa *et al.* 2005, van Lieverloo *et al.* 2009), and the usual technique of tracking from the early morning would mean most studies include portions of crepuscular and possibly nocturnal activities. We encourage the continued use of this technique, recommending researchers to incorporate and acknowledge the inclusion of nocturnal browsing. Black rhino browsing assessments not using backtracking techniques (Oloo *et al.* 1994, Muya & Oguge 2000) would benefit largely by setting transects randomly (Emslie & Adcock 1994), rather than in 'known' rhinos areas based on diurnal sightings (Muya & Oguge 2000). This would enable researchers to encompass nocturnal and diurnal browse events indiscriminately.

In the past many wildlife management decisions have been implemented only once a species' has shown declines in distribution and population sizes and growth rates (Morris 2003b). However a better method is to rather follow a pre-emptive adaptive approach using habitat utilisation and behavioural cues as indicators of population stability (Morris 2003b). Wildlife conservation managers therefore have a vital task evaluating and monitoring habitat use, which is essential for understanding limitations that the environment can impose on these animals (Adcock *et al.* 2001). Previously, these evaluations have largely been done using diurnal sightings as an indication of habitat utilisation. However, different factors may affect day and night decisions made by the same animal (Hill 2006, Tattersall 2006) and we need to be aware of resultant circadian variations on an animal's movement and habitat selection. Variations in movements and selection are not restricted to only day/night differences, but may occur throughout the day or night due to a variety of selection forces (Kronfeld-Schor & Dayan 2003), including predation (Druce *et al.* 2006), competition (Wasserberg *et al.* 2006) and ambient temperature (Kinahan *et al.* 2007). To encompass these differences managers and researchers will need to develop innovative techniques to monitor and study these species more effectively.

Table 3.1 The extent of black rhino nocturnal movements overlapping with diurnal ranging areas. The size (mean ± standard error for totals**)** of black rhino diurnal core (50 % probability kernel) and home ranges (95 % probability kernel) and the number of nocturnal tracks falling completely within these ranges on the Mun-ya-wana Game Reserve. The number of nocturnal tracks which had all its browse points falling completely within each individual's 95 % diurnal browse range is shown. We calculated expected values based on the relevant kernel's probability of occurrence.

Rhinos [a]	n [b]	Core range (km^2)	Nocturnal points in core range		Home range (km^2)	Nocturnal points in home range		Nocturnal browse points in browse range
			Expected	Actual		Expected	Actual	Actual
F1	16	2.2	8	3	18.4	15.2	12	13
F2 [c]	3	2.1	-	-	19.5	-	-	-
F3 [c]	5	1.2	-	-	12.3	-	-	-
F4	0	4.6	-	-	28	-	-	-
F5	11	2.8	5.5	1	18.8	10.5	6	7
F6	0	1.3	-	-	15.9	-	-	-
F7	8	1.7	4	1	10.8	7.6	8	4
F average	43	2.27	17.5	5	17.67	33.3	26.0	24.0
M1	8	5.5	4	1	20.7	7.6	8	3
M2	9	4.5	4.5	2	24.8	8.6	6	5
M3	11	4.9	5.5	1	16.4	10.5	7	9
M4	13	3	6.5	3	19	12.4	12	12
M average	41	4.48	20.5	7	20.23	39.0	33.0	29.0
SM1	0	1.4	-	-	10.5	-	-	-
SM2	13	3.1	6.5	3	25.2	12.4	10	11
SM3	0	6.7	-	-	31.6	-	-	-
SM4	10	2.5	5	2	11.6	9.5	9	10
SM average	23	3.43	11.5	5	19.73	21.9	19.0	21.0
Population average	107	3.2	49.5	17	18.9	94.1	78.0	74.0

[a] F = female, M = adult male and SM = sub-adult male, the number identifies individual rhino.

[b] Number of nocturnal backtracks recorded

[c] Both these females data were not analysed due to small sample sizes. No calculations were made for these rhino.

Table 3.2 Black rhino diurnal browsing and resting habitat selection on the Mun-ya-Wana Game Reserve. We grouped rhino with overlapping core ranges into clusters. A significant Pearson correlation (*r*), between the total number of a black rhino's locations in a habitat and the number of browsing or resting locations in the same habitat (bold *P* values), is an indication of non-selection of habitats for these behaviours.

			Browsing locations			Resting locations		
Cluster	Rhino	n[a]	n	*r*	*P*	n	*r*	*P*
1	F1	7	29	0.988	**≤ 0.001**	20	0.989	**≤ 0.001**
	F2	7	20	0.939	**0.002**	15	0.777	**0.04**
	F5	6	16	-0.308	0.552	23	0.366	0.476
	F7	5	7	0.835	0.079	22	0.993	**0.001**
2	F6	5	24	0.9	**0.037**	14	0.181	0.771
	M1	7	14	0.911	**0.004**	25	0.928	**0.003**
	SM1*	7	39	-	**-**	21	-	**-**
3	F4	6	23	0.677	0.139	38	0.848	**0.033**
	M4	6	19	0.546	0.263	28	0.811	**0.05**
	SM3	7	19	0.855	**0.014**	26	0.936	**0.002**
4	M3	9	28	-0.331	0.385	19	0.132	0.735
	SM2	9	61	0.981	**≤ 0.001**	30	0.933	**≤ 0.001**
	SM4	7	31	-0.14	0.764	13	-0.23	0.62
5	M2	6	18	-0.047	0.93	15	-0.375	0.463

[a] The number of habitats each rhino utilised.

[b] Removed from analyses due to a biased number of unknown sightings in certain habitats.

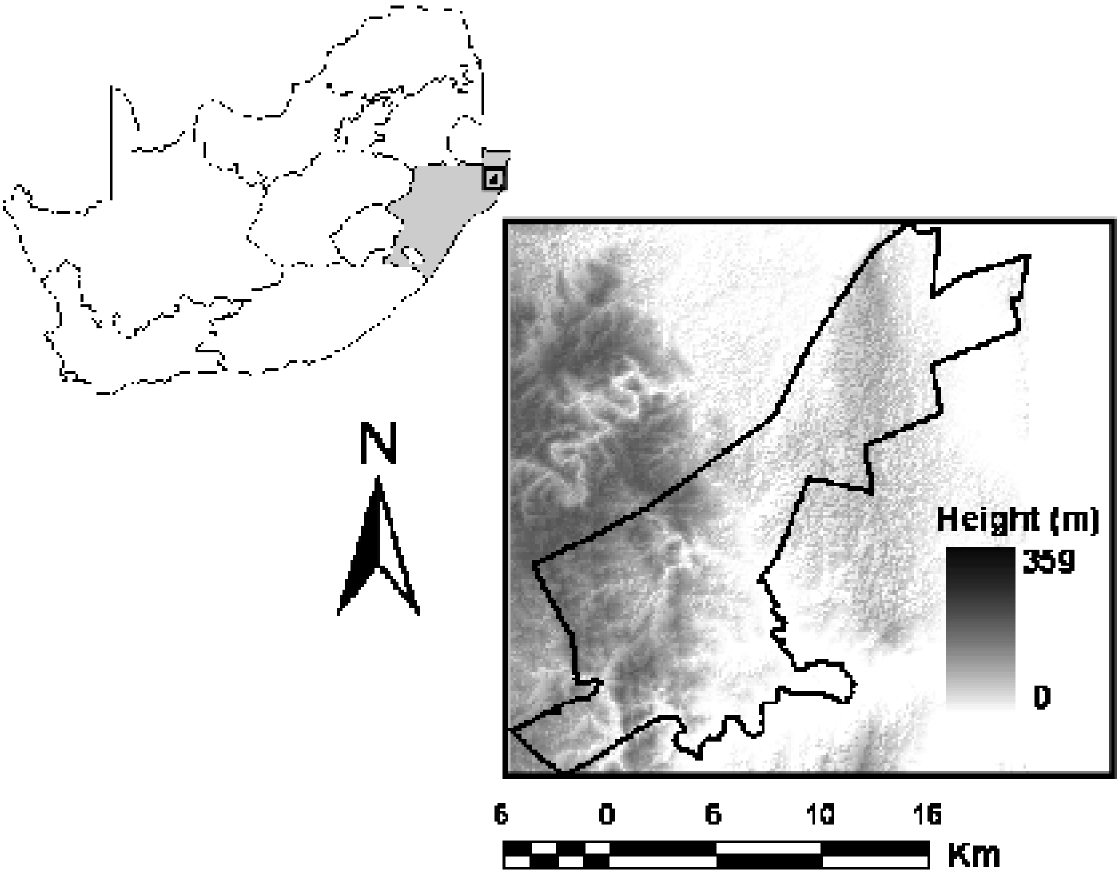

Figure 3.1 Location of the Mun-ya-Wana Game Reserve in South Africa.

CHAPTER 4

Interindividual niche variation in black rhino *Diceros bicornis*

4.1. Summary

Conclusions about resource use at a population level do not necessarily translate to behaviour at an individual level, and often the degree of interindividual niche variation among conspecifics is not tested or considered. However, conclusions about utilisation at a population level do not necessarily translate to behaviour at an individual level. We investigated the degree of interindividual niche variation of a selective forager, the black rhino (*Diceros bicornis*). Clusters of black rhinos had a significant degree of niche variation among individuals, which increased from one cluster to the next as the total niche width increased. Within a cluster, black rhinos did not show a change in the degree of habitat variation among individuals as the total niche width changed, but at a diet level, the niche variation increased noticeably as the total niche width increased. There was a significant increase in the degree of interindividual habitat and dietary niche variation between clusters of black rhinos as the total niche width increased from one cluster to the next. The majority of the dietary niche variation is due to large variations in the use of ancillary browse species among individuals, especially during the dry season. Consequently, pooling habitat location data and diet selection data for individuals within a population will average out patterns of utilisation, however, this average does not reflect the actual selection by any, or many, individuals. We suggest a re-assessment of methods for evaluating use of habitat and browse by black rhinos, especially in regions with highly heterogeneous resources.

4.2. Introduction

Habitat use and selection by animals is an extensively studied subject (e.g. Aebischer *et al.* 1993, Morris 2003b, Carter *et al.* 2006) due to the importance it plays in wildlife conservation and management decisions (Luck 2002, Morris 2003a). The diet composition within different habitats determines the quantity and quality of food intake, and therefore, the nutritional status of individual animals, their physiological condition, and hence, potential fitness (Hanley 1997). However, conclusions about use at a population level do not necessarily translate to behaviour at an individual level (Bolnick *et al.* 2003). The potential for interindividual niche variation requires us to first study species at an individual level, or for social species at the functional group level, so that we can understand population level patterns (Aebischer *et al.* 1993, Bolnick *et al.* 2003, Osko *et al.* 2004). Niche variation among individuals, whether based on age, sex or morphology, is generally the result of a trade-off between various resources (Bolnick *et al.* 2003, Svanbäck & Bolnick 2005) and has been documented within different species; however, the degree of variation among conspecifics is often not considered (Bolnick *et al.* 2003).

The niche variation hypothesis (NVH) suggests that populations with greater niche widths exhibit greater niche variation among individuals (Van Valen 1965). For example a decrease in resource abundance, possibly driven by an increase in population density may drive individuals to include alternative resources, increasing the population’s total niche width (TNW) and the level of variation among individuals (Svanbäck & Bolnick 2007). The NVH has been empirically tested and has been exhibited in a range of generalist species, including three-spine stickleback *Gasterosteus aculeatus*, Eurasian perch *Perca fluviatilis*, *Anolis* lizards, *Nucella* snails, a number of Brazilian leptodactylid frog species (Bolnick *et al.* 2007) and recently in grey wolves *Canis lupus* (Darimont *et al.* 2009).

In the case of the grey wolves a sub-population with a comparatively larger TNW was comprised of individuals which were making use of ‘vacant niches’ and under-utilised resources differently to one another (Darimont *et al.* 2009). Identifying the importance of these different resources used by individuals makes us aware of the conservation implications associated with increased niche variation among individuals as the population's niche width expands. Specifically, the management of an 'average' resource base may lead to mismanagement of resources that are significantly important to certain individuals (Bolnick *et al.* 2003, Darimont *et al.* 2009). This would be particularly risky for small populations, or if use is sex or age based, as a change in demographics could result in unfavourable population effects (Durell 2000).

Previously we noted variation in the selection of habitats by black rhinoceros (*Diceros bicornis*) at three different scales of selection on the Mun-ya-Wana Game Reserve (MGR) in South Africa (Morgan *et al.* 2009). Current management and research strategies for black rhino are aimed at the population level, as niche variation among individuals at a habitat and diet level has never been addressed in detail. Specifically, many studies for black rhino have pooled information, averaging results across individuals and making deductions at the population level for this 'selective' forager (Muya & Oguge 2000, e.g. Ganqa *et al.* 2005). Considering the potential variation in resource abundance across seasons and the array of habitats which black rhino can occupy (Emslie & Brooks 1999) it would be important to identify whether the NVH applies to this endangered species (IUCN 2008) and to what extent. This may have previously been ignored, as we would expect a selective forager to have a narrow TNW and therefore limited options for individuals to diverge into separate niches.

Our aim, therefore, is to determine whether any interindividual variation in diet and habitat niches exists within populations of black rhino and to empirically test the NVH on this ecologically important species. For the context of this study, a niche is defined within specific categories, such that a population can have numerous niche categories (i.e., fine and broad scale diet and habitat niches). Our objectives in this study were to: (1) establish the degree of interindividual habitat and diet niche variation for two geographically separated populations of black rhino; (2) investigate the degree of variation among individual's subsidiary diets for each of these two populations; and (3) interpret the results in terms of conservation management.

4.3. Materials and methods

The Mun-ya-Wana Game Reserve (MGR; S 27^{o} 40‘– 27^{o} 55’ and E 32^{o} 12’ – 32^{o} 26’) encompasses an area of 180 km^{2} in the northeastern section of South Africa, at the southern end of the East African coastal plain. The local climate is typified by dry and warm winters (April - September) and hot and wet summers (October - March). During the study period the annual rainfall was 840 mm, which falls within the ten year mean (± standard error) annual rainfall of 758 ± 65 mm. The broad scale vegetation types identified in the region are Southern Lebombo Bushveld, Zululand Lowveld, Maputaland Coastal Belt, Makatini Clay Thicket, Sand Forest and Western Maputaland Clay Bushveld (Mucina *et al.* 2005). A total of sixteen habitat types have been identified across MGR; this high number in such a small area is due to high variability in the geological formations across the reserve (Anon 1988). The elevation of MGR ranges from 50 m in the northeastern region of the reserve to 340 m in the southwestern corner.

Tswalu Kalahari (Tswalu; S 27°04' - 27°44' and E 22°10' - 22°36') encompasses an area of 1,080 km^{2} in the northwestern section of South Africa. The climate is semi-arid with a warm and dry season (April - September) and a hot and wetter season (October - March). The rainfall is seasonal but highly variable among years, with a mean (± standard error) annual rainfall of 280 ± 28 mm for the last 30 years. During the study period, the rainfall was 235 mm for the first wet season of 2003 – 2004, 400 mm for the following wet season of 2004 – 2005, and 510 mm for the wet season of 2005 –2006. The predominant vegetation types have been classified as Gordonia Plains shrubveld and Gordonia duneveld (Mucina *et al.* 2005), which have a relatively open structure. For the purposes of this study, we identified five habitat types at a smaller scale from a vegetation map of the reserve (van Rooyen 1999). The elevation of Tswalu ranges from 1,020 m in the west to 1586 m in the southeastern corner (van Rooyen 1999).

4.1.1. Data collection

In October 2004, 15 black rhinos were translocated to the MGR, and the population comprised seven adult females and eight males (4 adult and 4 sub-adult males). These rhinos originated from game reserves in the surrounding Maputaland region. From January through December of 2005, we used radio transmitters implanted in the horns to locate all 15 rhinos at least once every 4 days (see Linklater *et al.*, 2006 for details on horn implant methods). The rhino all showed site fidelity within 6 days of release (Linklater *et al.* 2006) and an analysis of their response to various ecogeographical variables, including habitat and browse availability, indicate the acclimatisation phase to be over and the majority of their changes to variables to have occurred within 25 days of release (SM, unpublished results). We used an indirect track-based method to collect foraging information for 10 individuals. This was done by back-tracking their spoor (footprints) and recording information from each feeding station where the rhino stopped to browse (Oloo *et al.* 1994, Ganqa *et al.* 2005). The characteristic "pruning" of plants by black rhino, which occurs when the prehensile upper lip is used to pull branches into the mouth and the twigs are then cut off by the proximal molars, leaves a distinctive diagonal cut (Joubert & Eloff 1971); this evidence was used to identify browse utilisation by black rhinos. We defined a separate browse event as any fresh browse identified more than a rhino length away from the previous browse event. In the majority of cases, this constituted a single plant species; in cases in which the rhino targeted more than one species, we recorded the species that exhibited the greatest estimated biomass removed. This method relied on a single observer documenting all events and ensuring consistency throughout the study. From this method, we were able to estimate the proportional contribution that a species made to a rhino's decision to stop and browse (see Morgan *et al.*, 2009 for detailed track data collection methods).

Eight black rhinos were translocated to a 450 km^2 fenced section of Tswalu from Etosha National Park in Namibia in June 1995. The population had increased to 22 by the end of 2005, which suggests that this population was well settled and productive. The focal animals for this study were the five adult females from the original founder population,. There were 392 sightings of the focal animals (range = 71 to 86 per individual) throughout the data collection period of January – December 2004 and 2005; 192 sightings were made during the wet seasons (October-March) and 200 during the dry seasons (April-September). We identified individual rhinos using unique ear-notch patterns and gathered data on their diets by using the same back-tracking methods described above. A more detailed diet study was conducted at this study site, and at each feeding station the plant species, number of new bites, leaf phenology (immature, mature, yellow and dry), and total leaf retention using a five point scale (Dekker & Smit 1996) was recorded. A bite was scored for any isolated severed shoot or branch, or where numbers of contiguous shoots or branches were bitten off at the same level, all severed shoots < 5 mm thick occurring within a circle of 5 cm in diameter were recorded as one bite (following (Hall-Martin *et al.* 1982). For five days during each season in both years we measured and categorized the diameter of all shoots within a bite into three size classes, 0≤1 mm, 1≤3 mm and 3≤6 mm (Helary *et al.* 2009). The greatest diameter of twig recorded as utilised at this site was 6mm. We collected twenty twigs of *Acacia haematoxylon*, *Acacia mellifera*, *Grewia flava*, *Rhigozum trichotomum*, *Monechma incanum*, *Lycium cinerum* and *Lycium hirsutum* in each of the 3 diameter size classes (0≤1 mm, 1≤3 mm, 3≤6 mm) during the wet season when mature leaf retention was greatest. Twigs and leaves were stored in paper bags and air-dried before the mass was obtained on an Ohaus Precision Plus TP4000D scale calibrated to an accuracy of 3 decimal places. The relationships between stem and leaf dry weight and twig diameter value for each sample of each species were determined using regression equations (Basile & Hutchings 1966). The total dry mass contribution of leaves and stems of a given species was calculated by applying the appropriate regression equation to the standard mean diameter for each twig diameter class, and then multiplying this value by the total number of twigs recorded in that same diameter class for that species. The total dry mass contribution for a plant species each month was the sum in each diameter class of the dry mass of stems and proportion of leaves retained (Helary *et al.*, 2009). We recorded 150 feeding tracks during the study period, totalling 33,218 rhino bites.

4.1.2. Data analyses

For analysis we grouped all rhinos into clusters (Tatman *et al.* 2000, Lent & Fike 2003, Morgan *et al.* 2009). This method groups rhinos that have overlapping core home ranges, deemed as a 50 % kernel home range of the years' locations (see Morgan *et al.*, 2009 for details on kernel development and cluster selection). For purposes of this paper we assumed that all rhinos in a designated cluster had unrestricted access to the same resources, thereby eliminating potential differences in use due to varying availabilities of resources (Osko *et al.* 2004). This was based on repeated observations of cluster ‘buddies’ browsing and socialising alongside one another (SM, unpublished data).

In total, we identified five clusters on MGR (Table 4.1). Four females had overlapping core ranges with more than one adult male and we therefore assigned them to a female-only cluster and to a cluster with both the adult males. We acknowledge the assumption of equal availabilities may not strictly apply in this cluster (Cluster 3, $n = 8$), as the adult males did not traverse each other’s core ranges and we could therefore expect this cluster to have a greater TNW and potentially greater variation amongst its members. We analyzed the Tswalu data as a single cluster (Table 4.1), as the five focal rhinos on Tswalu all had overlapping core home ranges (JS, unpublished data). For analyses we did not separate the sexes in the clusters, due to small sample sizes; however, cluster four (n = 4) and cluster five (n = 3) on MGR were made up of only females and males, respectively and the Tswalu rhino were all female.

There are various methods to measure the degree of niche variation among individuals, each with pros and cons and all highly correlated with one another (see Bolnick *et al.*, 2002 for a review). We used a program devised by Bolnick *et al.* (2002), IndSpec1, to calculate the different indices of niche variation. Firstly, we calculated an index of total niche width (TNW) for each of the clusters, which uses the Shannon diversity index as a measure of the variation in resource use within a population (Roughgarden 1979). We then used IndSpec1 to measure the overlap between an individual’s and the cluster’s diet. IndSpec1 uses an adaptation of the proportional similarity index (Schoener 1968b) as an index of niche variation among individuals,

$$PS_{\mathrm{i}} = 1 - 0.5 \sum_{\mathrm{j}} \left| p_{ij} - q_j \right|$$

in which p_{ij} represents the proportion of category j in individual i’s diet and q_j is the proportion of category j in the cluster’s diet. For an individual that utilises resources in direct proportion to the cluster and therefore shows complete niche overlap, $PS_{\mathrm{i}} = 1$, while for maximal individual variation $PS_{\mathrm{i}} = 0$. To make PS_{i} more intuitive, we followed (Bolnick *et al.* 2002) and expressed the niche variation among individuals as $V_{\mathrm{i}} = 1 - \mathrm{PS}_{\mathrm{i}}$;

therefore, V_i ranges from 0 to 1. The mean V_i of a cluster (V) is an indication of the average individual variation within the cluster. IndSpec1 runs a nonparametric Monte Carlo procedure for each individual of 1,000 replicates drawn from the cluster's niche distribution. This procedure generates a replicate null distribution model from which we can calculate *P*-values for the cluster.

To determine which habitats individual rhinos used, we imported all GPS location data into ArcGIS 9.2 © (ESRI, California, USA) and calculated the number of locations for individual rhino in each of the habitat types across MGR and Tswalu. We assigned a value of 0 to those habitats in which a rhino never occurred. Black rhino potentially shift their ranges from one season to the next and from one year to the next (Lent & Fike 2003). We therefore split the habitat data into wet and dry seasons for both reserves, and on Tswalu we analysed each year's data separately.

On MGR, we used the total number of browse events per plant species as an indication of an individual's diet composition. We analysed browse use within the 3 clusters we had gathered this information on, with 10 individuals across the clusters. We pooled the browse data across the year, due to a small sample size of foraging tracks completed per individual seasonally, which might enhance interindividual variation on MGR. On Tswalu, we used the mass of estimated off-take per species as the indicator of browse use among individuals. We compared data from the wet and dry seasons across the two years (average number of 100 m sections completed per rhino in the wet season $N = 266 \pm 57$ and dry season $N = 281 \pm 78$).

To determine whether diet variation among individuals was related to all the plant species in the diet, or only to those species making up the larger proportion of a rhino's diet, we also identified subsidiary diets for the clusters of rhino. We removed the dominant species from their diet in the dry season, using an arbitrary cut-off value of 20 % contribution to a cluster's seasonal diet to identify dominant species. We defined the remaining plant species as the subsidiary diet of the cluster, as identified during the period of resource scarcity in the case of the Tswalu rhino. Any difference observed in the diet variation among individuals between the entire and the subsidiary diets will be due to those dominant species we removed from the cluster's diet.

We eliminated those habitat types or browse species that were poorly represented in a cluster (Krebs 1989). We removed any category representing < 5 % of the cluster's use, unless it made up more than 10 % of any individual's use. This decreased the variability among the individuals in the dataset (Burke 2001), making this method conservative; any detected differences will be biologically relevant. Each cluster's data were then entered into IndSpec1 to determine the TNW of the cluster, each individual's V_i and then each cluster's V. We ran nonparametric Monte Carlo procedures to calculate P-values of the observed results against a null-model of 1,000 simulations.

We tested for a change in V_i from the wet to the dry season and we tested for a difference between the primary and subsidiary diet V for each cluster using paired sample t-tests in To test for an effect of TNW on the observed interindividual variation within a cluster, we conducted linear regressions of TNW against V_i or the corresponding V. We used an alpha of 0.05 for statistical significance, and statistical analyses were conducted in SPSS 15.0 (SPSS Inc., Illinois, USA).

4.2. Results

There was evidence of niche variation among black rhino on MGR, with levels of variation significantly higher than would be expected by a random null model (Table 4.1; Fig. 4.1a and b). As expected Cluster 3, which had potentially unequal availabilities amongst its individuals, had the largest TNW and the highest levels of variation amongst individuals for all the tests. Individual black rhinos did not change their degree of variation of habitat use with the rest of their cluster from one season to the next (Table 4.1). We therefore conducted a linear regression of TNW against the average interindividual variation (V) in use of habitat types for the clusters. In support of the NVH there was a significant positive relationship between TNW and V from one cluster of rhinos to the next ($F_{1,8} = 54.44$; $P < 0.001$; Fig. 4.1a and b).

The small degree of dietary interindividual variation (V_i) for black rhinos on MGR (Fig. 4.1c) was significantly higher than would have been expected from a random null model (Monte Carlo procedure of 1,000 simulations: $P < 0.01$ for each of the three clusters of rhinos). There is a significant effect of TNW on the resulting degree of V_i from one rhino cluster to the next ($F_{1,11}$ = 5.37; P = 0.041), which is in support of the NVH, with an increase in variation among individuals as the population's TNW increased (Fig. 4.1c).

On Tswalu, during the two wet seasons and the first dry season, there was evidence of a degree of habitat V that was significantly higher than that generated by a random null model, while during the dry season of 2005, the variation was markedly lower and showed no difference to the null model (Table 4.1; Fig. 4.2a). Individual black rhinos did not change the degree of habitat niche overlap with the rest of the cluster from one season to the next, in either 2004 or 2005 (Table 4.1). The regression analysis did not indicate an effect of TNW on the V across the seasons and years ($F_{1,2}$ = 0.003; P = 0.946).

We plotted the V and TNW for each of the clusters on MGR and Tswalu to establish whether the rhino showed similar trends across geographically varied areas (Fig. 4.3). We ran a linear regression of TNW against V and found a significant effect of TNW on V at both the habitat level ($F_{1,12}$ = 15.08; P = 0.002) and the diet level ($F_{1,3}$ = 60.19; P = 0.004), again in support of the NVH.

Black rhinos on Tswalu exhibited less of a degree of V at the diet level than at the habitat level, but the degree of niche variation was still significantly higher than would be expected from a random null model (Table 4.1; Fig. 4.2). There was a significant increase in each individual's V_i from the dry to the wet season for mass of browse offtake (Table 4.1). As the TNW increased, there was a corresponding significant increase in individual's V_i based on the browse off-take in the diet ($F_{1,8}$ = 7.17; P = 0.028), highlighting how the NVH can apply to individuals within a population exposed to changing resources.

MGR - We removed the top two species, *Dichrostachys cinerea* (minimum of 35 % and maximum of 43 % contribution) and *Spirostachys africana* (minimum of 20 % and a maximum of 27 % contribution), from each of the 3 cluster's diets. Two clusters of black rhinos on MGR had a significantly higher degree of V_i in their subsidiary diet choice than that noted across their entire diet (Paired T-Test cluster three: t_6 = -6.65, P = 0.001; cluster four: t_2 = -4.88, P = 0.039), while a third cluster showed a similar trend, but to a lesser degree (Paired T-Test cluster five: t_2 = -3.32, P = 0.080) (Fig. 4.4).

Tswalu - We removed one species (*Acacia haematoxylon*) from this cluster's dry season diet, which comprised 71% contribution to the off-take. To determine if there was a seasonal effect, we removed only this one species during the wet season (49% of off-take). Black rhino on Tswalu had a significantly higher degree of V_i in their subsidiary diet species than that noted across their entire diet during the dry season (Paired T-Test: $t_4 = -5.41$, $P = 0.006$), but not during the wet season (Paired T-Test: $t_4 = 0.34$, $P = 0.749$) (Fig. 4.4b).

4.3. Discussion

Here, we investigated whether the niche variation hypothesis (NVH) applies to individual's and clusters of black rhino use of both habitat and diet resources. In support of the NVH there was an increase in the level of variation among individual black rhino's use of resources as the total niche width (TNW) increased from one cluster to the next. In areas with a high heterogeneity of habitats or available browse and a resultant high population TNW, we would expect individual black rhino to have lower levels of niche overlap with other members of the population. Niche variation among individuals has been noted in a wide range of mammals, including snowshoe hares *Lepus americanus* (Pietz & Tester 1983), grizzly bears *Ursus arctos* (Nielsen *et al.* 2002) and moose *Alces alces* (Osko *et al.* 2004), and at a habitat level this has been attributed to differences in availabilities (Nielsen *et al.* 2002, Osko *et al.* 2004). However, black rhinos with similar availabilities of resources have significant degrees of variation in their strategies of habitat and browse species utilisation. It is important to note that the levels of niche variation among individuals here may not be as large as those recorded in other species (Bolnick *et al.* 2003, Svanbäck & Persson 2004, Araujo *et al.* 2007, Svanbäck & Bolnick 2007), but are significantly higher than expected from a null model. Regardless, pooling data among black rhino individuals in a population may cause errors (Aebischer *et al.* 1993, Osko *et al.* 2004), as it would average out unrelated patterns of use (Schooley 1994, Osko *et al.* 2004, Bowyer & Kie 2006) and provide biases (Nielsen *et al.* 2002, Osko *et al.* 2004), whereby the average does not reflect the actual use of any, or many, individuals.

We did not have large enough sample sizes to evaluate differences among the sexes. Since there has been limited studies on the variation in the use of resources between and or among the sexes of black rhino, it is difficult for us to make assumptions on the influence this may have. We could assume that females and males or even females at different stages of the reproductive cycle have different foraging needs and constraints. A more detailed study would be able to establish whether we could attribute differences we noted here to these factors, although the detailed diet data from the similar aged, all female Tswalu clusters' data indicates that differences do occur among adult females.

No studies have specifically investigated the degree of diet variation among individual black rhino, with the majority of foraging studies not discerning diets among individuals (Muya & Oguge 2000, Brown *et al.* 2003, Ganqa *et al.* 2005, Ganqa & Scogings 2007). A single report of diet variation among individuals within a cluster was mentioned from a project on the Lewa Wildlife Conservancy in Kenya, where individuals showed a clear difference in their preference of some diet species, but an overall similarity in their selection (von Holdt 1999). Black rhinos on MGR and Tswalu showed similar trends to those on Lewa with clusters of rhino having low but significant degrees of diet variation among individuals. What is important to note here is the scale of diet utilisation we are looking at. The diet niche we identified here represents the use individuals make within the cluster's range, within which we noted unrestricted movement. Black rhinos, therefore, may bias their diet composition by deciding to use areas within their range which have different availabilities of browse species to other rhinos (noted in the degree of habitat variation for the clusters), this still represents a difference among individuals choices to use a different area of their common range. We have, however, not tested whether rhinos presented with the same availabilities of plants in a foraging patch make a different selection or not. Indeed, initial indications are that black rhinos show similar levels of selection when presented with key resources at a foraging patch (JS, unpublished results). These apparently contradictory results emphasise the need to incorporate and clarify the scale of investigation when drawing conclusions (sensu Cumming *et al.* 2006).

The majority of variation among black rhino's browse use is within the subsidiary composition of their browse species. During the dry season on Tswalu, the majority of plant species are lower in quality due to leaf loss, black rhino therefore make extensive use of *A. haematoxylon* (71 % of the browse offtake), which is semi-evergreen and retains leaves throughout the year (JS, unpublished data). This species heavily influences the low levels of diet variation among individuals in the dry season. This supports the NVH, with an increase in diet variation among individuals as the population increase its niche width during the wet season. The information we have from MGR is limited from a seasonal perspective, but still indicated a difference in utilisation strategies of primary and subsidiary diet species by black rhinos, with more variation among individuals use of subsidiary species. We would need to study the seasonal effects of this phenomenon to infer whether the seasonal trends noted on the species poor Tswalu reserve apply to more heterogeneous environments, such as that on MGR. Black rhinos are not faced with the same tradeoffs that exist during dry season browse selection (Robinson & Wilson 1998), as during the wet season most plant species nutrient availabilities increase (Ganqa *et al.* 2005). Most studies of interindividual diet variation changes are based on density shifts in populations (Svanbäck & Bolnick 2005) and have only been hypothesised about on a seasonal scale (Bolnick *et al.* 2007); here we confirm that this variation can occur at a smaller scale due to fluctuations in resource abundance across seasons.

Interestingly, black rhinos within clusters responded differently to changes in TNW at a habitat level than what we would expect according to the NVH. Individual black rhinos did not change their degree of niche variation from one season to the next on either reserve, and the female cluster on Tswalu did not increase its average variation among individuals as the TNW increased. Therefore, within clusters, black rhinos increased their respective habitat niche widths similarly to one another irrespective of the degree of variation already existing (i.e., an increase of the with-in individual component as the TNW increases, while the between individual component remains constant). Black rhinos within the same cluster would be affected by similar variables, which influence an increased habitat niche width, for example the presence of new water points in the wet season. A detailed study on the way rhinos increase their habitat niche width would give insight as to how rhinos within clusters take a similar approach to habitat niche expansion.

Management strategies and studies of black rhino are primarily aimed at a population level (Brown *et al.* 2003, Ganqa *et al.* 2005, Adcock 2006, Ganqa & Scogings 2007); we suggest future research should try and incorporate the individual and that variation among individual selection is explored, particularly in those populations with high TNW. Management habitat strategies based at the population level could benefit from being defined at a cluster level, while management and studies of forage use by black rhino should try and incorporate individuals, especially if it concerns those plant species which make up the subsidiary diet of black rhino. Further, we must clarify the scale at which individual variation occurs, specifically investigating the finer level of plant species or plant part selection. We need to be cautious in assuming that interindividual variation only occurs at high-density levels, especially in heterogeneous landscapes, and that due to changes in environment it is good to be aware of and to preserve variation among individuals as a conservation strategy (Bolnick *et al.* 2003).

Table 4.1 The degree of niche variation among individuals (*V*) for black rhinos on the Mun-ya-Wana Game Reserve (MGR) and Tswalu Kalahari (Tswalu) during the dry and wet seasons (*V* ranges from 0 to 1; 0 = no niche variation among individuals and 1 = maximum niche variation among individuals). *P*-values were calculated by Monte Carlo procedures based on 1,000 simulations.

			Dry Season			Wet Season			Test for change in *V*i from Dry to Wet season
MGR	Cluster	N	*V*	N[a]	*P*	*V*	N[a]	*P*	*P*[b]
Habitat	1	3	0.161	4	0.026	0.113	3	0.018	0.411
	2	4	0.242	6	0.016	0.275	6	< 0.001	0.280
	3	8	0.367	7	< 0.001	0.357	6	< 0.001	0.827
	4	4	0.237	5	< 0.001	0.257	5	< 0.001	0.778
	5	3	0.165	4	0.005	0.208	4	< 0.001	0.418
Tswalu	Year								
Habitat	2004	5	0.295	4	< 0.001	0.300	5	< 0.001	0.959
	2005	5	0.191	4	0.117	0.280	3	< 0.001	0.215
Diet	2004-2005	5	0.031	3	< 0.001	0.157	5	< 0.001	0.032

[a] The number of habitats or plant species tested within each niche, represented by only those with a > 5 % contribution to the clusters use, or a > 10 % contribution to any one individual's use.

[b] Determined using paired T-tests.

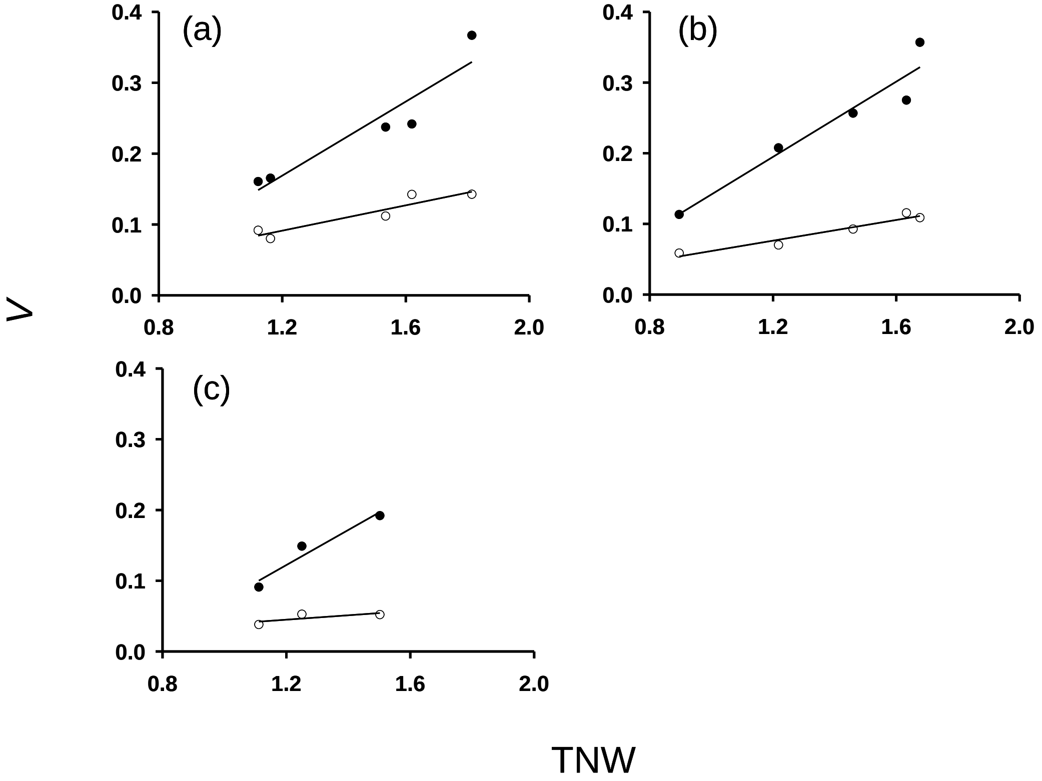

Figure 4.1 The correlation between the degree of interindividual variation (*V*) and the total niche width (TNW) for clusters of black rhino on the Mun-ya-Wana Game Reserve. This is shown at a habitat level in (a) the dry season and (b) the wet season and at a diet level (c) across both seasons. Filled in circles represent empirical results while the open circles represent a null model, with the random re-sampling of a 1 000 permutations from the population. The regression lines are drawn to help illustrate the effect of TNW on *V*.

