

**Food Preferences and Feeding Interactions Among
Browsers, and the Effect of an Exotic Invasive Weed
Chromolaena odorata on the Endangered Black Rhino
(*Diceros bicornis*), in an African Savanna**



**Ruth Howison
November 2009**



**FOOD PREFERENCES AND FEEDING
INTERACTIONS AMONG BROWSERS AND THE
EFFECT OF AN EXOTIC INVASIVE WEED
CHROMOLAENA ODORATA ON THE
ENDANGERED BLACK RHINO (*DICEROS
BICORNIS*), IN AN AFRICAN SAVANNA**

by

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**Submitted in fulfilment of the academic
requirements for the degree of
Master of Science in the School of Biological &
Conservation Sciences,
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Background, Nzimani River, Hluhluwe-iMfolozi Park, R Howison
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Black rhino, www.news.bbc.co.uk
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ABSTRACT

Biodiversity changes, often resulting from climate change, land transformation, and the transportation of organisms across geographical barriers are among the most important human induced global changes. To optimize the spatial allocation of conservation efforts, and how to best protect indigenous species, requires an understanding of the principal determinants that structure ecological communities and ecosystems. We studied community-level interaction among a diverse assemblage of specialist and generalist browsers in an African savanna. Hluhluwe-iMfolozi Park (HiP), South Africa, hosts a complete assemblage of vertebrate species across all trophic levels and contains a diverse guild of large browsers. Using species abundance distributions (SADs) we graphically illustrate the diversity and abundance of woody species that comprise six structural habitat types within HiP. We calculated the Shannon-Wiener index and Pianka's niche overlap to characterise the utilization of forage across habitat types among different browser groups. By using individual plant traits we investigated mechanisms of resource partitioning. We specifically investigated the effect of the temporal expansion of an exotic invasive plant (*Chromolaena odorata*) on the critically endangered black rhino using GIS and statistical analyses. We found that lower lying habitat types were important forage resources for browser species and individual plant traits that are highly correlated with digestibility strongly predicted browser preference. Black rhino used different strategic and metabolic mechanisms to successfully compete within the same forage height range of other, smaller, browsers. *C. odorata* has negatively impacted forage species utilization and has led to a spatial reorganization of the population of black rhino. This may partly explain the recent decline in the population. The principles within metapopulation management can be used to successfully conserve endangered species. High diversity of browse across three dimensions (diversity, abundance and maximum height) relative to area facilitates a high diversity and abundance of different browsing herbivores. Therefore the spatial configurations of resources ranging from topological attributes to the individual plant traits are essential to maintaining viable populations of many co-occurring species within conservation areas of limited extent.

To my mother Rosalie Gene Fraser
and my dear family
Owen, Skyla and Caleigh Howison

PREFACE

The experimental work described in this dissertation was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville, under the supervision of Professor Robert Slotow and co-supervised by Professor Han Olff from the Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, Rijksuniversiteit Groningen, Haren, the Netherlands, and these supervisors are acknowledged for their guidance as co-authors of Chapters 2 and 3.

These studies represent original work done 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 has been duly acknowledged in the text.

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DECLARATION 1 – PLAGIARISM

I, Ruth Alison Howison, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
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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: Howison, R.^{1,2,3}, Slotow, R.¹ and Olf, H.³ (in preparation) Food preferences and feeding interactions among browsers, in a diverse African savanna

The work was done by the first author, under guidance and with reviews by the second and third authors. The third author assisted with statistical analyses.

Publication 2: Howison, R.^{1,2,3}, te Beest, M.³, Slotow, R.¹ and Olf, H.³ (in preparation) The effect of the invasive weed *Chromolaena odorata* on the critically endangered black rhino in Hluhluwe-iMfolozi Park, South Africa

The work was done by the first author, under guidance and with reviews by the third and fourth authors. The second author is acknowledged for her contribution to the experimental design and data collection. The fourth author assisted with GIS and statistical analyses.

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Date:

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1. GENERAL INTRODUCTION

Biodiversity changes, often resulting from climate change and land transformation are among the most important human induced global changes (Sala et al. 2000; Olff et al. 2002; Ogutu and Owen-Smith 2003). The human population is expanding at an exponential rate (Lutz and Qiang 2002) causing a highly negative impact on natural ecosystems both in biodiversity and ecosystem services (Chapin et al. 2000; Sala et al. 2000). Humans have caused the extinction of 5 – 20 % of the species in many groups of organisms, and human mobility has transported organisms across geographical barriers, leading to the risk of biotic homogenization through species invasions (McKinney and Lockwood 1999; Chapin et al. 2000; Sala et al. 2000). Africa and tropical Asia have been less affected by extinctions and have a relatively intact diversity of large mammals. However human predation is reducing these populations to precariously low numbers (Owen-Smith 1989; Prins and Olff 1998). Biodiversity can only persist in a natural setting through protection (Western 1987; Chapin et al. 2000; Sala et al. 2000). Optimizing the spatial allocation of conservation efforts, and how to best protect different endangered species requires an understanding of the principal determinants that structure ecological communities and ecosystems (Owen-Smith 1988, 1989).