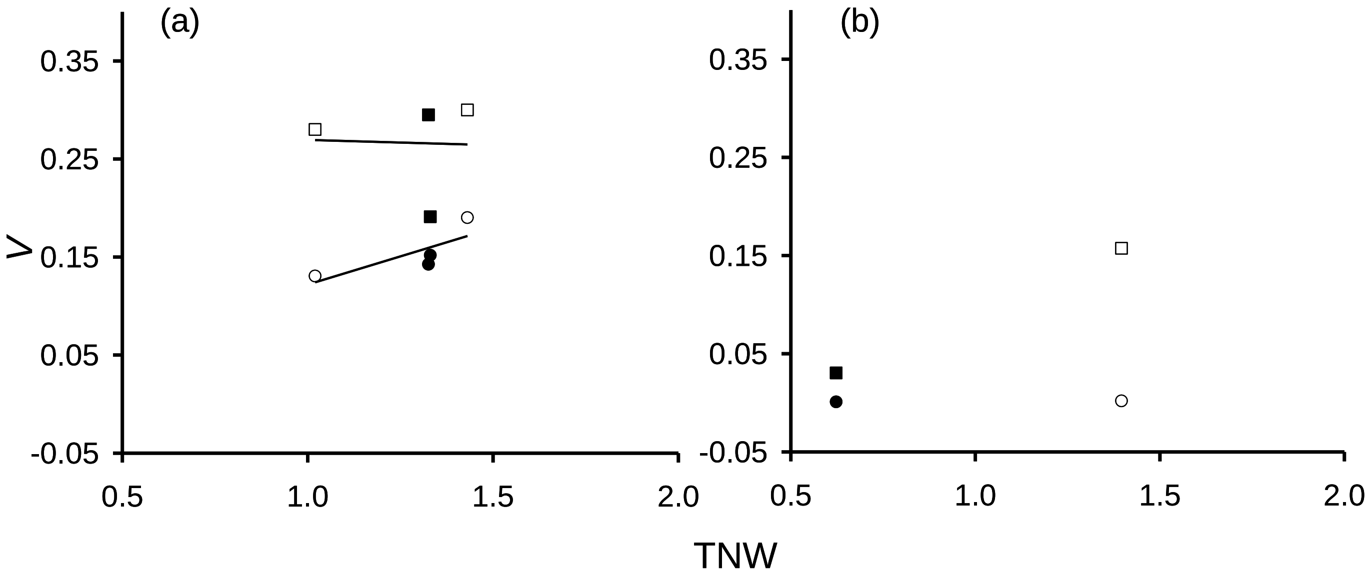

Figure 4.2 The correlation between the degree of interindividual variation (*V*) and the total niche width (TNW) for black rhino on Tswalu Kalahari at (a) a habitat level and (b) a diet level. Squares represent empirical results and the circles represent a null model, with shaded symbols representing the dry season and open symbol the wet season. The regression lines are drawn to help distinguish the seasons and the effect of TNW on *V*. The null model was calculated from the random re-sampling of a 1 000 permutations from the population.

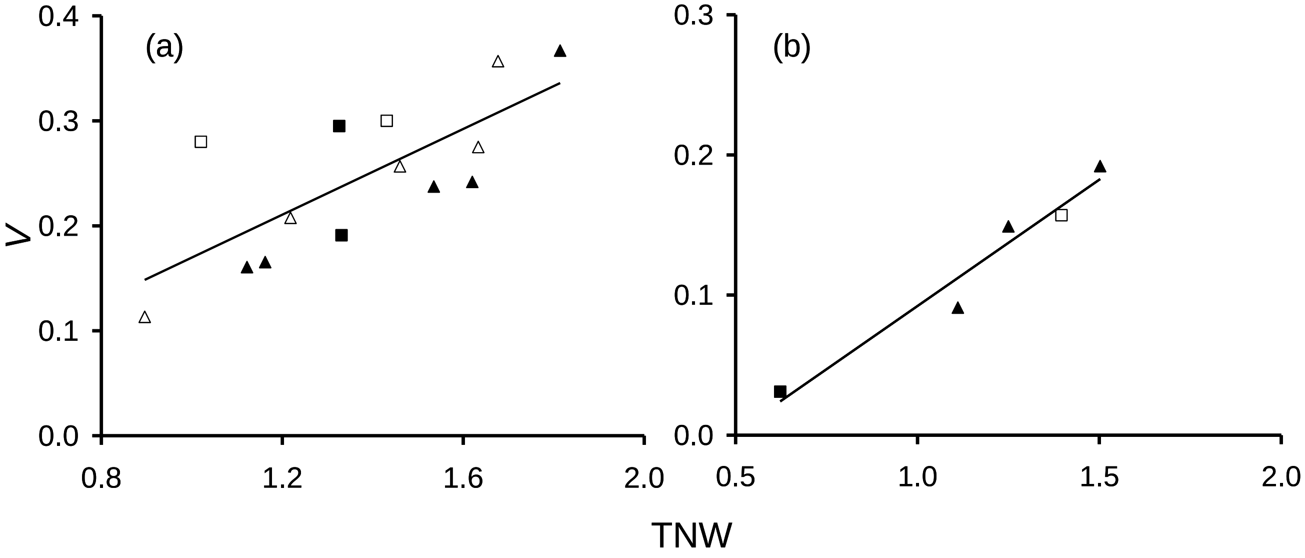

Figure 4.3 The increasing degree of niche variation among individuals (*V*) of black rhino clusters with an increasing total niche width (TNW) for two geographically separated populations. Tswalu Kalahari is represented by a square symbol and Mun-ya-Wana Game Reserve (MGR) is represented by a triangle at (a) a habitat level and (b) a diet level. In (a) the shaded symbol represents the dry season and open symbol the wet season and in (b) MGR results were calculated from year round data, while Tswalu's shaded square represents the dry season and open square the wet season.

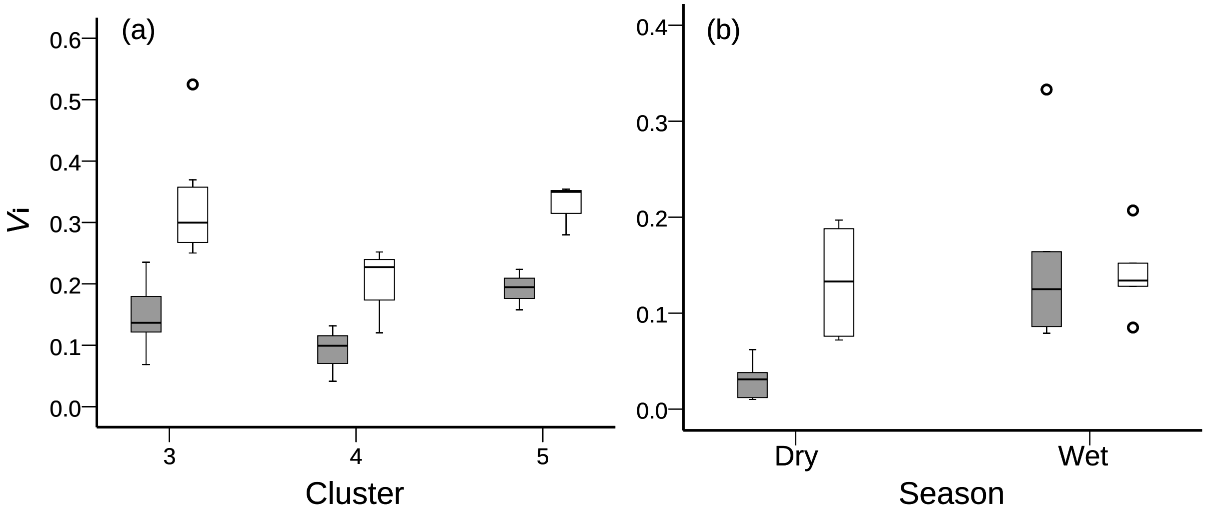

Figure 4.4 The difference between black rhino primary (shaded box plots) and subsidiary (open box plots) diets' degree of interindividual diet niche variation (V_{i}) across the Mun-ya-Wana Game Reserve (MGR) and Tswalu Kalahari (see section 3 for details). (a) We divided the black rhino on MGR into three clusters. (b) Black rhino on Tswalu comprised of one cluster, but the more detailed diet data, determined by the mass of off-take of each species, was separated by season. Data are box plots: thick line within box is the median; box represents the 25th and 75th percentiles; and the whiskers indicate the 5th and 95th percentiles. Outliers are designated by an open circle.

CHAPTER 5

The importance of incorporating individual variation in modelling habitat suitability

5.1. Summary

User-friendly habitat suitability models rely on the assumption that averaging the response of individuals to ecogeographical variables (EGVs) is suitable to deduce population level responses. However, this may blur differences between the utilisation of specific EGVs by individuals, resulting in the potential mismanagement of resources to the disadvantage of certain individuals, resulting in a loss of population productivity. We therefore tested a Maximum entropy (Maxent) model, which incorporated inter-individual niche variation, in a population of black rhino *Diceros bicornis*. We did this by developing a Maxent model for each member of the population (n = 15) and merged the outputs to produce two individual models, one which allocated the highest individual suitability value to a grid cell (Individual Max model), and a second model (Corrected Individual model) which added a measure of population deviation to the Individual Max model, and compared their outputs and predictive capabilities to a pooled location model (Pooled model). The Pooled model blurred black rhino responses to EGVs, providing incorrect indications of how the population was responding to EGVs. The Individual Max model out-performed the Corrected Individual model, while all the models had accepted levels of predictive omission. During resource limiting periods (dry season), the Individual Max model was able to predict the occurrence of non-modelled individuals, and of future occurrences of the modelled population, as effectively as the Pooled model. By modelling and analysing each individual's responses to EGVs across the landscape, we were able to understand individual black rhino decisions and discuss the results in the context of black rhino conservation management. By incorporating individual responses conservation mangers are able to answer the question "What ecogeographical variables influence a population's movements?" and to model future occurrences of the population

using a select number of individuals. We suggest that model development should have the ability to compensate for differences in individual sample sizes and inter-individual niche variation. This would allow user-friendly models to compete with more complex analytical approaches, such as eigenanalyses and generalised additive mixed models.

5.2. Introduction

Conservationists and land managers use habitat suitability models (HSM) to define landscape properties, map the distribution of suitable wildlife habitat and to produce probability maps depicting the likelihood of species occurrence and their response to environmental change (Guisan & Thuiller 2005). HSM are therefore vital in conservation planning strategies (Store & Kangas 2001, Wintle *et al.* 2005) and answering the question "What ecogeographical variables influence a population's movements?"(Basille *et al.* 2008). Presently we design models to answer this question by measuring a population's association, through occurrence and sometimes absence, with selected indirect-, direct- and resource-gradient variables (Austin 1985), and produce a numerical representation of their potential distribution throughout a landscape (see Elith and Graham, 2009 for a discussion on a number of different HSM and how they function). Current modelling techniques rely on the assumption that averaging the response of individuals to these ecogeographical variables (EGVs) is suitable to deduce population level responses (Manly *et al.* 2002). However, using pooled location data may blur differences between strong and weak selection of specific EGVs by individuals (Calenge & Dufour 2006, Aarts *et al.* 2008). This is particularly risky for small populations (Durell 2000) due to the mismanagement of resources which are significantly important to specific individuals (Bolnick *et al.* 2003, Darimont *et al.* 2009).

As a result of rapid increases in technology (Moll *et al.* 2007, Kozak *et al.* 2008), researchers are increasingly presented with accurate occurrence data of individuals within a population, but lose this detail by pooling the location data for modelling purposes (Calenge & Dufour 2006, Monterroso *et al.* 2009) and averaging out individual selection (Manly *et al.* 2002). The importance of recognising the individual within a population is not new (Johnson 1980, Judson 1994) and is used extensively in the modelling of home range and population dynamics (Grimm & Railsback 2005, Wang & Grimm 2007). Developments in eigenanalyses (K-select analysis, Calenge *et al.* 2005a) and generalised additive mixed models (Aarts *et al.* 2008) acknowledge the importance of individual variation, and ensure that biases in sample sizes (Thomas & Taylor 2006) and individual selection (Calenge *et al.* 2005a, Aarts *et al.* 2008) do not influence the data. However, these techniques often require expertise and an in-depth understanding of statistical analysis.

Species distribution models which are more user friendly, and only require an understanding of GIS analysis, include BIOMAPPER (Hirzel *et al.* 2006), which computes an ecological niche factor analysis, and Maxent (Phillips *et al.* 2006), a maximum entropy model. To understand how individual variation may affect these distribution model outputs we decided to use Maxent which performed consistently well in a number of comparative studies (Elith *et al.* 2006, Phillips *et al.* 2006, Pearson *et al.* 2007, Wisz *et al.* 2008, Elith & Graham 2009). Maxent is a machine learning HSM using presence-only location data and continuous or categorical EGVs to model species distribution. It is robust in its inclusion of unnecessary EGVs as it uses regularisation techniques to avoid over-parameterisation and ignores non-informative EGVs (Phillips *et al.* 2006), which alleviates the need for further statistical procedures such as an information theoretic approach to model building (Burnham & Anderson 2002). Maxent performs well at small sample sizes (Pearson *et al.* 2007, Wisz *et al.* 2008), but still follows the trend of other models by performing better with increased sample sizes (Wisz *et al.* 2008). Therefore, if we assume concurrence amongst a population, we would expect a Maxent model developed with the maximum number of sample locations available to perform better than any number of Maxent models developed with subsets of the same locations.

During model generation Maxent repeatedly tries to improve the fit of the model within the constraints of the EGVs and the distribution of the location data, such that a final probability distribution of maximum entropy (closest to uniform) is achieved (Phillips *et al.* 2006). It does this through a number of iterations which attempt to maximise the average probabilities of the sample location’s assigned EGVs values by weighting the EGVs accordingly (Phillips *et al.* 2006). Model results are adversely affected by biases towards higher sampled individuals or groups (Thomas & Taylor 2006) and large variations around the average EGVs values, for example due to changes in animal responses to EGVs across seasons (Suarez-Seoane *et al.* 2008) or geographically distinct areas (Calenge *et al.* 2005a). Present methods to deal with these two issues are to partition the data accordingly (Osborne & Suarez-Seoane 2002), for example spatially (Murphy & Lovett-Doust 2007) or temporally (Suarez-Seoane *et al.* 2008). This ultimately leaves the researcher with a number of models depicting different distributions, which can be more informative than a pooled model (Murphy & Lovett-Doust 2007, Estrada-Peña & Thuiller 2008). We propose to similarly partition data by individuals, and produce a number of more informative outputs which we can merge into one output. We will combine the maximum suitability values of all the individuals, meaning the model will incorporate all areas deemed important by any one individual.

Our aim is to therefore to establish whether a habitat suitability model based on individual data will provide conservation managers with a better understanding of population responses. We have chosen a known population of 15 black rhinoceros *Diceros bicornis* within a fenced game reserve in South Africa to test our premise. Black rhino are critically endangered (http://www.iucnredlist.org) and the conservation plans for several African countries specify the need for the establishment of new breeding populations and increased meta-population growth rates (Emslie & Brooks 1999, Emslie 2001, Metzger *et al.* 2007). Consequently, we were interested in learning more about the ecology of the black rhino for improved planning and implementation of reintroductions and supplementations. We developed separate habitat suitability models for each member of the population and combined these results to produce two outputs. Firstly, a merged model of maximum suitability, and, secondly, a corrected version of the maximum suitability model incorporating a factor of individual deviation. We compared these models to a third model developed from pooled location data for the population, and tested the predictive performance of each model using (1) location data of non-modelled individuals during the same period and (2) using location data of modelled individuals from the following year. We hypothesised that an individual based model would provide a more accurate prediction of habitat suitability for black rhino in the study area.

5.3. Materials and methods

The study area was restricted to the Mun-ya-Wana Game Reserve (MGR) (See Chapter 1 for full study area details). Locations of the entire MGR black rhino population (*n* = 15) were collected over a three year period from the beginning of January 2006 to October 2009 (*n* = 966). We used radio-telemetry in the first year and conventional tracking techniques in the last few years, once the radio transmitter's batteries had expired (see Chapter 2 for methods of capturing location data). We collected a larger number of locations during the wet season (*n* = 558, mean = 35 per individual, SD = 12) than in the dry season (*n* = 408, mean = 23 per individual, SD = 18), as it is easier to track an animal's spoor once it has rained than when it is dry. This artifact of conventional tracking methods to locate animals may also have biased the areas in which we located individual rhino, and the resultant sample size for each individual. However, since the same locations were used for all model development and testing, the same biases would be evident across all the models.

We downloaded all location data into ArcMap ® 9.3 (ESRI, California, USA) for analysis and used Maxent (Version 3.3.1; Phillips *et al.* 2006) for development of the habitat suitability models.

5.3.1. Ecogeographical Variables (EGVs)

The scale at which EGVs are measured will ultimately set the scale at which a study is measured. The inclusion of indirect parameters, for example slope, aspect and habitat type, confine the application of a model to a limited region due to changes in direct and resource gradients responses to indirect parameters in different regions (Guisan & Zimmerman 2000). For this study we were interested in the suitability of the habitat only for a single reserve (200 km^2), and therefore included direct, indirect and resource gradients. There were 17 EGVs in total (Table 5.1). We used the same EGVs as developed and selected for in Chapter 4, other than the distance to closest territorial male.

We excluded this variable as we wanted to use ‘conventional’ EGVs with respect to HSM. The various habitat types and an explanation of the development of the habitat map are included in Appendix 2.

5.3.2. Model development

Maxent evaluates the overall fit of the model using a receiver operating characteristic (ROC) curve, where the model’s sensitivity versus (1 – specificity) is plotted (Phillips *et al.* 2006). The area under the ROC curve (AUC) is then calculated, with AUC = 1 being the best fit, and AUC = 0.5 being expected from a random model. AUC values greater than 0.75 are considered useful (Elith *et al.* 2006). Maxent’s output is a predicted habitat suitability grid of the study area, with grid cell values being a function of the relevant EGVs, ranging from 0 – 1, with higher values corresponding to more suitable conditions for the species (Phillips *et al.* 2006). Maxent also evaluates the importance of each variable by doing a jackknife analysis of each EGV separately to determine how well the each variable explains the observed distribution.

We developed three Maxent suitability models for each of the two seasons (i.e. hot wet and cool dry), namely the Individual Max, Corrected Individual Max and Pooled models. Black rhino potentially change their selection of resources from one season to the next (Oloo *et al.* 1994, Ganqa *et al.* 2005) and we wanted to ensure that this variation in selection did not confound our model comparisons.

i) Individual Max model - We developed a Maxent model for each individual black rhino for each season. Maxent produces a raster file, which is a grid covering the area of the reserve, and allocates a suitability value for each grid cell; 0 being the lowest and 1 the maximum suitability (Phillips *et al.* 2006). A partitioned based HSM, for the tick species *Boophilus decoloratus*, which was developed from the mean values of partitioned models did not perform as well as non-averaged models (Estrada-Peña & Thuiller 2008). Subsequently we overlaid all the individual models and selected the maximum value for each grid cell for the dry and the wet seasons. The resultant dry and wet season Individual Max models represent the maximum predictions for the population based on individual black rhino locations. We selected the maximum rather than the mean of the results, as the mean would average out potentially important and non-used areas by different black rhino.

ii) Corrected Individual model - We might expect that by using the maximum values of the individual models the predictions in some areas may be biased to single individuals who are not the 'norm' and that these areas would have resulting low use in the long term. We therefore decided to compensate for variation within the population using the standard deviation (SD) incorporated in the following correction factor:

Corrected Individual Max value = (1 – SD) x (Individual Max value)

Since suitability values were all between 0 and 1, multiplying by (1 – SD) had an effect of decreasing the maximum value proportionally by the SD. High maxima with low SD would retain high corrected values, whereas corrected values for high maxima with high SD would become proportionally lower, and so on.

iii) Pooled model - We developed a Maxent model using pooled location data of all the black rhino separately for the dry and wet seasons, and as such we did not recognise individuals, or variation among individuals, in the formulation of this model.

5.3.3. Model comparisons

To assess the amount of agreement between the initial individual suitability maps, we calculated the degree of niche overlap using the program ENMTools (Warren *et al.* 2008). ENMTools calculates the niche overlap using two different statistics, namely the Schoener's *D* (Schoener 1968a) and the *I* statistic (Warren *et al.* 2008). We used only the *D* statistic to evaluate overlap due to the similarity in the outputs of the two statistics (Warren *et al.* 2008). The higher the Schoener's *D* value the greater the agreement amongst the models. We assessed the degree of overlap between individuals within the whole population, then within the sexes and finally within clusters of rhinos of both sexes. Clusters are groups of individuals with overlapping home ranges and which associate with one another on a regular basis (sensu Lent and Fike, 2003; see Chapter 2 for more details on cluster identification).

We calculated the same Schoener's *D* niche overlap statistic between the final three models. We were also interested in how these models differed statistically in their allocation of suitability values spatially. However, we decided to use bar graphs to illustrate the expected distribution of black rhino (see Test 1 and 2 below), rather than statistical tests between the models' spatial distribution for a number of reasons. Firstly, Warren *et al.* (2008) devised randomisation tests for the Schoener's *D* statistics, but since our location data were the same for each model we were unable to complete these tests. Secondly, the models had non-normal distributions (One-Sample Kolmogorov-Smirnov Test, $P < 0.05$) so we could not use a pair-wise t-test (Levine *et al.* 2009). The effect size of our comparisons was large (lowest Cohen's $d > 1.2$), which means that there was less than a 40 % distribution overlap between samples (Cohen 1988), and with such large sample sizes (the number of grid cells on the HSM was in excess of 1.5 million) we were concerned with overpowering any test we did. Finally, none of these tests suitably show the comparisons between how the models are responding to each of the EGVs.

In order to evaluate how the individual models differed from each other and from the Pooled model, we examined the Jackknife AUC results, which show how well each EGV explain the observed distribution. We recorded the results of the individuals as bar graphs and marked the respective EGV score for the Pooled model on the same graph. To assess whether any agreement amongst individuals was a true reflection, we selected three rhino with the most similar AUC scores to the Pooled model's AUC score for Habitat and again for Browse Availability (BA) in the dry season. We selected these variables (one a categorical and one a continuous variable) as examples of the potential variation amongst seemingly similar responses, and which managers typically use in decision-making. We then graphed the response curves (generated automatically by Maxent) of the individuals, and the Pooled model, to the variables.

5.3.4. Variation in model predictive capabilities

i) Test 1 - To test how well a model would predict the occurrence of other black rhino from the same period as model development we allocated 3 individuals (20 % of the population) location data (n = 181) as testing data and excluded them from the first set of model generation. The test rhino included a female (PDF78), dominant male (DM2) and subordinate male (PDM03) from different areas throughout the reserve (see Chapter 2 as to how we established social structure amongst the males).

ii) Test 2 - To test how well a model would predict the occurrence of the population in the period following model development we generated models using all 15 rhinos' location data and tested the variation in their capabilities using location data of the same individuals from the year after model data was collected. The proceeding data were collected so as to incorporate both seasons over the nine month collection period, from January – October 2009 (wet season n = 67; dry season n = 59). There were fewer locations during this period as we only used conventional spoor tracking techniques to find the rhino.

5.3.5. Statistical analyses

We ran two extrinsic tests to test how well the models performed under our Test 1 and Test 2 scenarios. We assigned each testing location relevant habitat suitability values from each of the three models. We calculated the extrinsic commission index (the proportion of grid cells predicting presence locations), using the lowest probability value of each category as a 'threshold' value (Anderson *et al.* 2003). We therefore had 10 commission indices for each model. We plotted these against the omission error (proportion of locations falling outside the predicted area) for the relevant categories and connected each model's points with a straight line. Omission/commission graphs are an effective means of comparing the performance of predictive models, with intrinsic and extrinsic test results closely related (Anderson *et al.* 2003). We were then able to read approximate omission error values at nine commission index values (0.1; 0.2; 0.3;…0.9) so that we could make equalised predicted area comparisons between the models (Phillips *et al.* 2006). We used a non-parametric Friedman's test to test for differences among the three model's omission error values, to assess whether the three models' performance differed for equal areas of prediction. However, a good predictive model will identify the most suitable areas for a population to inhabit, whether the areas are inhabited or not (Anderson *et al.* 2003). This plays a role in the perceived commission index error, with uninhabited areas having no testing locations present and therefore falsely decreasing the performance of the model. The individual models may fall into this category of predicting too large an area for occurrence. Anderson *et al.* (2003) propose that "the ideal value of the commission index equals the true proportion of pixels that hold potential distribution for the species". Here, based on expert opinion, we estimate the optimal modelling area to be between 70 – 85 % of the study area. We are therefore able to visually assess whether the models have acceptable levels of less than 5 % omission error (Anderson *et al.* 2003) in this estimated area.

For the second extrinsic comparison of the models we tested their performance using receiver operating characteristic (ROC) curves. The area under the ROC curve (AUC) has the advantage of being a continuous evaluation of the prediction of the models rather than relying on categories of threshold values. Since we have only presence locations and no source of absence locations to measure specificity, we used a random selection of 10 000 absence points (pseudo-absences) as described by Phillips *et al.* (2006). By assigning model suitability values to our test locations, and to the pseudo-absences, we were able to calculate both the sensitivity and the specificity of the models, and calculate AUC for each model. A random prediction would still correspond to an AUC value of 0.5 (Phillips *et al.* 2006). We were then able to compare the resultant AUC values statistically to determine whether the models differed significantly in their performance using Analyse-it for Microsoft Excel (version 2.20, Analyse-it Software, Ltd. http://www.analyse-it.com/; 2009). The software uses the non-parametric Delong, Delong, Clarke-Pearson method (DeLong *et al.* 1988) to compare the resultant AUC values, and reports a *P* value for the test.

All other statistical analyses were performed in SPSS 15.0 (SPSS Inc., Illinois, USA). Significance was tested at a level of 0.05 unless stated otherwise.

5.4. Results

We designed and tested predictive habitat models to assess whether pooling location data for black rhino was meaningful, or whether developing a model based on individual predictions was more informative. The Pooled dry and wet season models for Test 1, had an AUC of 0.875 and 0.885 respectively. For Test 2 the Pooled dry and wet season models, had an AUC of 0.871 and 0.851. The individual black rhinos' dry and wet season models had, on average, higher AUC values, with an average of 0.938 (SD = 0.044; min = 0.865) and 0.922 (SD = 0.067; min = 0.769), with the lowest AUC > 0.75, and therefore still considered useful (Elith *et al.* 2006).

For easier viewing we increased the raster cell size using a nearest neighbourhood analysis and categorised the map outputs into five categories (Fig. 5.1). There was little inter-individual niche overlap of the predicted suitable habitats for the rhinos, for either the dry or the wet season, with a higher degree of overlap between individuals within the same clusters (Table 5.2), although this overlap was still low. The overlap between the Test 2 Pooled model's distribution map and the Corrected and Individual Max maps was slightly higher in the wet season (Schoener's *D* of 0.69 and 0.70 respectively) than in the dry season (Schoener's *D* of 0.65 and 0.67 respectively; Fig. 5.1). The Corrected Individual and Individual Max models overlapped completely (Schoener's *D* of 0.96 for both seasons; Fig. 5.1).

The Pooled model (Test 2 model) restricted higher suitability values to smaller areas than the more even allocation of suitability scores of the two individually generated maps (Fig.5.1). Across all the models, there was an increased area and more even distribution of suitable habitat for the rhino during the wet season than during the dry season.

We inspected the Maxent jackknife AUC outputs for each EGV, which is run independent of all the other EGVs, to determine the importance of the individual data (Fig. 5.2). At this fine scale we can now see the variation amongst individual black rhino responses to EGVs. During the cold dry season, when resource limitation would occur, there was individual variation in the rhinos' response to water and the presence of herbs and agreement among individuals' responses towards the important habitat, elevation and shading variables. Interestingly, there was a large amount of variation in the individual and the pooled model outputs for these same important variables, meaning the pooled model was unable to quantify an ‘average’ response for these important variables. This is largely because the rhino were not necessarily responding to EGVs in the same manner (Fig. 5.3), although they are ranking their importance similarly to one another (Fig. 5.2).

We therefore need to analyse each individual’s response curves to better understand the increase of suitable areas in the wet season (Fig. 5.1). For example, habitat types explain the seasonal response of PDF79 better during the dry season (AUC = 0.88) than in the wet season (AUC = 0.76). She used habitat types 4 (*Spirostachys africana* woodlands), 6 (*Combretum apiculatum*-Lebombo open woodlands) and 13 (Floodplain grasslands) in the wet season (Fig. 5.3), while in the dry season her response changed to an increased use of habitat type 4 (*Spirostachys africana* woodlands), 5 (*Acacia luderitzii* thickets and woodlands) and 15 (Riparian woodlands and forests) while exhibiting less importance to 13 (Floodplain grasslands). Her change in habitat use may be due to the increase in grass quality and the presence of seasonally available herbs in the grasslands during the wet season, which are both components of black rhino browse when available (Brown *et al.* 2003, van Lieverloo *et al.* 2009), while the riparian areas, forests and woodlands would continue to provide available forage going into the dry season. Her response to browse availability (BA) and herbs support this notion, with browse availability being more important during the dry (AUC = 0.90) than the wet season (AUC = 0.54), and herbs being more important during the wet season (AUC = 0.76) than the dry season (AUC = 0.62). Her movements in the dry season would therefore be more limited than in the wet season, during which time she would have an abundance of available forage in a number of various habitats (explaining the lower habitat type AUC value in the wet season).

The models differed significantly in their performance based on the equalised area comparison of their omission errors (Friedman’s χ^2 $P < 0.05$ for all tests), other than for Test 1 in the dry season (Friedman’s $\chi^2 = 1.64$, $P = 0.441$). The Pooled model had slightly lower omission errors than the other two models, and appeared to make more accurate predictions, specifically for low commission index values. However, all the models had acceptable levels of less than 5 % omission error in the optimal modelling area (between

0.70 – 0.85 commission index), other than during the dry season for Test 2 (Fig. 5.4). The latter result may be due to small sample sizes, but further analysis would be required to understand these results better.

Based on the extrinsic formulated ROC curves (Fig. 5.5) the Pooled and the Individual Max models performed similarly well during the dry season, while during the wet season the Pooled model outperformed the two individual models (Table 5.3). The Individual Max model generally outperformed the Corrected Individual model.

The Individual Max model response to the EGVs was a more accurate prediction of rhino habitat suitability, and it performed similarly well during the resource limiting dry season. We therefore developed a final model to illustrate the dry season habitat suitability for black rhino on MGR for management purposes (Fig. 5.6). We used the Individual Max model to illustrate areas of suitability, namely low (0.00 – 0.33), medium (0.34 – 0.66) and high (0.67 – 1.00), and graded each raster cell in relation to the level of agreement amongst individuals. We did this by using the standard deviation map we calculated to grade the level of population variation (min SD = 0 and max SD = 0.40) into three equal categories of low (SD = 0 – 0.13), medium (SD = 0.14 – 0.26) and high (SD = 0.27 – 0.40). Each grid cell therefore could fall into one of nine categories relating to the combination of suitability and individual variation categories. Interestingly, there was no incidence of high suitability with low variation and low suitability with high variation.

5.5. Discussion

Partitioning of location data into subsets exhibiting similar responses to EGVs (in our case individuals), provides more accurate models of population responses (this study; Murphy & Lovett-Doust 2007, Estrada-Peña & Thuiller 2008, Suarez-Seoane *et al.* 2008). During resource limiting periods, an individual Maxent model, using maximum suitability values from each individual, was able to make predictions of occurrences of non-modelled individuals, and of future occurrences of the modelled population, as effectively as a model using pooled location data. Pooled black rhino responses to EGVs were different to how individuals were actually responding. By modelling each individuals' responses to EGVs across the landscape, we were better able to understand individual black rhino decisions and the trends of the models. For example we were able to understand why there was an increased suitable area during the wet season, by analysing individuals' responses to the various EGVs, and thus answer the question "What ecogeographical variables influence a population's movements?".

The EGVs included in this study were at a fine scale which we did in order to achieve a better understanding of the population's ecology and future habitat use in one geographical area. At a larger ecological scale, partitioning of geographically separated populations would be more applicable (Osborne & Suarez-Seoane 2002), as would the inclusion of larger scale climatic variables, for example rainfall and temperature. The results from this study and others (e.g. Calenge & Dufour 2006) do suggest, however, that individual level responses to the proposed EGVs for model development should first be tested before their locations are pooled.

Black rhino have low levels of agreement amongst their social clusters' responses to EGVs (this study; Chapter 4), however it is still higher than the variation amongst individuals at a population level. Therefore, if data collection is to be restricted to a few individuals from a population, then representatives from clusters of black rhino should be selected rather than a random selection. A more detailed analysis of individuals' niche equivalency (Warren *et al.* 2008) and to which EGVs they respond similarly to, would yield further insight into a population's ecology, and how best to present a population level response for management purposes. For example an assessment and comparison of individuals' response curves to each variable (as exemplified in Fig. 5.3) may lead to identifying groups of similarly responding individuals (Estrada-Peña & Thuiller 2008).

We expected a Maxent model using the maximum number of locations from a population to perform better during model development than a number of models using a sub-sample of locations (Wisz *et al.* 2008). However, due to the variation in individuals' niche selection, Maxent struggled to achieve higher levels of entropy than the partitioned models representing the individuals. This is ultimately an artefact of the individuals having narrower niche ranges (i.e. more agreement amongst their locations) relative to the area described by the environmental data (Phillips *et al.* 2006). By identifying each individual's niches accurately the predicted Maxent model, and hence the EGVs deemed important, was more accurate. By analysing the individual we also eliminated problems of sample size bias (Thomas & Taylor 2006) evident between individuals in the study population.

5.5.1. Black rhino management

Black rhino responses to EGVs varied amongst individuals. However, there was more agreement among black rhino responses during the dry season, which will make management decisions during these important periods of resource limitation easier. Since black rhino agree more on the areas which they avoid, we needed to understand how individuals are responding to EGVs to get a picture of population responses. For example, since habitat types and shading were important to black rhino during the dry season, then management decisions, i.e. burning and bush clearing, in those habitats which individuals considered important, should be managed accordingly.

5.5.2. Conclusion

The utility of Maxent and other similar machine learning habitat suitability models make them attractive choices for conservation planners and land managers. The adaptation of these models to incorporate an error structure which has the ability to compensate for intrapopulation variation in sample sizes and habitat preferences would allow it to compete with more advanced methods in this regard (K-select analysis, Calenge *et al.* 2005a, e.g. generalised additive mixed models, Aarts *et al.* 2008). A single output would provide a more user-friendly model for conservation managers, rather than a number of individual responses which the researcher needs to manipulate. This is particularly relevant for endangered species, for which intensive management is essential. Ultimately, prediction models based on relevant partitions within a population perform better than those models which attempts to average out variation.

Table 5.1 List of ecogeographical variables used for measuring habitat suitability for black rhino on the Mun-ya-Wana Game Reserve in South Africa.

Code	Ecogeographical variable
BA	Browse Availability - measured for each habitat using the browse availability method as outlined by Adcock (2004).
CC	Carrying capacity - calculated for each habitat using the index of black rhino browse availability, soil fertility, annual rainfall and minimum July temperature (Adcock 2006)
Grass	Grass abundance, calculated as a percentage of grass ground cover for each habitat, as outlined by Adcock (2004).
Herbs	Herb abundance, calculated as a percentage of herbaceous ground cover for each habitat, as outlined by Adcock (2004).
Dist_water	Distance to the closest permanent water source.
Habitat	Habitat types - as determined by van Rooyen and Morgan (2007), see Appendix 2 for full details.
Habitat_rich	Habitat richness - a measure of the diversity of habitats surrounding a grid cell on the map, equated as the number of different habitat types present in a 500m diameter surrounding a grid cell.
Shading	Shading was the average of the shading site index recorded at the browse assessments sites across the reserve for each habitat type. Shading index ranges from 1= Deep shade to 13 = No shade.
DEM	A 50-m resolution digital elevation model, also used for the calculation of slope and aspect. Elevation is measured in meters above sea level, to the maximum height of the study site at 305m.
Aspect	Aspect as calculated from the digital elevation map, measured in degrees.
Slope	Slope as calculated from the digital elevation map, measured in degrees.
Rd_density	We calculated road density using a line density calculation in ArcMap, using all the roads on the reserve. It was calculated as the kilometres of road per square kilometre area (km/km^2).
Dist_rds	For the road distance variable we included only main access routes to the lodges, due to the large amount of traffic that they receive on a daily basis, and the two public roads that run through the length of the reserve. The rest of the road system on the reserve is extensive but was not included, because of relatively infrequent use. This is thus a measure of potential disturbance from human activity as opposed to the ecological influence of roads per se which is captured in road density above.
Dist_fence	Distance to the boundary fence.
Sand	Percentage ground cover of sand, such that cover between sand, stones and rocks equals 100%. The cover was estimated for each browse assessment site across the reserve and the mean was calculated for each habitat type.
Stone	Percentage ground cover of stones (< 20cm in diameter), such that cover between stones, sand and rocks equals 100%. The cover was estimated for each browse assessment site across the reserve and the mean was calculated for each habitat type.
Rocks	Percentage ground cover of rocks (> 20cm in diameter), such that cover between rocks, stones and sand equals 100%. The cover was estimated for each browse assessment site across the reserve and the mean was calculated for each habitat type.

Table 5.2 The overlap between 15 individual black rhino Maxent models with one another, quantified by the mean of the Schoener's *D* statistic across overlaps. The higher the *D* value the greater the overlap, and hence agreement, amongst the models. The overlap was initially calculated for all individuals within the population, then within the sexes and finally within each identified cluster of rhino for each season (see Chapter 3 for details on cluster identification).

		Dry season		Wet season	
	N	Mean *D*	SD	Mean *D*	SD
All Individuals	105	0.30	0.16	0.27	0.21
Females	21	0.26	0.15	0.23	0.20
Males	28	0.30	0.17	0.28	0.21
Cluster 1	3	0.67	0.01	0.73	0.03
Cluster 2	6	0.42	0.13	0.39	0.18
Cluster 3	6	0.52	0.07	0.59	0.07
Cluster 4	6	0.43	0.09	0.47	0.19

Table 5.3 Results of extrinsic receiver operating characteristic (ROC) analyses for Maxent derived black rhino habitat suitability models for the Mun-ya-Wana Game Reserve (see text for details on development of the different models) and the difference between the models' performances. A significant *P* value implies that the model with the highest AUC is significantly better than the other. The models were built and tested with location data spanning three years and six seasons. Test 1 was conducted with location data of three individuals removed from model development. Test 2 was conducted with location data of the modelled population from the following year.

				Individual Max		Pooled	
	Season	Model	AUC	Difference	*P*	Difference	*P*
Test 1	Dry	Corrected	0.847	0	0.740	0	0.854
		Individual Max	0.848			0.01	0.806
		Pooled	0.843				
	Wet	Corrected	0.750	0.01	< **0.001**	0.07	< **0.001**
		Individual Max	0.755			0.06	< **0.001**
		Pooled	0.763				
Test 2	Dry	Corrected	0.700	0.02	**0.003**	0.08	**0.004**
		Individual Max	0.717			0.06	0.021
		Pooled	0.778				
	Wet	Corrected	0.750	0.01	0.070	0.08	< **0.001**
		Individual Max	0.750			0.07	< **0.001**
		Pooled	0.824				

For each model the area under the ROC curve (AUC) is given. All model's AUC values were significantly better than a random model (all models $P < 0.0001$; model *P* values not shown). The difference between model AUC scores for each test is cross tabulated, with significant differences noted in **bold** (Bonferroni corrected significance level of $P = 0.004$).