Individual species and populations of large herbivores are influenced by spatial heterogeneity in their environments at scales ranging from individual plant traits to the biome (Iason and van Wieren 1999; du Toit 2003). Herbivore diversity within a heterogeneous food resource is determined by how evenly community resources are shared by species of different size (du Toit and Owen-Smith 1989; Skarpe et al. 2000). In addition to height, specific morphological and chemical features of individual plant species determine forage acceptability and palatability (Owen-Smith and Cooper 1987; Iason and van Wieren 1999; Skarpe et al. 2000). Body size, metabolic adaptations and mouth morphology allow co-occurring browsers to partition a multi dimensional forage resource (dimensions include: vertical stratification (height), canopy texture (branches and leaves), chemical (plant secondary metabolites (PSM's), digestibility) and structural defence (spinescence)) (Jarman and Sinclair 1979; Demment and van Soest 1985; Owen-Smith and Cooper 1987; du Toit and Owen-Smith 1989; Ritchie and Olff 1999; Wilson and Kerley 2003). Interspecific interactions among herbivores mainly occur at lower heights within the canopy, or in the case of elephant browsing on tall trees, by ultimately bringing the canopy level down to a level accessible to smaller browsers (Owen-Smith 1988; Skarpe et al. 2000; du Toit 2003; Wiseman et al. 2004; Fornara and du Toit 2008). Herbivores maximize intake of nutrients and digestible energy, while avoiding chemical and structural deterrents (Skarpe et al. 2000). Larger herbivores have larger bite size and utilize the forage resource at a coarser patch

scale than smaller herbivores, which results in poorer quality forage being consumed (Jarman and Sinclair 1979; Ritchie and Olff 1999; Wilson and Kerley 2003). Large herbivores require lower quality forage (but larger absolute quantity of food) due to lower per mass energy requirements than smaller herbivores (Jarman and Sinclair 1979; Owen-Smith and Cooper 1987; du Toit and Owen-Smith 1989; Ritchie and Olff 1999).

The richest assemblages of large herbivores on this planet can be found in Africa (Kingdon 1989; Owen-Smith 1989) with 172 plant-eating mammals heavier than 2 kg described for the continent (Estes 1991; Prins and Olff 1998; du Toit 2003). The African savanna biome is a tropical grassland characterized by high spatial heterogeneity and takes up almost half the continent (about 13 million km²), extending over a large and continuous landmass between the Sahel and Karoo semi deserts and is partially separated over the equator by the equatorial forest biome (Prins and Olff 1998; du Toit 2003). Across the entire African continent the distribution of ungulate species richness is closely associated with the distribution of the savanna biome (Turpie and Crowe 1994) with hotspots of diversity under intermediate rainfall and high soil fertility (Olff et al. 2002). Despite the establishment of many protected areas, savannas are threatened by fragmentation through land transformation for agriculture and urbanisation and invasion by exotic invasive species (McKinney and Lockwood 1999; Chapin et al. 2000). Dispersal is an important process in population regulation, but in small isolated conservation areas dispersal is limited, often by fenced boundaries, leading to accelerated overutilization of the natural vegetation and rapid losses of biodiversity (Western and Ssemakula 1981; Owen-Smith 1983b; Chapin et al. 2000). Therefore, successful protection of diverse co-existing assemblages of herbivores is dependent on the spatial vegetation heterogeneity (Cromsigt and Olff 2006) and direct intervention by population management (Owen-Smith 1983b; du Toit 2003), especially if fenced park boundaries are restricting animal movements (Owen-Smith 1983a).

Biotic homogenization through replacement of native vegetation with exotic monocultures is occurring at a global scale as a result of two influences: environmental modification and transportation of exotic species (McKinney and Lockwood 1999). The consequent habitat degradation threatens African savannas and their herbivores and the result is loss of biodiversity (Mooney and Drake 1986; Leslie and Spotila 2001; Keane and Crawley 2002; Turpie 2003; Strayer et al. 2006). Few studies have shown what the true impacts are of invasive species on endangered herbivore species, and especially for large mammals greater than 2 kg (McKinney and Lockwood 1999; Leslie and Spotila 2001; Gaston and Fuller 2007). Large specialist herbivores are more prone to extinction because they are poorly equipped to adapt to habitat degradation. Extinction biasing traits include low fecundity, low population numbers, slow dispersal and

selective forage behaviour (Owen-Smith 1988, 1989; McKinney and Lockwood 1999). A thorough knowledge of invasive plant species ecology is required to ascertain the level of risk the invader poses to endangered indigenous herbivores (Mooney and Drake 1986; Leslie and Spotila 2001; Strayer et al. 2006). Therefore we must know how such invaders affect the resource utilization of browsers on native woody plants.

1.1. STUDY SITE

My primary study site was the Hluhluwe-iMfolozi Park (HiP), an 890 km² fenced game reserve situated in the north-eastern KwaZulu-Natal, South Africa. The Park comprises three historical proclaimed conservation areas: Hluhluwe (north, proclaimed in 1895), iMfolozi (south, proclaimed in 1895 but deproclaimed in the early 1920s for veterinary purposes and reproclaimed in 1952) and the Corridor (central) (Brooks and MacDonald 1983; Brooks 2005). The three areas were formally proclaimed as one conservation area now known as Hluhluwe-iMfolozi Park (HiP) in 1989, but have been managed as a single conservation area from the early 1950s (MacDonald 1978; Conway et al. 2001; Brooks 2005). This study site was chosen for its long natural history and high diversity of African mammalian species (Brooks and MacDonald 1983). A diverse browser guild occurs within the Park and provides a unique opportunity to study a diverse assemblage of herbivores and woody species at the community level. HiP is world renowned for the successful recovery of the white rhino (*Ceratotherium simum simum*) (Slotow et al. 2001) and is currently the custodian of one of the largest populations of the critically endangered black rhino (*Diceros bicornis*) and most other black rhino populations in South Africa are derived from animals exported from HiP (Slotow et al. 2001; Reid et al. 2007). The Park is threatened by the invasion of *Chromolaena odorata* (MacDonald 1978; Howison, O. et al. unpublished data), which is an aggressive invasive plant species (Richardson and Van Wilgen 2004) and therefore warrants investigation into the potential threat this species poses to endangered wildlife.

1.2. OVERALL AIMS AND OBJECTIVES

Black rhino are the key species within this study because of their endangered status. This study aims to improve our understanding of how best to protect this endangered species. There are two main chapters, both written as papers for publication. In Chapter Two the responses of large browsers to spatial vegetation heterogeneity are investigated. Hluhluwe-iMfolozi Park provides a unique opportunity to study mechanisms of resource partitioning among a diverse guild of browsers within a heterogeneous savanna. Differential plant species selection by competing browsers across the range of habitat types and the influence of plant traits on such selection are assessed. Species abundance distributions (SADs) graphically illustrate the diversity and abundance of woody species that comprise six structural vegetation communities within HiP. Species abundance distributions are used as a null hypothesis (diversity and abundance independent of browser utilization) to compare the utilization of the vegetation community by black rhino, elephant and a group of other browsers'. The Shannon-Wiener diversity index is used as a comparative measure between the diversity of each of the vegetation communities and shows the relative importance of vegetation community to diet composition for each browser group. Pianka's (1973) niche overlap is used to assess the degree of forage species overlap in relation to the total species diversity and species abundance sampled. Finally the individual plant traits of abundant species are aligned along two out of four main independent "plant ecological dimensions" (specific leaf area (SLA) and maximum plant height (MaxHgt)) that have been suggested in literature (Westoby et al. 2002). The palatability of these woody species in relation to utilization by black rhino, elephant and other browsers' is assessed.

In Chapter Three the effect of an invasive plant (*Chromolaena odorata*) on the critically endangered black rhino (*Diceros bicornis*) is investigated at a finer level of vegetation categorization, i.e. 32 vegetation communities that fall within the seven structural vegetation types (Whateley and Porter 1983; EKZNW unpublished data). Sophisticated GIS and statistical analyses are used to evaluate the population trends and spatial distribution of the rhinos. Secondly, the spatial reorganization of the black rhino is investigated, through the calculation of home ranges from individual sightings, which are compared in location, size and presence of *C. odorata* between two time periods (before and after the major invasion of *C. odorata*) for male and female rhino. Finally, shifts in foraging preference and selection due to *C. odorata* invasion through diet observations are explored along transects situated across the gradient of *C. odorata* prevalence and where browsing by black rhino could be uniquely identified from other browsers'.

In the final chapter the implications and broader relevance of the results are discussed bringing together the various elements in the following way: Resources are partitioned among a guild of coexisting browsers where preferences are differentially aligned to chemical and morphological traits and this relates both to differences in body size and metabolic adaptations. Carrying capacity relates to the realized area utilized by herbivores (based on topological characteristics, some areas are not suitable to include in carrying capacity calculations) and behavioural constraints. Black rhino are affected by the temporal spread of an exotic invasive species which has invoked structural and species composition changes in the natural vegetation. Finally metapopulation management principles can be used to manage diverse populations of naturally occurring megafauna within a fragmented landscape.

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2. FOOD PREFERENCES AND FEEDING INTERACTIONS AMONG BROWSERS, IN A DIVERSE AFRICAN SAVANNA

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2.1. ABSTRACT

Mechanisms for resource partitioning related to plant diversity and consequent herbivore diet diversity are poorly understood. Classifications of herbivores into grazers, mixed feeders and browsers are therefore thought to represent the main axis of resource partitioning. Our study site, Hluhluwe-iMfolozi Park (HiP), South Africa, hosts a complete assemblage of naturally occurring vertebrate species across all trophic levels and contains a diverse guild of large browsers that utilise a wide variety of woody species. In the field we distinguished which woody plants were browsed by elephant, black rhino and other browsers'. We used species abundance distributions (SADs) of woody plants to capture the main plant diversity differences among six habitat types. We calculated the Shannon-Wiener index and Pianka's niche overlap to characterise the utilization of forage across habitat types among different browser groups. Finally we used morphological and chemical plant traits to predict which plant traits were the main determinants of food plant selection of different herbivores. Within habitats we found that the group of other browsers' had a significantly higher diet diversity than black rhino and elephant. Diet overlap between other browsers' and elephant was significantly higher compared to all other contrasts. Using ordination plants whose traits were positively aligned along the specific leaf area (SLA) gradient (high digestibility) comprised the most important forage species. Black rhino have different strategic and metabolic mechanisms that allow them to successfully utilize abundant but toxic woody species. However they require a high diversity of forage species to mitigate the effects of toxicity. We conclude that resource partitioning at the level of individual woody species strongly promotes the coexistence of many browser species within a heterogeneous landscape. High diversity of browse across three dimensions (diversity, abundance and maximum height); relative to area facilitates a high diversity and abundance of different browsing herbivores.