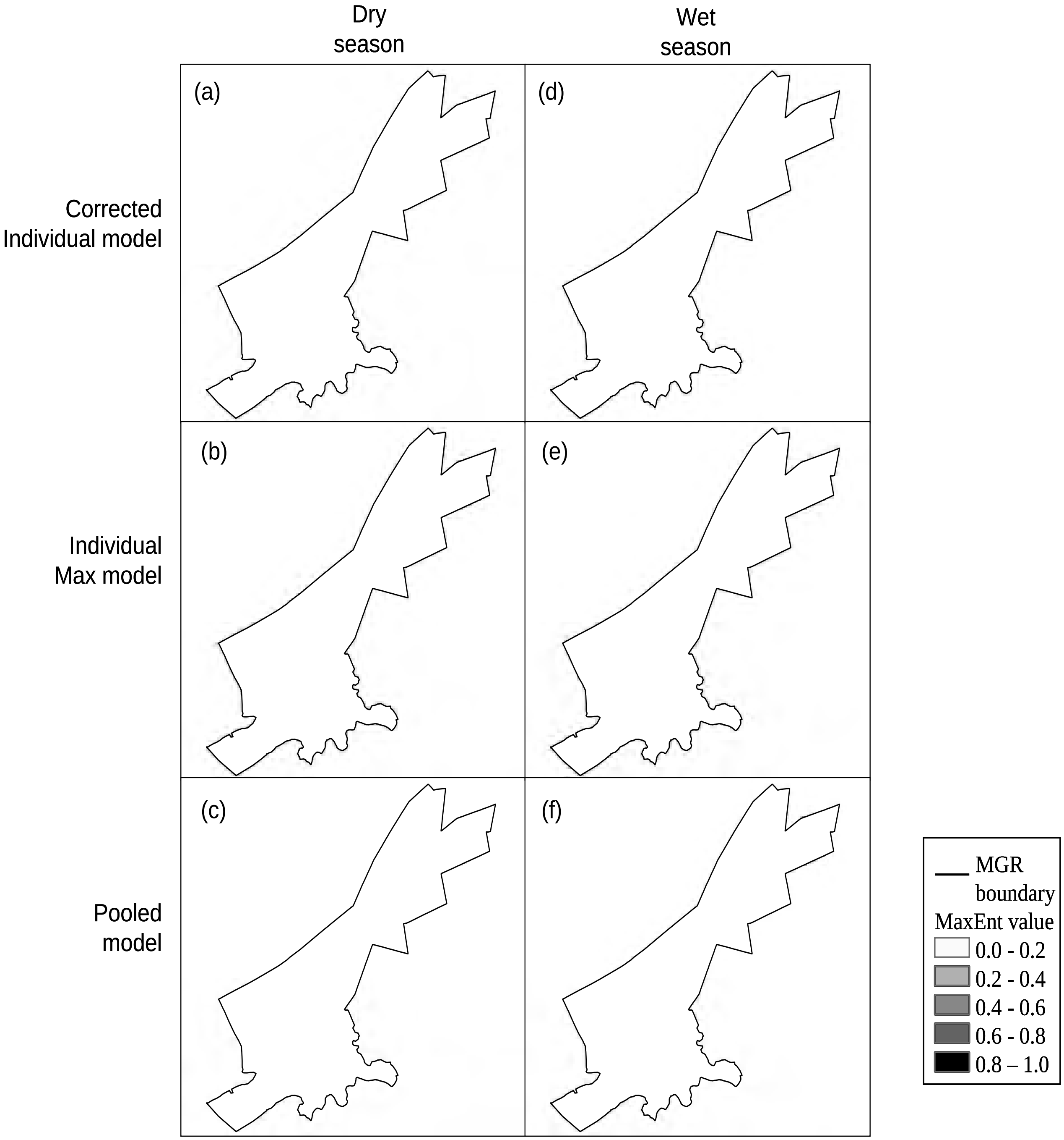

Figure 5.1 Maximum entropy (Maxent) distribution models for black rhino on the Mun-ya-Wana Game Reserve, in the dry and the wet seasons. Darker areas represent more suitable habitat for black rhino. The Individual Max model was developed using maximum predictive values from models generated for each individual. The Corrected Max model is a result of applying a correction factor, based on the standard deviation of the individual's results, to the Individual Max model (see text). The Pooled model pools the location data of all the individuals to generate one map, thereby not accounting for inter-individual niche variation.

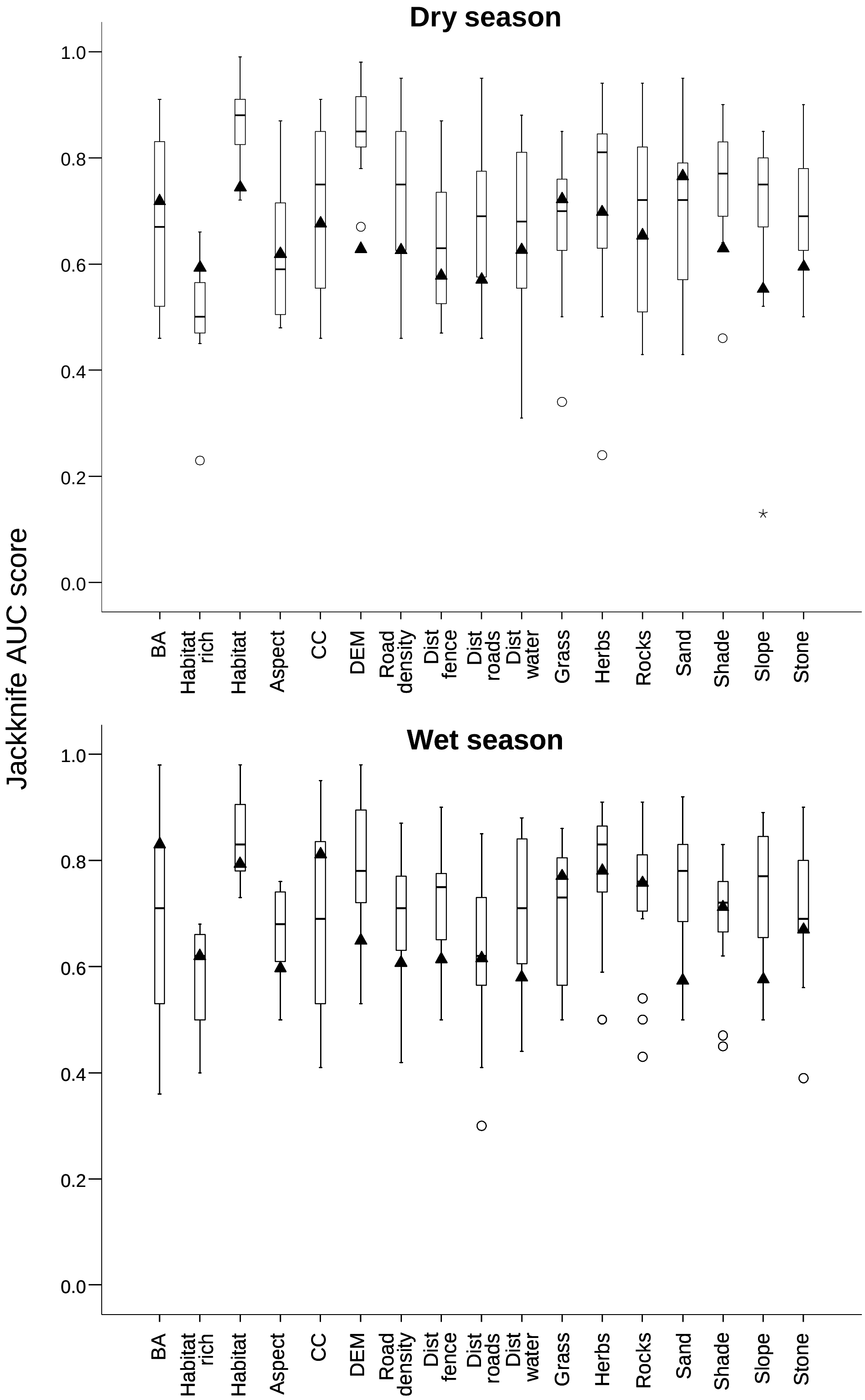

Figure 5.2 The variation of ecogeographical variables (EGVs; see Table 1 for details) importance for individual black rhino, as calculated by individual Maxent habitat suitability models. A

pooled location model's predictions are also shown for each season (filled triangles). Bar graph represents the variation among the individual models' (n = 15) importance for each EGV. The importance is measured using area under the receiver operating curve (AUC) statistics calculated on Jackknife tests for each EGV. The line across the box is the median; box represents the 25th and 75th percentiles; and the whiskers indicate the 5th and 95th percentiles. Outliers and extreme outliers are designated by open circles and asterisks. Variables most affected by pooling are those where the median is furthest from the triangle and those where the ranges are large.

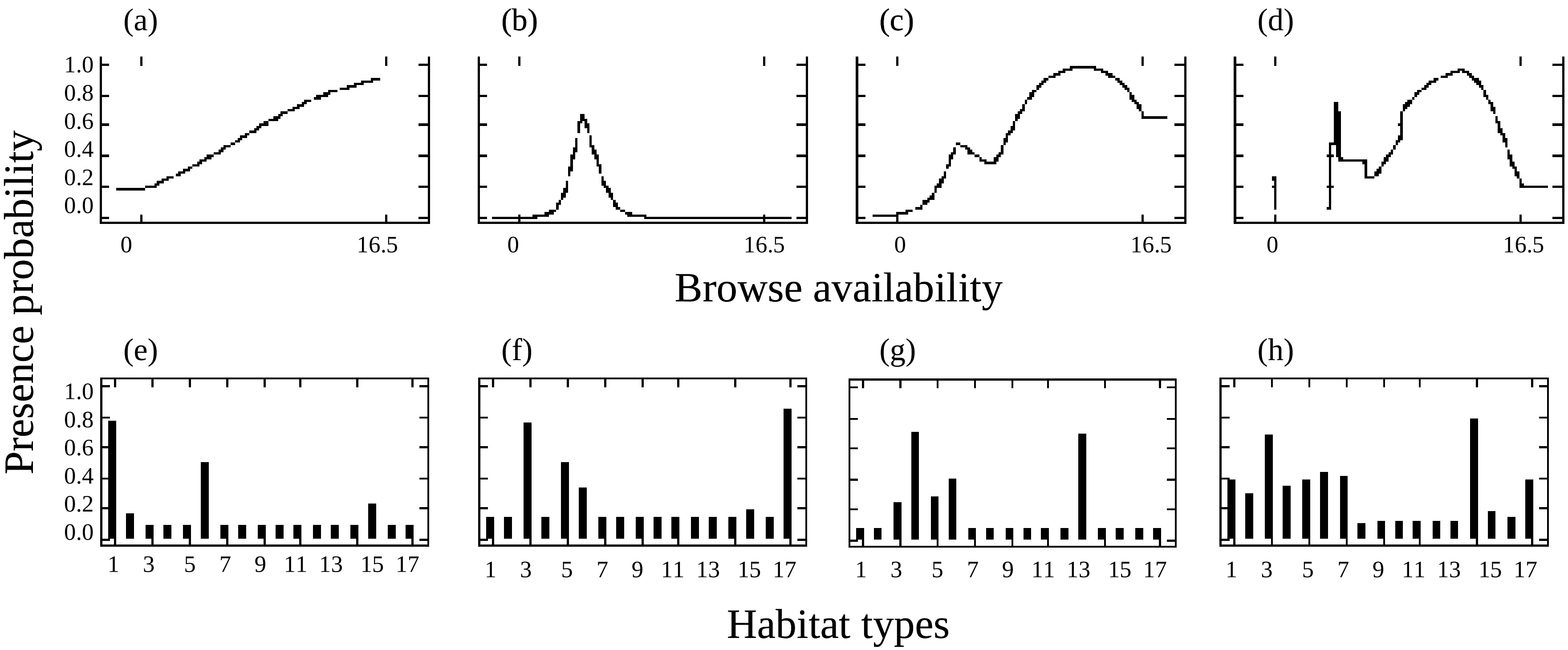

Figure 5.3 Response of black rhino to browse availability (BA) and habitat types in the wet season. BA is measured as the percentage volume of suitable browse available for black rhino within 2 m of the ground. Habitats are numbered according to the list in Appendix 2. BA response curves (a) PDM81 (AUC = 85), (b) PDF01 (AUC = 82), (c) PDF85 (AUC = 83) and (d) Pooled model (AUC = 83). Habitat response curves (e) DM4 (AUC = 78), (f) DM3 (AUC = 78), (g) PDF79 (AUC = 77) and (h) Pooled model (AUC = 79).

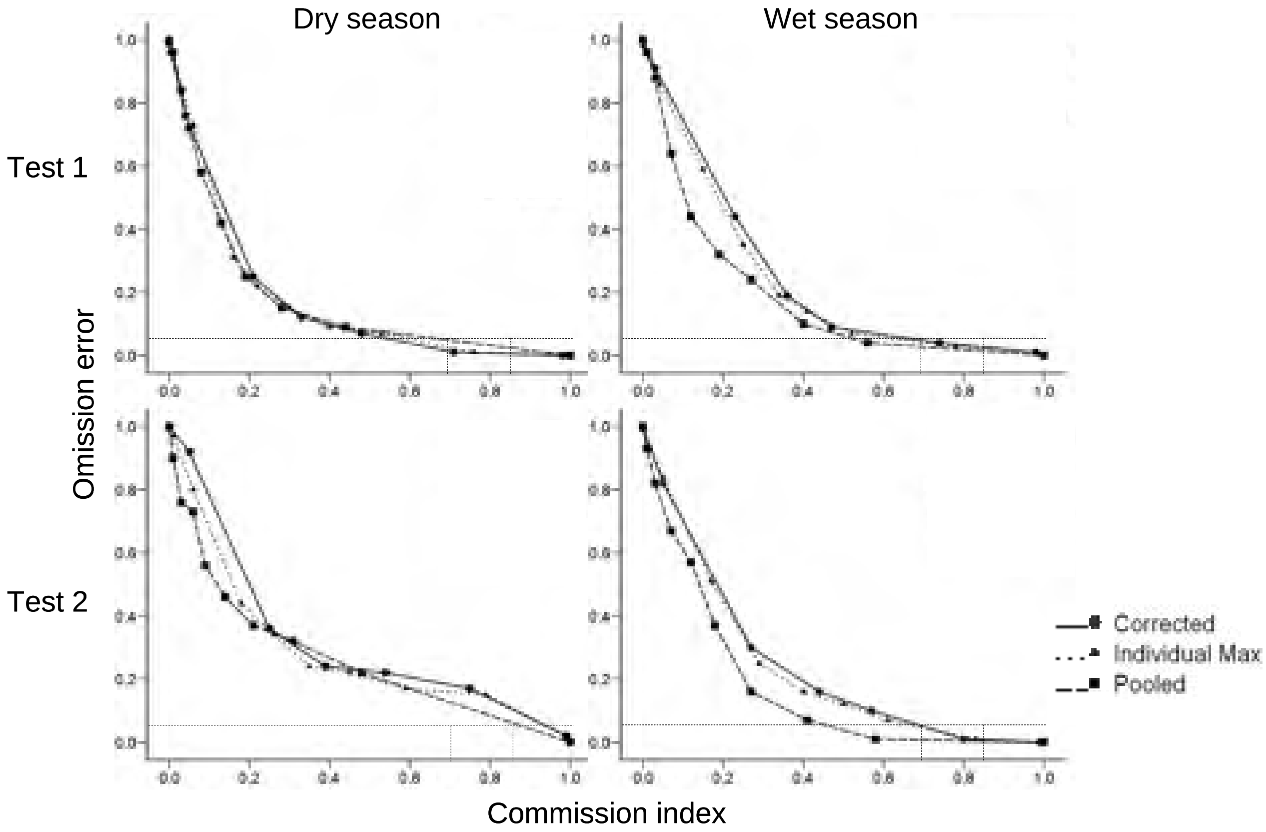

Figure 5.4 The performance of three habitat suitability models for black rhino on the Mun-ya-Wana Game Reserve (see text for details on model development). The commission index is the proportional area where the model predicts occurrences of black rhino, while the omission error is the proportion of testing locations falling outside of the predicted area. The areas were calculated for each of 10 predictive value thresholds, spread equally by a value of 0.1 between the Maxent logistic output suitability values of 0 and 1. Test 1 was conducted with location data of three individuals removed from model development. Test 2 was conducted with location data of the modelled population from the following year. Dotted reference lines (*y*-axis 0.05; *x*-axis 0.70 and 0.85) represent optimal modelling areas and accepted 5 % omission error levels. Models falling into this region would be considered useful.

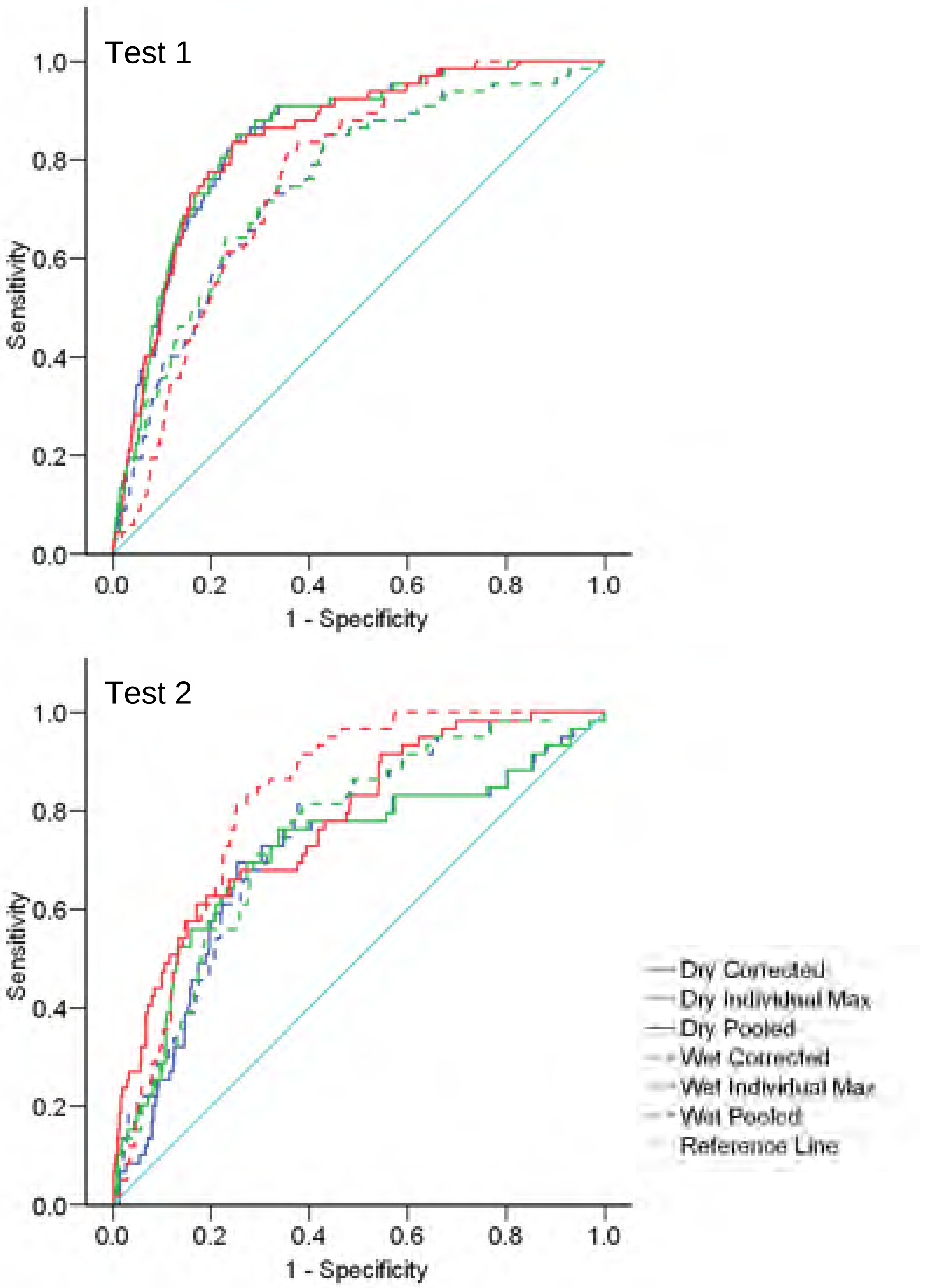

Figure 5.5 Extrinsic receiver operating characteristic (ROC) curves for three black rhino habitat suitability models generated by Maxent, for the Mun-ya-Wana Game Reserve (see text for details on the different models). The models were built and tested with location data spanning three years and six seasons and specificity was calculated using 10 000 pseudo-absence points. Each test was conducted using location data from the cool dry

season and warm wet season data. Test 1 was conducted with location data of three individuals removed from model development. Test 2 was conducted with location data of the modelled population from the year following model development.

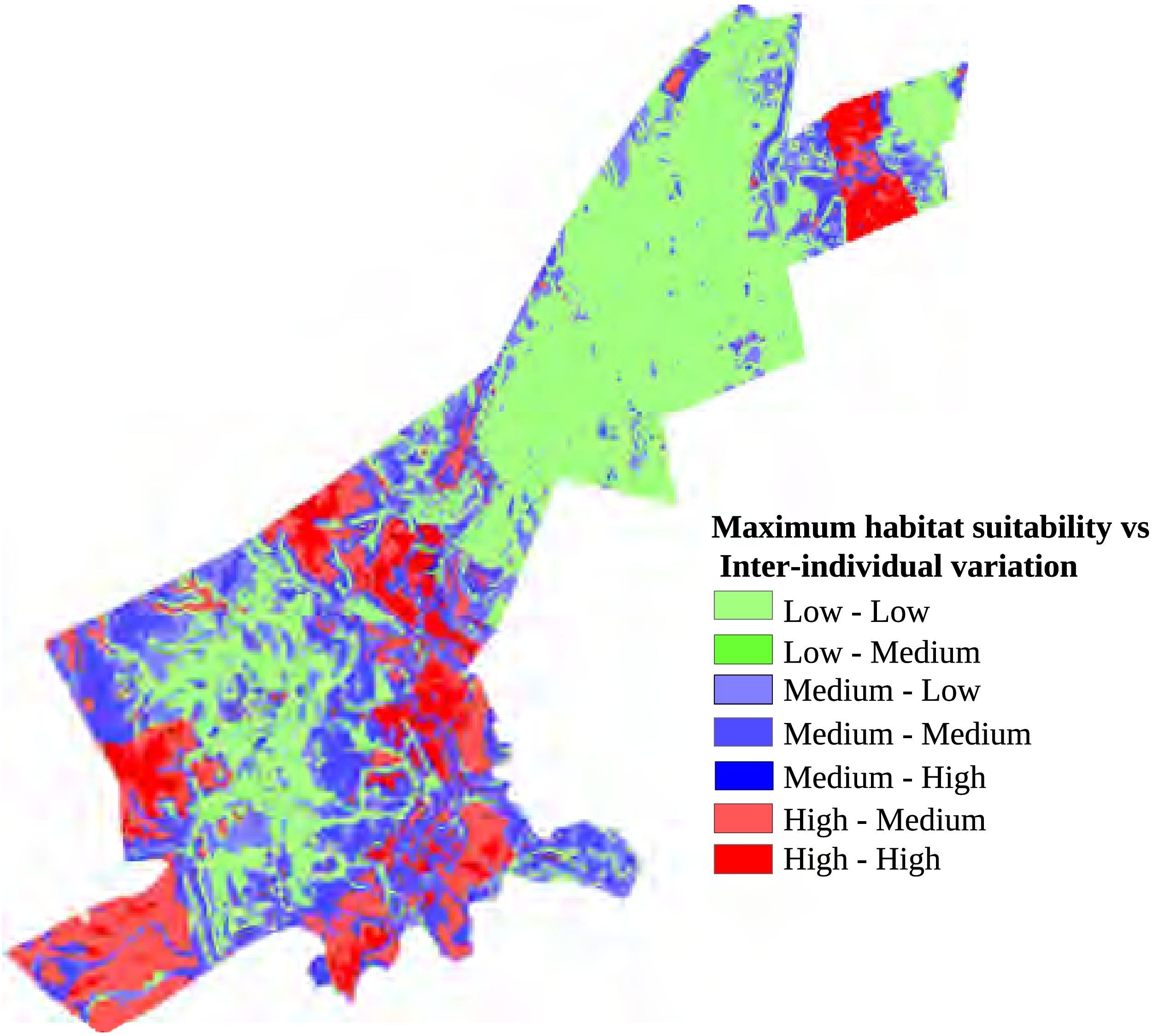

Figure 5.6 A habitat suitability model for black rhino on the Mun-ya-Wana Game Reserve during the dry season. The map illustrates the suitability of each grid cell according to the suitability value of the individual in the population which ranked that cell the highest and the degree of inter-individual variation amongst the population. Low variation indicates agreement amongst the populations predicted suitability values for a cell, while high variation indicates disagreement.

CHAPTER 6

Evaluating the settling response of reintroduced black rhinoceros to ecogeographical variables

6.1. Summary

Understanding how ecogeographical variables (EGVs) affect the settling response of a population of reintroduced animals could enhance future reintroduction efforts. Using a machine learning maximum entropy model (Maxent), we assessed the response of individuals in a population of reintroduced black rhino *Diceros bicornis* to various EGVs over a 12 month period divided into 7 phases based on known black rhino ecology. Based on these responses, we could delineate three phases: the acclimation phase (first 25 days), the establishment phase (26 – 281 days) and the settlement phase (282+ days). The most important settling variable for all demographic groups was the social response of rhino to dominant males, which occurred during the acclimation phase. The adult males established themselves into the new area more quickly than either females or sub-adult males, and made fewer changes from the establishment to the settlement phase. By the settlement phase, the rhino had settled into a fixed area relative to their release sites, were using specific habitat types and, although there were differences amongst the demographic groups, they had settled into responses to most of the EGVs. Following the responses of the rhino towards different EGVs we make a number of management suggestions for future release strategies for black rhino, including (1) black rhino are free released onto reserves with no conspecifics, (2) black rhino release periods should be as short as possible and span no longer than the acclimation phase of 25 days, (3) adult males should be released in spatially distinct areas (the size of an estimated home range for the region) such that they have access to a water resource which is distant (>1 km) from a fence. Here we have shown that understanding the response of reintroduced animals to EGVs provides us with valuable insights into the ecology of the species, and allows us to develop management interventions which may help improve the settling rate of reintroduced populations.

6.2 Introduction

A large majority of reintroductions are conducted for conservation purposes to either establish new breeding populations or to supplement existing populations of endangered species (Fischer & Lindenmayer 2000). The aim of such translocations is to increase the growth and breeding success of the meta-population. However, reintroductions may be unsuccessful, either due to animals trying to 'home' after translocation (Miller & Ballard 1982, Linnell *et al.* 1997), competition at the release site (Linklater & Swaisgood 2008), environmental factors encountered at the release site which are different to the source site (Fischer & Lindenmayer 2000, Stamps & Swaisgood 2007) or through stress induced from the translocation (Letty *et al.* 2007). Presently reintroduction studies focus on the afore mentioned factors in combination with the age and sex of individuals (Moehrenschlager & Macdonald 2003, Wear *et al.* 2005, Hardman & Moro 2006), behavioural ecology (Bremner-Harrison *et al.* 2004, Watters & Meehan 2007) and release techniques (Eastridge & Clark 2001, Hardman & Moro 2006) as the factors affecting the settling rate and subsequent success of reintroductions.

Ecogeographical variables (EGVs) are often ignored (Eastridge & Clark 2001) or assumptions are made about their influence on the post-release movement patterns of animals (Vandel *et al.* 2006, Spinola *et al.* 2008). However, a number of environmental factors influence the ranging patterns of animals, including habitat availability (Arthur *et al.* 1996), habitat suitability (Winnie Jr. *et al.* 2008), seasonality (Schooley 1994) and social dynamics (Fretwell & Lucas Jr. 1970). The success of an introduction and the future breeding potential of a population may be dependant on the EGVs influencing settling patterns of the population (Jean-Baptiste *et al.* 2009). For example water vole *Arvicola terrestris* post-release settlement and future survival rates are influenced by vegetation abundance (Moorhouse *et al.* 2009), while the Eurasian badger *Meles meles* are negatively affected by human disturbances during their settling phase (Balestrieri *et al.* 2006, Gusset *et al.* 2008). We therefore suggest another important indicator and aspect of the settling phases is how individuals' responses to EGVs change after their release. Conservation managers reintroducing animals would be better equipped to implement measures to decrease search efforts and the associated stress, mortality risks and deferred costs associated with finding and settling into a new range, by understanding the various factors being selected for, or influencing, an animal's settling process.

Three phases of post-release movement have been identified (Moehrenschlager & Macdonald 2003). First, the acclimation phase describes initial movements after release that are highly variable in distance and direction. Daily displacements can be unusually large (e.g. flight response, or individuals extremely sedentary and hiding). The acclimation phase has also been referred to as the dispersal phase and ends when an individual moves into its future home range for the first time (Richard-Hansen *et al.* 2000). Second, the establishment phase encompasses the period when an individual's distance from the release site stabilizes, but its movement patterns are dissimilar to those of established animals, for example higher daily displacements. Lastly, during the final settlement phase an individual's daily movement and ranging patterns are similar to those of established animals (Moehrenschlager & Macdonald 2003).

Armstrong and Seddon (2008) outline the need for us to understand which habitat conditions a population requires to persist. Within this context they note that we need to ensure that the data captured on EGVs is relevant to the species. Presently our understanding of these variables in relation to black rhino *Diceros bicornis* with regard to reintroductions is lacking. Reintroductions are an important management tool for the future conservation of this endangered species (http://www.iucnredlist.org; Emslie 2001, Metzger *et al.* 2007), but there are high mortality rates amongst reintroduced black rhino (Brett 1998, Linklater & Swaisgood 2008). Here we propose the novel application of Maxent (Phillips *et al.* 2006), a maximum entropy model used for the prediction of presence-only species occurrences (Phillips *et al.* 2006), to better understand black rhino post-release settlement phases with regard to EGVs. Previous work indicate the acclimation phase to take about 5 days and the establishment phase to last up to 25 or over 100 days (Linklater & Swaisgood 2008), with no clear indication of a settlement phase due to a lack of comparable settled black rhino data. No longer-term study has been conducted to establish at what stage black rhino enter the settlement phase, or what factors affect the settlement rate.

We aimed to define the influence of EGVs on black rhino settlement and establishment, and to propose potential management interventions to increase the settling rate. Our objectives were therefore to (1) establish provisional post-release phases based on prior knowledge of black rhino ecology and ranging patterns; (2) use Maxent to calculate the importance of the different EGVs and how they influenced the distribution of black rhino for each of the provisional post-release phases; (3) determine which of the provisional phases could be grouped together to form the different post-release settlement phases, namely the acclimation, establishment and settlement phases; (4) discuss the implications of these findings for developing a better understanding of reintroduction biology.

6.3. Materials and methods

6.3.1. Capture, translocation and release

The capture, translocation and release procedures for the 15 black rhino released on the Mun-ya-Wana Game Reserve (MGR) is described in Linklater *et al.* (2006). All rhino received horn-implant transmitters, either a MOD-80 or the larger MOD-125 (Telonics, Inc., Mesa, USA; www.telonics.com). Seven females (six adults and one sub-adult) and eight males (four adult and four sub-adults) originated from four different reserves in KwaZulu-Natal Province, South Africa. Linklater *et al.* (2006) describe the details of the initial post-release monitoring efforts and Morgan *et al.* (2009) describe the details of monitoring efforts during the first year after release. We located the rhino daily for the first three weeks following release and then at least once every three days thereafter, with a final average of 2.1 ±0.1 days between locations for the first 60 locations. In total, 1 857 locations were recorded during the first 14 months following release of the rhino (Table 1). Over the course of the study we identified the four adult males to be dominant, because they had established non-overlapping territories with one another, but allowing one or two sub-adult males to range within their territories (Adcock 1994). We therefore divided our analysis into females, dominant males and subordinate males.

A detailed scent-broadcasting and social interaction study during the acclimation phase of the MGR black rhino is being completed and for this reason we will largely concentrate on the establishment and settlement phases of these populations. The preliminary analyses indicated that black rhino move away from their own dung which was spread at their release site, but settled in to areas adjacent to where other released rhinos' dung has been spread (Linklater *et al.* 2006). This suggests that conspecific cues may play a role in the settling behaviour of back rhino (Linklater *et al.* 2006). Within three days, the black rhino from the study entered the area of their future home ranges and decreased their daily movement rates considerably after six days (Linklater *et al.* 2006). We do not believe that this scent broadcasting study will confound the effects of the rhino's responses towards EGVs following this six day period.

6.3.2. Maximum entropy program (Maxent)

There are a number of resource selection analyses which are capable of using presence-only location data, including commonly used weighted (Millspaugh *et al.* 2006) and unweighted (Aebischer *et al.* 1993) compositional analyses, and eigenanalyses such as K-select analysis (Calenge *et al.* 2005a). These analyses need a measure of availability to be calculated, which assumes an animal has some concept and knowledge of its surrounding environment. However, when released into a new area an animal still needs to acquire that knowledge, and we could expect selection to rather be based on its immediate surrounds, conspecific cues (Linklater *et al.* 2006) or conspicuous environmental cues based on previous experiences from their natal environment (Stamps & Swaisgood 2007). Therefore the analysis we chose needed to exclude resource availabilities in its calculations. We also needed to use a method which could analyse small numbers of locations, due to potentially short settling phases (Moehrenschlager & Macdonald 2003, Linklater & Swaisgood 2008). The resource selection analyses mentioned above need an absolute minimum of 30 locations (Kernohan *et al.* 2001, Millspaugh *et al.* 2006), which would be too large a sample size for a phase lasting only 6 days (Linklater & Swaisgood 2008). Maxent suits a post-release study as it does not use a measure of availability to determine the influence of variables on locations, it can use less than ten locations to infer suitability (Pearson *et al.* 2007, Wisz *et al.* 2008), it uses presence-only location data in conjunction with continuous or categorical EGVs, and performs well with respect to other suitability models (Wisz *et al.* 2008, Elith & Graham 2009).

Maxent evaluates the overall fit of the model using a receiver operating characteristic (ROC) curve, where the model's sensitivity versus (1 – specificity) is plotted (Phillips *et al.* 2006). The area under the ROC curve (AUC) is then calculated, with AUC = 1 being the best fit, AUC = 0.5 being expected from a random model and values greater than 0.75 being considered useful (Elith *et al.* 2006). Maxent's output is a predicted habitat suitability grid of the study area, with grid cell values being a function of the relevant EGVs, ranging from 0 – 1, with higher values corresponding to more suitable conditions for the species (Phillips *et al.* 2006). Maxent produces two outputs based on each EGV. The first is a response curve developed from a Maxent model run using only the selected EGV. These response curves reflect how the dependence of predicted suitability is based on the selected variable and conversely on any other variable correlated with it. We will analyse these curves to determine how individual rhino respond to the various EGVs and how this response changes with increasing time after their release. The second output evaluates the importance of each variable by doing a jackknife analysis of each EGV separately to determine how well the variable explains the observed distribution (Phillips *et al.* 2006). We will use these results to illustrate the relative importance of each EGV for each of the different post-release phases.

6.3.3. Post-release phases

We divided the first 14 months since the release date into seven provisional phases based on the three post-release settlement phases as described by Moehrenschlager and Macdonald (2003).

Acclimation phase - This phase has previously been identified using daily displacements and the distances of animals relative to their release sites (Moehrenschlager & Macdonald 2003). Black rhino daily displacements are highest over the first five to six days post-release and they decrease their minimum daily displacement within 25 days of being released (unpublished data; Linklater & Swaisgood 2008). We could not analyse the first five days response to the EGVs, as approximately ten locations are needed for accurate results from Maxent (Pearson *et al.* 2007, Wisz *et al.* 2008). We therefore split the first 25 days into two phases, the first ten locations as Phase 1, then until the end of 25 days as Phase 2. To determine whether there was variation in their movements relative to their release sites we calculated the straight line distances for each location back to the relative release site for each of the phases described below. We made boxplots of the distances and then ran an ANOVA or, if the assumptions of the ANOVA were not met a Kruskal-Wallis test, across the phases for each rhino to determine how they established themselves relative to their release sites.

Establishment and settlement phases - Since there was no existing population on the reserve we investigated whether their changes in response to different EGVs over time would enable us to identify these two phases, and then explain factors influencing them. We divided the time since their release into different sub-phases based on black rhino ecology and previous studies of black rhino post-release movements. In Southern Africa black rhino establish and utilise home ranges (Conway & Goodman 1989, Adcock *et al.* 1998, Lent & Fike 2003, Reid *et al.* 2007), although home range spatial and size shifts may occur across seasons (Lent & Fike 2003, Reid *et al.* 2007). We therefore decided to analyse the first 26 -100 days since their release, for comparison to other black rhino post-release movement studies (Linklater & Swaisgood 2008), and then to split the rest of their year, until the end of October 2005, into seasonal phases. By using seasonal phases we would be able to assess whether any changes could be attributed to seasonal responses to the EGVs. To be able to make direct comparisons between the rhinos' responses during the first 100 days since their release we ensured Phase 7 encapsulated the same months a year later (November – December 2005). Based on the results from these phases we are hoping to be able to group these 5 phases into establishment and settlement phases.

6.3.4. Ecogeographical Variables (EGVs)

Three types of ecological gradients can be identified to classify EGVs, specifically resource-, direct- and indirect-gradients (Austin 1980, Austin & Smith 1989). Resource-gradients deal with those variables that are consumed by the relevant species (e.g. water and food), direct-gradients are non-consumed environmental constraints (e.g. shade and the different habitat types), while indirect-gradients have no direct physiological relevance to the species' functioning (e.g. topographical features, distance to roads and fences). We would expect these gradients to influence animals differently during the various phases they go through after being released. For example the distribution of resource gradients would be largely unknown to a recently released animal while direct gradients could play a role in animal's movements at the release site.

There is little peer reviewed literature available on factors thought to influence the post-release settling rate of black rhino or any other large mammal, so we drew on our previous experience and information from unpublished literature to identify a combination of selected variables. One source was from habitat suitability models developed for black rhino in Augrabies National Park (ANP), South Africa (Buk 2004), and Liwonde National Park (LNP), Malawi (Van der Heiden 2005). In ANP the EGVs which had the greatest influence on black rhino distribution were slope, distance to water and roads, and a measure of habitat heterogeneity, available forage and rockiness (Buk 2004). Shade cover and distance to fences were significant in some of the models, but were left out in the final model (Buk 2004). In LNP road, river and water hole densities, distance to permanent water holes and plant species diversity were all significant in the utilisation distribution of black rhino (Van der Heiden 2005). We included a number of similar measures for the EGVs in these two studies and included a number of other variables which could potentially affect the settling rate or help explain the movement patterns of black rhino (Table 2). We calculated all the EGVs at a grid cell size of 20 x 20 m across the study area.

An advantage of Maxent is that it is robust in its inclusion of unnecessary and correlated EGVs, as it uses regularisation techniques (i.e. penalises features with strong weights, λ) to avoid over-parameterisation and ignores non-informative EGVs (Phillips *et al.* 2006), which alleviates the need for further statistical procedures such as an information theoretic approach to model building (Burnham & Anderson 2002). We included a number of variables which may not seem informative initially, but which may lead to responses that we had not considered (Aarts *et al.* 2008). We investigated how EGVs were related by selecting 20 000 random points and allocating them values for each of the EGVs across the study area. We then ran a regression analysis between the values of potentially similar EGVs to ascertain which of them were related.

An important aspect of the settling process are the rhinos' social interactions with one another, as evident from the sent broadcasting study (Linklater *et al.* 2006) and the problems encountered due to negative social interactions between recently released black rhino (Linklater & Swaisgood 2008). Generally, a number of black rhino ranges will appear to overlap on the landscape forming social groups or ‘clusters’ (sensu Lent & Fike 2003) that reflects intra- and inter-sexual relationships amongst same- and opposite-sexed neighbours (Conway & Goodman 1989, Tatman *et al.* 2000, Lent & Fike 2003). Territorial males do not overlap their ranges with one another (Adcock 1994), and accept subordinate males into their ranges, which normally range exclusively within this single territorial males range, while females may bridge across male territories (Estes 1993, Adcock *et al.* 1998, Lent and Fike 2003). For this reason we decided that a measure of how the subordinate males and females associated with the territorial males resident within their ranges would provide us with an understanding of the formation of the clusters and social bonds. We therefore calculated the central point of each dominant male’s location for each phase. We did this in ArcMap using the Central Feature tool, which calculates a point in space associated with the smallest accumulated distance to all the selected locations. The distance to the central point of each dominant male was calculated as separate variables and inputted into the relevant models. We excluded a dominant male’s own central location from its models.

6.3.5. Analysis of Maxent outputs

Maxent’s final output is a habitat suitability map based on the inputted locations. This would be an indication of the areas we could expect an individual to occupy had it not changed its response to the inputted EGVs. We could therefore assess the degree of change in an individual’s response to the EGVs by analysing the overlap of consecutive phase’s suitability maps. We calculated the degree of niche overlap using the program ENMTools (Warren *et al.* 2008). ENMTools calculates the niche overlap using two different statistics, namely the Schoener’s D (Schoener 1968a) and the I statistic (Warren *et al.* 2008). We used only the D statistic to evaluate overlap due to the similarity in the outputs of the two statistics (Warren *et al.* 2008). We did this between consecutive phases for each rhino, and plotted how the predicted Maxent distributions of the population changed since their release.

Maxent runs a jackknife test on each EGV separately, building a model with it to see how well it can describe the locations (Phillips *et al.* 2006). Maxent calculates the fit of this model using the AUC statistic based on the locations it set aside for model testing. The EGV AUC values are not directly comparable from one phase to the next, due to the effect that sample sizes may have on the accuracy of the statistic (Wisz *et al.* 2008), however the order of their importance is comparable. We therefore ran a Kruskal-Wallis test on the ranks of the EGVs within each phase to assess the change in their importance since the rhino were released. This will only tell us about potential changes in the importance of the EGVs, but will not tell us how an individual's response to a variable changes, or whether responses between individuals is similar.

Maxent produces response curves for each EGV based on a model built using only that variable, which produces a measure of how the model's predicted suitability is dependent on the selected variable, and those variables correlated with it. To help us understand the effect of the EGVs across the phases we assessed the changes in the response of the rhino to those EGVs which were either ranked highly, or for which the mean rank of importance changed noticeably from one phase to the next for the population. For example, suitability may decrease with distance from water. We also assessed those indirect gradients which could be manipulated by conservation managers to see how black rhino might respond to their manipulation during different phases. To do these assessments for each rhino we aligned each EGVs phases' response curves below one another in tables. We recorded a change point between phases if there was a change from a positive to a negative response to a variable or whether a response curve changed notably in its shape. We then recorded whether the rhino made a number of changes in their responses to EGVs and across which phases the changes were occurring more frequently.

For some of continuous variables we could assess whether a rhino's response was negative or positive in relation to the variable for a phase. For example the suitability score for distance to water may increase closer to water (a positive/attracted response) or farther from water (a negative/avoidance response). This could be a strong response (an exponential response curve) or a gradual response (a linear response curve). Based on these assessments we rated the response of the rhino to each EGVs for the different phases as either a weak (1) or a strong (2) positive (+) or negative (-) response or alternatively as no response (Schmitz). It is important to note here that a strong response as defined here does not mean that an individual considered the variable more or less important for a phase (the AUC values from the jackknife tests tell us that), but rather how the rhino responded to the relevant variable. Due to small sample sizes we relied on box-plots to assess the agreement amongst the rhino for the different phases, and to identify differences between the phases.

There is an extensive game-viewing road network on MGR, with 28 % of the reserve having road densities above 5 km/km^2 and only 20 % of the reserve with densities less than 2.5 km/km^2. The majority of the low density areas occur in very mountainous terrain or in the unsuitable habitat barrier mentioned earlier. We therefore assessed whether the rhino had a negative response to road densities only above a 5 km/km^2 threshold.

Rhino PDF73 VHF transmitter failed before Phase 6, so we were not able to analyse her movements during the last two phases. We performed all statistical tests using SPSS 15.0 (SPSS Inc., Illinois, USA) and used a significance level of 0.05, unless stated.

6.4. Results

Although the sample sizes were small for each group, there was sufficient agreement amongst individuals' responses for us to make deductions about settling phases from the results, and to postulate reasons for the rhinos' responses. All the predictive models for each individual and each phase had an AUC > 0.75, meaning the models were useful (Elith *et al.* 2006). None of the EGVs used for model development were able to explain related EGVs with an $r^2 > 0.50$, so we assumed the jackknife and response curves developed for each EGV were largely a direct response without dependencies induced by other variables (Phillips *et al.* 2006).

In many cases the rhino changed their responses to EGVs (noted by a low overlap of the Maxent predicted distributions) across those phases for which they had a notable change in their distance from their release site (Fig. 1). A good example is between Phases 2 and 3 for rhinos DM4, PDF73, PDF98 and PDM81. However, in some incidences a change in response to EGVs did not correspond to a change in distances from their release site. The majority of black rhino had significant changes in the distance they were from their release sites over the 7 phases (all $p < 0.05$), with the exceptions being DM1 ($p = 0.947$), PDF79 ($p = 0.239$) and PDM03 ($p = 0.059$). These three rhino all settled immediately into a set distance relative to their release site, yet they continued to show changes in the way they were reacting to EGVs (Fig. 1). If a rhino has a similar ranging distance from the release site from one phase to the next it does not necessarily indicate it is exhibiting site loyalty, as it is possible for an animal to move in an arc relative to a release site. However, there were no major arc movements by any of the black rhino in this study. The only two phases with consecutively similar ranging distances from the release site are the last two phases, suggesting that these two phases could represent a separate settling phase to the previous phases.

Based on the Maxent predicted distributions, although not statistically strong, the rhino had the least amount of change between Phase 1 and 2 and again between Phase 6 and 7, the most change between Phases 2 to 5 and a decreasing change towards the last phases (Fig. 1). At this stage we could potentially delineate these three periods as the acclimation (Phase 1 and 2), establishment (Phases 2 – 5) and settlement (Phase 6 and 7) phases. Nonetheless, without understanding how the rhino were responding to specific EGVs it is difficult to ascertain whether any of these ranging patterns noted here are due to seasonal or settling processes.

6.4.1 Ecogeographical variables importance

The only EGV for which importance changed noticeably over the phases was habitat richness (Kuskal-Wallis $\chi^2 = 31.8$, $p < 0.001$; all other EGVs $p > 0.07$), however it was unimportant in Phase 1 (mean rank of 12) and got progressively less important. The most important EGVs to the rhino, across all the phases, were habitat type, elevation and the distance to the closest dominant male. We therefore analysed these response curves and included distance to fence, distance to busy roads, road density and distance to water which we felt would be informative for conservation managers, and have been noted as important factors in past black rhino release studies (Linklater & Swaisgood 2008).

All rhino made the first, and the majority, of their changes in response to the EGVs between Phase 2 and 3 (Table 3; Fig.2), which supports our previous delineation of phases. The dominant males had one major settling change by Phase 3, while the females and sub-adult males had two settling changes, one by Phase 3 and the second by Phase 6. There are, however, variations amongst the individuals as to whether the second settling phase occurs or not. The dominant males settled more similarly to one another than the other two groups of rhino.

All the rhino changed their responses to elevation, distance to water and the distance to the nearest dominant male by Phase 3 (Table 3). The response to elevation would suggest that each rhino had selected specific environments of the reserve to settle in by Phase 3. We can interpret the responses to the dominant males as avoidance or association responses (Fig. 3). By Phase 3 the dominant males had already started avoiding one another, and we can regard this as the starting point of their territorial exclusivity. By Phase 3 all but one female were associating with dominant males, which was during the same phase we saw three female rhino mating with dominant males. We attribute this to a ‘getting-to-know-you’ response by the adult male, as none of these matings resulted in known births. Interestingly, PDF79’s avoidance response in Phase 5 coincided with her giving birth, while PDF71’s negative response coincided with her shifting her range into the neighbouring dominant male’s territory in Phase 7.

PDF85, DM1 and PDM03 all formed one cluster, and were the only rhino to consistently respond negatively towards water. Either there was an unknown water point within their range which was not included in the model development, or an unseen factor. We have therefore removed them from the response to water to gain an understanding of how the rest of the population responded (Fig. 4a). The other black rhinos’ response to water gained strength by Phase 3 for the females and dominant males, while the subordinate males took longer. The subordinate males’ delayed response to water in Phase 6 and 7 may have been a seasonal response, as these phases were during the dry season; however this is not evident from the female and dominant male responses.

The population ranked the distance to fence as slightly more important during Phase 1 than the other phases (although not significantly) and responded either neutrally or negatively to the fence during this same phase (Fig. 4b). This response is unexpected, as tracks of black rhino are commonly found along the fence boundary during the initial days after their release (personal observation at five different release sites, totalling 40 black rhinos; Morkel & Kennedy-Benson 2007). It is possible that the rhino were avoiding the fences during the day when they mostly rest (Schenkel and Schenkel 1969, Tatman *et al.* 2000, Rice and Jones 2006) and made exploratory trips along the fences at night only. It is unclear why the dominant males would take longer than the females and subordinate males to habituate themselves to the fence.

The black rhino did not avoid busy roads or regions with high road densities (Fig. 5) during the first two phases, which may have been due to their use of roads to explore a new area (personal observation at five different release sites, totalling 40 black rhinos), their habituation to vehicle noise during their time in the bomas (from between 31 – 61 days) or due to distress caused by an extended period in the bomas (Linklater *et al.* 2010). Following Phase 1 and 2, the rhino avoided regions with road densities > 5 km/km^2, which could be because of the large edge effects on the habitat (Andrews 1990, Forman & Alexander 1998). The females generally avoided busy roads following Phase 2, as they may seek out areas of fewer disturbances for their young in the future, while the male’s responses varied and they were seemingly indifferent to the busy roads.

In summary black rhino post-release phases can be delineated into the three phases proposed by Moehrenschlager and Macdonald (2003); the acclimation phase (first 25 days), the establishment phase (26 – 281 days) and the settlement phase (282+ days), although this may be later for the dominant males. During the acclimation phase black rhino have large daily displacements, potentially move large distances from their release sites, avoid fences during the day, yet are not adverse to busy roads or areas with high road densities and have yet to associate themselves with a water source. During the establishment phase the rhino have established themselves relative to the dominant males (meaning the dominant males have identified themselves), they have selected broad-scale environments and areas with road densities < 5 km/km^2 to settle in, have varied responses to most EGVs during the phase, but the adults associate themselves with water sources. The dominant males make fewer changes from this phase to the settlement phase than the females and subordinate males. By the settlement phase the rhino have settled into a fixed area relative to their release sites, use specific habitat types and, although there are differences amongst the demographic groups, have settled responses to all the EGVs.

6.5. Discussion

This exploration of the effect of EGVs on the settling process of black rhino reveals the importance of social structure, and how responses of demographic groups differ and change differently during settlement. Some of the responses to variables in this study did not correspond to previous suitability models developed for black rhino (Buk 2004, Van der Heiden 2005), however this study was done at an individual level, allowing for more in depth responses to be assessed, rather than averaged population level responses. Black rhino movements and responses to the selected variables indicate that there is a clear distinction between the acclimatisation (Phase 1 and 2) and the establishment phase, while the division between the establishment and settlement phase, specifically for the adult males, was less distinct.

The adult males, later identified as dominant individuals, were more cohesive in their settling responses and established territorial boundaries within 25 days, settling quicker than the subordinate males and females. This supports the theory proposed by Linklater *et al.* (2006) that reproductively ready males are quicker to respond to an opportunity to defend a territory and females. They are presented with a unique position to do so in an area devoid of resident conspecifics, and possibly grab the opportunity, organising themselves into spatially distinct areas relative to one another by the end of the acclimatisation phase. Being older, they may also be able to respond quicker to conspicuous cues based on previous experiences from their natal environment (Stamps & Swaisgood 2007). The role which natal environments play in the settling response of animals to EGVs warrants further investigation.

Here the population had organised itself socially within the first 100 days since their release, frequently socialising with one another (unpublished data), especially after Phase 2 when females were even recorded mating with males. However, on 6 other large reserves (i.e. reserves > 18 000 ha) with similarly low densities (< 0.1 rhino/km^2) there were no recorded associations between black rhino during the first 100 days since release, other than a single breeding relationship between a resident male and an introduced female (Linklater & Swaisgood 2008). Interestingly all these rhino were released one-by-one from holding enclosures, rather than being free-released across the reserve, like they were on the MGR, and all but one of these reserves had resident conspecifics. This would suggest that either one of these factors could have facilitated a quicker settling response by the rhino on the MGR. Since the black rhino on MGR were all having to establish themselves at the same time, they may have been more apt to socialise since none of their conspecifics were protecting well known resources, and they did not have to get accepted into an existing social group, but rather to form their own. It is also possible that the scent broadcasting study (Linklater *et al.* 2006) had an increased settling response on the rhino.

Even though the rhino were regularly associating with one another in their clusters, it would seem that the social bonds may take longer than we perceive to develop. This is evident from the length of time it took the subordinate males to associate with water points within a dominant male's territory and that the first conception in this population happened after 15 months (unpublished data). It is hard to decipher whether the female's conception was delayed by stress factors due to the translocation and the new area or the time it took for social bonds to form between the rhino. We saw females mating soon after the acclimation phase and attribute this mating as an initial 'getting-to-know-you' response, since none of these recorded mating events resulted in known births (unpublished data) or a dominance act by a dominant male, as black rhino adult males do attempt to mate immediately with females supplemented into existing populations (SM, WL personal observations). To reduce the delay in the formation of social bonds it may be prevalent to capture and reintroduce established clusters of black rhino into new areas.

While the adult rhino found and associated positively with water resources quickly, they took longer to identify with specific habitats. Water is largely a stationary resource which can be easily learnt once found, while assessing the suitability of the surrounding habitat would take longer. It is likely that we measured the resource gradients at an incorrect scale, as the rhino ranked habitats as more important than the resource gradients they had to offer. Animals possibly select for specific combinations of variables within habitats, rather than any single averaged estimate of a resource gradient measured across a habitat. This is in accordance with black rhino not selecting identified habitat units based on the availability of suitable browse or the perceived importance of the habitat based on carrying capacity estimates (Morgan *et al.* 2009).

6.5.1. Black rhino management

Following the results here we suggest that, where possible, black rhino are free released onto reserves with no resident conspecifics and those regions with road densities > 5 km/km^2 are excluded from estimates of available area for black rhino. Releases should occur as soon after one another as possible, ideally within 6 days, as previously suggested by Linklater *et al.* (2006). No black rhino should be released into a population after the acclimation phase of 25 days, as we can assume adult males will respond to any newcomers aggressively, like they would in an established population (Brett 1998, Linklater & Swaisgood 2008), thereby delaying the settling process. Adult males should be released in spatially distinct areas (the size of an estimated home range for the region) such that they have access to a water resource which is distant (>1 km) from a fence and which they do not need to share with other adult males. Females should not be released in areas close to busy roads. This study was potentially affected by the small sample size and by the diurnal nature of the location records. We suggest continued investigations into future black rhino releases and that researchers endeavour to include some form of nocturnal movement information to enhance our understanding of the responses we have noted here.

6.5.2. Conclusion

Understanding the response of reintroduced animals to EGVs gives us an insight into how we can manage reintroductions better, and teaches us valuable lessons about the ecology of animals. Previously those studies which have taken EGVs into account were constrained by small sample sizes (Larkin *et al.* 2004, Rittenhouse *et al.* 2008) and were unable to analyse the data statistically (Larkin *et al.* 2004) or across different settling phases (Rittenhouse *et al.* 2008). Here we have shown that Maxent is a useful tool in the investigation of post-release animal responses to EGVs even when sample sizes are low, and or when a dominance hierarchy potentially confounds our understanding of settling processes.

Table 6.1 The number of locations recorded for individual black rhino for the first year since their release on the Mun-ya-Wana Game Reserve. The movements of the rhino were studied across seven phases and the number of locations recorded per phase is shown (see text for details on phase descriptions).

Phase Season	Phase 1 and 2 Early wet	Phase 3 Early wet	Phase 4 Late wet	Phase 5 Early dry	Phase 6 Late dry	Phase 7 Early wet	
Days since release	1 – 25	25 – 100	101 – 182	183 – 281	282 – 380	380 – 440	Total
PDF01*	22	36	31	29	32	20	150
PDF71	21	30	22	24	27	20	124
PDF73	20	23	21	17	-	-	81
PDF78	19	27	27	26	25	18	124
PDF79	16	23	17	28	23	20	107
PDF85	21	27	23	22	22	17	115
PDF98	21	26	20	23	27	21	117
DM1	20	28	23	24	27	20	122
DM2	19	25	20	22	28	20	114
DM3	22	37	28	27	28	20	142
DM4	23	29	27	28	26	17	133
PDM03	21	31	23	22	26	19	123
PDM57	20	33	24	33	32	20	142
PDM59	20	24	27	26	24	17	121
PDM81	23	36	30	27	26	20	142
Total	308	435	363	378	373	279	1857

*PDF = Female; DM = Dominant male; PDM = Subordinate male

Table 6.2 Ecogeographical variables used for measuring responses of black rhino during different post-release phases on the Mun-ya-Wana Game Reserve.

Code	Ecogeographical variable
BA	Browse Availability - measured for each habitat using the browse availability method as outlined by Adcock (2004).
CC	Carrying capacity - calculated for each habitat using the index of black rhino browse availability, soil fertility, annual rainfall and minimum July temperature (Adcock 2006)
Grass	Grass abundance, calculated as a percentage of grass ground cover for each habitat, as outlined by Adcock (2004).
Herbs	Herb abundance, calculated as a percentage of herbaceous ground cover for each habitat, as outlined by Adcock (2004).
Dist_water	Distance to the closest permanent water source.
Habitat	Habitat types - as determined by van Rooyen and Morgan (2007), see Appendix 2for full details.
Habitat_rich	Habitat richness - a measure of the diversity of habitats surrounding a grid cell on the map, equated as the number of different habitat types present in a 500m diameter surrounding a grid cell.
Shading	Shading was the average of the shading site index recorded at the browse assessments sites across the reserve for each habitat type. Shading index ranges from 1= Deep shade to 13 = No shade.
DEM	A 50-m resolution digital elevation model, also used for the calculation of slope and aspect. Elevation is measured in meters above sea level, to the maximum height of the study site at 305m.
Aspect	Aspect as calculated from the digital elevation map, measured in degrees.
Slope	Slope as calculated from the digital elevation map, measured in degrees.
Rd_density	We calculated road density using a line density calculation in ArcMap, using all the roads on the reserve. It was calculated as the kilometres of road per square kilometre area (km/km^2).
Dist_rds	For the road distance variable we included only main access routes to the lodges, due to the large amount of traffic that they receive on a daily basis, and the two public roads that run through the length of the reserve. The rest of the road system on the reserve is extensive but was not included, because of relatively infrequent use. This is thus a measure of potential disturbance from human activity as opposed to the ecological influence of roads per se which is captured in road density above.
Dist_fence	Distance to the boundary fence.
Sand	Percentage ground cover of sand, such that cover between sand, stones and rocks equals 100%. The cover was estimated for each browse assessment site across the reserve and the mean was calculated for each habitat type.
Stone	Percentage ground cover of stones (< 20cm in diameter), such that cover between stones, sand and rocks equals 100%. The cover was estimated for each browse assessment site across the reserve and the mean was calculated for each habitat type.
Rocks	Percentage ground cover of rocks (> 20cm in diameter), such that cover between rocks, stones and sand equals 100%. The cover was estimated for each browse assessment site across the reserve and the mean was calculated for each habitat type.

Table 6.3 The occurrence of changes in the response of black rhino to ecogeographical variables (EGVs) since their release. Changes are indicated as the proportion of changes to an EGV made by a demographic group (F = female, n = 7; DM = dominant male, n = 4; SM = subordinate male, n = 4) across the different post-release phases.

Phase*	Habitats			Elevation (DEM)			Distance to water			Road density		
	F	DM	SM	F	DM	SM	F	DM	SM	F	DM	SM
1 - 2	-	-	-	0.20	0.20	-	-	0.60		0.07	0.40	0.40
2 - 3	0.40	-	0.29	0.70	0.60	0.80	0.70	0.40	0.50	0.36	0.40	0.40
3 - 4	0.20	0.67	0.43	-	-	-	0.10	-	-	0.36	0.20	0.20
4 - 5	0.20	0.33	0.14	0.10	-	-	0.10	-	0.33	0.14	-	-
5 - 6	0.20	-	0.14	-	-	-	0.10	-	0.17	-	-	-
6 - 7	-	-	-	-	0.20	0.20	-	-	-	0.07	-	-

Phase	Distance to roads			Distance to fence			Distance to DM			Total EGV		
	F	DM	SM	F	DM	SM	F	DM	SM	F	DM	SM
1 - 2	0.08	-	-	0.23	-	0.33	0.08	0.11	-	0.10	0.18	0.10
2 - 3	0.38	0.50	0.38	0.31	0.50	0.33	0.33	0.78	0.60	0.44	0.51	0.45
3 - 4	0.08	-	0.13	0.08	0.17	0.17	0.25	-	0.20	0.16	0.11	0.17
4 - 5	0.15	0.17	0.25	0.15	-	-	0.17	0.11	-	0.14	0.08	0.12
5 - 6	0.15	0.17	0.13	0.15	-	0.17	0.08	-	0.20	0.10	0.03	0.12
6 - 7	0.15	0.17	0.13	0.08	0.33	-	0.08	-	-	0.06	0.11	0.05

*See text for details on phase descriptions

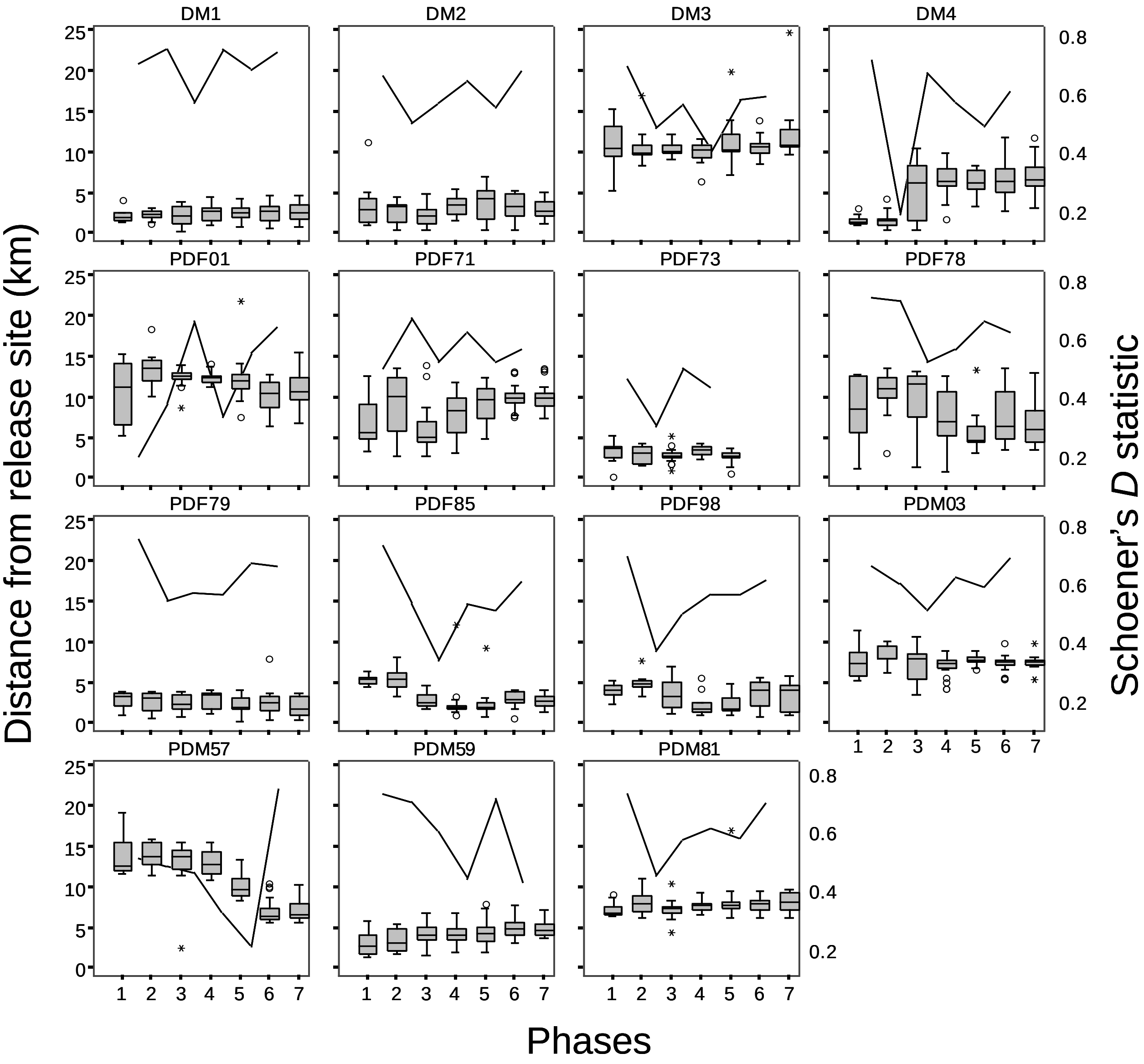

Figure 6.1 The settling process of individual black rhino in relation to their distance moved from their release sites (boxplots) and the overlap in the way they responded to different ecogeographical variables (lines) from one post-release phase to the next (see text for details on phase descriptions). The distance to the release site is calculated as straight line distances from recorded locations during each of the phases. The overlap between successive phases is calculated using Schoener's *D* statistic, with 0 = no overlap and 1 = maximum overlap. The line across the box is the median; box represents the 25th and 75th percentiles; and the whiskers indicate the 5th and 95th percentiles. Open circles and asterisks respectively designate outliers and extremes.

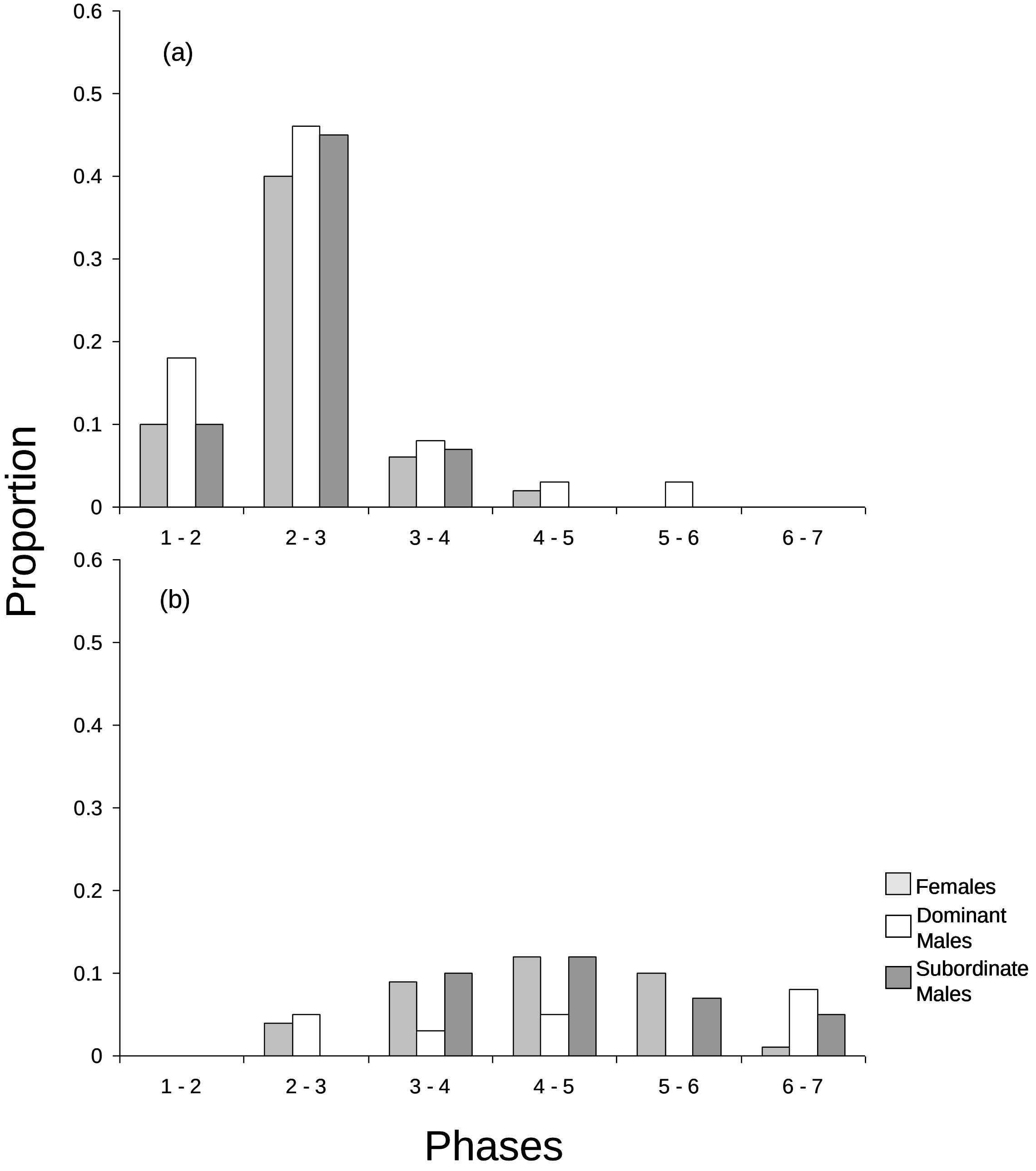

Figure 6.2 The incidence of black rhino responses to EGVs for seven different post-release phases. The bars represent the total proportion of changes made by a demographic group in response to the EGVs for (a) the first and (b) the second time changes were made during the different post-release phases. The incidences of a third change in response to an EGV were negligible and are not graphed.

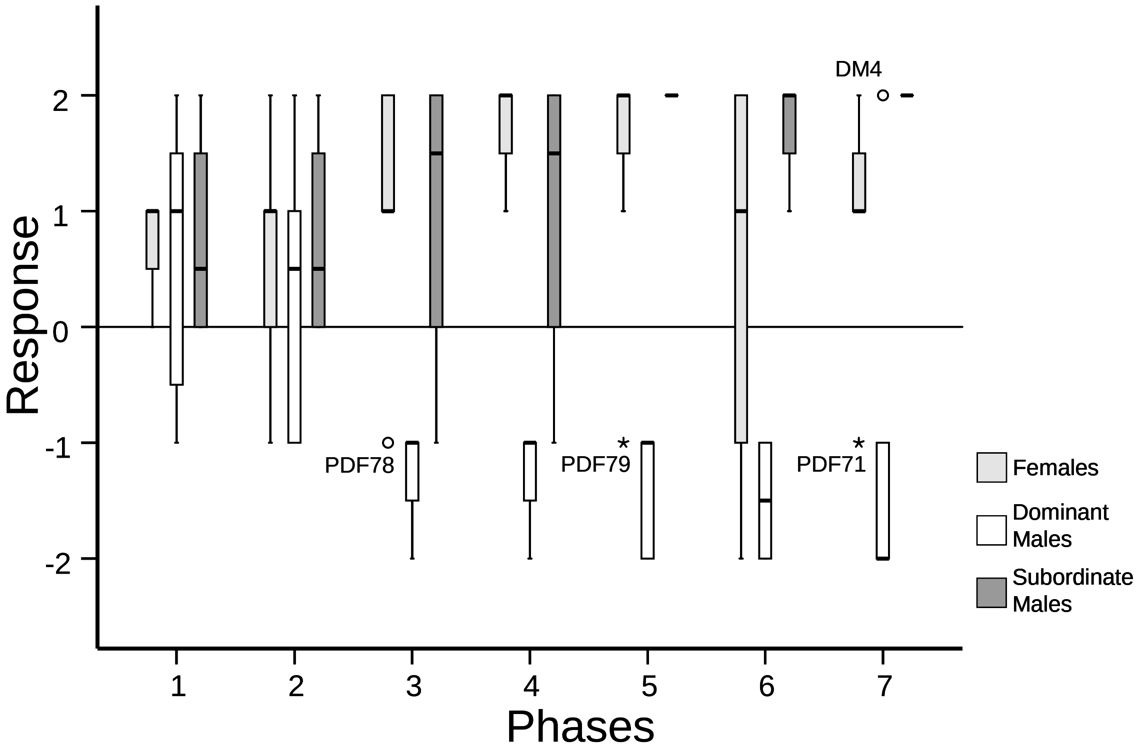

Figure 6.3 The variation in the response of individual black rhino to dominant males for different post-release phases on the Mun-ya-Wana Game Reserve. The response of the females and subordinate males is to the dominant male closest to them during the first three phases, while the response of the dominant males is their response to the closest two other dominant males. Responses are gauged as either a weak (1) or strong (2) response, as association (+) or avoidance (-) or alternatively as no response (Schmitz). The response of the rhino were assessed across seven different post-release phases (see text for details on phase descriptions). The line across the box is the median; box represents the 25th and 75th percentiles; and the whiskers indicate the 5th and 95th percentiles. Open circles and asterisks respectively designate outliers and extremes.

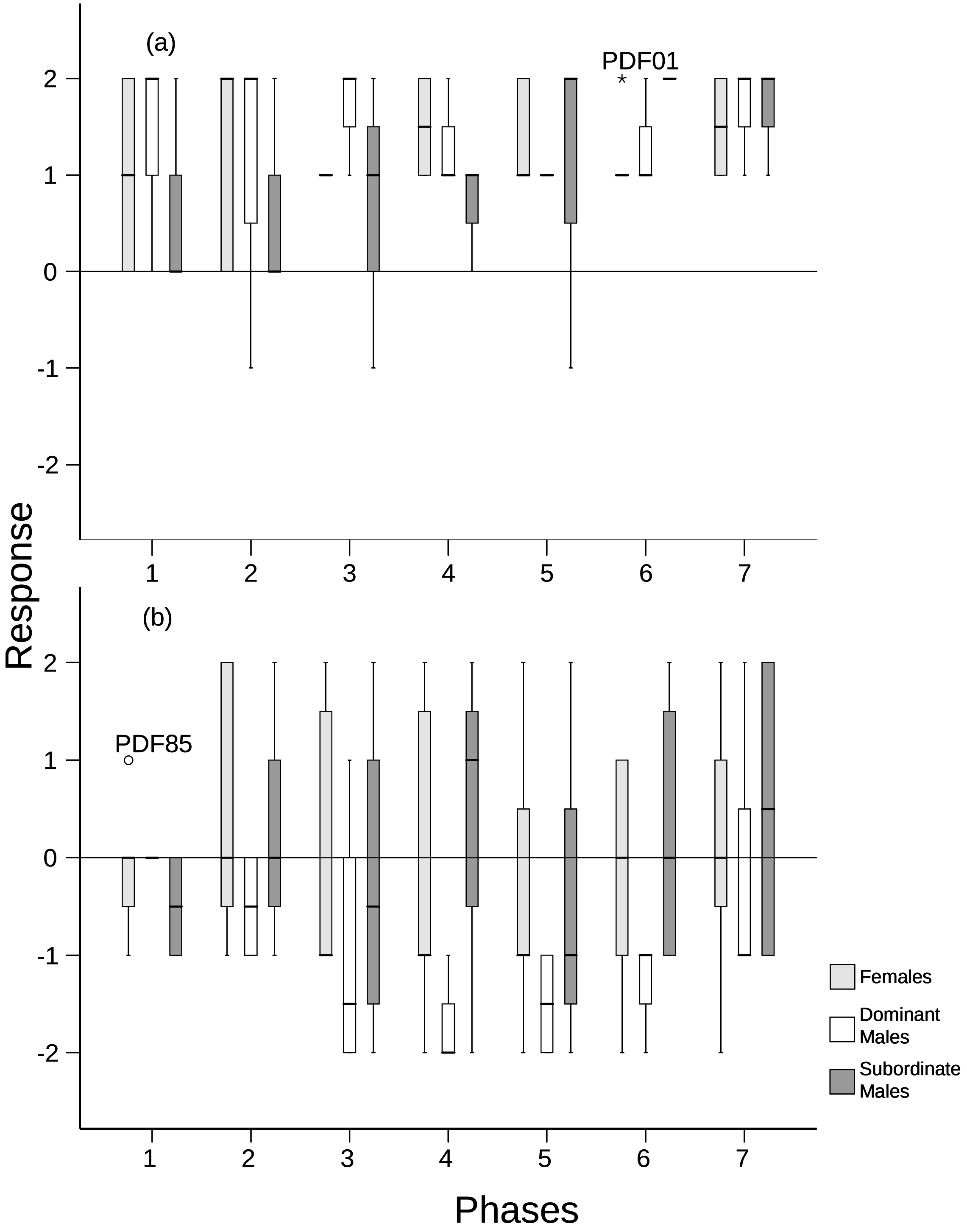

Figure 6.4 The variation in the response of individual black rhino to water points and the fence for different post-release phases on the Mun-ya-Wana game Reserve. (a) Response to the permanent water sources in the study area. (b) Response to the distance to fence. Responses are gauged as either a weak (1) or strong (2) response, as positive (+) or

negative (-) or alternatively as no response (Schmitz). The response of the rhino were assessed across seven different post-release phases (see text for details on phase descriptions) and during the dry and wet seasons once the population had settled. The line across the box is the median; box represents the 25th and 75th percentiles; and the whiskers indicate the 5th and 95th percentiles. Open circles and asterisks respectively designate outliers and extremes.