2.2. INTRODUCTION

Ecological communities of plants and herbivores in Africa are exceptionally diverse due to unique combinations of high spatial heterogeneity and preserved co-evolutionary radiations on multiple trophic levels (McNaughton and Georgiadis 1986; Owen-Smith 1989; Prins and Olff 1998). Mammalian herbivores are important both economically and ecologically but their diversity is threatened by fragmentation and isolation of natural ecosystems (McNaughton and Georgiadis 1986; Olff et al. 2002). Vegetation communities form the forage resource for large herbivores, which in turn directly affect changes in the structure and dynamics of vegetation communities (Skarpe et al. 2000; Wright et al. 2004; Makhabu et al. 2006). As protected areas become smaller and more isolated, large herbivores must often be managed to prevent loss of diversity, both in the vegetation and in herbivore assemblages (Skarpe et al. 2004; Makhabu et al. 2006; Fornara and du Toit 2008; Guldmond and van Aarde 2008; Woolley et al. 2008). In order to set conservation priorities (Where can high abundance and diversity of herbivores be maintained best? Where is it most at risk? What will introduction of new species mean for existing populations?) it is important to understand food choices and resource partitioning among herbivores (Western 1987; Skarpe et al. 2000; Fornara and du Toit 2008).

Resource overlap is greatest during periods of low resource abundance (Gordon and Illius 1989) and this is when interspecific competition is expected to be strongest (de Boer and Prins 1990; Prins et al. 2006). These periods of food scarcity also can determine the limit to population size for different species, and determine which species will outcompete each other and which will coexist (Lawlor 1980; Breebaart 2000). Such coexistence can partly be induced by differential use of resources (Schoener 1974; Voeten and Prins 1999; Makhabu 2005). Body size and associated metabolic adaptations allow herbivores to differentially utilize forage that is vertically stratified and varying in digestibility (Gordon and Illius 1989; Iason and van Wieren 1999; Voeten and Prins 1999). Several different measures have been developed to capture the degree of niche overlap between species pairs (Pianka 1973; Lawlor 1980; Gotelli and Entsminger 2008) that vary in the importance they place on forage selectivity, forage abundance and rate of resource renewal (Lawlor 1980). The niche overlap index developed by Pianka (1973) can be used to capture instantaneous dietary overlap at a particular moment in the seasonal cycle, however the index is not a true measure of competition, because it does not take into account the renewal rate of the resources (Lawlor 1980; Gotelli and Entsminger 2008).

Forage quality for herbivores is dependent on plant community structure (the number, nature and abundance of different species) and lower quality forage species are often more abundant than

high quality species (Demment and van Soest 1985; Woolnough and du Toit 2001), although this depends on rainfall and soil nutrient availability (Olf and Ritchie 1998). Species abundance distributions (SADs) which are the most basic description of an ecological community (Whittaker 1965; Krebs 1985; Etienne and Olf 2005; Yin et al. 2005; McGill et al. 2007) can be used to compare individual woody species utilization by browsers across habitats, in relation to relative abundance or availability. They can be used to explore to what extent the diet composition of the herbivore reflects the plant community composition, where deviations are interpreted as preferences or avoidances. These can then in turn be explained by morphological, nutritional and chemical properties and accessibility of plants to herbivores (Krebs 1985; Begon et al. 1996; Skarpe et al. 2000; Fornara and du Toit 2008). The Shannon-Weiner index, which summarizes aspects of the shape of the SAD relating to species richness and evenness (Krebs 1985; Begon et al. 1996; Gotelli and Colwell 2001; Gotelli and Entsminger 2008) is useful for standardizing and comparing the combination of diet breadth and quantity each woody species contributes to the diet among co-occurring herbivores (Krebs 1985; Begon et al. 1996; Gotelli and Colwell 2001; Gotelli and Entsminger 2008).

In addition to height, specific morphological and chemical features of individual plant species determine forage acceptability and palatability (Owen-Smith and Cooper 1987; Iason and van Wieren 1999; Skarpe et al. 2000). Morphological features that are important to browsers include specific leaf area (SLA), leaf fractal dimension (LFD), maximum tree height (MaxHgt) and spinescence. Chemical features, including phenolics, condensed tannins and other secondary plant metabolites and lastly digestibility strongly affected the balance between protein and cell wall (fibre) components (Demment and van Soest 1985; Owen-Smith and Cooper 1987; Iason and van Wieren 1999; Iason and Villalba 2006). With regard to morphological plant traits, four independent multivariate plant ecological dimensions (or axes) have been suggested to explain the variation among vascular plants (Westoby et al. 2002). Two out of four ecological dimensions are considered. The first dimension, specific leaf area (SLA), varies inversely with leaf lifespan (SLA-LL) while correlating positively with digestibility (Westoby et al. 2002). Leaves from species with low SLA and high LL are generally less digestible because of high investments in structural and chemical defence (high fibre and secondary compound content) (Westoby 1998; Westoby et al. 2002; Iason and Villalba 2006; Kurokawa and Nakashizuka 2008). The second dimension, maximum height (MaxHgt), is positively correlated with wood density (more structural support allows taller growth) and leaf size (taller trees can afford to have smaller leaves); the traits that fall along this axis may be less important for browsers than the nutritional (SLA-LL) axis, although taller trees are able to escape non-climbing browsers (Westoby 1998; Birkett 2002; Westoby et al. 2002).

Herbivores tend to increase diet breadth when forage is dominated by suboptimal quality species (Jenkins and Wright 1988; Dearing and Cork 1999; Provenza 2003). By utilizing an array of different nutritious and toxic species that are biochemically complimentary, herbivores maximise nutrient intake and mitigate the effects of toxicity (Provenza 2003; Shaw et al. 2006). Diet composition and digestion has been well documented for domestic herbivores (Provenza 1995; Dearing and Cork 1999; Provenza 2003; Shaw et al. 2006) and specific principles within the literature (e.g. palatability of forage, nutrient extraction and detoxification pathways) can broadly be compared to herbivores in their natural habitat (Owen-Smith and Cooper 1987; Dearing and Cork 1999). However, domestic herbivore diet composition is artificially centred on maximum production rather than optimal maintenance (Provenza 2003). Differential forage resource utilization by naturally co-occurring herbivores promotes plant species diversity, however the composition of the herbivore assemblage determines the extent to which specific nutrients are selected for and consequently which plant species are removed or promoted (Skarpe et al. 2000; Provenza 2003). Therefore insight into the diet composition and mechanisms of resource partitioning among a guild of different browser species within their natural habitat will promote holistic management of the natural forage resource (du Toit 2003; Provenza 2003).