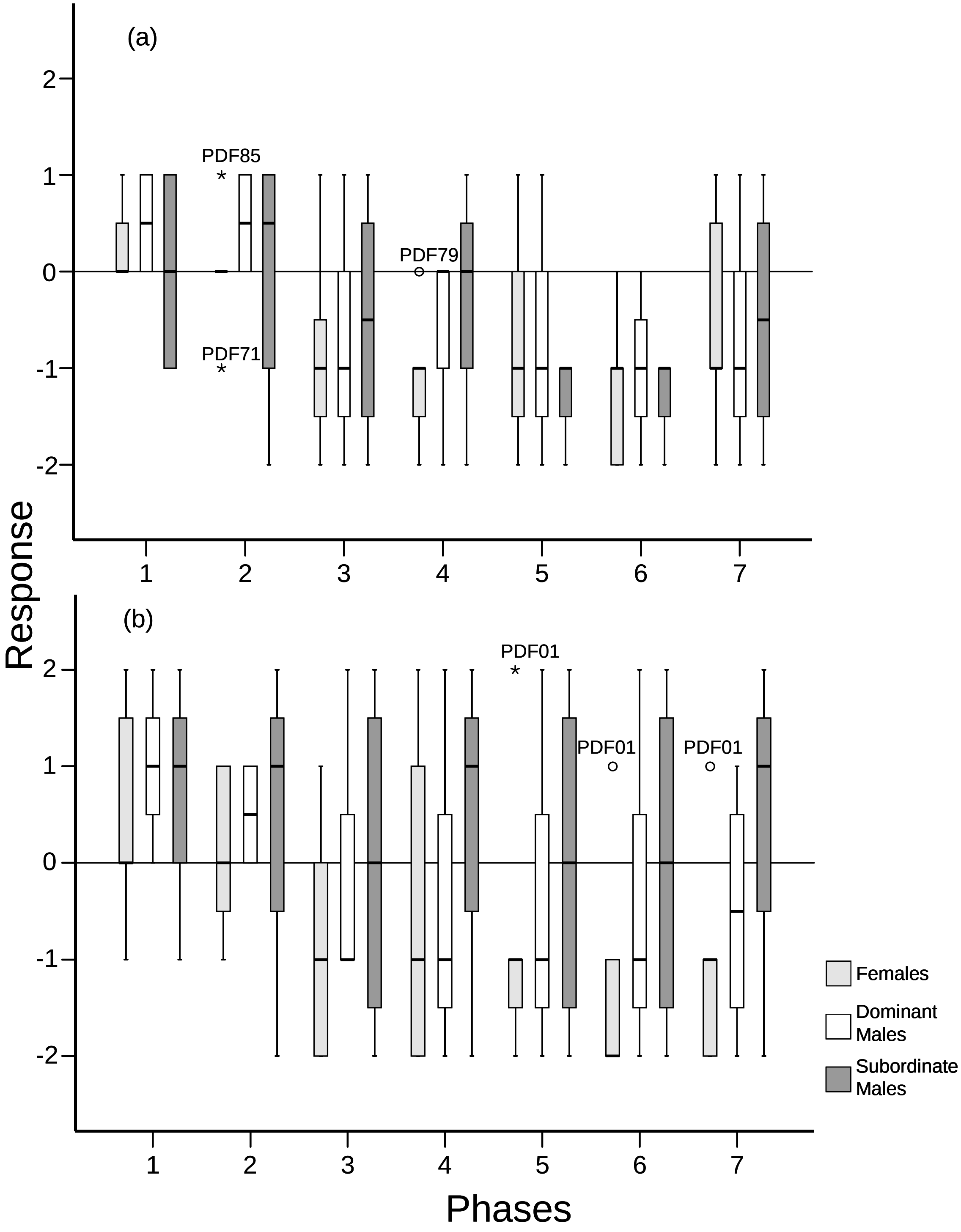

Figure 6.5 The variation in the response of individual black rhino to the density and distance to roads for different post-release phases on the Mun-ya-Wana game Reserve. (a) Response to the density of roads in the study area. (b) Response to the distance to

busy roads in the study area. Responses are gauged as either a weak (1) or strong (2) response, as positive (+) or negative (-) or alternatively as no response (Schmitz). The response of the rhino were assessed across seven different post-release phases (see text for details on phase descriptions) and during the dry and wet seasons once the population had settled. The line across the box is the median; box represents the 25th and 75th percentiles; and the whiskers indicate the 5th and 95th percentiles. Open circles and asterisks respectively designate outliers and extremes.

CHAPTER 7

Summary and conclusions

The aim of this study was to address variance in our current perspective of habitat value from that of the focal animals themselves. This was interrogated at a range of spatial, temporal and behavioural scales, allowing us to better recognise ecological-species interactions at the appropriate level or scale. In addition I focussed on the concept of the individual and whether our previous assumptions of average population responses are correct when studying and planning conservation measures. I did this by exploring variation among individual black rhino *Diceros bicornis* ecology while testing and developing a number of modelling and statistical techniques. Such techniques will further enhance our understanding and conservation management of wildlife. My approach was to use alternative methods, based on different assumptions, and pose the results against each other in order to assess which performed best, and which would be the most prudent approach in the applied context of conservation of threatened species. In this chapter I summarise my findings, and discuss further those which have broad scale implications and conservation application. Finally, I highlight gaps in our knowledge.

7.1. A priori valuation of land use for conservation purposes

In Chapter 2 I questioned the appropriateness of using carrying capacity (CC) estimates to indicate habitat utilisation for a particular species, and thus as a tool for conservation planning. This is an approach which has been used by conservation managers in the past (Bothma *et al.* 2004, Hayward *et al.* 2007), but, at various scales, does not necessarily correlate with individuals' selection within a population (Chapter 2). The current BrCC-Model v2_1, designed by Adcock (2006), and which is used as a basis of conservation management decisions, would not be able to predict habitat utilisation of black rhino, especially in low density populations. I was not able to study the process driving this variation in this Chapter 2, but suggested a number of plausible reasons (density-dependence, environmental variables, scale of selection, individual variation and intraand inter-specific dynamics) why we got these results. In some of the following chapters I was able to further unravel some of the reasons behind these results.

By studying how individuals responded not only to habitats in Chapter 6, but a myriad of ecogeographical variables, we can see how the concept of basing a predictive model primarily on the available habitats and the abundance of browse is flawed. This is also supported by my study of individual niche variation in Chapter 4, which highlighted how important the individual can be in a population, and that using a predictive model based on the population rather than the individual may be flawed. If CC estimates developed in this manner were unable to help us understand individual utilisation of habitats, then we must query the use of such methods to manage population numbers in a demarcated area. Perhaps a more integrated CC model taking into account home range sizes, social dynamics (which play a large role in the rhino's spatial utilisation, see Chapter 6) and combined with established resource selection functions (Manly *et al.*, 2002) or predictive distribution models (for example the maximum habitat suitability model developed in Chapter 5, Figure 5.6) could provide conservation managers with a better understanding of the CC of an area.

7.2. Circadian variation in spatial and behavioural habitat utilisation

I questioned whether current methods of analysing diurnal location data of animals provide accurate ecological or conservation conclusions and in Chapter 3 found, in the case of the black rhino, that it did not. I mentioned in the previous paragraph that black rhino movement patterns and social dynamics should be included in CC estimates, but by using only their diurnal range, i.e. a smaller than actual ranging area, we would underestimate areas of utilisation and overestimate CC estimates.

The limitation in my study was the variation in the means of data collection between the diurnal and nocturnal data. This limited the conclusions I could make about the factors driving the circadian variation and the ecogeographical variables influencing the rhino during the different periods. A study using point location data of black rhino during the night and day is difficult due to the nature of the rhino and the environment the data needs to be collected in. Many other mammal species' body shape allow them to be fitted with GPS collars, which has allowed researchers a greater understanding of circadian variations in habitat selection and movement patterns, for example the African elephant (Kinahan *et al.* 2007). Unfortunately the technology of GPS horn implants for black rhino are still in their infancy, with no measured success to date. However, I was still able to show that browsing areas for black rhino differed during the day and night, and believe that the continued use of backtracking techniques to understand the nocturnal ranging and browsing habits of black rhino is an important management and research tool.

Variations in a mammal's ecology can make interpretations using pooled data largely inaccurate. Although seemingly obvious, before researchers pool data they should establish whether there may be variations across different periods of the day and night (Chapter 3; Kronfeld-Schor & Dayan 2003), for different behaviours (Chapter 3; Schmitz 1991), amongst conspecifics (Chapter 4; Bolnick *et al.* 2003), or between seasons (Schooley 1994). Unfortunately pooling data is often the result of a trade-off between quality and quantity of data available for analysis based on the constraints of data collection. For example, in Chapter 5 and 6 I did not differentiate between the behaviours of the black rhino for modelling purposes as I was limited in the number of locations and behaviours I could record in one day. Ideally being able to model the settling response of the rhino for both foraging and resting behaviours across the day and night would have yielded a greater insight into their settling response. With the increase in modern technologies, for example GPS movement and behaviour recording collars, researchers are able to gather both good quality and quantities of data allowing them to analyse the collected data as suggested above.

7.3. Interindividual niche variation

After noting a variation amongst individual animal's responses in Chapter 3, I explored the degree of this variation at various scales, exploring various individual's habitat and diet niches in Chapter 4. My study is the first to use IndSpec1.0 (Bolnick *et al.* 2003) to understand variations among individuals from a habitat perspective rather than just a dietary point of view, although interindividual variations in habitat use have been noted using K-select analysis (Calenge *et al.* 2005a) and compositional analysis (Aebischer *et al.* 1993). I found significant, although not large, niche variation among black rhino, at both a dietary and habitat level. The variation was higher in those clusters with greater niche widths, which supports the Niche Variation Hypothesis (NVH), which suggests that populations with greater niche widths exhibit greater niche variation among individuals (Van Valen 1965).

By using IndSpec 1.0 to analyse habitat and dietary niches I was able to show that black rhino interindividual variation is not limited to just a single scale of utilisation, but that it permeates through various levels of niche use. It is difficult to understand which level of niche use is driving the variation in a species for which we cannot manipulate field conditions to test hypotheses. In this low density population, clusters of rhino, which appear to have equal access to the same habitats as one another, still showed variation amongst themselves in habitat and dietary choices. Were black rhino utilising different habitats to one another based on individually preferred patches of known browse, meaning the variation is driven at the diet level (Searle *et al.* 2006)? Or is variation in habitat utilisation driven by a number of ecogeographical variables (Calenge *et al.* 2005a), meaning individuals are ultimately presented with different dietary choices? As more habitats were used by a cluster, the variation amongst individuals did not increase as we would have expected it to; however, it did at a diet level. The variation at a diet level was driven by the subsidiary diet choices of individuals, with an increase in the interindividual niche variation of these species during times when resources were limited. This suggests that the variations at the habitat level are driven by individual diet preferences, specifically of plants in their subsidiary diets, rather than any other ecogeographical variable. This highlights the importance of subsidiary diets, as I noted here with black rhino, and that wildlife managers need to be aware of the importance these food species play during periods of resource scarcity or in high density populations. By pooling diet information researchers may well underestimate the importance of subsidiary resources to specific individuals, resulting in the mismanagement of these resources.

7.4. The importance of incorporating individual variation in modelling habitat suitability

Following the results in Chapter 4 I wanted to establish what effect inter-individual variation had on the outcomes of modelling suitable habitats for a population. I did this in Chapter 5 using a machine learning modelling technique, a Maximum Entropy (Maxent) model (Phillips *et al.* 2006), and a number of relevant ecogeographical variables (EGVs).

Developing a number of Maxent outputs allowed us to understand individual responses to EGVs, but the population outputs were limited to a manually merged output. The current abilities of machine learning models, like Maxent, are limited with regards to incorporating individual based data into the population level model, which weakens their applicability for wildlife research and management (this study; Baldwin 2009). Automation of incorporation of individual level data into interpretations would greatly enhance the value of such tools to managers. However, modelling a population using individual responses to EGVs is useful, as we can understand the forces driving individual's decisions, as in the case of black rhino. I therefore suggest the collection and analysis of individual specific movement data when the resources are available.

7.5. Understanding individual changes in response to ecogeographical variables over time

In Chapter 6 I used a novel individual based modeling approach, as explored in Chapter 5, to analyse how individual black rhino settled into a new area. The population of black rhino I studied were reintroduced into the MGR and I was interested to understand what ecogeographical variables (EGVs) affected their settling responses in a new environment. Interestingly the Maxent models highlighted how much more important social dynamics in the population were than any other resource or variable used in the modeling procedure. The dominant males appeared to settle fairly quickly, and made fewer changes in their responses to EGVs, than the females and sub-adult males. The results indicate that all the rhino' acclimation phase lasted no longer than 25 days and that to minimize disturbance to the settling process, all individuals in a newly released cohort should be released within this period. It was also during this period that the dominant males and females showed an affiliation with a water point, suggesting that releasing animals near permanent water sources to minimize searching would improve the settling rate.

Previously, Maxent has largely been used to query where we could expect animals to move, and to a degree what EGVs animals were influenced by. Here I have managed to extend the use of Maxent for a temporal analysis of EGV influences on their movements. This will allow us to understand how EGV influence animals over time using only a small number of presence-only locations from different periods. We can apply this to not only reintroduction biology, but also seasonal or density changes that a population may experience over time, establishing how these factors influence animal's responses to EGVs. Incorporating a temporal functionality into a machine learning model like Maxent, which has the ability to construct useful models with few presence locations, would greatly strengthen the value of the model to wildlife researchers and managers.

7.6. Black rhino ecology, conservation and gaps in our knowledge

I have discovered and confirmed a number of aspects of black rhino ecology through the course of the study. Notably, black rhino

i. do not select habitats based on the availability of relevant browse species or on our estimates of habitat quality,
ii. do not select habitats to browse in during the day, yet they do at night,
iii. use different areas to browse in during the day than the night,
iv. move outside of their diurnal ranges at night,
v. have a variation amongst individuals in their response to and the selection and use of ecogeographical variables, which is less pronounced, although still significant,
    a. among individuals with similar availabilities of variables,
    b. among their use of primary browse species and more so in their use of subsidiary browse species,
    c. during the dry season,
vi. share home ranges and form social clusters, often spending short periods together,

vii. adult males exhibit territorial behaviour, using exclusive ranges relative to other adult males, in the KwaZulu-Natal province,
viii. use social cues to settle and establish home ranges once released into a new area,
ix. demographic groups have different post-release settling strategies and respond to ecogeographical variables differently,
x. dominant males settle quicker than other males and females once released into a new area.

The main points which I discovered or confirmed about black rhino conservation management and research are:

i. The use of existing black rhino carrying capacity and browse assessments to determine areas used by black rhino is flawed. I rather suggest the use of individual based habitat suitability models to estimate these areas.
ii. I caution the use of carrying capacity models which fail to take into account the social and many other ecogeographical variables which influence the use of the landscape by black rhino.
iii. Recording and understanding the nocturnal movements of black rhino will provide researchers and managers with a more complete view of black rhino movements, their use of the landscape and their foraging ecology.
iv. Pooling location or foraging data of black rhino individuals in a population will cause errors, whereby the average does not reflect the actual use of any, or many, individuals.
v. One aspect which is evident from all the research I completed was the importance of monitoring not only the population, but specific individuals within the population too. Understanding the individual and specific decisions made by different members of a population will allow managers to predict individual and population level responses (e.g. fitness of individuals ultimately drives mortality and birth rates).
vi. Regions with road densities > 5 km/km^2 should be excluded from estimates of available area for black rhino.
vii. Black rhino reintroductions:

   a. Should occur as quickly as possible, ideally within 6 days, but never over more than 25 days.
   b. Adult males should be released in spatially distinct areas (the size of an estimated home range for the region) such that they have access to a water resource which is distant (>1 km) from a fence and which they do not need to share with other adult males.
   c. Females should not be released in areas close to busy roads.
   d. To accelerate the formation of social bonds it may be relevant to capture and reintroduce established clusters of black rhino into new areas.

I have identified a number of gaps in our understanding of black rhino ecology and conservation. Namely:

i. We need to develop new technologies to enable researchers to understand the nocturnal movements of rhino better. Understanding the extent to which rhino move from their diurnal ranges would allow managers to better understand the capacity of their reserves to support rhino, and those specific parts of the reserve that are important to rhino. Currently there are trials on GPS devices which can be fitted in the horn of a rhino (TramirLoc Pty. Ltd, Stellenbosch). If successful, this will greatly advance our understanding of general and post-release rhino ecology.

ii. Here I have shown that black rhino individuals can vary in their decisions, and that conclusions about use at a population level do not necessarily translate to behaviour at an individual level (Bolnick *et al.* 2003; this study). We are yet to fully understand decisions made by the individual, as focus has been at the population level (Brown *et al.* 2003, Ganqa *et al.* 2005, Adcock 2006, Ganqa & Scogings 2007). Future research and management should strive to incorporate and understand the individual, not only the population.

iii. I was unable to evaluate interindividual niche variation differences between the sexes of black rhino. The initial indications are that the sexes still exhibit differences amongst themselves, meaning that the variation is not driven by sex. A more detailed study with larger sample sizes would allow us to confirm this.

This will hopefully provide more of indication of what is driving the variation amongst individuals.

iv. I could not determine how rhino within a cluster all increased their habitat niche width similarly to one another. A more detailed study on niche expansion would give us an insight into what is driving the expansion, and how this would influence their conservation in different areas.

v. Throughout the study and during observations in the field, I noted very few occurrences of black rhino and African elephant *Loxodonta africana* at the same time. It could be possible that black rhino avoid elephant (Slotow *et al.* 2001), which would further influence their movements across the landscape. This warrants further research, as high densities of elephant may be negatively influencing black rhino populations, not only from a resource perspective, but also due to stress.

7.7. Conclusion

I have queried a number of previously accepted methodologies in the management and study of large mammal ecology in general, with lessons I learnt about black rhino being applicable to the conservation management of many other species. In this study I have discovered a number of new aspects to add to our understanding of black rhino ecology. This will require us to re-evaluate our current research methodologies, the management of species and the scale at which we do this. This includes changing the way we perceive and apply carrying capacity models, which are extensively used in the management of this and many other endangered species. I was able to develop novel applications of machine learning models to answer questions related to the ecology of black rhino and any other species. I have shown the importance of understanding what EGVs influence an individual's niche use, to what degree individuals vary in this use and whether they display temporal variations in niche use over a 24 hour period and during different seasons. I managed to investigate post-release animal responses to EGVs, regardless of low sample sizes and potentially confounding social factors. I was then able to add to our understanding of settling rates of black rhino, potentially improving the reintroduction success of the endangered species. I identified that the amalgamation of carrying capacity, habitat suitability and individual variation models with an added temporal functionality would be best suited to the future conservation and management of species.

An important message from this study is that of understanding individuals within populations and how they respond to the environment rather than averaged responses of the population. This gives us greater insight into the biology of species, specifically the nature of social interactions of social species and how this influences the behaviour of individuals, and thus of populations. This information allows conservation managers to consider social implications of interventions and management practices (Wittemyer *et al.* 2007). To obtain this level of understanding researchers and managers need to initiate and maintain long-term monitoring programs to record individual behaviours and movements, providing an insight into unique environments and the effect they have on local populations.

APPENDIX I

VEGETATION TYPES

of

PHINDA GAME RESERVE

January 2007

CONTENTS

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CHAPTER 1

INTRODUCTION

The identification and description of vegetation units across the landscape forms the basis of scientifically based environmental and veld management plans and are critical first steps in building a framework for ecosystem management planning. It provides a structure to gain information on:

the origin and geographic distribution of vegetation communities;
the relative importance of individual communities;
the overall species composition and variability within communities; and
the relationship of vegetation units to environmental and ecological processes.

Ideally an area should be managed to be self-sustaining, while the quality and diversity of the resources should not be allowed to decrease, as this would inevitably lead to ecosystem degradation and lower productivity. The primary purpose of vegetation management should be to maintain genetic diversity, and ensuring that this diversity does not compromise the continued capacity of the area to support life.

Information on the spatial, temporal and ecological properties of the vegetation units can lead to improved understanding, protection and management of natural resources. These management goals can be achieved by following a policy whereby sensitive communities are protected and existing plant species composition in the natural vegetation is maintained. The invasion of natural vegetation by alien invader plant species should be prevented and attempts should be made to systematically remove existing infestations. Acceptable levels of ungulate-induced change to the vegetation should be established and the collection of plant products should be controlled. Research should be encouraged to determine the dynamics of the plant communities and management strategies (e.g. fire) needed for their long term survival.

The aim of this report is therefore to classify, describe and map the different plant assemblages on Phinda Game Reserve, which could be used for vegetation management as well as for studying plant-animal interactions.

CHAPTER 2

STUDY AREA

Location

Phinda Game Reserve is situated south of the Mkhuze Game Reserve in northern KwaZulu-Natal, at the southern foothills of the Lebombo Mountains. It is located approximately between 27° 40’ S and 27° 55’S latitudes, and 32° 13’ East and 32° 26’ East longitudes on the western coastal plains of Maputaland and covers approximately 21 402 ha (Figures 1 & 6). The grid references for the reserve are 2732 CA, 2732 CB, 2732 CC and 2732 CD. The reserve consists of the following farms or portions of these farms: Harrowgate, Sutton, Ufumba, Iseme, Ntabankosi, Zuka, Tebelwane, Fagolweni, Bube, Monte Rosa, Indabana, Izwelihle, Umgotsha, Golweni, Humseni, Shotton and part of the Katema Settlement and Mnqobokazi area.

Climate

Rainfall

The Maputaland region forms the southerly tip of the Tropical Climate Region, which is characterised by the coldest month (July) having a mean temperature of above 18ºC. Phinda Game Reserve lies just south of the 18ºC isotherm and hence coincides roughly with the southern boundary of Köppen's Tropical Savanna climatic type. The reserve has a warm to hot, humid, tropical to subtropical climate with hot summers and cool to warm winters. Tropical cyclones occur infrequently along the coast, generally from January to March, and are often accompanied by high wind speeds and are regarded as a significant disturbance factor in the coastal areas and hinterland. As a result of these tropical cyclones moving down the Mozambique Channel episodic large-scale river floods occasionally occur.

Phinda Game Reserve lies in the summer rainfall region. The mean monthly and annual rainfall recorded at weather stations in the area are summarised in Table 1. In general, the mean annual rainfall varies from about 600 mm in Mkhuze Game Reserve to as high as 1 044 mm at St Lucia to the southeast and near the coast, and up to 1128 mm against the escarpment to the west at Hlabisa. The mean annual rainfall measured at False Bay is 667 mm. This rainfall gradient significantly influences the plant assemblages within the area. In general, the highest rainfall occurs from October to April, when more than 75% of the annual rainfall occurs, and the lowest from June to August (Figure 2). Along the coast there is no pronounced dry season, and the driest months still receive a fair amount of rain. The absolute maximum annual and absolute minimum annual rainfall measured at Makatini were 1 144 mm in 1984 and 433 mm in 1968 respectively. The absolute maximum and minimum annual rainfall measured at St Lucia were 1987 mm in 1984 and 576 mm in 1979.

Temperature

The mean annual temperature for Mkhuze is 21.8°C (Table 2) with the mean monthly temperature for January 25.5°C and for July 16.4°C. The absolute maximum and minimum temperatures measured at Makatini were 44.2 and 0.1°C respectively (Table 3) while the absolute minimum measured at Hlabisa is 3.3°C. Frost is therefore a rare occurrence in the area.

Wind, humidity, dew and evapotranspiration

Northeasterly and southwesterly winds predominate in the coastal plain, with the rain-bearing winds coming from the southwest. Gale-force winds are most frequent from September to December, and wind speeds of 26 to 40 km per hour and gusts of up to 140 km per hour have been recorded. Wind speeds greater than 50 km per hour occur on average on 12 days per year.

The air humidity is relatively high throughout the area for most of the year. The monthly relative air humidity ranges between 79% and 88% at 08:00 and between 68% and 74% at 14:00. The high relative air humidity coupled with high summer temperatures result in a high discomfort index during the summer months. Dew is experienced throughout the year on calm, windless nights and is particularly heavy during winter. The mean annual evaporation rate is approximately 1660 mm in the interior region.

Terrain morphology

The Phinda Game Reserve lies at the southwestern end of the extensive Mozambican coastal plains. The altitude of Phinda ranges from 50 m in the north-eastern to 340 m in the south-western corner. To the north in the Mkhuze Game Reserve, the height above sea level rises to 474 m at Khombe peak in the Lebombo Mountains.

Hydrology

Phinda Game Reserve is drained by a number of drainage lines towards the Mkhuze and Mzunduzi Rivers in the north (outside the reserve); the Mhlosinga River in the south and tributaries of the Mhlosinga River such as the Munywane and Mungwana Rivers (Figure 1). The Mhlosinga River and its tributaries cover the major portion of the catchment in the reserve. The rivers are seasonal, flowing during the wet summer months, and are reduced to isolated pools and subterranean seepage through bed sediments in winter.

Geology

The geology of Phinda Game Reserve consists of the following (see Figure 3):

- Rhyodacite, rhyolite and flow breccia of the Jozini Formation, Lebombo Group;
- Rhyolitic lava and pyroclastic rocks of the Fenda Formation;
- Rhyolitic tuff and perlite of the Nxwala Formation; rhyolite of the Ntabankosi Suite;
- Amygdaloidal trachybasalt and trachyandesite of the Mpilo Formation, Lebombo Group;
- Conglomerate, siltstone and sandstone of the Makatini Formation, Zululand Group;
- Marine glauconitic siltstone with shelly and concretionary horizons from the Mzinene Formation, Zululand Group;
- Siltstone and sandstone of the St Lucia Formation, Zululand Group;
- Syenite and microsyenite of the Bombeni Complex;
- Red dune cordon sand of the Berea Formation;
- Argillaceous sand of the Muzi Formation; and
- Alluvium

The geological variation and the associated soils of the Phinda region, contribute a great deal to the diversity of vegetation types in the area (see Figures 3 & 6). The Lebombo Mountains were formed by erosion-resistant rhyolites, while weathering and erosion of the early Cretaceous sediments at the base of the mountains resulted in a gently undulating landform with moderate relief. The eastern coastal plain borders on the Lebombo Mountains (continental shelf) (KZN 1999). On the coastal plain the rhyolite and basalt are overlain by Cretaceous terrestrial and marine sediments of the Zululand Group. These sediments comprise three formations exposed in striking north-south zones parallel to the eastern foot slopes of the Lebombo Mountains. The first to be deposited was the lower Cretaceous Makatini Formation consisting of non-marine, fluviatile coarse sandstone and conglomerate. The overlying Mzinene Formation consists of shallow marine silts and sands, while the St Lucia Formation near the coast is the youngest and comprises of buff and greenish grey glaucanitic silts and fine sands.

The cretaceous sediments of the Zululand Group are overlain by the Maputaland Group of relict sandy beach dune ridges which record a succession of depositional events related to sea level fluctuations. The high dune cordons mark stillstands during the Mio-Pliocene marine regressions and decrease in age from west to east. The oldest and most westerly dune cordon occurs adjacent to the Lebombo Mountains in the Mkhuze and Phinda Game Reserves and is probably early Pleistocene (3 million to 30 000 years ago). To the east a younger dune ridge runs west of the Muzi Pan, east of Phinda and along the western boundary of False Bay Park. The youngest dune ridges are probably late Pleistocene (30 000 to 10 000 years ago) and are some of the youngest formations in southern Africa (Hobday 1976).

Land Types and soils

In contrast to the infertile soils over most of the coastal plains, weathering of rhyolite and basalt on the Lebombo Mountains has produced relatively fertile soils with high clay contents. Soil derived from the rhyolite and basalt to the west was deposited on the coastal plain below as clayey but shallow lithosols. To the east there is a belt of rich clay-loam soils formed primarily *in situ* on the Cretaceous strata. These vary from red loamy to clayey soils in the higher-lying areas and black vertisols on lower-lying valley bottoms.

Land types are areas with a uniform climate, terrain form and soil pattern (see Figure 4). A terrain unit is any part of the land surface with homogeneous form and slope. Terrain unit 1 represents a crest, 2 = scarp, 3 = midslope, 4 = footslope and 5 = valley bottom. The following land types are found in Phinda Game Reserve:

Land Types Ae, Ah and Ai;
Land Types Db and Dc;
Land Type Ea; and
Land Type Ib

Land Types Ae, Ah and Ai refer to yellow and red soils without water tables and have one or more of the following soil forms: Inanda, Kranskop, Magwa, Hutton, Griffin and Clovelly.

Land Type Ae is characterised by red, high base status soils more than 300 mm deep (no dunes). A small area on the plains in the north of Phinda, and an area to the east of the reserve fall within this land type (Figure 4).

Land Type Ah is characterised by red and yellow, high base status soils with less than 15% clay content. A small sandy area in the northwestern part of Phinda Game Reserve falls within this Land Type (Figure 4). Terrain units 1 and 3 are the main units found in Land Type Ah and cover 80% and 20% of the area respectively. The slopes vary from 1% to 3% in terrain unit 1, but are up to 10% in terrain unit 3. The dominant soil forms include Bonheim, Arcadia, Glengazi and Rensburg. The soils are deeper than 1 200 mm and rocks are absent in this land type. The percentage clay of the soils ranges from 0 - 15% in the A- and B-horizons. These soils are classified as medium textured sand to loamy sand.

Land Type Ai is characterised by yellow freely drained sandy soils with a high base status. This land type occurs over most of the plains in the north and east of the reserve (Figure 4).

Land Types Db and Dc accommodate land where duplex soils are dominant. Upland soils that display duplex character include Estcourt, Sterkspruit, Swartland, Valsrivier and Kroonstad soil forms.

Land Type Db is characterised by duplex soils that cover more than 50% of the area, but the B-horizons are not red. In the Phinda Game Reserve, this land type is particularly prominent on the borders of sandy areas and near low-lying drainage lines. Small areas in the northeastern, eastern and southeastern parts of Phinda Game Reserve fall within this land type (Figure 4).

Land Type Dc is characterised by duplex soils that cover more than 50% of that land type. In addition, one or more vertic, melanic, red-structured diagnostic horizons occur. A small area in the southern part of the reserve along the Mhlosinga River falls within this land type (Figure 4). Terrain units 3 and 5 are found in this land type and cover 50% each of the landscape. The slopes vary from 1% to 3%. The soils are from 500 mm to 1 200 mm deep and rocks are mostly absent. The percentage clay in the soils ranges from 30 - 45% in the A-horizon and 40 - 65% in the B-horizon. These soils are classified as medium textured sandy clay to clay soils. In some areas deep sandy, sandy loam and sandy clay-loam soils occur with clay contents varying from 5% to 35%.

Land Type Ea covers land with dark coloured or red soils with a high base status, usually clayey, more than half of which is covered by soil forms with vertic, melanic and red structured diagnostic horizons. The basaltic plains in the southwest of the reserve fall within this land type (Figure 4).

Terrain units 4 and 5 are found in this land type and cover approximately 80% and 20% of the area respectively. The slopes vary from 1% to 3%. The dominant soil forms include Bonheim, Arcadia, Glengazi and Rensburg. The soils are deeper than 600 mm and rocks are mostly absent. The percentage clay in the soils varies from 45 - 65% in the A- and B-horizons. These soils are classified as medium textured sandy clay to clay soils.

Land Type Ib consists of exposed rocky areas (covering 60% to 80% of the area), with miscellaneous soils. This land type covers the foothills of the Lebombo Mountains in the southwest and south-central areas of Phinda Game Reserve (Figure 4).

CHAPTER 3

METHODS

Two separate data sets, each compiled by a different researcher, were used for the vegetation classification. Unfortunately no stratification of aerial photographs was made prior to conducting the field surveys to ensure optimal placement of sampling plots. For proper and efficient surveying, an ecological stratification of, for example, 1: 50 000 scale stereo aerial photographs on the basis of terrain morphology and vegetation cover should be made beforehand. This stratification should be used to determine the position and number of sample plots, and is the basis for identifying habitat types and compiling a vegetation map of the area.

Only the woody stratum was sampled during the surveys. Each species was allocated an ‘importance value’ which was based on cover and/or density. An assessment of the habitat, e.g. topography, geology, rock cover, soil texture, soil depth, slope and aspect were made at each sampling plot of one of the two data sets (163 sample plots). No habitat information is available for the second data set. As a result of the absence of information on the herbaceous stratum (grasses and forbs), the classification of the vegetation units for the Phinda Game Reserve (Table 4 – *excluded from this copy due to size of table*) produced in this report is preliminary and is valid only for the woody stratum. For a true classification of the vegetation knowledge of the herbaceous stratum is essential.

The classification of the vegetation data was done with the TURBOVEG and MEGATAB computer programmes (Table 4). The description of the plant communities includes the tree and shrub layers. All plant species recorded in the sample plots are listed in Table 4. The descriptions of the plant communities are based partially on Table 4 as well as descriptions of other vegetation types identified physiognomically during field visits. The environmental description of each plant community is based on the environmental data that was recorded when the woody vegetation was sampled by the researchers concerned (Table 5). The table matrix consists of mean values for each of the vegetation types.

A field visit was undertaken to finalise the vegetation map. To create a Geographical Information System (GIS) ready map, the vegetation map will be classified into ‘intelligent’ GIS classes by a semi-automatic classification in a digital image processing system environment. Refinement of the geo-referencing will be done by using global positioning system (GPS) points on conspicuous localities such as fence corners, pans and lodges. The final raster map will be vectorised and boundary smoothing applied on the vector lines. The main roads were recorded by GIS and will be included in the final vegetation map. Other visible roads will be digitised ‘on screen’ using maps and aerial photographs as reference.

CHAPTER 4

VEGETATION

The general vegetation of the area was classified by Acocks (1953, 1988) as (1) Typical Coast-belt Forest and Zululand Palmveld (under the Coastal Forest and Thornveld vegetation types), and (2) Lowveld, which forms part of the Tropical Bush and Savanna Types. According to Low & Rebelo (1998) the vegetation of Maputaland is part of both the Savanna and Forest Biomes. Savanna vegetation types occurring in the area are Sweet Lowveld Bushveld, Natal Lowveld Bushveld and Coastal Bushveld-Grassland. The Sand Forest belongs to the Forest Biome. The Sand Forests that occur in the reserve are considered endemic to Maputaland. Hunter (2000) distinguished nine vegetation types in Phinda Game Reserve, i.e.

- Closed mixed bushveld
- Open mixed bushveld
- Closed red sand bushveld
- Open red sand bushveld
- Palmveld
- Grassland
- Sand Forest
- Dry mountain bushveld
- Riparian.

Mucina *et al.* (2005) distinguishes nine vegetation types in the Phinda Game Reserve (see Figure 5), i.e.

- Zululand Lowveld
- Southern Lebombo Bushveld

- Western Maputaland Clay Bushveld
- Maputaland Coastal Belt
- Makatini Clay Thicket
- Sand Forest
- Subtropical Salt Pan
- Lowveld Riverine Forest
- Subtropical freshwater wetlands

In the present study, the vegetation of the Phinda Game Reserve has been classified into 25 plant communities. The total area covered by the reserve is approximately 21 402 ha. However, it should be noted that grasses and most of the non-grassy herbaceous plant species were not included in the original surveys and were therefore not part of the data sets used in the classification. The distribution of the main plant communities found in the study area is depicted in the vegetation map (Figure 6).

1. *Acacia nilotica* open shrub savanna

This open to dense shrub savanna occurs on dark clayey soils on relatively flat terrain in the north-eastern, central and western part of the reserve, west of the main road (Figures 6 & 7). It covers 184 ha (0.9% of the total area). *Acacia nilotica* is sometimes the dominant species occurring on abandoned fields. It falls within Land Types Db113 and Ah29 (Figure 4). The sandy loam to sandy clay soils are derived from siltstone (Figure 3). Stones and rocks are absent from the soil surface (Table 5). Rill erosion occurs locally. Fire is a rare event and herbivory is light.

There are no diagnostic species for this community and the community is generally very species poor (Table 4). The most common woody species is *Acacia nilotica*, while other shrub species such as *Dichrostachys cinerea*, *Gymnosporia senegalensis* and *Euclea* *divinorum* occur locally in low numbers. Perennial semi-woody and herbaceous species include *Solanum incanum, Sida* sp. and *Tephrosia* sp. Grasses and forbs cover on average 63% and 9% of the area respectively.

2. *Acacia nilotica-Dichrostachys cinerea* open shrub savanna

This open shrubland occurs on relatively flat terrain along drainage lines and on abandoned fields in the central and southern part of the reserve (Figures 6 & 8). It covers 1695 ha (7.9% of the total area). It falls within various land types, notably the Ea and Db land types (Figure 4). The fine sandy loam to sandy clay soils are derived from siltstone, rhyolite and basalt (Figure 3). Stones and rocks are mostly absent from the soil surface (Table 5). The community has a low woody vegetation cover and is exposed to wind. Rill erosion occurs locally. Fire is a rare event and herbivory is light.

There are no diagnostic species for this community and the community is generally species poor (Table 4). The common species of species groups 18 and 19 (Table 4) characterise this vegetation type. *Acacia nilotica* and *Dichrostachys cinerea* are the most common species together with the trees *Ziziphus mucronata, Berchemia zeyheri, Spirostachys africana*, *Sclerocarya birrea* and *Dovyalis caffra*. The most prominent shrub species include *Euclea divinorum, Gymnosporia senegalensis, Rhus quenzii, Coddia rudis and Euclea racemosa.* Grasses and forbs cover on average 63% and 9% of the area respectively.

3. *Acacia nilotica* grasslands on clay

These grasslands occur on flat terrain in the north-east and south-west of the reserve on dark clayey soils (Figures 6 & 9). It falls within Land Types Db113 and Ea48 (Figure 4). It covers 448 ha (2.1% of the total area). Stones and rocks are absent from the soil surface (Table 5). A large number of small flattish termitaria occur in this community. The sandy clay-loam to clayey soils are derived from rhyolite in the south-west and alluvial sediments in the north-east. The soil substrate is occasionally moist, but mostly dry. Rill erosion occurs locally. Fire is a rare event and herbivory is light.

There are no diagnostic species for this community and the community is generally very species poor (Table 4). The woody layer is poorly developed with the tree layer almost absent. The shrubs are small with *Acacia nilotica* the dominant species. Other shrub species such as *Hyphaene coriacea*, *Dichrostachys cinerea, Gymnosporia senegalensis, Acacia nilotica*, *Acacia borleae* and *Euclea divinorum* occur locally in low numbers. The grasses cover more than 80% of the area and include species such as *Themeda triandra, Sporobolus africanus, Bothriochloa insculpta, Ischaemum afrum, Digitaria eriantha, Eustachys paspaloides* and *Setaria incrassata*.

4. *Acacia nilotica-Hyphaene coriacea* open savanna of drainage systems, including pans, termitaria and bushclumps

This community occurs in the central and northern part of the reserve along flat open drainage lines on the edge of the sandy plains. It is characterized by open savanna, pans and isolated bushclumps on termitaria (Figures 6 & 10). It covers 719 ha (3.4% of the total area). It falls within Land Types Ai9 and Db111 (Figure 4). The coarse sandy loam to sandy clay loam soils are derived from argillaceous sand and siltstone (Figure 3). The soil surface is lightly capped and is covered by pebbles, stones and small rocks (Table 5). Besides the bushclumps, the community has a low woody vegetation cover and is exposed to wind. Trampling and wash were recorded. Fire is a rare event and herbivory is light to moderate.

The open savanna is generally species poor represented by species such as *Acacia burkei, Acacia nilotica, Ziziphus mucronata* and *Hyphaene coriacea,* while *Sclerocarya birrea, Berchemia zeyheri, Acacia robusta* and *Phoenix reclinata* are found locally. Other shrub species include *Coddia rudis, Dichrostachys cinerea, Euclea divinorum, Gymnosporia buxifolia, Gymnosporia senegalensis, Croton steenkampiana, Rhus guenzii* and *Euclea* *racemosa* (see species groups 18 and 19, Table 4). Grasses and forbs cover on average 56% and 6% of the area respectively.

The distinctive bushclumps occur mostly on old termitaria and is dominated by species usually found along drainage lines on clayey soils and is characterized by large trees such as *Spirostachys africana, Schotia brachypetala, Balanites maughamii, Acacia robusta, Acacia burkei, Sclerocarya birrea, Newtonia hildebrandtii, Galpinia transvaalica, Mystroxylon aethiopicum, Sideroxylon inerme and Ziziphus mucronata.* The most common shrub species *include Euclea divinorum, Schotia afra, Euclea natalensis, Euclea racemosa, Carissa tetramera, Azima tetracantha, Rhus guenzii, Rhoicissus digitata* and *Capparis tomentosa.*

5. *Acacia borleae* open shrub savanna

This community occurs in the central and south-eastern part of the reserve on flat terrain and gentle east facing midslopes on fine and dark sandy clay to clayey soils derived from siltstone and rhyolitic lava (Figures 3, 6 & 11). It covers 602 ha (2.8% of the total area). It falls within Land Types Ea48 and Db111 (Figure 4). The soils are shallow in places and the surface is capped and covered by pebbles, stones and small rocks (Table 5). The community has a low woody vegetation cover and is exposed to wind. Wind and gully erosion occur locally. Fire is a rare event and herbivory is light.

Acacia borleae is the diagnostic shrub species for this vegetation type and it occurs locally in dense stands on clayey soils (see species group 1, Table 4). This community is generally species poor and the tree layer is poorly developed. The most prominent shrubs include *Acacia borleae, Acacia nilotica, Dichrostachys cinerea* and *Euclea divinorum,* while other less common shrub species such as *Schotia capitata, Rhus guenzii, Acacia karroo, Acacia luederitzii, Grewia bicolor, Hyphaene coriacea* and *Gymnosporia senegalensis* are locally conspicuous. The herbaceous *Abutilon angulatum* is found in some localities. Grasses and forbs cover on average 65% and 2% of the area respectively.

6. *Acacia karroo* open shrub savanna

This community occurs on red clayey soils in the central and south-eastern part of the reserve on relatively flat terrain and gentle south- and east-facing midslopes (Figure 6). It covers 795 ha (3.7% of the total area). It falls within Land Types Ea48, Db111 and Db113 (Figure 4). The coarse sandy clay to clayey soils are derived from siltstone (Figure 4). The soil surface is strongly capped and is covered by pebbles, stones and small rocks (Table 5). The soil substrate is mostly dry to very dry. The community has a low woody vegetation cover and is exposed to wind erosion. Fire occurs occassionally and herbivory is light.

This community is generally species poor and is characterised by *Acacia karroo*, *Euclea divinorum, Acacia nilotica, Berchemia zeyheri* and *Ziziphus mucronata.* The shrub layer includes prominent species such as *Acacia borleae*, *Dichrostachys cinerea, Gymnosporia senegalensis* and *Gymnosporia buxifolia.* Other shrub species that occur more locally include *Euclea racemosa, Rhus guenzii, Gymnosporia buxifolia, Dovyalis caffra, Grewia flavescens, Scutia myrtina*, *Kraussia floribunda* and *Solanum incanum.* The herbaceous *Abutilon angulatum* is found in some localities. Grasses and forbs cover on average 68% and 2% of the area respectively.

7. *Acacia tortilis* savanna

This savanna occurs on the basaltic plains in the southwest of the reserve. It falls within Land Type Ea56 (Figure 4). It covers 1731 ha (8.1% of the total area). The coarse sandy clay to clayey soils are derived from basalt (Figure 4). The soil surface is capped and is covered by pebbles, stones and small rocks (Table 5). The soil substrate is mostly dry to very dry. The community has a low woody vegetation cover and is exposed to wind erosion. Fire occurs occasionally and herbivory is light.

This community is generally species poor and is dominated by the trees *Acacia tortilis, Acacia nilotica, Sclerocarya birrea* and *Ziziphus mucronata*, while the shrub layer includes prominent species such as *Euclea divinorum, Dichrostachys cinerea* and *Gymnosporia senegalensis.* Other shrub species that occur more locally include *Euclea racemosa, Kraussia floribunda, Acacia karroo, Acacia borleae* and *Capparis tomentosa.* The alien invader *Chromolaena odorata* occurs locally in high densities. Grasses and forbs cover on average 65% and 2% of the area.

8. *Spirostachys africana* dense woodlands on floodplains and riverbanks

This community occurs locally along the Mhlosinga River and in stands along other drainage lines throughout the reserve (see community 23) (Figures 6 & 12). It covers 1092 ha (5.1% of the total area). It is generally found on flat, poorly drained lowlands on clayey soils, often of alluvial origin. It falls within various land types (Figure 4). The slopes vary from 1% to 3%. The fine- to coarse-textured sandy clay to clay soils are derived from rhyolite, siltstone and alluvium (Figure 3). The clay content of the soils varies from 30 - 45% in the A-horizon and 40 - 65% in the B-horizons. The soils are from 500 mm to 1200 mm deep and grit, pebbles, stones and rocks are absent (Table 5). The community has a medium to high woody vegetation cover and is partially protected from wind. Rill erosion is visible. Fire is mostly absent and herbivory is light to moderate.

Species group 5 is the differential species group for communities 7, 8 and 9 with *Spirostachys africana* the most prominent tree species occurring in all three communities (Table 4). Communities 7, 8 and 9 are therefore floristically closely related.

The diagnostic species for this community are *Schotia brachypetala, Pappea capensis, Ehretia rigida and Capparis tomentosa* (species group 5, Table 4). The tree layer is characterized by *Spirostachys africana, Sideroxylon inerme* and *Berchemia zeyheri,* while *Ziziphus mucronata, Acacia nilotica, Mystroxylon aethiopicum, Galpinia transvaalica, Acacia robusta* and *Harpephyllum caffrum* occur locally. The most prominent shrub species include *Euclea divinorum, Rhus guenzii, Euclea racemosa, Carissa bispinosa and Gymnosporia buxifolia,* while *Dovyalis longispina, Capparis tomentosa, Pyrostria hystrix, Scutia myrtina, Cissus rotundifolius, Phyllanthus reticulatus, Acalypha glabrata, Kraussia floribunda* and *Coddia rudis* are less common. Grasses and forbs cover on average 52% and 4% of the area respectively.

9. *Spirostachys africana-Sideroxylon inerme* woodlands

This community occurs in the southern part of the reserve (Figures 6 & 13) on flat lowlands to gentle northeast facing footslopes (Figure 4). It covers 710 ha (3.3% of the total area). The fine to medium-textured loamy to sandy clay soils are derived from rhyolite and siltstone (Figure 3). The soil surface is lightly capped and is covered by some stones and rocks (Table 5). In some areas deep sandy, sandy loam and sandy clay-loam soils occur with clay contents ranging from 5% to 35%. The community has a medium to high woody vegetation cover and is partially protected from wind. Gully erosion occurs locally. Fire is a fairly rare event and herbivory is light to moderate.

The tree layer is well-developed and characterized by *Spirostachys africana* and *Sideroxylon inerme*, while other common tree species such as *Berchemia zeyheri, Ziziphus mucronata, Acacia nilotica* and *Dombeya rotundifolia* occur locally. *Sideroxylon inerme* is locally prominent on slopes and flat bottomlands along drainage lines in the western and south-eastern parts of the reserve. Noteworthy is the absence of *Spirostachys africana* from these areas. The most prominent shrub species include *Rhus guenzii, Euclea racemosa, Euclea divinorum, Cissus rotundifolius, Phyllanthus reticulatus, Coddia rudis, Carissa bispinosa, Kraussia floribunda, Scutia myrtina, Pyrostria hystrix, Dovyalis longispina, Grewia flavescens, Gymnosporia buxifolia, Gymnosporia senegalensis* and *Azima tetracantha*. The alien invader *Chromolaena odorata* occurs locally in high densities. Grasses and forbs cover on average 56% and 2% of the area.

10. *Acacia luederitzii-Euclea divinorum* thickets and dense woodlands

These thickets and woodlands occur as local stands along drainage lines in the southern half of the reserve (Figures 6 & 12). It covers 1160 ha (5.4% of the total area). The community is generally found on flat, poorly drained lowland on clayey soils, often of alluvial origin and it falls within the Ea and Db land types (Figure 4). The medium to coarse textured sandy clay to clayey soils are derived from siltstone and rhyolite (Figure 3). The soil surface is lightly capped and is covered by grit, pebbles, stones and small rocks (Table 5). The community has a medium to high woody vegetation cover and is partially protected from wind. Rill erosion is visible. Fire is a fairly rare event and herbivory is moderate.

This woodland is species rich in comparison to communities 1 to 5. The diagnostic species include *Cissus rotundifolius, Rhoicissus tridentata, Phyllanthus reticulatus* and *Dombeya rotundifolia*. The tree layer is characterized by *Acacia luederitzii, Berchemia zeyheri, Ziziphus mucronata* and *Dombeya rotundifolia. The trees Acacia nilotica, Spirostachys africana, Balanites maughamii, Euphorbia cooperi, Schotia brachypetala, Galpinia transvaalica, Mystroxylon aethiopicum, Elaeodendron transvaalense, Olea europaea* subsp. *africana*, *Strychnos spinosa* and *Sideroxylon inerme* occur locally. The most prominent shrub species is *Euclea divinorum.* Other shrub species include *Coddia rudis, Rhus guenzii, Euclea racemosa, Cissus rotundifolius, Carissa bispinosa*, *Carissa tetramera, Kraussia floribunda, Grewia flavescens, Gymnosporia buxifolia, Gymnosporia senegalensis*, *Capparis tomentosa*, *Ximenia americana*, *Phyllanthus reticulatus*, *Pyrostria hystrix, Scutia myrtina*, *Cissus rotundifolia* and *Azima tetracantha*. The alien invader *Chromolaena odorata* occurs locally in high densities. Grasses and forbs cover on average 51% and 2% of the area.

11. *Combretum apiculatum* mountain bushveld

This woodland is found in the southwest on the rhyolitic foothills of the southern Lebombo Mountains, which rise from the coastal plain (Figures 6 & 14). It covers 2543 ha (11.9% of the total area). This community occurs on gentle northeast-facing midslopes and falls within Land Types Ea48 and Ib133 (Figure 4). The fine sandy clay soils are derived from rhyodacite and rhyolite (Figure 3). The soil surface is moderately capped and is covered by grit, pebbles, stones and rocks (Table 5). The community has a low to moderate woody vegetation cover and is exposed to wind and gully erosion. Fire is a fairly regular event and herbivory is light.

The diagnostic species for this vegetation type is *Combretum apiculatum* (Table 4). The community is generally species poor and besides the dominant *Combretum apiculatum,* other tree species include *Ziziphus mucronata, Acacia burkei, Dombeya rotundifolia, Ozoroa paniculata, Peltophorum africanum, Sclerocarya birrea, Combretum molle, Pappea capensis, Galpinia transvaalica, Acacia nilotica* and *Aloe spectabilis*. The shrub layer is represented by a dense cover of *Dichrostachys cinerea*, while less common species include *Euclea divinorum, Euclea racemosa, Rhus guenzii, Gymnosporia senegalensis, Gymnosporia buxifolia, Ozoroa engleri* and *Solanum incanum*. Grasses and forbs cover on average 89% and 1% of the area respectively.

12. *Ziziphus mucronata-Euclea divinorum* dense bushveld on west, south-west and south-facing slopes

This dense bushveld is found on rhyolite on south-west and south-facing slopes with isolated patches of forest where local conditions are sufficiently moist (Figures 6 & 15). It covers 305 ha (1.4% of the total area).

The most prominent species include the trees *Ziziphus mucronata, Berchemia zeyheri, Sideroxylon inerme, Ficus ingens, Ekebergia capensis, Acacia burkei, Sclerocarya birrea, Combretum kraussii, Aloe spectabilis* and the shrubs *Euclea divinorum, Euclea* *racemosa, Pavetta edentula, Kraussia floribunda, Zanthoxylum capense, Diospyros lycioides, Grewia flavescens, Catunaregam spinosa, Gymnosporia buxifolia, Rhoicissus tridentata, Coddia rudis, Acacia kraussiana* and *Cissus rotundifolia.*

13. *Combretum apiculatum* open savanna and grasslands

This community occurs on the hills and slopes in the west and falls within Land Type Db111 and Ea48 (Figures 4, 6 & 16). It covers 849 ha (4.0% of the total area). The fine sandy clay soils are derived from rhyolite, rhyolitic lava and pyroclastic rocks (Figure 3). The soil surface is moderately capped and is covered by grit, pebbles, stones and rocks (Table 5). The community is exposed to wind and gully erosion. Fire is a fairly regular event and herbivory is light.

This open savanna consists of a mosaic of grassland and isolated patches of woodland on rocky outcrops. The community is generally species poor and besides *Combretum apiculatum,* other tree species include *Ziziphus mucronata, Acacia burkei, Pavetta edentula, Sclerocarya birrea, Ficus stuhlmannii, Ficus abutilifolia* and *Acacia nilotica*. The shrub layer is represented by *Dichrostachys cinerea, Euclea divinorum, Rhus guenzii, Rhus gracillima, Gymnosporia senegalensis and Gymnosporia buxifolia. Aloe spectabilis* are locally common. The grass layer is characterized by species such as *Hyperthelia dissoluta, Themeda triandra* and *Bothriochloa insculpta.* Grasses and forbs cover on average 89% and 1% of the area respectively.

14. *Terminalia sericea* bushveld and woodlands

Communities 13, 14 and 15 are floristically related because they share species such as *Terminalia sericea, Hyphaene coriacea, Combretum molle* and *Strychnos madagascariensis* (Table 4). Community 14 covers 1858 ha (8.7% of the total area).

This community occurs on pallid sands on the plains and gentle north-facing slopes in the north (Figures 6 & 17) and falls within Land Type Ai9, which is characterised by yellow freely drained fine sandy soils with a high base status (Figures 3 & 4). Pebbles, stones and rocks are absent from the soil surface (Table 5). The soil substrate is mostly dry. The community has a medium woody vegetation cover and is partially protected from wind. Sheet erosion occurs locally. Fire is a fairly rare event and herbivory is light to moderate.

The tree layer is characterized by locally common tree species such as *Terminalia sericea, Combretum molle, Brachylaena discolor, Strychnos madagascariensis, Strychnos spinosa, Acacia burkei, Ziziphus mucronata, Sclerocarya birrea* and *Mystroxylon aethiopicum*. The most prominent shrubs include *Rhus guenzii, Dalbergia obovata, Grewia monticola, Schotia capitata, Coddia rudis, Dichrostachys cinerea, Gymnosporia senegalensis* and *Euclea divinorum.* Grasses and forbs cover on average 52% and 3% of the area respectively.

15. *Terminalia sericea-Hyphaene coriacea* bushveld

This palmveld occurs in different places on the deep whitish and fine sandy soils on the plains in the north, north-east and east of the reserve (Figures 6 & 18). It covers 576 ha (2.7% of the total area). It falls within Land Type Ai9 which is characterised by freely drained sandy soils with a high base status (Figures 3 & 4). Pebbles, stones and rocks are absent from the soil surface (Table 5). The soil substrate is mostly dry. The community has a medium woody vegetation cover and is partially protected from wind. Sheet erosion occurs locally. Fire is a fairly rare event and herbivory is light to moderate.

The tree layer is characterized by *Terminalia sericea* and dense stands of *Hyphaene coriacea.* Other tree species include *Combretum molle, Strychnos madagascariensis, Trichilia emetica, Euphorbia ingens* and *Strychnos spinosa*. The most prominent shrub species include *Catunaregam spinosa, Zanthoxylum capense, Coddia rudis, Euclea divinorum, Euclea natalensis, Dichrostachys cinerea, Acacia nilotica* and *Gymnosporia* *senegalensis*. The thatch grass *Hyperthelia dissoluta* is locally prominent.

16. *Terminalia sericea-Dichrostachys* cinerea old fields and other disturbed areas (open woodlands)

This community occurs in the northern half of the reserve (Figures 6 & 19) on old fields and in areas where partial bush clearing occurred. It falls within Land Type Ai9, which is characterised by deep whitish to yellow freely drained fine sandy loam soils with a high base status (Figures 3 & 4). It covers 446 ha (2.1% of the total area). Pebbles, stones and rocks are absent from the soil surface (Table 5). The soil substrate is mostly dry to very dry. The community has a low to moderate woody vegetation cover and is partially exposed to wind. Fire is an occasional event and herbivory is light to moderate.

Prominent tree species include *Terminalia serice, Strychnos spinosa, Combretum molle, Sclerocarya birrea, Acacia burkei, Brachylaena discolor, Pteleopsis myrtifolia* and *Strychnos madagascariensis.* The palm *Hyphaene coriacea* is prominent locally. The common shrub species include *Dichrostachys cinerea, Catunaregam spinosa, Euclea divinorum, Rhus guenzii, Croton steenkampiana, Euclea natalensis, Grewia micrantha, Euclea crispa, Schotia capitata, Mundulea sericea, Grewia caffra, Rhoicissus digitata* and *Gymnosporia senegalensis*. The dwarf shrub *Helichrysum kraussii* is a dominant species of these areas. Grasses and forbs cover on average 47% and 1% of the area respectively.

17. *Pteleopsis myrtifolia* open to dense bushveld/woodland

Communities 16 and 17 are related to Sand Forest proper (community 18) through sharing species such as *Monadenium caffra, Toddaliopsis caffra* and *Salacia leptophylla* (Table 4). Community 17 covers 2333 (10.9% of the total area).

This dense woodland occurs on the sandy lowland plains in the central-northern part of the reserve. It surrounds many of the dense stands of Sand Forest (Figure 6) and falls within Land Type Ai9 that is characterised by yellow, freely drained coarse sandy loam soils with a high base status (Figures 3 & 4). Pebbles, stones and rocks are absent from the soil surface (Table 5). The soil substrate is mostly dry to very dry. The community has a high woody vegetation cover and is partially to fully protected from wind. Rill erosion occurs locally in this community. Fire is virtually absent from this area and herbivory is moderate.

This woodland is species rich in comparison to the other communities found in Phinda Game Reserve. The extensive list of diagnostic species include species such as *Hymenocardia ulmoides*, *Balanites maughamii, Tricalysia capensis, Landolphia kirkii* and *Tricalysia lanceolata* (see species group 13, Table 4). Of note is the absence of *Terminalia sericea* and *Hyphaena coriacea* (see communities 10, 11 and 12 and species group 12 (Table 4).

The dominant tree species include species such as *Pteleopsis myrtifolia, Strychnos spinosa*, *Balanites maughamii, Combretum molle, Dialium schlechteri, Mystroxylon aethiopicum, Commiphora neglecta, Strychnos spinosa, Brachylaena discolor, Acacia burkei, Maerua cafra* and *Strychnos madagascariensis*. The shrub layer is characterised by *Hymenocardia ulmoides, Salacia leptophylla, Hypericum revolutum, Tricalysia capensis, Tricalysia lanceolata, Rhus guenzii, Landolphia kirkii, Euclea divinorum, Uvaria caffra, Vitex ferruginea, Carissa tetramera, Ochna arborea, Dalbergia nitidula, Canthium setiflorum, Croton steenkampiana, Zanthoxylum capense* and *Catunaregam spinosa*.

Sand Forest species (community 18) present in this community include *Monadenium caffra, Uvaria caffra, Salacia leptophylla, Toddaliopsis bremekampii, Rhoicissus digitata, Strychnos henningsii, Croton pseudopulchellus, Croton steenkampianus* and *Wrightia natalensis* (see species group 22, Table 4). Grasses and forbs cover on average

19% and 6% of the area respectively.

18. *Dialium schlechteri* woodland

This woodland is related to communities 16 and 18 through sharing species from species group 22. It is particularly related to the Sand Forest community (community 18) (Table 4).

This community occurs locally in the north of the reserve in association with Sand Forest patches (Figure 6). It covers 285 ha (1.3% of the total area). It falls within Land Type Ai9 which is characterised by yellow, freely drained coarse sandy loam soils with a high base status (Figure 4). Pebbles, stones and rocks are absent (Table 5). The soil substrate is mostly dry to very dry. The community has a high woody vegetation cover and is partially to fully protected from wind. Rill erosion occurs locally in this community. Fire is virtually absent from this habitat and herbivory is moderate.

The diagnostic species for this community include *Erythrophleum lasiantum, Drypetes natalensis, Croton sylvaticus* and *Tricalysia sonderi* (see species group 20, Table 4). The most common tree species found in this community are *Dialium schlechteri, Pteleopsis myrtifolia, Cleistanthus schlechteri, Drypetes natalensis, Erythrophleum lasiantum, Cryptocarya woodii* and *Strychnos decussata.* The shrub layer is characterized by *Croton sylvaticus, Tricalysia sonderiana, Toddaliopsis bremekampii, Dovyalis caffra* and *Cola greenwayi. Salacia leptophylla, Grewia caffra* and *Blighia unijugata* are locally common.

19. *Drypetes arguta* Sand Forest

This vegetation type is also called the Licuati Sand Forest (Mucina *et al*. 2005). Sand Forest is a type of dry forest and is best developed on the north-south trending dune cordons in the hinterland of the coastal plains of Maputaland where the water table is deep. The soils developed *in situ* from the relatively homogeneous, grey, silicaceous, aeolian sands and are highly leached (dystrophic) and relatively acidic. Structurally this forest is from 5 to 12 m tall and forms dense vegetation with different strata.

The Sand Forests occur as distinct stands on the sandy plains in the central, northern and eastern parts of the reserve (Figures 5, 6 & 20). It covers 509 ha (2.4% of the total area). They fall within Land Type Ai9 which is characterised by yellow, freely drained coarse sandy loam soils with a high base status (Figures 3 & 4). No pebbles, stones and rocks occur on the soil surface (Table 5). The soil substrate is occasionally moist but mostly dry. The community has a high woody vegetation cover and is fully protected from wind. Fire is rare in this community and herbivory is light to moderate.

The differential species include *Cola greenwayi, Salacia leptophylla, Drypetes arguta, Newtonia hildebrandtii, Toddaliopsis bremekampii* and *Uvaria caffra* (see species groups 21 and 22, Table 4). The dominant tree species include *Drypetes arguta, Newtonia hildebrandtii, Cleistanthus schlechteri, Wrightia natalensis* and *Strychnos henningsii.* The shrub layer is represented by *Uvaria caffra, Salacia leptophylla, Toddaliopsis bremekampii, Cola greenwayii, Croton steenkampiana, Hyperacanthus amoenus* and *Vitex ferruginea*. Grasses and forbs cover on average 2% and 3% of the area respectively.

20. Thatch grass (*Hyperthelia dissoluta*) old fields

This community occurs in the north of the reserve on old fields on deep sand. It is dominated by the yellow thatch grass *Hyperthelia dissoluta* (Figure 6). It covers 53 ha (0.2% of the total area). The sparse shrub layer is characterized by *Sclerocarya birrea, Dichrostachys cinerea, Acacia nilotica, Strychnos spinescens* and *Gymnosporia senegalensis*.

21. Palmveld (*Hyphaene coriacea*)

This palmveld occurs on the plains in the north-east of the reserve and is dominated by

Hyphaene coriacea (Figures 6 & 21). Notably is the absence of *Terminalia sericea* in this vegetation type. It covers 298 ha (1.4% of the total area).

22. Floodplain grasslands

The floodplain grasslands occur in the south-east of the reserve (Figures 6 & 22). It covers 228 ha (1.1% of the total area). Shrub species include *Dichrostachys cinerea*, *Azima tetracantha, Coddia rudis, Rhus guenzii* and *Flueggia virosa*. The prominent grass species include *Panicum maximum*, *Echinochloa pyramidalis, Hemarthria altissima*, *Echinochloa pyramidalis* and *Setaria incrassata.*

23. Streams (seasonal drainage lines)

The stream vegetation as mapped in Figure 6 includes the vegetation occurring on the streambanks as well as on the floodplains next to the streams. It covers 1068 ha (5.0% of the total area). The dominant woody species include trees such as *Spirostachys africana, Sideroxylon inerme, Acacia luederitzii,* and *Schotia brachypetala* (see communities 4, 7, 8 and 9)

24. *Acacia xanthophloa* riparian forests

These riparian forests are best developed along the Mhlosinga and Mungwana Rivers and the lower reaches of their main tributaries (Figures 6 & 25). It covers 615 ha (2.9% of the total area). The following description of this vegetation type is also based on description provided by Van Rooyen (2004) for the Mkhuze and GSLWP area. *Acacia xanthophloea* stands occur on floodplains that experience frequent seasonal, short-duration floods and also on pan edges. These stands are associated with a dense cover of grasses such as *Echinochloa pyramidalis, Hemarthria altissima, Cynodon dactylon* and stands of *Phragmites australis.* Other prominent species include *Ficus sycomorus, Rauvolfia* *caffra, Syzygium guineense, Ziziphus mucronata, Trichilia emetica* and *Ekebergia capensis*. Where a riverine thicket develops it is mostly composed of the shrubs *Acacia schweinfurthii, Azima tetracantha* and *Grewia caffra,* with *Ficus capreifolia* and the palm *Phoenix reclinata* on the river banks close to water. These species are extremely important for stabilizing the river banks and to prevent erosion of low-lying areas.

25. Pan and dam vegetation

The vegetation on the small pans and depressions found interspersed throughout the central and north-eastern lowlands of the reserve was not surveyed but has been mapped (Figures 6 & 26). It covers 217 ha (1.0% of the total area). The following description of this vegetation type is based on description provided by Van Rooyen (2004) for the Mkhuze and GSLWP area. These wetlands differ in size and duration of standing water. They are associated with sandy substrates or dark grey to black soils with high organic content and with water table levels just below or at the surface. The dominant grass species are *Ischaemum fasciculatum, Leersia hexandra, Hemarthria altissima, Acroceras macrum, Panicum meyerianum, Agrostis lachnantha, Brachiaria arrecta, Digitaria albomarginatum* and *Sporobolus subtilis.* Other common wetland species found in these areas are the sedges *Scirpus littoralis, Pycreus polystachyos, Fuirena obcordata, Cyperus tenax* and *Eliocharis dulcis,* and the forbs *Centella asiatica* and *Hydrocotyle bonariensis*.

26. Lodges, houses, airfields etc.

These areas cover approximately 84 ha (0.4% of the total area).

ACKNOWLEDGMENTS

The following institutions and persons are thanked for their contributions and support for this study:

Management and staff of Phinda Game Reserve, especially Kevin Pretorius GM

Matt Repton for providing data.

Gretel van Rooyen for editorial support.

Wayne Matthews for his support.

Table 1 Mean monthly rainfall (mm) for different weather stations in the vicinity of Phinda Game Reserve

Month	Makatini	Mkhuze	Hlabisa	St Lucia Lake	Mbazwana	Ndumu
January	102	64	172	153	133	151
February	112	88	142	125	140	91
March	78	30	167	124	108	70
April	42	28	61	87	76	57
May	24	31	40	60	47	22
June	14	9	16	42	40	8
July	12	16	26	41	42	19
August	15	28	28	49	40	16
September	43	50	64	69	50	54
October	59	77	120	87	83	54
November	77	80	132	114	90	93
December	83	77	160	93	86	91
Year	661	578	1128	1044	935	726

Table 2 Mean monthly temperature (C) for different weather stations in the vicinity of Phinda Game Reserve

Month	Makatini	Mkhuze	Hlabisa	St Lucia Lake	Ndumu
January	26.7	25.5	22.7	25.4	26.9
February	26	25.8	23.1	25.4	26.6
March	25.3	24.7	21.9	24.5	25.7
April	22.8	23	20.5	22.1	23.4
May	20	19.7	18.6	19.4	21.1
June	16.9	16.6	16.8	16.7	18.7
July	17.1	16.4	16.5	16.9	18.6
August	19	18.3	17.5	18.5	20.1
September	21.3	20.4	18.7	20.3	21.8
October	22.6	22.5	19.7	21.3	22.8
November	23.9	23.4	20.9	22.5	24.1
December	25.7	24.8	22.3	24.2	26
Year	22.3	21.8	19.9	21.4	23

Table 3 Absolute maximum and minimum temperatures recorded at different weather stations near Phinda Game Reserve

Station	Maximum	Minimum
Makatini	44.2	0.1
St Lucia	43.5	1.4
Hlabisa	40.6	3.3
Ndumu	44.5	6.2

Table 5 Mean values of site characteristics for the different plant communities identified for Phinda Game Reserve

Site number	1	2	3	4.1	4.2	5	6	7	8	9	10	11*	12	13	14*	15
GPS alt	53.8	50.8	68.9	50.8	51.6	67.9	63.7	44.6	47.2	41.4	54.2		38.3	39.6		40.4
Topographic position	6.0	5.3	6.4	6.1	6.3	5.5	2.0	6.9	7.1	8.1	4.9		6.0	6.4		4.6
Microrelief	2.1	1.9	1.8	1.9	1.4	1.0	1.7	1.6	1.8	1.7	1.7		1.3	2.3		2.4
Direction (deg)	35.6	74.4	101.5	105.6	167.2	52.4	32.5	80.3	69.0	101.1	5.2		245.0	7.0		29.0
Aspect	NE	E	E	E	S	NE	NE	E	NE	E	N		W	N		NE
Slope 1m drop	632.9	171.7	172.0	99.8	32.1	175.7	50.0	101.6	189.2	230.0	1177.1		41.7	900.0		386.7
Dom. erosion Cell pos.	2.2	1.8	2.0	1.8	1.8	1.6	2.3	1.6	1.9	1.6	2.2		2.3	1.9		1.9
Soil texture	7.2	5.4	6.2	5.4	5.2	6.0	7.3	5.5	6.1	5.4	6.1		6.3	4.1		4.7
Grasses canopy cover	62.8	55.6	64.6	64.7	68.3	89.4	51.7	50.9	56.2	52.9	51.8		46.7	18.9		1.6
Forbs canopy cover	8.7	6.2	4.8	1.7	2.2	1.1	3.7	2.0	2.1	9.0	2.8		0.7	5.9		3.0
Boulders	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0		0.0
Large rocks	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0		0.0	0.0		0.0
Small rocks	0.0	0.1	0.4	0.1	0.0	1.6	0.0	0.7	0.0	0.0	0.0		0.0	0.0		0.0
Large stones	0.0	0.6	1.2	0.3	0.8	1.6	0.0	0.2	1.2	0.0	0.0		0.0	0.0		0.0
Small stones	0.0	1.4	0.2	0.3	0.8	3.6	0.0	2.2	0.0	0.0	0.0		0.0	0.0		0.0
Large pebbles	0.0	1.4	1.5	0.3	0.4	3.1	0.0	0.4	0.0	0.0	0.0		0.0	0.0		0.0
Small pebbles	0.0	0.6	3.2	2.2	0.0	3.1	0.0	0.4	0.0	0.7	0.0		0.0	0.0		0.0
Grit	0.0	0.3	2.3	0.6	0.0	3.1	0.0	0.9	0.0	0.7	0.0		0.0	0.0		0.0
Coarse sand	4.4	2.5	3.1	2.2	5.8	2.5	0.0	7.4	10.8	7.1	0.0		30.0	12.9		0.0
Fine sand	77.8	16.9	15.0	18.1	12.9	5.6	0.0	35.6	31.2	50.0	90.0		70.0	72.9		85.7
Sandy clay	17.8	59.1	24.6	30.0	21.7	51.9	100.0	26.3	48.5	27.1	5.0		0.0	14.3		14.3
Broken clay	0.0	0.0	1.5	0.0	0.0	0.0	0.0	7.4	0.0	0.0	5.0		0.0	0.0		0.0
Capped clay	0.0	17.2	46.2	45.9	57.5	25.6	0.0	13.7	7.7	14.3	0.0		0.0	0.0		0.0
Moisture status	5.4	5.7	5.4	6.3	6.1	5.3	5.7	5.6	5.2	5.3	6.0		6.3	5.9		5.6
Shading	11.9	11.6	12.3	11.8	12.3	12.4	10.7	9.1	8.8	7.6	9.5		7.7	4.0		2.3
Protection from wind	2.9	2.4	2.9	2.6	2.9	3.0	2.7	2.3	2.2	2.0	2.3		1.7	1.6		1.0
Erosion type	2.1	7.3	4.6	4.9	6.0	3.8	0.0	6.0	3.6	4.6	1.0		5.7	1.9		0.9
Erosion intensity	0.2	0.7	0.9	0.8	0.9	0.5	0.0	1.0	0.5	1.1	0.2		0.7	0.3		0.0
Deposition type	0.7	1.7	2.0	2.4	3.0	1.9	0.3	1.4	1.1	1.9	0.5		2.3	0.6		0.6
Deposition intensity	0.4	0.8	0.9	0.7	0.8	0.6	0.3	0.6	0.4	0.6	0.2		1.0	0.1		0.3
Indications of fire	0.4	0.7	0.7	1.2	1.3	0.8	0.0	0.5	0.5	0.6	0.3		1.3	0.0		0.0
Intensity of herbivory	1.3	1.7	1.3	1.4	1.2	1.0	1.3	1.9	1.5	1.4	1.1		1.3	1.6		1.1

*Community 11 - related to communities 10 and 12

*Community 14 related to community 15

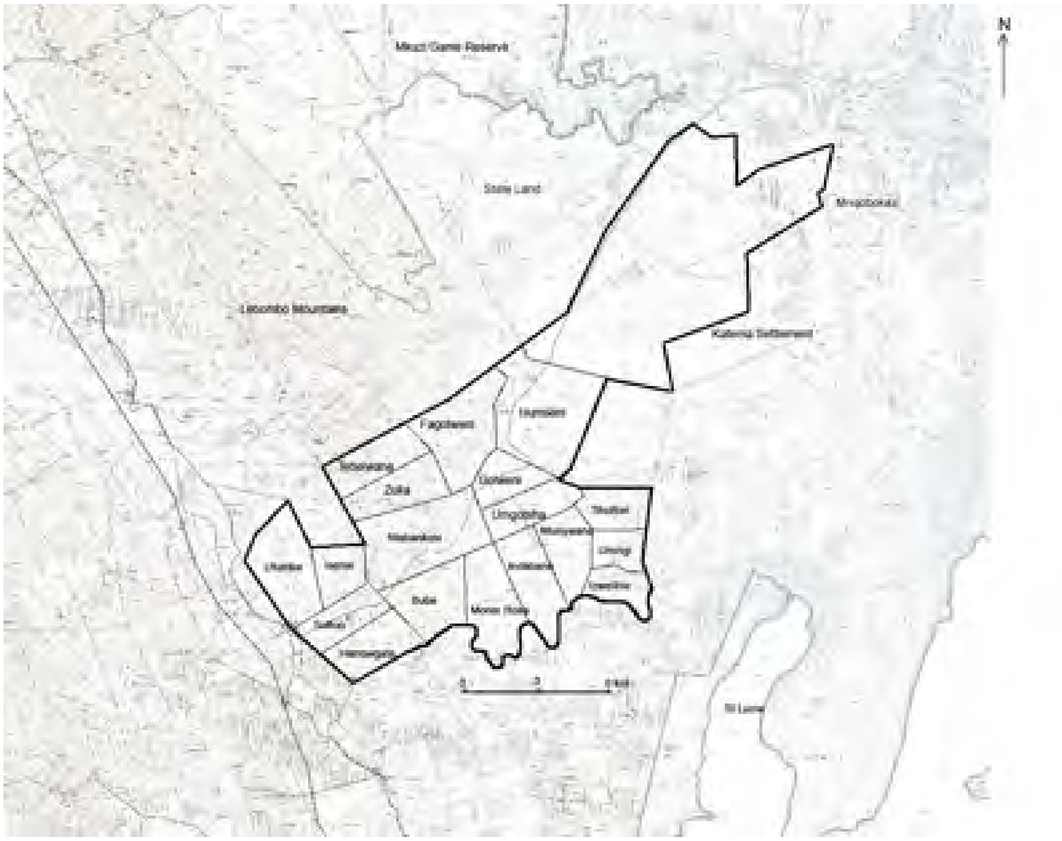

Figure 1 Location map of Phinda Game Reserve

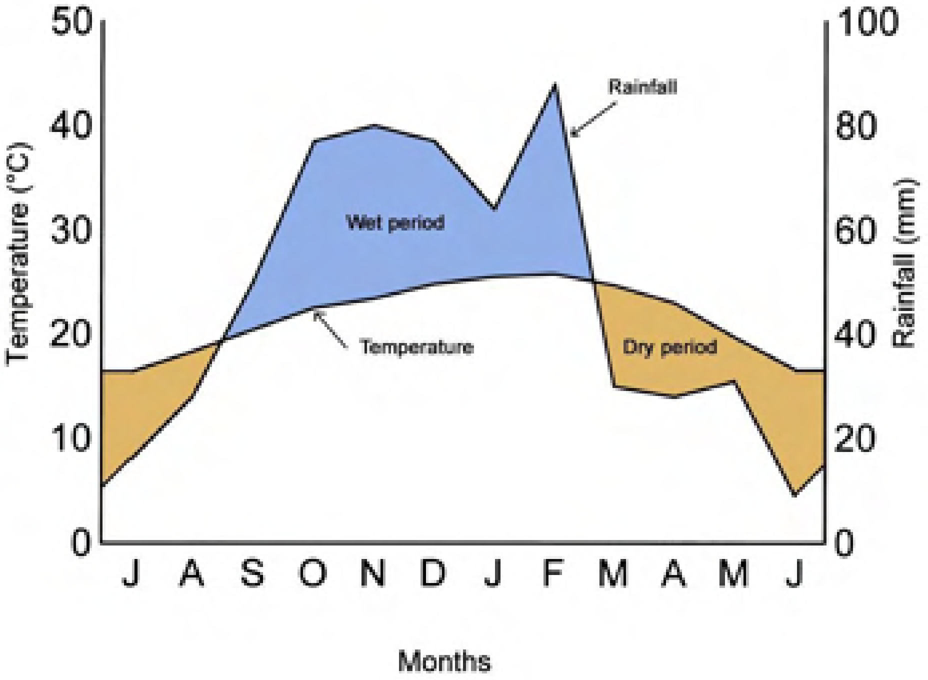

Figure 2 Climate diagram for Phinda region (Mkuze data)