Browsers require a range of woody species, which exhibit many different morphological and chemical traits, to satisfy their nutritional needs (Westoby 1978; Belovsky and Schmitz 1994; Provenza 2003). This is partly because no single browse species can fulfil all of the nutritional requirements of a browser and the plants themselves are adapted morphologically and chemically to defend themselves against excessive utilization by herbivores (Skarpe et al. 2000; Westoby et al. 2002; Provenza 2003). Herbivores are differentially capable of extracting nutrients and eliminating harmful substances from the forage resource, thereby creating opportunities for partitioning resources based on specific plant traits e.g. plant secondary metabolites (Dearing and Cork 1999). In this study we explored diet diversity, resource overlap and preference for morphological and chemical plant traits by a diverse browser guild, including black rhino (*Diceros bicornis*), elephant (*Loxodonta africana*) and a group of other browsers comprising giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*), bushbuck (*Tragelaphus scriptus*), common duiker (*Silvicapra grimmia*) and impala (*Aepyceros melampus*).

Our hypotheses were: (1) Habitat structure across the full spectrum of available species can be defined by the distribution of plant species and captured by a classic species abundance distribution (SAD) curves which capture abundance and species richness. We predicted that

dietary breadth and percentage dietary contribution (species preference), among the browser groups, could be determined from habitat structure. (2) We predicted that different browser groups would differentially utilize the available forage resource; therefore by using the Shannon-Weiner index we could compare dietary diversity. (3) Browsers utilize the available forage resource along the vertical (height) and horizontal (species composition) planes. A certain amount of resource overlap is predicted because all browsers will utilize forage within the lower reaches and only the taller browsers will be able to claim a specialized niche through utilizing forage above the accessible height of other shorter browsers. We use Pianka's (1973) niche overlap index to compare dietary overlap among the different browser groups. (4) Westoby et al. (2002) ascribes variation among plant traits along four independent axes, plants in general maximise growth, but allocate part of their resources to physical and chemical defences that minimise resource loss to herbivory. Conversely herbivores adapt to overcome plant defences to maximise nutrient intake. We predicted that browsers differentially utilize forage species based on the variation among plant traits.

2.3. METHODS

2.3.1. Study site

Hluhluwe-iMfolozi Park (HiP) is an 890 km² fenced nature reserve situated in north-eastern KwaZulu-Natal, South Africa (Fig. 2.1a). The mean annual rainfall decreases from 985 mm in the north to 650 mm in the south and increases with elevation (Fig. 2.1b). The highest elevation (584 m) is found at the northwest corner of the park, with a steady south-eastward decline in elevation towards the confluence of the black and white Umfolozi rivers (38 m) (Fig. 2.1c) (Whateley and Porter 1983; Schulze 2003; Cromsigt and Olff 2008). Despite its small size, the park hosts a wide range of geological formations from granites and basalts alternated with dolerite dykes in Hluhluwe to a mosaic of dolerites and shales in iMfolozi (King 1970; Downing 1980), leading (in combination with the superimposed topographic and climatic variation) to a high heterogeneity of soil types (Downing 1980; Barrow 1986; EKZNW unpublished data). The fire return interval is spatially heterogeneous, ranging from two to ten years (Balfour and Howison 2001), depending on vegetation, rainfall, topography and herbivore density. As a consequence of the variation in elevation, topography, rainfall, geology, soil types and fire return interval, the vegetation is highly heterogeneous with vegetation types ranging from open grasslands to closed *Acacia* and broad-leaved woodlands (Whateley and Porter 1983; Archibald et al. 2005). Daily temperatures range from a minimum of 13 °C in the cooler and drier winter season (May-October) to a maximum of 35 °C in the warmer and wetter summer (November – April) (Brooks and MacDonald 1983).

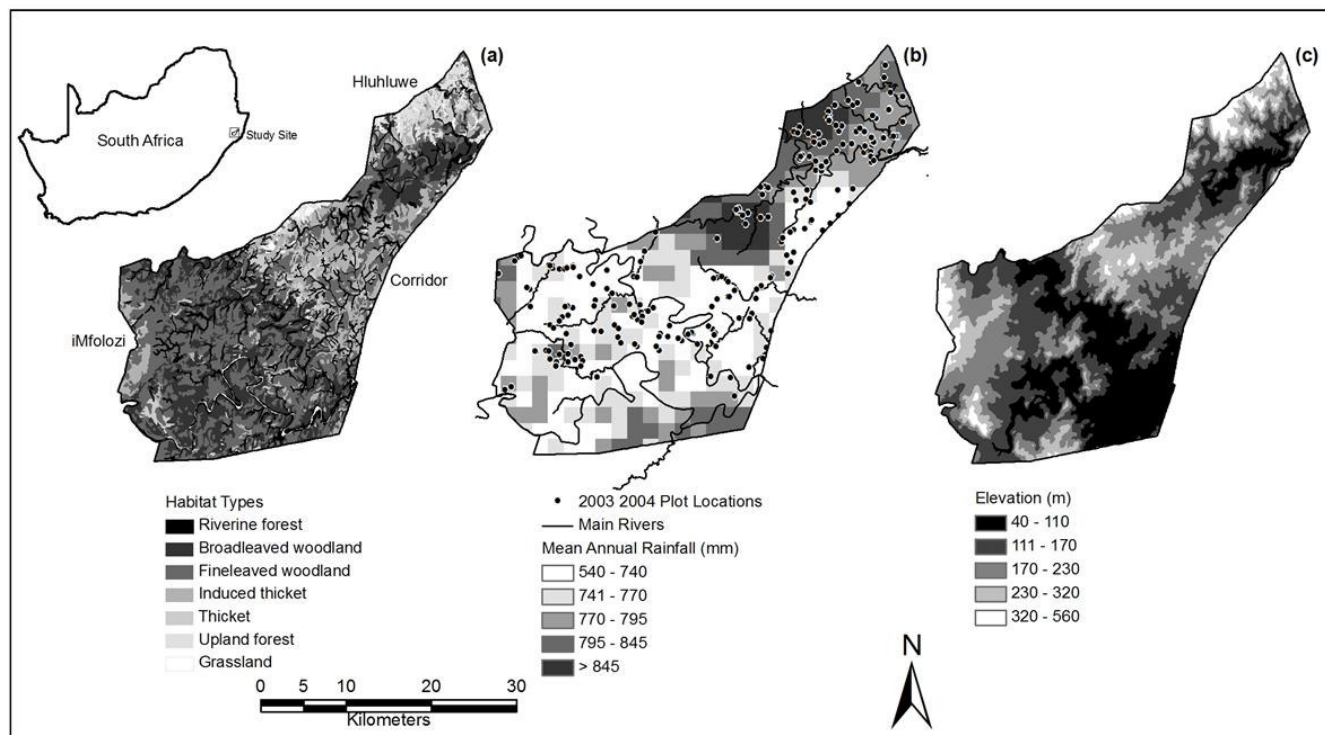


Figure 2.1: Geographic context of the study site: (a) The location of Hluhluwe-iMfolozi Park within South Africa, showing the distribution of the seven habitat types and location of the Hluhluwe, Corridor and iMfolozi areas. Six habitat types (grasslands excluded due to low sample size) were investigated for browser utilization. (b) The 2003 and 2004 plot locations and mean annual rainfall. Average rainfall (Schulze 2003) ranges from 980 mm p.a. in the north to 540 mm p.a. in the south. Most rainfall is received between October and March each year. (c) Elevation of Hluhluwe-iMfolozi Park (NASA 2004), ranging from 584 m in the north to 38 m in the south east.

2.3.2. Utilization by browsers of the main habitat types

Whateley & Porter (1983) identified 20 different vegetation communities which we aggregated into seven morphologically distinct habitat types: riverine forest, broadleaved woodland, fineleaved woodland, induced thicket, thicket, upland forest and grassland (Fig. 2.1a and Table 2.1). Open grassland patches were found along ridges of the highest peaks within the Park and was the least abundant habitat type occupying 1.5 % of the Park. *Dichrostachys cinerea*, *Rhoicissus tridentate*, *Acacia caffra* and ten other sparsely occurring woody species were located within this habitat type (Shannon-Wiener diversity index: $e^H = 9.0$). Browser utilization could not be assessed within this habitat type because the area was too small to permit sufficient sample plots to be surveyed. The six remaining habitat types were distributed within the landscape in direct association with changes in geology, elevation and rainfall patterns. (1) Riverine forest was confined to narrow bands along the main rivers and major tributaries throughout HiP (Whateley and Porter 1983) and of all the main habitat types, was the most highly diverse in woody species

composition, with $n_{\text{species}} = 82$ and $e^H = 34.5$, but occupies only 11 % of HiP (Fig. 2.2a). *D. cinerea*, *Acacia karroo* and *Gymnosporia senegalensis* were the three most abundant woody species. (2) Broadleaved woodlands were the second most abundant habitat type occupying 26 % of HiP and hosting 96 woody species with a diversity $e^H = 33.7$. *Dichrostachys cinerea*, *Spirostachys africana* and *Diospyros lycioides* were the three most abundant species in this type (Fig. 2.2b). (3) Fineleaved woodlands were the most abundant habitat type in the park occupying 38 % of HiP, with $n_{\text{species}} = 106$ and $e^H = 30.1$. *D. cinerea*, *A. karroo* and *G. senegalensis* were the three most abundant species found in this habitat type (Fig. 2.2c). (4) Induced thicket was the third most abundant woody habitat type (16 % of HiP, $n_{\text{species}} = 53$) (Fig. 2.2d) and was composed of grassland encroached by few species of native shrubs that can resprout from rootstocks after fire, mostly *A. karroo* and *D. cinerea* (Whateley and Porter 1983; Wakeling and Bond 2007; Balfour and Midgley 2008). (5) Thickets comprise four percent of the area of HiP ($n_{\text{species}} = 38$ and $e^H = 21.33$). *Hippobromus pauciflorus*, *D. cinerea* and *A. caffra* were the three most abundant woody species (Fig. 2.2e). (6) Upland forest occur in only 3.5 % of the area of HiP, with $n_{\text{species}} = 66$ and $e^H = 32.9$ and *Acalypha glabrata*, *A. karroo*, and *D. cinerea* were the three most abundant species (Fig. 2.2f).