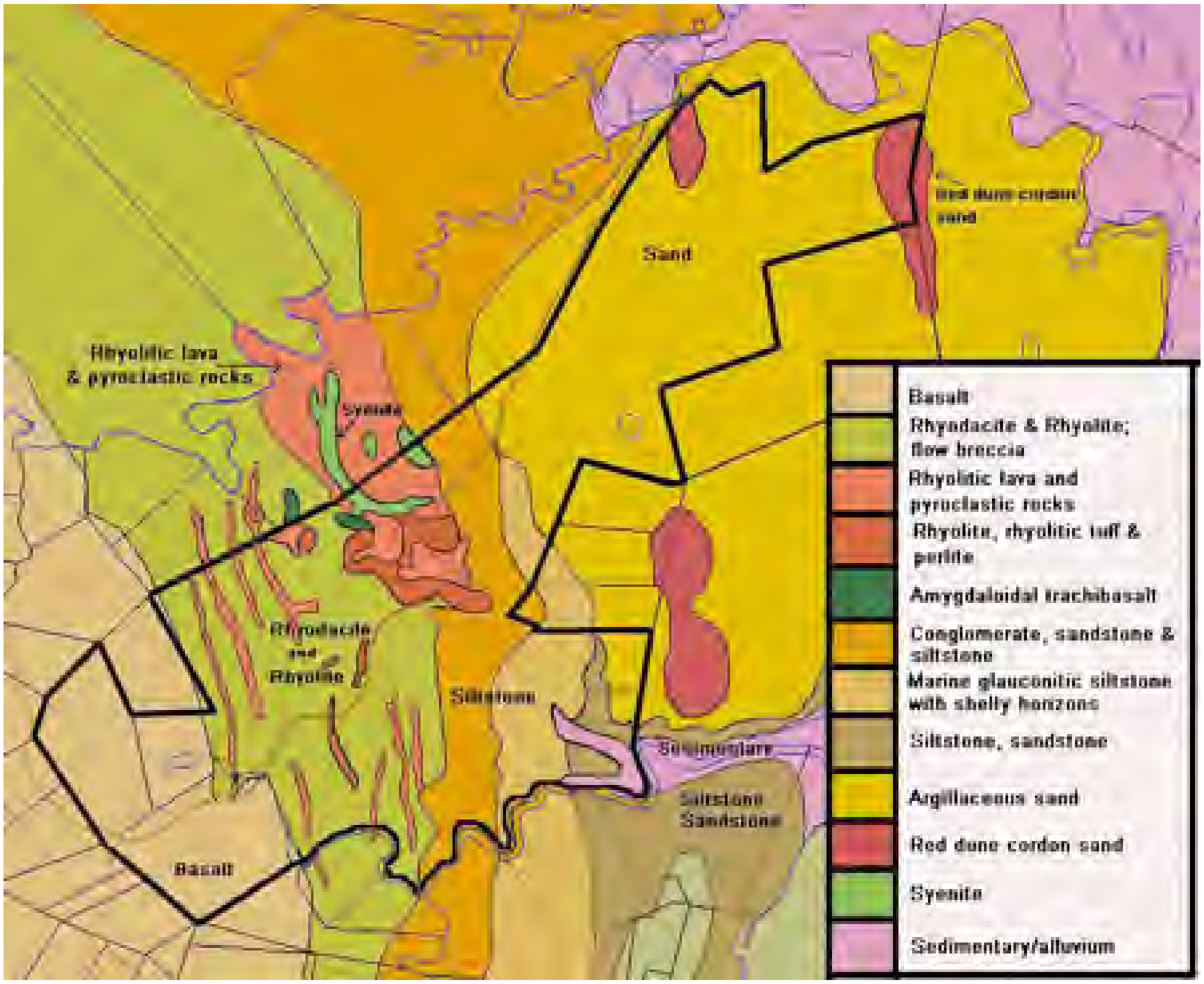

Figure 3 Geology map of Phinda Game Reserve

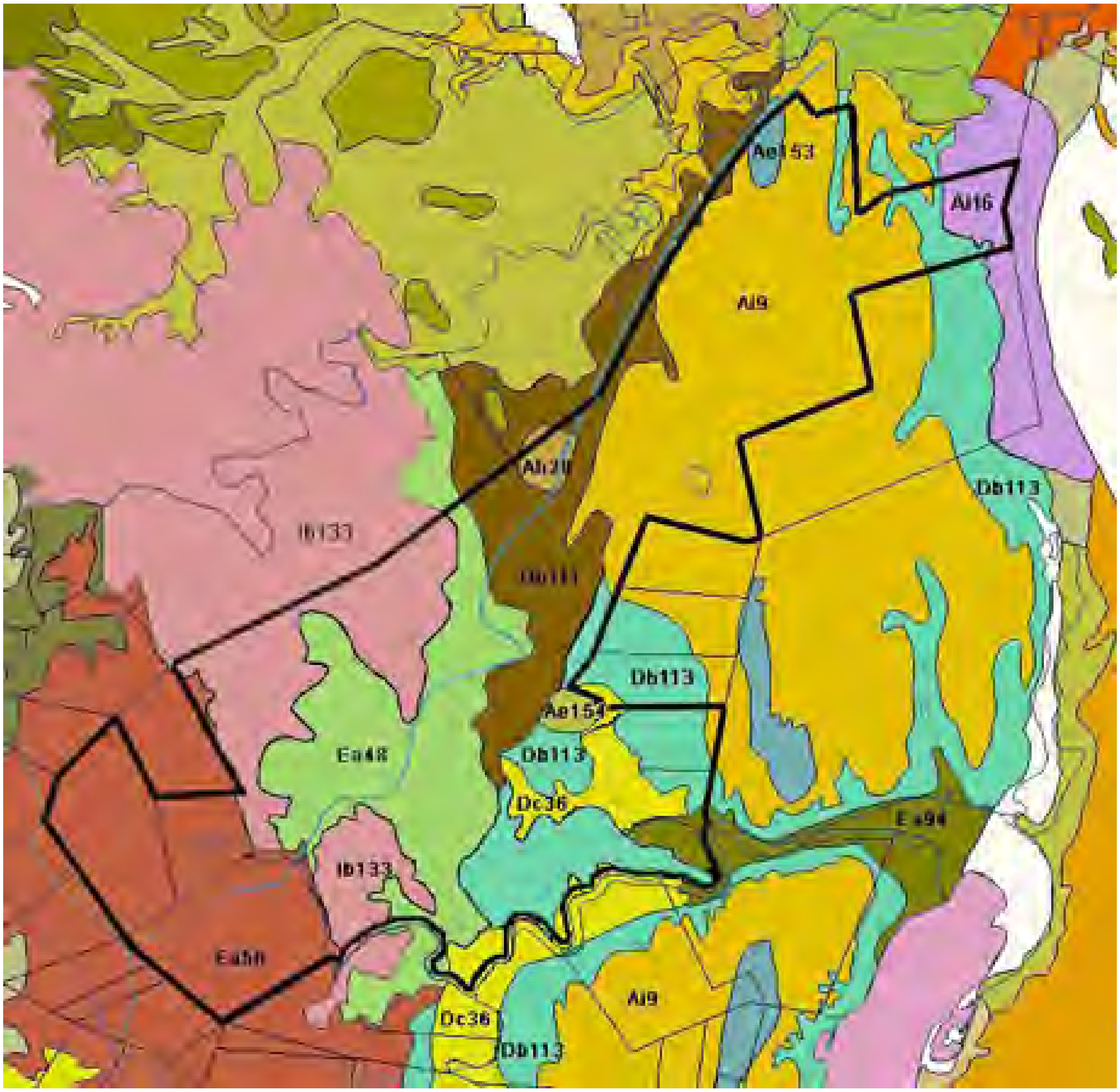

Figure 4 Land Types of Phinda Game Reserve

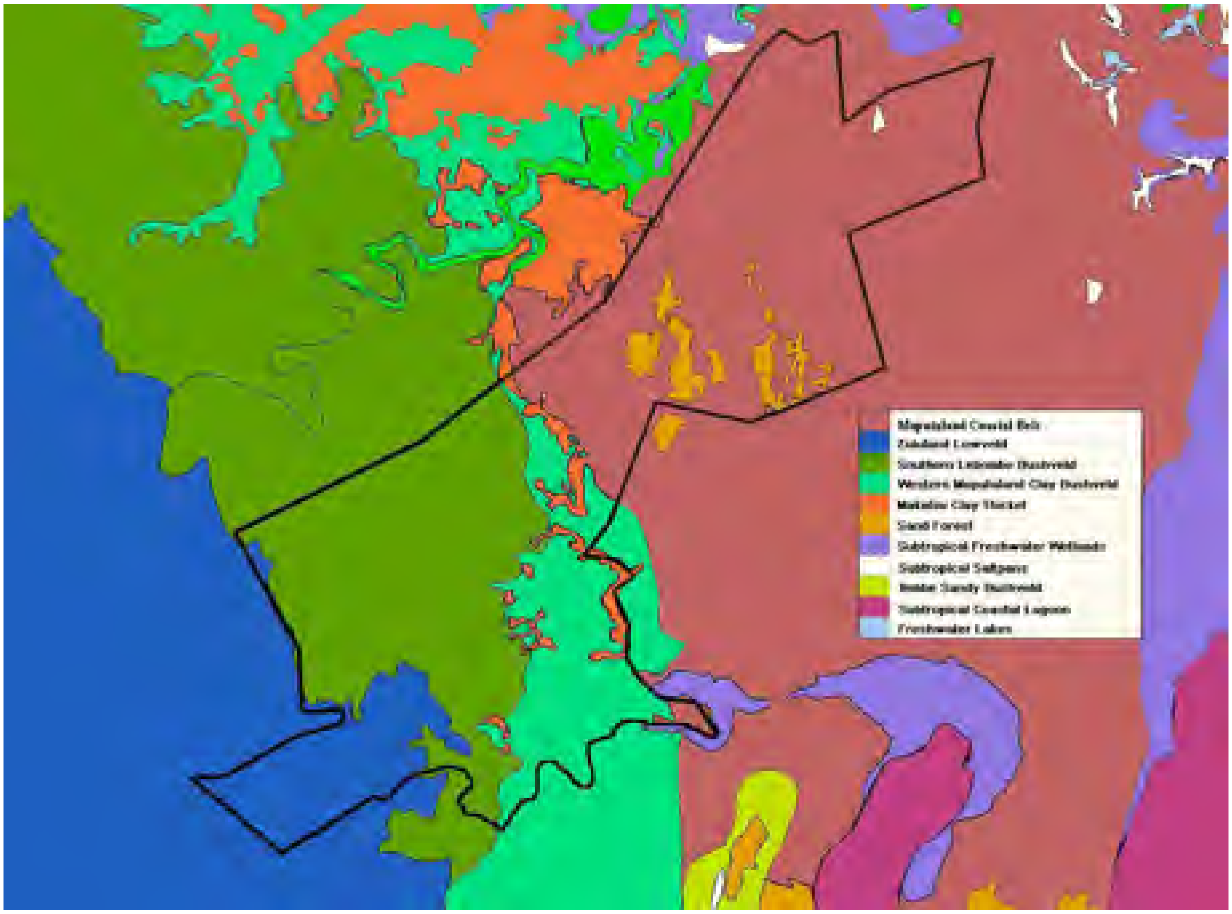

Figure 5 Vegetation of Phinda Game Reserve according to Mucina *et al.* (2005)

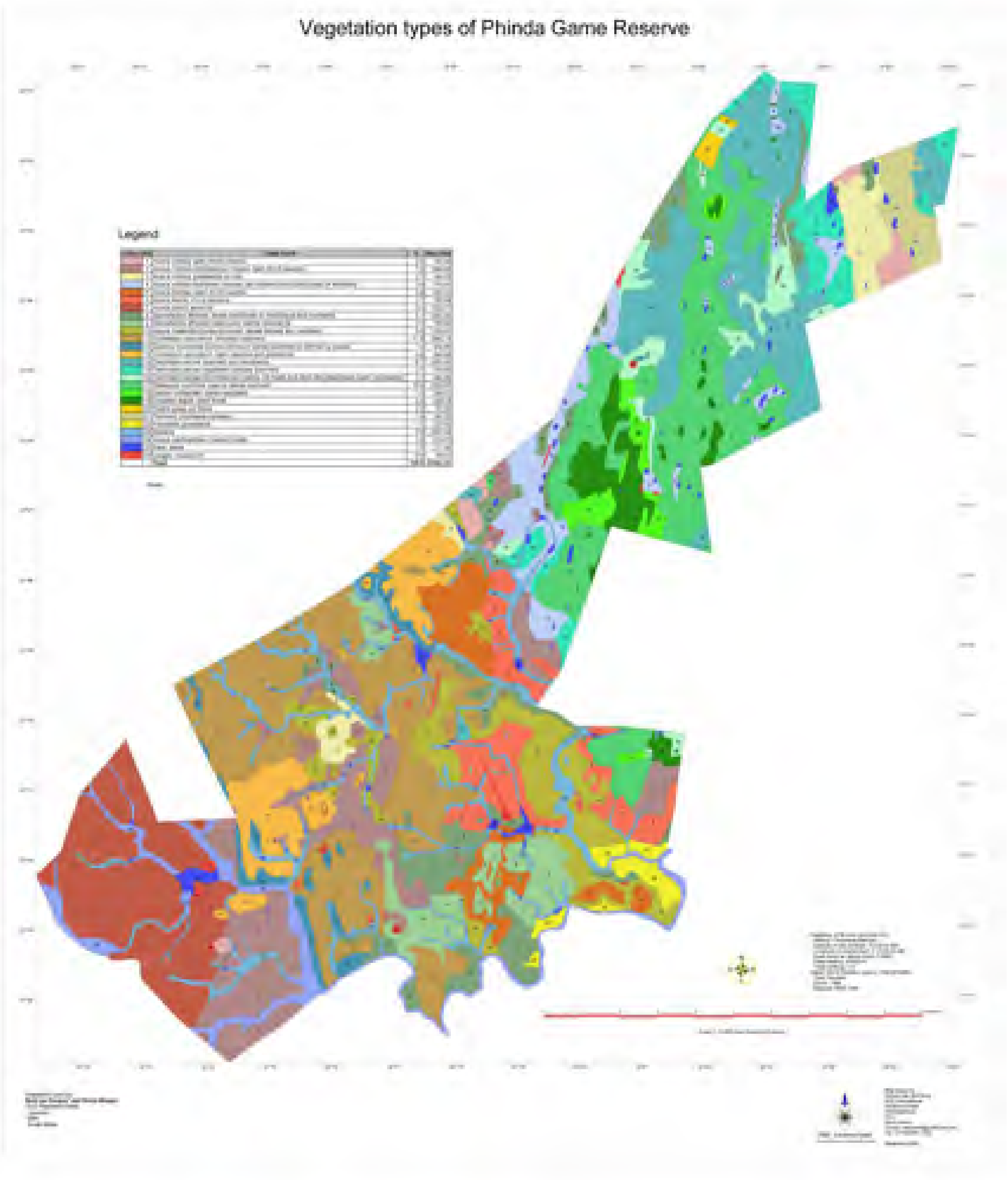

Figure 6 Final vegetation types on Phinda Game Reserve.

Figure 7 ***Acacia nilotica*** **shrub savanna (community 1)**

Figure 8 ***Acacia nilotica-Dichrostachys cinerea*** **open shrub savanna (community 2)**

Figure 9 ***Acacia nilotica*** **grasslands on clayey soils (community 3)**

Figure 10 ***Acacia nilotica-Hyphaene coriacea*** **pan systems and bushclumps on termitaria (community 4)**

Figure 11 ***Acacia borleae*** **open shrub savanna (community 5)**

Figure 12 ***Spirostachys africana*** **dense woodlands (community 8) along the drainage line with** ***Acacia luederitzii-Euclea divinorum*** **dense thickets and woodland (community 10) on the floodplains**

Figure 13 ***Spirostachys africana-Sideroxylon inerme*** **woodlands (community 9)**

Figure 14 ***Combretum apiculatum*** **mountain bushveld (community 11)**

Figure 15 ***Ziziphus mucronata-Euclea divinorum*** **dense bushveld on SW-facing slopes (on left of picture) (community 12)**

Figure 16 ***Combretum apiculatum*** **open savanna and grasslands on the right (community 13)**

Figure 17 ***Terminalia sericea*** **bushveld and woodlands (community 14)**

Figure 18 ***Terminalia sericea-Hyphaene coriacea*** **bushveld (community 15)**

Figure 19 ***Terminalia sericea-Dichrostachys cinerea*** **old fields and other disturbed areas (community 16)**

Figure 20 ***Drypetes arguta*** **sand forest (community 19)**

Figure 21 Palmveld (*Hyphaene coriacea*) (community 21)

Figure 22 Floodplain grasslands (community 22)

Figure 23 Floodplain grasslands with *Acacia xanthophloea* riparian forests in the background (communities 22 and 24)

Figure 24 One of the pans in the area

REFERENCES

ACOCKS, J.P.H. (1953, 1988). Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* 57: 1-146.

GEOLOGICAL SERIES. 1985. 2732 St Lucia. 1: 250 000 map. Government Printer, Pretoria.

GOODMAN, P.S. (1990). *Soil, vegetation and large herbivore relations in Mkhuzi Game Reserve, Natal*. PhD thesis. University of the Witwatersrand, Johannesburg.

HOBDAY, D.K. (1979). Geological evolution and geomorphology of the Zululand coastal plain. IN; ALLANSON, B.R. (Ed.) *Lake Sibaya*. pp. 19. Junk, The Hague.

IDMP (2000). *Integrated Development Management Plan*. pp. 280. DEAT, KwaZulu-Natal Nature Conservation Services, Pietermaritzburg.

LAND TYPES (1988). Land types of the map 2830 Richards Bay. *Memoirs of the Agricultural Natural Resources of South Africa* 11: 1-823.

LOW, A & REBELO, A. (1996). *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs & Tourism, Pretoria.

LUBBE, R.A. (1996). *Vegetation and flora of the Kosi Bay Coastal Forest Reserve in Maputaland, northern KwaZulu-Natal, South Africa.* MSc dissertation. University of Pretoria, Pretoria.

MACDEVETTE, D.R. & GORDON, I.G. (1991). Current vegetation patterns on the Zululand coastal dunes. In: EVERARD, D.A. & VON MALTITZ, G.P. (Eds.), *Dune forest dynamics in relation to land use practices*, pp. 55-71. CSIR, Pretoria.

MATTHEWS, W.S., VAN WYK, A.E. & VAN ROOYEN, N. (1999). Vegetation of the Sileza Nature Reserve and neighbouring areas, South Africa, and its importance in conserving the woody grasslands of the Maputaland Centre of Endemism. *Bothalia* 29: 151-167.

MATTHEWS, W.S., VAN WYK, A.E., VAN ROOYEN, N. & BOTHA, G.A. (2003). Vegetation of the Tembe Elephant Park, Maputaland, South Africa. *South African Journal of Botany* 67: 573-594

MOLL, E.J. (1978). The vegetation of Maputaland - a preliminary report on the plant communities and their present and future conservation status. *Trees in South Africa* 29: 31-58.

MOLL, E.J. (1980). Terrestrial plant ecology. IN: BRUTON, M.N. & COOPER, K.H. (Eds). *Studies on the ecology of Maputaland*. Rhodes University and the Natal branch of the Wildlife Society of southern Africa.

MUCINA, L., RUTHERFORD, M.C. & POWRY, L.W. 2005. Vegetation map of South Africa, Swaziland and Lesotho. SANBI, Pretoria.

REPTON, M. 2005. Vegetation utilization by elephants in the Mkhuze and Phinda Game Reserve. MSc dissertation. School of Biological and Conservation Sciences. University of Kwa-Zulu Natal, Durban

SCHULZE, R.E. (1982). Agrohydrology and agroclimatology of Natal. Report no. 14. Pietermaritzburg, Agricultural Catchment Research Unit, University of Natal.

TINLEY, K.L. (1985). *Coastal dunes of South Africa.* FRD report 109, Pretoria.

VAN ROOYEN, N. 2004. Vegetation types and wildlife re-establishment in the Greater St Lucia Wetland Park. Report to GSLWP Authority, KwaZulu-Natal.

VAN WYK, A.E. (1996). Biodiversity of the Maputaland Centre. In: VAN DER MAESEN,L.J.G. & et al. (Eds.), *The biodiversity of African plants,* pp. 198-207. Kluwer Academic Publishers, Amsterdam.

VON MALTITZ, G.P., VAN WYK, G.F. & EVERARD, D.A. (1996). Successional pathways in disturbed coastal dune forest on the coastal dunes in north-east KwaZulu-Natal, South Africa. *South African Journal of Botany* 62: 188-195.

WATKEYS, M.K., MASON, T.R. & GOODMAN, P.S. (1993). The role of geology in the development of Maputaland, South Africa. *Journal of African Earth Sciences* 16, 205-221.

WEATHER BUREAU. (1988). *Climate of South Africa*. WB 40. Government Printer, Pretoria.

WEATHER BUREAU. (1998). *Climate of South Africa*. WB Series. Government Printer, Pretoria.

APPENDIX II

HABITAT/LANDSCAPES
of
PHINDA GAME RESERVE

January 2008

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INTRODUCTION

A report has been compiled detailing the classification, description and mapping of the vegetation types of Phinda Game Reserve (Van Rooyen & Morgan 2007). However, a need has been expressed for a more simplified habitat/landscape map of the reserve. The identification and description of vegetation units across the landscape forms the basis of scientifically based environmental and veld management plans and are critical first steps in building a framework for ecosystem management planning as well as for studying plant-animal interactions.

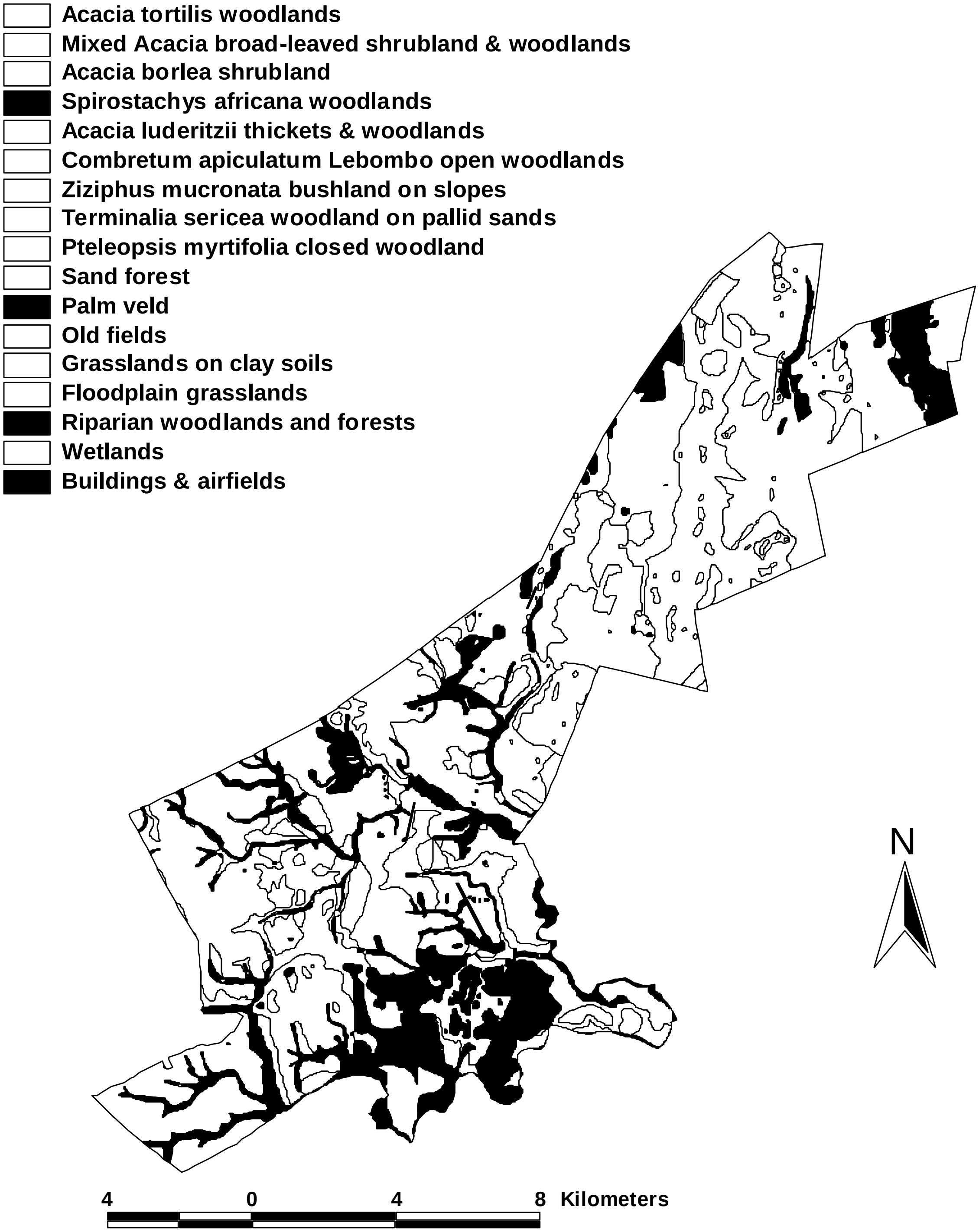
Phinda Game Reserve is situated south of the Mkhuze Game Reserve in northern KwaZulu-Natal, on the western coastal plains of Maputaland and southern foothills of the Lebombo Mountains. It is located approximately between 27° 40’ S and 27° 55’S latitudes, and 32° 13’ East and 32° 26’ East longitudes and covers approximately 21 402 ha (Figure 1). The grid references for the reserve are 2732 CA, 2732 CB, 2732 CC and 2732 CD. The reserve consists of the following farms or portions of these farms: Harrowgate, Sutton, Ufumba, Iseme, Ntabankosi, Zuka, Tebelwane, Fagolweni, Bube, Monte Rosa, Indabana, Izwelihle, Umgotsha, Golweni, Humseni, Shotton and part of the Katema Settlement and Mnqobokazi area.

The aim of this second report is therefore to produce a simplified habitat map by merging vegetation types that are closely related in terms of plant species composition and habitat characteristics.

VEGETATION

The vegetation of the Phinda Game Reserve has originally been classified into 25 plant communities. Based on floristic affinities and by merging related plant communities, the vegetation of the area was then simplified into 16 habitats/landscapes, which could be used as management units (Figure 1). The total area covered by the reserve is approximately 21 402 ha.

Figure 1 Habitat/Landscapes Phinda Game Reserve



i. *Acacia tortilis* (umbrella thorn) woodlands

This savanna occurs on the plains in the southwest of the reserve and covers approximately 3 200 ha (15 % of the total area). The coarse sandy clay to clayey soils are derived from basalt. The soil surface is capped and is covered by pebbles, stones and small rocks.

This community is generally species poor and is dominated by the trees *Acacia tortilis*, *Acacia nilotica*, *Sclerocarya birrea* and *Ziziphus mucronata*, while the shrub layer includes prominent species such as *Euclea divinorum, Dichrostachys cinerea* and *Gymnosporia senegalensis.* Other shrub species that occur more locally include *Euclea racemosa*, *Kraussia floribunda*, *Acacia karroo*, *Acacia borleae* and *Capparis tomentosa.* The alien invader *Chromolaena odorata* occurs locally in high densities. Grasses and forbs cover on average 65 % and 2 % of the area.

ii. Mixed *Acacia/*broad-leaved shrubland and woodland

This woodland occurs on the plains, around pans and along flat open drainage lines on the edge of the sandy plains, on old fields and termitaria. The coarse to fine sandy loam to dark clayey soils are derived from alluvium sediments, argillaceous sand, siltstone, rhyolite and basalt. This shrubland and woodland covers 1 113 ha (5 % of the total area). A large number of small flattish termitaria occur in some areas. Stones and rocks are mostly absent from the soil surface although pebbles, stones and small rocks occur in places.

There are no diagnostic species for this community and the community is generally very species poor. The most common tree species are *Acacia nilotica*, *Acacia tortilis*, *Acacia* *burkei, Acacia nilotica, Ziziphus mucronata, Sclerocarya birrea, Ziziphus mucronata, Berchemia zeyheri, Spirostachys africana* and *Acacia robusta.* The palms *Hyphaene coriacea* and *Phoenix reclinata* are found locally. The prominent shrub species include *Dichrostachys cinerea, Gymnosporia senegalensis, Acacia borleae, Acacia karroo, Euclea divinorum, Euclea natalensis, Rhus quenzii, Coddia rudis, Euclea divinorum, Gymnosporia buxifolia, Croton steenkampianus, Kraussia floribunda* and *Euclea racemosa*. Grasses cover from 50 % to more than 80 % of the area and include species such as *Themeda triandra, Sporobolus africanus, Bothriochloa insculpta, Ischaemum afrum, Digitaria eriantha, Eustachys paspaloides* and *Setaria incrassata*. Forbs cover less than 10 % of the area.

Distinctive bushclumps occur mostly on old termitaria and are dominated by species usually found along drainage lines on clayey soils. The most common large tree species are *Spirostachys africana, Schotia brachypetala, Balanites maughamii, Acacia robusta, Acacia burkei, Sclerocarya birrea, Newtonia hildebrandtii, Galpinia transvaalica, Mystroxylon aethiopicum, Sideroxylon inerme* and *Ziziphus mucronata.* The most common shrub species *include Euclea divinorum, Schotia afra, Carissa tetramera, Azima tetracantha, Rhus guenzii, Rhoicissus digitata* and *Capparis tomentosa.* The alien invader *Chromolaena odorata* occurs locally in high densities.

iii. *Acacia borleae* (sticky thorn) open shrub savanna

This community occurs in the central and south-eastern part of the reserve on flat terrain and gentle south and east facing midslopes on fine and red to dark sandy clay to clayey soils derived from siltstone and rhyolitic lava. It covers 1 397 ha (6 % of the total area). The dry soils are shallow in places and the surface is capped and covered by pebbles, stones and small rocks.

Acacia borleae and *Acacia karroo* are the diagnostic shrub species for this species-poor vegetation type and they occur locally in dense stands on clayey soils. Other woody species of note are *Euclea divinorum, Acacia nilotica, Berchemia zeyheri* and *Ziziphus mucronata*. The most prominent shrubs are *Acacia borleae, Acacia nilotica, Dichrostachys cinerea* and *Euclea divinorum*. The herbaceous *Abutilon angulatum* is found in some localities. Grasses and forbs cover on average 66 % and 2 % of the area respectively.

iv. *Spirostachys africana* (tamboti) woodlands

This community occurs locally on flat lowlands and along the rivers and other drainage lines throughout the reserve. It covers 1 802 ha (8 % of the total area). It is generally found on flat, poorly drained lowlands on fine to medium-textured loamy to clayey soils derived from rhyolite and siltstone, often of alluvial origin. In some areas deep sandy, sandy loam and sandy clay-loam soils occur and are locally covered by grit, pebbles, stones and rocks.

The diagnostic species for this community are *Schotia brachypetala, Pappea capensis, Ehretia rigida, Capparis tomentosa, Cissus rotundifolia, Rhoicissus tridentata* and *Phyllanthus reticulatus*. The tree layer is well-developed and characterized by *Spirostachys africana, Sideroxylon inerme* and *Berchemia zeyheri. Sideroxylon inerme* is prominent on slopes and flat bottomlands along drainage lines in the western and south-eastern parts of the reserve. Noteworthy is the absence of *Spirostachys africana* from these areas. The most prominent shrub species are *Euclea divinorum, Rhus guenzii, Euclea racemosa, Carissa bispinosa* and *Gymnosporia buxifolia*. The alien invader *Chromolaena odorata* occurs locally in high densities. Grasses and forbs cover on average 54 % and 3 % of the area respectively.

v. ***Acacia luederitzii*** **(false umbrella-thorn) thickets and woodlands**

These thickets and woodlands occur as local stands along drainage lines in the southern half of the reserve. It covers 1 160 ha (5.4 % of the total area). The community is generally found on flat, poorly drained lowland on clayey soils, often of alluvial origin. The medium to coarse textured sandy clay to clayey soils are derived from siltstone and rhyolite. The soil surface is lightly capped and is covered by grit, pebbles, stones and small rocks.

The tree layer is characterized by *Acacia luederitzii, Berchemia zeyheri, Ziziphus mucronata* and *Dombeya rotundifolia.* The most prominent shrub species is *Euclea divinorum.* The characteristic shrub species include *Coddia rudis, Rhus guenzii, Euclea racemosa, Cissus rotundifolia, Carissa bispinosa, Carissa tetramera, Kraussia floribunda, Grewia flavescens, Gymnosporia buxifolia, Gymnosporia senegalensis, Capparis tomentosa, Ximenia americana, Phyllanthus reticulatus, Pyrostria hystrix, Scutia myrtina* and *Azima tetracantha*. The alien invader *Chromolaena odorata* occurs locally in high densities. Grasses and forbs cover on average 51 % and 2 % of the area.

vi. ***Combretum apiculatum*** **(red bushwillow) Lebombo open woodland**

This rocky open woodland is found in the southwest on the rhyolitic foothills and slopes of the southern Lebombo Mountains, which rise from the coastal plain. It covers 3 392 ha (16 % of the total area). The fine sandy loam to clay soils are derived from rhyolitic lava, pyroclastic rocks, rhyodacite and rhyolite. The soil surface is moderately capped and is covered by grit, pebbles, stones and rocks.

The diagnostic species for this vegetation type is *Combretum apiculatum*. This open woodland consists of a mosaic of grassland and patches of woodland on rocky outcrops. The community is generally species-poor and besides the dominant *Combretum apiculatum,* other tree species include *Ziziphus mucronata, Acacia burkei, Dombeya rotundifolia, Ozoroa paniculosa, Peltophorum africanum, Sclerocarya birrea, Combretum molle, Pappea capensis, Galpinia transvaalica, Acacia nilotica, Pavetta edentula, Ficus stuhlmannii, Ficus abutilifolia* and *Aloe spectabilis*. The shrub layer is represented by a dense cover of *Dichrostachys cinerea,* while less common species are *Euclea divinorum, Euclea racemosa, Rhus guenzii, Gymnosporia senegalensis, Gymnosporia buxifolia, Ozoroa engleri* and *Rhus gracillima*. The grass layer is characterized by species such as *Hyperthelia dissoluta, Themeda triandra* and *Bothriochloa insculpta.* Grasses and forbs cover on average 89 % and 1 % of the area respectively.

vii. ***Ziziphus mucronata*** **(buffalo thorn) bushland on slopes**

This dense bushland is found on rhyolite on south-west and south-facing slopes with isolated patches of forest where local conditions are sufficiently moist. It covers 305 ha (1.4 % of the total area). The most prominent species include the trees *Ziziphus* *mucronata, Berchemia zeyheri, Sideroxylon inerme, Ficus ingens, Ekebergia capensis, Acacia burkei, Sclerocarya birrea, Combretum kraussii, Aloe spectabilis* and the shrubs *Euclea divinorum, Euclea racemosa, Pavetta edentula, Kraussia floribunda, Zanthoxylum capense, Diospyros lycioides, Grewia flavescens, Catunaregam spinosa, Gymnosporia buxifolia, Rhoicissus tridentata, Coddia rudis, Acacia kraussiana* and *Cissus rotundifolia.*

viii. *Terminalia sericea* (silver cluster-leaf) woodland on pallid sand

The characteristic species for this community are *Terminalia sericea, Hyphaene coriacea, Combretum molle* and *Strychnos madagascariensis*. This community covers 2 880 ha (14 % of the total area). This community occurs on deep and fine pallid sands on the plains and gentle north-facing slopes in the north. It is also found on old fields and in areas where partial bush clearing occurred. This community is characterised by yellow freely drained fine argillaceous sandy soils with a high base status. Pebbles, stones and rocks are absent from the soil surface.

The diagnostic species include *Terminalia sericea, Canthium spinosum, Hyphaene coriacea, Sclerocroton integerrimum, Dalbergia obovata, Grewia monticola, Rawsonia lucida, Psydrax obovata* and *Grewia caffra*. The tree layer is characterized by locally common tree species such as *Terminalia sericea, Combretum molle, Brachylaena discolor, Strychnos madagascariensis, Strychnos spinosa, Acacia burkei, Ziziphus mucronata, Trichilia emetica, Euphorbia ingens* and *Sclerocarya birrea*.

The most prominent shrubs are *Rhus guenzii, Coddia rudis, Dichrostachys cinerea, Croton steenkampianus, Gymnosporia senegalensis, Euclea divinorum, Euclea crispa,* *Canthium spinosum, Sclerocroton integerrimum, Schotia capitata, Mundulea sericea*, *Grewia micrantha*, *Dovyalis caffra*, *Catunaregam obovata, Zanthoxylum capense*, *Grewia monticola*, *Euclea natalensis, Acacia nilotica, Gymnosporia senegalensis* and *Grewia caffra.* The thatch grass *Hyperthelia dissoluta* is locally prominent. The dwarf shrub *Helichrysum kraussii* is a dominant species of these areas. Grasses and forbs cover on average 50 % and 2 % of the area respectively.

ix. *Pteleopsis myrtifolia* (stink-bushwillow) closed woodland

This closed woodland occurs on the sandy lowland plains in the central-northern part of the reserve. It surrounds many of the dense stands of Sand Forest (community x.) and is characterised by yellow, freely drained coarse sandy loam soils with a high base status. It covers 2 333 (11 % of the total area). Pebbles, stones and rocks are absent from the soil surface.

This woodland is species rich in comparison to the other communities found in Phinda Game Reserve. The extensive list of diagnostic species includes species such as *Hymenocardia ulmoides, Balanites maughamii, Tricalysia capensis, Landolphia kirkii* and *Tricalysia lanceolata.* Of note is the absence of *Terminalia sericea* and *Hyphaena coriacea.* The dominant tree species include *Pteleopsis myrtifolia, Strychnos spinosa*, *Balanites maughamii, Combretum molle, Dialium schlechteri*, *Mystroxylon aethiopicum, Commiphora neglecta, Strychnos spinosa, Brachylaena discolor, Acacia burkei, Maerua cafra* and *Strychnos madagascariensis*. The shrub layer is characterised by *Hymenocardia ulmoides, Salacia leptoclada, Hypericum revolutum, Tricalysia capensis, Tricalysia lanceolata, Rhus guenzii, Landolphia kirkii, Euclea divinorum, Uvaria caffra,* *Vitex ferruginea, Carissa tetramera, Ochna arborea, Dalbergia nitidula, Canthium setiflorum, Croton steenkampianus, Zanthoxylum capense* and *Catunaregam obovata*.

Sand Forest species (community x.) present in this community include *Monadenium caffra, Uvaria caffra, Salacia leptoclada, Toddaliopsis bremekampii, Rhoicissus digitata, Strychnos henningsii, Croton pseudopulchellus, Croton steenkampianus* and *Wrightia natalensis*. Grasses and forbs cover on average 19 % and 6 % of the area respectively.

x. Sand forest

The Sand Forests occur as distinct stands on the sandy plains in the central, northern and eastern parts of the reserve. It covers less than 3 % of the reserve. Sand Forest is a type of dry forest and is best developed on the north-south trending dune cordons where the water table is deep. The soils developed *in situ* from the relatively homogeneous, grey, silicaceous, aeolian sands and are highly leached (dystrophic) and relatively acidic. Structurally this forest is from 5 to 12 m tall and forms dense vegetation with different strata. Open to dense woodlands occur in close association with Sand Forest patches. These dense woodlands and sand forests cover 794 ha (4 % of the total area). It is characterised by yellow, freely drained coarse sandy loam soils with a high base status. Pebbles, stones and rocks are absent.