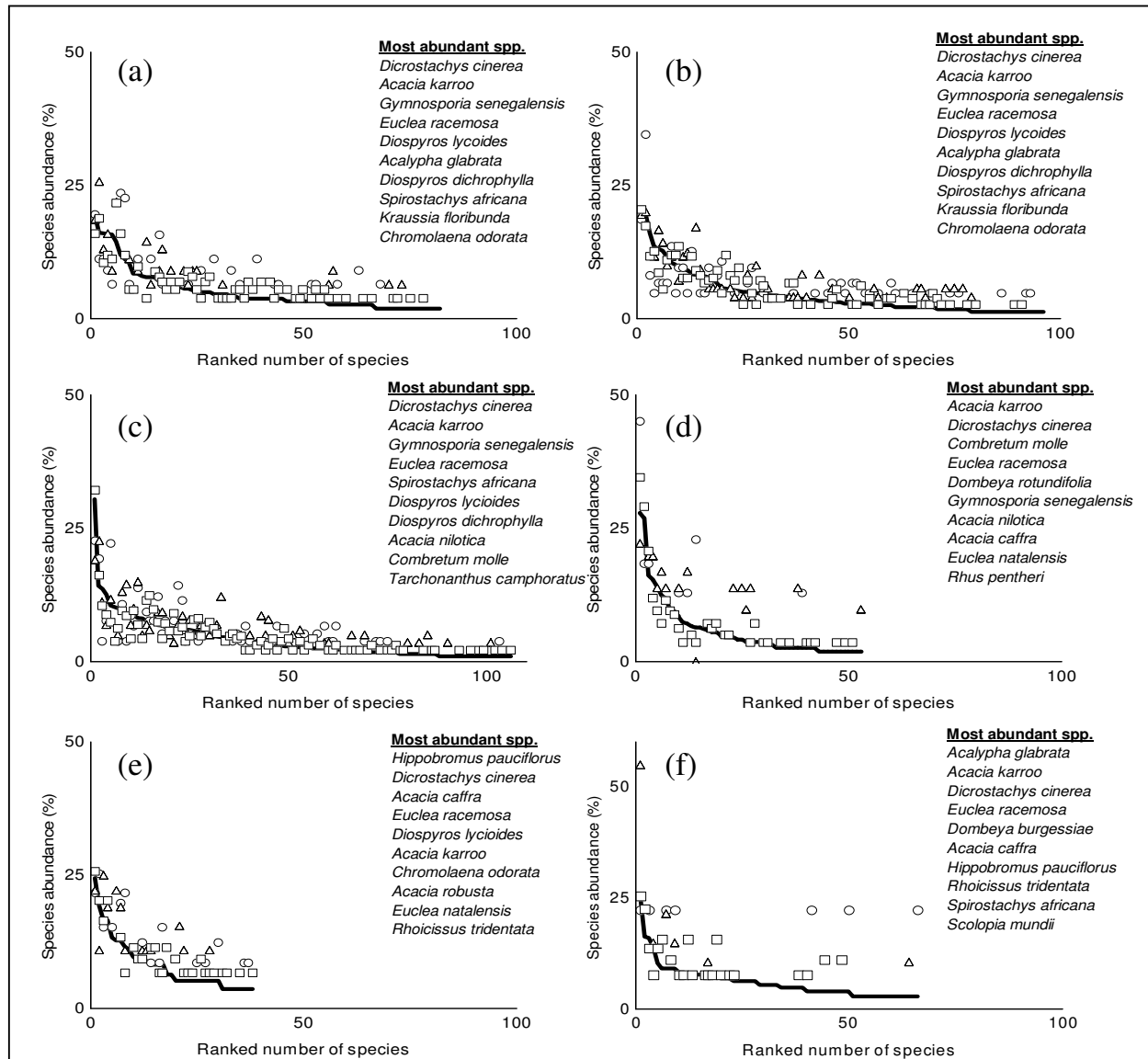


Figure 2.2: Species abundance distribution (SAD) (solid line) within six habitat types (excluding grasslands): Showing percent contribution (Arcsine transformed) of individual woody species representing abundance and richness. Further showing the relative contribution of each woody species to the diet of black rhino (open circle), elephant (open triangle) and other browsers' (open square). Woody species were ranked from the most abundant (left) to least abundant (right) for the habitat type; the order is retained for contribution to browser diet, therefore comparing woody species % contribution to diet among browser species in relation to the woody species abundance (availability). Total number of species sampled within each habitat; (a) Riverine forest ($n_{spp} = 82$), (b) Broadleaved woodland ($n_{spp} = 96$), (c) Fineleaved woodland ($n_{spp} = 106$), (d) Induced thicket ($n_{spp} = 53$), (e) Thicket ($n_{spp} = 38$) and (f) Upland forest ($n_{spp} = 66$). Woody species that were not utilized were included in the habitat SAD but were excluded from the diet contribution curves.