The diagnostic species for this community include *Cola greenwayi, Salacia leptoclada, Drypetes arguta, Newtonia hildebrandtii, Toddaliopsis bremekampii, Uvaria caffra, Erythrophleum lasianthum, Drypetes natalensis, Croton sylvaticus* and *Tricalysia sonderiana*. The most common tree species found in this community are *Drypetes arguta, Newtonia hildebrandtii, Cleistanthus schlechteri, Wrightia natalensis, Strychnos* *henningsii, Dialium schlechteri, Pteleopsis myrtifolia, Drypetes natalensis, Erythrophleum lasianthum, Cryptocarya woodii* and *Strychnos decussata.* The shrub layer is characterized by *Croton sylvaticus, Tricalysia sonderiana, Toddaliopsis bremekampii, Dovyalis caffra, Uvaria caffra, Salacia leptoclada, Cola greenwayii, Croton steenkampianus, Hyperacanthus amoenus, Vitex ferruginea, Grewia caffra* and *Blighia unijugata*.

xi. Palm veld

The ilala palm *Hyphaene coriacea* is prominent locally and a stand of palms is particularly well-developed on the plains in the north-east of the reserve. Notable is the absence of *Terminalia sericea* in this area. It covers 298 ha (1.4 % of the total area).

xii. Old fields

The old fields occur locally but widespread throughout the reserve. This community is on deep sands and are dominated by the yellow thatch grass *Hyperthelia dissolute.* It covers 73 ha (< 1 % of the total area).The sparse shrub layer is characterized by *Sclerocarya birrea, Dichrostachys cinerea, Acacia nilotica, Strychnos spinescens* and *Gymnosporia senegalensis*.

xiii. Floodplain grasslands

The floodplain grasslands occur in the south-east of the reserve on the Mzinene-Munywana floodplains. It covers 228 ha (1 % of the total area). Shrub species include *Dichrostachys cinerea, Azima tetracantha, Coddia rudis, Rhus guenzii* and *Flueggia* *virosa*. The prominent grass species include *Panicum maximum*, *Echinochloa pyramidalis, Hemarthria altissima, Echinochloa pyramidalis* and *Setaria incrassata.*

xiv. Grassland on clay soils

These grasslands occur on flat terrain in the north-east of the reserve on dark sandy clay-loam to clayey soils. It covers 443 ha (2 % of the total area). A large number of small flattish termitaria occur in this community. Stones and rocks are absent from the soil surface.

There are no diagnostic species for this community and the community is generally very species poor. The woody layer is poorly developed with the tree layer almost absent. The shrubs are small with *Acacia nilotica* the dominant species. Other shrub species such as *Hyphaene coriacea*, *Dichrostachys cinerea*, *Gymnosporia senegalensis*, *Acacia nilotica*, *Acacia borleae* and *Euclea divinorum* occur locally in low numbers. The grasses cover more than 80% of the area and include species such as *Themeda triandra*, *Sporobolus africanus, Bothriochloa insculpta, Ischaemum afrum, Digitaria eriantha, Eustachys paspaloides* and *Setaria incrassata*.

xv. Riparian woodlands and forests

The woodlands of seasonal and perennial streams and rivers include the vegetation occurring on the streambanks as well as on the floodplains next to the streams. The woodlands and forests cover 1 682 ha (8 % of the total area). The dominant woody species include *Spirostachys africana, Sideroxylon inerme, Acacia luederitzii* and *Schotia brachypetala.* The riparian forests are best developed along the rivers and the lower reaches of their main tributaries. *Acacia xanthophloea* stands occur on floodplains that experience frequent seasonal, short-duration floods and also on pan edges. These stands are associated with a dense cover of grasses such as *Echinochloa pyramidalis, Hemarthria altissima*, *Cynodon dactylon* and stands of *Phragmites australis.* Other prominent species include *Ficus sycomorus, Rauvolfia caffra, Syzygium guineense, Ziziphus mucronata, Trichilia emetica* and *Ekebergia capensis*. Where a riverine thicket develops it is mostly composed of the shrubs *Acacia schweinfurthii, Azima tetracantha* and *Grewia caffra*, with *Ficus capreifolia* and the palm *Phoenix reclinata* on the river banks close to water. These species are extremely important for stabilizing the river banks and to prevent erosion of low-lying areas.

xvi. Wetlands

The vegetation of the dams, small pans and depressions found interspersed throughout the central and north-eastern lowlands of the reserve was not surveyed but has been mapped. It covers 218 ha (1 % of the total area). These wetlands differ in size and duration of standing water. They are associated with sandy substrates or dark grey to black soils with high organic contents and with water table levels just below or at the surface. The dominant grass species are *Ischaemum fasciculatum, Leersia hexandra, Hemarthria altissima, Acroceras macrum, Panicum meyerianum, Agrostis lachnantha, Brachiaria arrecta, Digitaria diversinervis* and *Sporobolus subtilis.* Other common wetland species found in these areas are the sedges *Scirpus littoralis, Pycreus polystachyos, Fuirena obcordata, Cyperus tenax* and *Eliocharis dulcis,* and the forbs *Centella asiatica* and *Hydrocotyle bonariensis*.

REFERENCES

Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31:140-160.

Adcock, K. 1994. The relevance of 'territorial' behaviour in black rhino to their population management. Pages 82-86 *in* B. L. Penzhorn, andN. P. J. Kriek, editors. Proceedings of a symposium on Rhinos as Game Ranch Animals. SAVA Wildlife Group, Onderstepoort South Africa.

_____. 2004. Visual assessment of Black Rhino browse availability V2.0. SADC Regional Programme for Rhino Conservation.

_____. 2006. Rhino Management Group Black Rhino Carrying Capacity Model V2.1. Darwin Initiative & SADC Regional Programme for Rhino Conservation.

Adcock, K., D. Balfour, K. Buk, W. Linklater, M. Mulama, and N. Owen-Smith. 2001. Report of working group 2: Monitoring resources. Pages 102-106 *in* Proceedings of SADC Rhino Management Group (RMG) workshop on biological management to meet continental and national black rhino conservation goals.:102-106.

Adcock, K., H. B. Hansen, and H. Lindemann. 1998. Lessons from the introduced black rhino population in Pilanesberg National Park. Pachyderm 26:40-51.

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Alldredge, J. R., and J. Griswold. 2006. Design and Analysis of Resource Selection Studies for Categorical Resource Variables. The Journal of Wildlife Management 70:337-346.

Amin, R., B. Okita-Ouma, K. Adcock, R. H. Emslie, M. Mulama, and P. Pearce-Kelly. 2006. An integrated management strategy for the conservation of Eastern black rhinoceros *Diceros bicornis michaeli* in Kenya. International Zoo Yearbook 40:118-129.

Anderson, R. P., D. Lew, and A. T. Peterson. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling 162:211-232.

Andrews, A. 1990. Fragmentation of habitat by roads and utility corridors: a review. Australian Zoologist 1:130-141.

Anon. 1988. Land types of the map 2830 Richards Bay.

_____. 1998. Climate of South Africa. *in* WB Series. Weather Bureau, Government Printer, Pretoria

Araujo, M. S., S. F. dos Reis, A. A. Giaretta, G. Machado, and D. I. Bolnick. 2007. Intrapopulation diet variation in four frogs (Leptodactylidae) of the Brazilian Savannah. Copeia:855-865.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing Habitat Selection when Availability Changes. Ecology 77:215-227.

Austin, M. P. 1980. Searching for a model for use in vegetation analysis. Vegetatio 42:11-21.

_____. 1985. Continuum concept, ordination methods and niche theory. Annual Review of Ecology and Systematics 16:39-61.

Austin, M. P., and T. M. Smith. 1989. A new model for the continuum concept. Vegetatio 83:35-47.

Baldwin, R. A. 2009. Use of Maximum Entropy Modeling in Wildlife Research. Entropy 11:854-866.

Balestrieri, A., L. Remonti, and C. Prigioni. 2006. Reintroduction of the Eurasian badger (Meles meles) in a protected area of northern Italy. Italian Journal of Zoology 73:227-235.

Basile, J. V., and S. S. Hutchings. 1966. Twig Diameter-Length-Weight Relations of Bitterbush. Journal of Range Management 19:34-38.

Basille, M., C. Calenge, E. Marboutin, R. Andersen, and J. M. Gaillard. 2008. Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. Ecological Modelling 211:233-240.

Ben-Shahar, R., and J. D. Skinner. 1988. Habitat preferences of African ungulates derived by uni- and multivariate analyses. Ecology 69:1479-1485.

Birkett, A. 2002. The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. African Journal of Ecology 40:276-282.

Bolnick, D. I., R. Svanba¨ck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forrister. 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist 161:1-28.

Bolnick, D. I., R. Svanbäck, M. Araújo, and L. Persson. 2007. More generalized populations are also more heterogeneous: comparative support for the niche variation hypothesis. Proceedings of the National Academy of Sciences, U.S.A 104:10075-10079.

Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanback. 2002. Measuring individual-level resource specialization. Ecology 83:2936-2941.

Bothma, J. d. P., N. v. Rooyen, and M. W. v. Rooyen. 2004. Using Diet and Plant Resources to Set Wildlife Stocking Densities in African Savannas. Wildlife Society Bulletin 32:840-851.

Bowyer, R. T., and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions 12:244-257.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, I. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by Elk in Yellowstone National Park. Ecoscience 10:421-431.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trend. Ecol. Evol 14:268-272.

Braunisch, V., K. Bollmann, R. F. Graf, and A. H. Hirzel. 2008. Living on the edge - Modelling habitat suitability for species at the edge of their fundamental niche. Ecological Modelling 214:153-167.

Bremner-Harrison, S., P. A. Prodohl, and R. W. Elwood. 2004. Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). Animal Conservation 7:313-320.

Brett, R. A. 1998. Mortality factors and breeding performance of translocated black rhinos in Kenya: 1984-1995. Pachyderm 26:69-82.

Brooks, P. 2001. Setting the scene: current co-ordination and management arrangements and aims of the workshop. Pages 1-8 *in* Proceedings of Proceedings of a SADC Rhino Management Group (RMG) workshop on biological management to meet continental and national black rhino conservation goals.1-8.

Brown, D. H., P. C. Lent, W. S. W. Trollope, and A. R. Palmer. 2003. Browse selection by black rhinoceros (*Diceros bicornis*) in four vegetation types of the Eastern Cape Province. Pages 509-512 *in* Proceedings of Proceedings of the VII International Rangeland Congress.509-512.

Buk, K. G. 2004. Diet selection of and habitat suitability for black rhino in Augrabies Falls National Park, South Africa. Unpublished MSc. thesis, University of Copenhagen, Denmark.

Burke, S. 2001. Missing values, outliers, robust statistics & non-parametric methods. Statistics and data online. LC.GC. Europe Online Supplement:19-24.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. A practical information-theoretic approach. Springer, New York, NY.

Butchart, D., and C. Roche. 2002. Phinda, Maputaland, KwaZulu-Natal, South Africa. Ecological Journal 4:171.

Calenge, C., and A. B. Dufour. 2006. Eigenanalysis of selection ratios from animal radio-tracking data. Ecology 87:2349-2355.

Calenge, C., A. B. Dufour, and D. Maillard. 2005a. K-select analysis: a new method to analyse habitat selection in radio-tracking studies. Ecological Modelling 186:143-153.

Calenge, C., D. Maillard, N. Invernia, and J. C. Gaudin. 2005b. Reintroduction of roe deer Capreolus capreolus into a Mediterranean habitat: female mortality and dispersion. Wildlife Biology 11:153-161.

Carter, G. M., E. D. Stolen, and D. R. Breininger. 2006. A rapid approach to modeling species-habitat relationships. Biological Conservation 127:237-244.

Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983-992.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences. 2nd edition. Lawrence Earlbaum Associates, Hillsdale, NJ.

Conway, A. J., and P. S. Goodman. 1989. Population characteristics and management of black rhinoceros *Diceros bicornis minor* and white rhinoceros *Ceratotherium simum simum* in Ndumu Game Reserve, South Africa. Biological Conservation 47:109-122.

Cumming, D. H. M., R. F. du Toit, and S. N. Stuart. 1990. African Elephants and Rhinos Status Survey and Conservation Action Plan. IUCN publication.

Cumming, G. S., D. H. M. Cumming, and C. L. Redman. 2006. Scale mismatches in social-ecological systems: causes, consequences, and solutions. Ecology and Society 11:14.

Darimont, C. T., P. C. Paquet, and T. E. Reimchen. 2009. Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. Journal of Animal Ecology 78:126-133.

De Alessi, M. 2000. Private Conservation and Black Rhinos in Zimbabwe: The Savé Valley and Bubiana Conservancies. Private Conservation Case Study.

Dekker, B., and G. N. Smit. 1996. Browse production and leaf phenology of some trees and shrubs in different Colophospermum mopane savanna communities. African Journal of Range and Forage Science 13:15-23.

del Monte-Luna, P., B. W. Brook, M. J. Zetina-Rejón, and V. H. Cruz-Escalona. 2004. The carrying capacity of ecosystems. Global Ecology and Biogeography 13:485–495.

DeLong, E. R., D. M. DeLong, and D. L. Clarke-Pearson. 1988. Comparing the Areas Under Two or More Correlated Receiver Operating Characteristic Curves: A Nonparametric Approach. Biometrics 44:837-845.

Donati, G., and S. Borgognini-Tarli. 2006. Influence of Abiotic Factors on Cathemeral Activity: The Case of *Eulemur fulvus collaris* in the Littoral Forest of Madagascar. Folia Primatologica 77:104-122.

Druce, D. J., J. S. Brown, J. G. Castley, G. I. H. Kerley, B. P. Kotler, R. Slotow, and M. H. Knight. 2006. Scale-dependent foraging costs: habitat use by rock hyraxes (*Procavia capensis*) determined using giving-up densities. Oikos 115:513-525.

Durell, S. E. A. L. V. d. 2000. Individual feeding specialisation in shorebirds: population consequences and conservation implications. Biological Reviews 75:503-518.

Eastridge, R., and J. D. Clark. 2001. Evaluation of 2 Soft-Release Techniques to Reintroduce Black Bears. Wildlife Society Bulletin 29:1163-1174.

Elith, J., and C. H. Graham. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. Ecography 32:66-77.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudı´k, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Sobero´n, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129-151.

Emslie, R. 2001. Plenary discussions and recommendations for an improved metapopulation management strategy. Pages 122-125 *in* Proceedings of Proceedings of a SADC Rhino Management Group (RMG) workshop on biological management to meet continental and national black rhino conservation goals.122-125.

_____. 2004. Rhino population sizes and trends. Pachyderm 37:107-110.

Emslie, R., and K. Adcock. 1994. Feeding ecology of black rhino. Pages 65-81 *in* B. L. Penzhorn, andN. P. J. Kriek, editors. Proceedings of a symposium on Rhinos as Game Ranch Animals. SAVA Wildlife Group, Onderstepoort South Africa.

Emslie, R., and M. Brooks. 1999. Status Survey and Action Plan - African Rhino. IUCN.

Erkert, H., and P. Kappeler. 2004. Arrived in the light: diel and seasonal activity patterns in wild Verreaux's sifakas (*Propithecus v. verreauxi*; Primates: Indriidae). Behavioral Ecology and Sociobiology 57:174-186.

Estes, R. D. 1993. The Safari Companion: A guide to watching African mammals. Russel Friedman Books CC, Halfway House.

Estrada-Peña, A., and W. Thuiller. 2008. An assessment of the effect of data partitioning on the performance of modelling algorithms for habitat suitability for ticks. Medical and Veterinary Entomology 22:248-257.

Fabricius, C., and M. T. Mentis. 1990. Seasonal habitat selection by eland in arid savanna in southern Africa. South African Journal of Zoology 25:238-244.

Fagen, R. 1988. Population Effects of Habitat Change: A Quantitative Assessment. The Journal of Wildlife Management 52:41-46.

Fischer, J., and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. Biological Conservation 96:1-11.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207 -231.

Frame, G. W. 1980. Black Rhinoceros (*Diceros bicornis L.*) sub-population on the Serengeti Plains, Tanzania. African Journal of Ecology 18:155-166.

Fretwell, S. D., and H. L. Lucas Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19:16-36.

Fritz, H., and P. Duncan. 1994. On the Carrying Capacity for Large Ungulates of African Savanna Ecosystems. Biological Sciences 256:77-82.

Ganqa, N. M., and P. F. Scogings. 2007. Forage quality, twig diameter, and growth habit of woody plants browsed by black rhinoceros in semi-arid subtropical thicket, South Africa. Journal of Arid Environments 70:514-526.

Ganqa, N. M., P. F. Scogings, and J. G. Raats. 2005. Diet selection and forage quality factors affecting woody plant selection by black rhinoceros in the Great Fish River Reserve, South Africa. South African Journal of Wildlife Research 35:77-83.

Garshelis, D. L. 2000. Delusions in habitat evaluation: Measuring use, selection, and importance. Pages 111-164 *in* L. Boitani, andT. K. Fuller, editors. Research Techniques in Animal Ecology, Controversies and Consequences. Columbia University Press,New York.

Goddard, J. 1967. Home range, behaviour and recruitment of two black rhino populations. East African Wildlife Journal 5:133-150.

_____. 1968. Food preferences of two black rhinoceros populations. East African Wildlife Journal 6:1-18.

Goodman, P. S. 2004. Phinda black rhino carrying capacity estimate (desktop analysis). Unpublished report.

Greene, C. M., and J. A. Stamps. 2001. Habitat selection at low population densities. Ecology 82:2091-2100.

Grimm, V., and S. F. Railsback. 2005. Individual-based Modelling and Ecology. Princeton University Press, Princeton.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993-1009.

Guisan, A., and N. E. Zimmerman. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147-186.

Gusset, M., S. J. Ryan, M. Hofmeyr, G. van Dyk, H. T. Davies-Mostert, J. Graf, C. Owen, M. Szykman, D. Macdonald, S. Monfort, D. M. Wildt, A. , M. G. L. Mills, R. Slotow, and M. Somers. 2008. Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa. Journal of Applied Ecology 45:100-108.

Hall-Martin, A., and J. Castley. 2003. The status of the black rhinoceros, *Diceros bicornis*, on private land in South Africa in 2001. Pachyderm 34:24-32.

Hall-Martin, A. J., T. Erasmus, and B. P. Botha. 1982. Seasonal variation of diet and faeces composition of black rhinoceros *Diceros bicornis* in the Addo Elephant National Park. Koedoe 25:63-82.

Halle, S., and N. C. Stenseth. 2000. Activity Patterns in Small Mammals. An Ecological Approach. Ecological Studies 141:235-251.

Hanley, T. A. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). Oikos 79:209-218.

Hardman, B., and D. Moro. 2006. Optimising reintroduction success by delayed dispersal: Is the release protocol important for hare-wallabies? Biological Conservation 128:403-411.

Harris, L. D., and P. Kangas. 1988. Reconsidering the habitat concept. Pages 137-144 *in* Proceedings of Transactions of the 53rd North American Wildlife and Natural Resources conference.137-144.

Hayward, M. W., J. O'Brien, and G. I. H. Kerley. 2007. Carrying capacity of large African predators: Predictions and tests. Biological Conservation 139:219-229.

Helary, S. F., N. Owen-Smith, J. A. Shaw, D. Brown, and D. Hattas. 2009. Comparison of the chemical composition of the diet of three free-ranging black rhinoceros (Diceros bicornis) populations with zoo diets. Pages 203-218 *in* A. M. Fidgett, J. M. Hatt, T. Huisman, J. Hummel, G. Janssen, J. Nijboer, andA. Plowman, editors. Zoo Animal Nutrition. Filander Verlag.

Hill, R. 2006. Why be diurnal? Or, why not be cathemeral? Folia Primatologica 77:72-86.

Hirzel, A. H., J. Hausser, and N. Perrin. 2006. Biomapper 3.2, Lab. for Conservation Biology. *in* http://www.unil.ch/biomapper. University of Lausanne,Lausanne.

Hobbs, N. T., and T. A. Hanley. 1990. Habitat evaluation: Do use/availability data reflect carrying capacity? Journal of Wildlife Management 54.

Hobday, D. K. 1979. Geological evolution and geomorphology of the Zululand coastal plain Pages 1-19 *in* B. R. Allanson, editor. Lake Sibaya. Junk,The Hague.

Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. The Animal Movement program. *in* USGS, Alaska Biological Science Center.

Hunter, L. T. B. 1998. *The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, KwaZulu-Natal, South Africa*. Phd thesis, University of Pretoria, Pretoria.

Idema, S. W. J. 1988. Land types of the Map / Landtipes van die Kaart: 2830 Richards Bay. ARC-Institute for Soil, Climate and Water.

IUCN. 2008. IUCN Red List of Threatened Species. *in* www.iucnredlist.org.

Jácomo, A., C. Kashivakura, C. Ferro, M. Furtado, S. Astete, N. Tôrres, R. Sollmann, and L. Silveira. 2009. Home Range and Spatial Organization of Maned Wolves in the Brazilian Grasslands. 90:150-157.

Jean-Baptiste, M., G. Pascaline Le, and S. François. 2009. Breeding habitat selection behaviors in heterogeneous environments: implications for modeling reintroduction. Oikos 118:663-674.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Joubert, E., and F. C. Eloff. 1971. Notes on the ecology and behaviour of the black rhinoceros in South West Africa. Madoqua 3:5-54.

Judson, O. P. 1994. The rise of the individual-based model in ecology. Trends in Ecology & Evolution 9:9-14.

Kausrud, K., A. Mysterud, Y. Rekdal, Ø. Holand, and G. Austrheim. 2006. Density-dependent foraging behaviour of sheep on alpine pastures: effects of scale. Journal of Zoology 270:63-71.

Kerley, G. I. H., and M. Landman. 2006. The impacts of elephants on biodiversity in the Eastern Cape Subtropical Thickets. South African Journal of Science 102:395-402.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125-166 *in* J. J. Millspaugh, andJ. M. Marzluff, editors. Radiotracking and animal populations. Academic Press,San Diego, California, USA.

Kinahan, A. A., S. L. Pimm, and R. J. van Aarde. 2007. Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. Journal of Thermal Biology 32:47-58.

Klar, N., N. Fernández, S. Kramer-Schadt, M. Herrmann, M. Trinzen, I. Büttner, and C. Niemitz. 2008. Habitat selection models for European wildcat conservation. Biological Conservation:308-319.

Kotze, D. C., and P. J. K. Zacharias. 1993. Utilisation of woody browse and habitat by the black rhino (*Diceros bicornis*) in Western Itala Game Reserve. African Journal of Range and Forage Science 10:36-40.

Kozak, K., C. Graham, and J. Wiens. 2008. Integrating GIS-based environmental data into evolutionary biology. Trends in Ecology & Evolution 23:141-148.

Krebs, C. J. 1989. Ecological Methodology. Chapman & Hall, New York.

Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics 34:153-181.

Largot, J. 2007. Made to measure. Pages 29-35 *in* Africa Geographic.

Larkin, J. L., J. J. Cox, M. W. Wichrowski, M. R. Dzialak, and D. S. Maehr. 2004. Influences on Release-Site Fidelity of Translocated Elk. Restoration Ecology 12:97-105.

Le Mar, K., and C. McArthur. 2005. Comparison of habitat selection by two sympatric macropods, *Thylogale billardierii* and *Macropus rufogriseus rufogriseus*, in a patchy eucalypt-forestry environment. Austral Ecology 30:674-683.

Lent, P. C., and B. Fike. 2003. Home ranges, movements and spatial relationships in an expanding population of black rhinoceros in the Great Fish River Reserve, South Africa. South African Journal of Wildlife Research 33:109-118.

Letty, J., S. Marchandeau, and J. Aubineau. 2007. Problems encountered by individuals in animal translocations: Lessons from field studies. Ecoscience 14:420-431.

Levine, R. S., K. L. Yorita, M. C. Walsh, and M. G. Reynolds. 2009. A method for statistically comparing spatial distribution maps. International Journal of Health Geographics 8:7.

Linklater, W., and R. Swaisgood. 2008. Reserve size, conspecific density, and translocation success for black rhinoceros. Journal of Wildlife Management 72:1059-1068.

Linklater, W. L., J. Flamand, Q. Rochat, N. Zekala, E. MacDonald, R. Swaisgood, D. F. Airton, C. P. Kelly, K. Bond, I. Schmidt, and S. Morgan. 2006. Preliminary analyses of the free-release and scent broad-casting strategies for Black Rhinoceros reintroduction. Ecological Journal 7:26-34.

Linklater, W. L., E. MacDonald, J. Flamand, and N. Czekala. 2010. Declining and low fecal corticoids are associated with distress, not acclimation to stress, during the translocation of African rhinoceros. Animal Conservation 13:104-111.

Linnell, J. D. C., R. Aanes, J. E. Swenson, J. Odden, and M. E. Smith. 1997. Translocation of carnivores as a method for managing problem animals: a review. Biodiversity and Conservation 6:1245-1257.

Linström, W., and L. G. Wolmarans. 1985. Council for Geoscience, 27½32 St Lucia.1: 250 000 map. *in* Geological Series. Government Printer Pretoria.

Luck, G. W. 2002. The habitat requirements of the rufous treecreeper (*Climacteris rufa*). 1. Preferential habitat use demonstrated at multiple spatial scales. Biological Conservation 105:383-394.

Luo, J., K. J. Hartman, S. B. Brandt, C. F. Cerco, and T. H. Rippetoe. 2001. A Spatially-Explicit Approach for Estimating Carrying Capacity: An Application for the Atlantic Menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. Estuaries 24:545-556.

Manly, B. F. J., T. L. McDonald, D. L. Thomas, and W. P. Erickson. 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Second edition. Kluwer Academic Publishers, London.

McLeod, S. R. 1997. Is the concept of carrying capacity useful in variable environments? Oikos 79:529-542.

Melton, D. A. 1987. Habitat selection and resource scarcity. South African Journal of Science 83:646-651.

Metcalfe, N. B., N. H. C. Fraser, and M. D. Burns. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. Journal of Animal Ecology 68:371-381.

Metzger, K. L., A. R. E. Sinclair, K. L. I. Campbell, R. Hilborn, J. G. C. Hopcraft, S. A. R. Mduma, and R. M. Reich. 2007. Using historical data to establish baselines for conservation: The black rhinoceros (*Diceros bicornis*) of the Serengeti as a case study. Biological Conservation 139:358-374.

Miller, S. D., and W. B. Ballard. 1982. Homing of Transplanted Alaskan Brown Bears. The Journal of Wildlife Management 46:869-876.

Mills, A., P. Morkel, V. Runyoro, A. Amiyo, P. Muruthi, T. Binamungu, M. Borner, and S. Thirgood. 2003. Management of Black Rhino in the Ngorongoro Crater. *in* Proceedings of A report on the workshop held at Serena Lodge, Ngorongoro.

Millspaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of Resource Selection Using Utilization Distributions. Journal of Wildlife Management 70:384-395.

Moehrenschlager, A., and D. W. Macdonald. 2003. Movement and survival parameters of translocated and resident swift foxes *Vulpes velox*. Animal Conservation 6:199-206.

Moll, R. J., J. J. Millspaugh, J. Beringer, J. Sartwell, and Z. He. 2007. A new 'view' of ecology and conservation through animal-borne video systems. Trends in Ecology & Evolution 22:660-668.

Monterroso, P., J. C. Brito, P. Ferreras, and P. C. Alves. 2009. Spatial ecology of the European wildcat in a Mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. Journal of Zoology 279:27-35.

Moorhouse, T. P., M. Gelling, and D. W. Macdonald. 2009. Effects of habitat quality upon reintroduction success in water voles: Evidence from a replicated experiment. Biological Conservation 142:53-60.

Morales, J. C., and D. J. Melnick. 1994. Molecular Systematics of the Living Rhinoceros. Molecular phylogenetics and evolution 3:128-134.

Morgan, S., R. L. Mackey, and R. Slotow. 2009. A priori valuation of land use for the conservation of black rhinoceros (*Diceros bicornis*). Biological Conservation 142:384-393.

Morkel, P., and A. Kennedy-Benson. 2007. Translocating black rhino: current techniques for capture, transport, boma care, release and post-release monitoring. Report to AfRSG.

Morris, D. W. 2003a. How can we apply theories of habitat selection to wildlife conservation and management? Wildlife Research 30:303-319.

_____. 2003b. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1-13.

Mucina, L., M. C. Rutherford, and L. W. Powry. 2005. Vegetation map of South Africa, Swaziland and Lesotho. South African National Botanical Institute, Pretoria.

Murphy, H. T., and J. Lovett-Doust. 2007. Accounting for regional niche variation in habitat suitability models. Oikos 116:99.

Muya, S. M., and N. O. Oguge. 2000. Effects of browse availability and quality on black rhino (*Diceros bicornis michaeli* Groves 1967) diet in Nairobi National Park, Kenya. African Journal of Ecology 38:62-75.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79:1435-1441.

Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modelling grizzly bear habitats in the Greater Yellowhead Ecosystem of Alberta: taking autocorrelation seriously. Ursus 13:45-56.

Oloo, T. W., R. Brett, and T. P. Young. 1994. Seasonal-Variation in the Feeding Ecology of Black Rhinoceros (Diceros-Bicornis L) in Laikipia, Kenya. African Journal of Ecology 32:142-157.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:29-49.

Osborne, P. E., and S. Suarez-Seoane. 2002. Should data be partitioned spatially before building large-scale distribution models? Ecological Modelling 157:249-259.

Osko, T. J., M. N. Hiltz, R. J. Hudson, and S. M. Wasel. 2004. Moose habitat preferences in response to changing availability. The Journal of Wildlife Management 68:576-584.

Owen-Smith, R. N. 1988. Megaherbivores. The influence of very large body size on ecology. Cambridge University Press, Cambridge.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102-117.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231-259.

Pietz, P. J., and J. R. Tester. 1983. Habitat Selection by Snowshoe Hares in North Central Minnesota. The Journal of Wildlife Management 47 686-696.

Reid, C., R. Slotow, O. Howison, and D. Balfour. 2007. Habitat changes reduce the carrying capacity of Hluhluwe-Umfolozi Park, South Africa, for Critically Endangered black rhinoceros *Diceros bicornis*. Oryx 41:247-254.

Rice, B. R., and M. Jones. 2006. Characteristics of black rhinoceros (*Diceros bicornis*) bedding sites. African Journal of Ecology 44:452-457.

Richard-Hansen, C., J.-C. Vie, and B. Thoisy. 2000. Translocation of red howler monkeys (*Alouatta seniculus*) in French Guiana. Biological Conservation 93:247-253.

Ritchie, A. T. A. 1963. The black rhinoceros (*Diceros bicornis* L.). East African Wildlife Journal 1:54-62.

Rittenhouse, C. D., J. J. Millspaugh, M. W. Hubbard, S. L. Sheriff, and W. D. Dijak. 2008. Resource selection by translocated three-toed box turtles in Missouri. Journal of Wildlife Management 72:268-275.

Robinson, B. W., and D. S. Wilson. 1998. Optimal foraging, specialization, and a solution to Liem's paradox. American Naturalist 151:223-235.

Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology 62:327-335.

Rossouw, D. J. 1998. Baseline survey of dietary preferences of black rhino on the Eastern Shores of Lake St. Lucia. B.Tech. Nature Conservation Degree thesis, Technikon Pretoria, Pretoria.

Roughgarden, J. 1979. Theory of Population Genetics and Evolutionary Ecology: An Introduction. Macmillan, New York.

Saltz, D. 1994. Reporting error measures in radio location by triangulation: a review. The Journal of Wildlife Management 58:181-184.

Schadt, S., E. Revilla, T. Wiegand, F. Knauer, P. Kaczensky, U. Breitenmoser, L. Bufka, J. ¡ Cerven´y, P. Koubek, T. Huber, C. Stani¡sa, and L. Trepl. 2002. Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. Journal of Applied Ecology 39:189-203.

Schenkel, R., and L. Schenkel. 1969. Ecology and Behaviour of the Black Rhinoceros (*Diceros bicornis* L.). Verlag Paul Parcy, Berlin.

Schmitz, J. 1991. Thermal constraints and optimization of winter feeding and habitat choice in white-tailed deer. Holarctic Ecology 14:104-111.

Schoener, T. W. 1968a. Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology and Society 49:704-726.

_____. 1968b. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology and Society 49:704-726.

Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. The Journal of Wildlife Management 58:367-374.

Searle, K. R., T. N. Hobbs, B. A. Wunder, and L. A. Shipley. 2006. Preference in patchy landscapes: the influence of scale-specific intake rates and variance in reward. Behavioral Ecology 17:315-323.

Sheriffs, P. 2003. The Black Rhino Range Expansion Project begins. Pachyderm 35:151-152.

Slotow, R., D. Balfour, and O. Howison. 2001. Killing of black and white rhinoceros by African elephant in Hluhluwe-Umfolozi Park, South Africa. Pachyderm 31:14-20.

Slotow, R., M. E. Garaï, B. Reilly, B. Page, and R. D. Carr. 2005. Population dynamics of elephants re-introduced to small fenced reserves in South Africa. South African Journal of Wildlife Research 35:23-32.

Slotow, R., G. van Dyk, J. Poole, B. Page, and A. Klocke. 2000. Older bull elephants control young males. Nature 408:425-426.

Spinola, R. M., T. L. Serfass, and R. P. Brooks. 2008. Survival and post-release movements of river otters translocated to western New York. Northeastern Naturalist 15:13-24.

Stamps, J., and R. Swaisgood. 2007. Someplace like home: Experience, habitat selection and conservation biology. Applied Animal Behaviour Science 102:392-409.

Stephens, P. A., S. W. Buskirk, G. D. Hayward, and C. Martínez del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. Journal of Applied Ecology 42:4-12.

Store, R., and J. Kangas. 2001. Integrating spatial multi-criteria evaluation and expert knowledge for GIS-based habitat suitability modelling. Landscape and Urban Planning 55:79-93.

Suarez-Seoane, S., E. L. G. de la Morena, M. B. M. Prieto, P. E. Osborne, and E. de Juana. 2008. Maximum entropy niche-based modelling of seasonal changes in little bustard (Tetrax tetrax) distribution. Ecological Modelling 219:17-29.

Svanbäck, R., and D. I. Bolnick. 2005. Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. Evolutionary Ecology Research 7:993-1012.

_____. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society of London, Series B: Biological Sciences 274:839-844.

Svanbäck, R., and L. Persson. 2004. Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. Journal of Animal Ecology 73:973-982.

Tatman, S. C., B. Stevens-Wood, and V. B. T. Smith. 2000. Ranging behaviour and habitat usage in black rhinoceros, *Diceros bicornis*, in a Kenyan sanctuary. African Journal of Ecology 38:163-172.

Tattersall, I. 2006. The concept of cathemerality: history and definition. Folia Primatologica 77:7-14.

Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. The Journal of Wildlife Management 70:324-336.

Traill, L. W., and R. C. Bigalke. 2006. A presence-only habitat suitability model for large grazing African ungulates and its utility for wildlife management. African Journal of Ecology 45:347-354.

Van der Heiden, C. 2005. Utilization distribution as a predictor in modelling black rhino (*Diceros bicornis*) habitat in Africa's Southern Rift Valley. MSc. thesis, Florida Atlantic University, Florida.

Van Horne, B. 1983. Density as a Misleading Indicator of Habitat Quality. The Journal of Wildlife Management 47:893-901.

van Lieverloo, R. J., B. F. Schuiling, W. F. de Boer, P. C. Lent, C. B. de Jong, D. Brown, and H. H. T. Prins. 2009. A comparison of faecal analysis with backtracking to determine the diet composition and species preference of the black rhinoceros (Diceros Bicornis minor). European Journal of Wildlife Research DOI 10.1007/s10344-009-0264-5.

van Rooyen, N. 1999. The vegetation types and veld condition of Tswalu Private Desert Reserve. Unpublished report for Tswalu Kalahari Reserve.

van Rooyen, N., and S. R. Morgan. 2007. Vegetation types of Phinda Game Reserve. Phinda Private Game Reserve, AndBeyond.

_____. 2008. Habitat/Landscapes of Phinda Game Reserve. Phinda Private Game Reserve, AndBeyond.

Van Valen, L. 1965. Morphological variation and the width of ecological niche. American Naturalist 99:377-390.

Vandel, J. M., P. Stahl, V. Herrenschmidt, and E. Marboutin. 2006. Reintroduction of the lynx into the Vosges mountain massif: From animal survival and movements to population development. Biological Conservation 131:370-385.

Verner, J., M. L. Morrison, and C. J. Ralph. 1986. Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates. The University of Wisconsin Press, Madison.

von Holdt, A. L. 1999. Ecological seperation by browsers on the Lewa Conservancy, Kenya. MSc., University of Pretoria, Pretoria.

Wang, M., and V. Grimm. 2007. Home range dynamics and population regulation: An individual-based model of the common shrew *Sorex araneus*. Ecological Modelling 205:397-409.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental Niche Equivalency Versus Conservatism: Quantitative Approaches to Niche Evolution. Evolution 62:2868-2883.

Wasserberg, G., B. P. Kotler, and Z. Abramsky. 2006. The role of site, habitat, seasonality and competition in determining the nightly activity patterns of psammophilic gerbils in a centrifugally organized community. Oikos 112:573-579.

Watters, J. V., and C. L. Meehan. 2007. Different strokes: Can managing behavioral types increase post-release success? Applied Animal Behaviour Science 102:364-379.

Wear, B. J., R. Eastridge, and J. D. Clark. 2005. Factors affecting settling, survival, and viability of black bears reintroduced to Felsenthal National Wildlife Refuge, Arkansas. Wildlife Society Bulletin 33:1363-1374.

Weston, M. A., G. C. Ehmke, and G. S. Maguire. 2009. Manage one beach or two? Movements and space-use of the threatened hooded plover (Thinornis rubricollis) in south-eastern Australia. Wildlife Research 36:289-298.

William, R., D. Steve, S. Elisabeth, B. Stefan, F. Sam Du, and W. Trudi. 2009. Kernel density estimates of alongshore home range of Hector's dolphins at Banks Peninsula, New Zealand. Marine Mammal Science 25:537-556.

Wing, M. G., A. Eklund, and L. D. Kellogg. 2005. Consumer-grade global positioning system (GPS) accuracy and reliability. Journal of Forestry 103:169-173.

Winnie Jr., J. A., P. Cross, and W. Getz. 2008. Habitat quality and heterogeneity influence distribution and behavior in African Buffalo (*Syncerus caffer*). Ecology and Society 89:1457-1468.

Wintle, B. A., J. Elith, and J. M. Potts. 2005. Fauna habitat modelling and mapping: A review and case study in the Lower Hunter Central Coast region of NSW. Austral Ecology 30:719-738.

Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, A. Guisan, and N. P. S. D. W. Group. 2008. Effects of sample size on the performance of species distribution models. Diversity and Distributions 14:763-773.

Wittemyer, G., W. M. Getz , F. Vollrath, and I. Douglas-Hamilton. 2007. Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. Behavioural Ecology and Sociobiology 61:1919-1931.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology and Society 70:164-168.

Zar, J. H. 1999. Biostatistical Analysis, Fourth Edition. Prentice Hall, New Jersey.