Table 2.1: Categorization of the 20 vegetation communities (Whateley & Porter 1983) into the seven main habitat types: Six habitat types (Grasslands excluded) were investigated for browser utilization, the table summarizes the proportion contribution of each habitat type to the total study site area, species richness within each habitat type and the Shannon-Wiener diversity index (e^H) for each habitat type and the median, range (between the first and third quartiles (Q25 – Q75)) and extremes (minimum and maximum) of elevation (m) at which each of the habitat types occurs. Data ordered by ascending median elevation (m).

| Vegetation Category Whateley & Porter 1983 | Habitat Type | Proportion area (%) | Species richness | eH' Habitat type | Elevation | | |
|---|----------------------|---------------------|------------------|------------------|------------|---------------------|---------------|
| | | | | | Median (m) | Range Q25 - Q75 (m) | Min - Max (m) |
| <i>Spirostachys africana</i> and <i>Euclea racemosa</i> Riverine Forest <i>Ficus sycamorous</i> and <i>Schotia brachypetala</i> Riverine Forest <i>Celtis africana</i> and <i>Euclea racemosa</i> Riverine Forest | Riverine forest | 10.8 | 82 | 34.5 | 142 | 100 - 188 | 41 - 381 |
| <i>Spirostachys africana</i> Woodland <i>Combretum apiculatum</i> Woodland <i>Combretum molle</i> Woodland <i>Euclea divinorum</i> Woodland | Broadleaved woodland | 25.8 | 96 | 33.7 | 142 | 116 - 182 | 38 - 501 |
| <i>Acacia burkeii</i> Woodland <i>Acacia nilotica</i> Woodland <i>Acacia gerrardii</i> Woodland <i>Acacia nigrescens</i> Woodland <i>Acacia tortilis</i> Woodland <i>Acacia karroo</i> Woodland | Fineleaved woodland | 39.0 | 106 | 30.1 | 183 | 139 - 233 | 52 - 542 |
| <i>Acacia karroo</i> and <i>Dicrostachys cinerea</i> Induced Thicket | Induced thicket | 15.9 | 53 | 16.3 | 220 | 180 - 268 | 59 - 568 |
| <i>Acacia caffra</i> Thicket <i>Acacia davyi</i> Thicket | Thicket | 3.7 | 38 | 21.3 | 253 | 210 - 299 | 57 - 541 |
| <i>Commiphora spp.</i> Upland Forest <i>Celtis africana</i> and <i>Harpephyllum caffrum</i> Upland Forest | Upland forest | 3.4 | 66 | 32.9 | 313 | 255 - 382 | 63 - 547 |
| <i>Sporobolus africanus</i> and <i>Cyperus textilis</i> (sedge) Grassland <i>Themeda triandra</i> Grassland | Grassland | 1.4 | 13 | 9.0 | 343 | 282 - 390 | 97 - 584 |

We sampled a total of 219 plots of 50 x 50 m, which were situated within the six main habitat types (excluding grassland) directly proportional to habitat type contribution to the total area of HiP (Linear regression: $y = 1.2743x - 4.2677$, $F_{1,4} = 48.57$, $R^2 = 0.92$, $p < 0.01$). The field work was done in June and July of 2003 and 2004. Starting from a random point in the approximate area for the plot a 50 m line transect was laid out in a north easterly direction and coordinates of the start and end points were recorded with a GPS. We sampled trees according to height class, and varied sampling area using a nested design (Walker 1976; Balfour 2003): Class 1 (4 x 50 m): all trees between 0.51 - 2.0 m were recorded; Class 2 (20 x 50 m): all trees between 2.01 - 4.0 m; Class 3 (50 x 50 m): all trees > 4.01 m. For each individual tree, we noted the species, its maximum height (ground to top of living material) and the number of stems originating from ground level up to 0.3 m height. Overall diversity of woody species per habitat type was calculated using the Shannon-Wiener index (e^H) (Shannon and Weaver 1949) (Table 2.1). Each individual tree was assessed for black rhino, elephant and other browser' impact. Elephant damage could be easily distinguished by the characteristic signs of branch twisting and chewing, bark stripping, branch breakage or whole tree toppling (Gadd 2002), black rhino characteristically clip branches off at a 45° angle (Emslie 1999), all 'other' browser damage could be identified by characteristic browser cropping or stripping of branch ends (Estes 1991), but could not be confidently assigned to a particular species. We acknowledge there are constraints with collecting only post foraging event data in that evidence of foraging by smaller herbivores may be masked by larger herbivore utilization should the latter remove plant parts that were previously browsed by the former. Our dataset is however sufficiently extensive throughout HiP to allow a minimum resource overlap between the various browser groups to be assessed.

Plot locations were stratified across habitats, and the distance between the 219 plots sampled, ranged from 100 m to 3410 m. Because we were interested in browsing, and some distances were relatively short relative to the range of the browsers, we checked for spatial dependence among plots. We calculated the percentage of the number of trees browsed by black rhino, elephant and other browsers' per plot. We then plotted all the plot locations as points in a GIS and calculated the nearest distance to another plot using proximity analysis tools (Arc Info 9.x, ESRI). We then plotted the percentage browsed for either black rhino, elephant or other browsers' per plot against distance to nearest plot then using linear regression (Statistica v.7) we investigated whether there were any inverse relationships between distance to nearest plot and black rhino, elephant and other browsers' utilization. No relationship was observed between black rhino (Linear regression: $F_{1,219} = 1.53$, $R^2 = 0.007$, $p = 0.22$), elephant (Linear regression: $F_{1,219} = 0.01$, $R^2 = 0.000$, $p = 0.91$) and 'other' browser species (Linear regression: $F_{1,219} = 1.95$, $R^2 = 0.01$, $p = 0.16$) in relation to utilization of woody species and distance to nearest plot. Therefore plot utilization by the

various browser groups was independent because there was no correlation between % browsed and distance to next plot. Interactions between black rhino, elephant and other browsers' were calculated within the height class 0.51 – 2.0 m, which represents the physically possible range of overlap between the species pairs studied. Within the height class 0.51 – 2.0 m black rhino and elephant plot utilization were significantly positively related (Linear regression: $F_{1,219} = 28.96$, $R^2 = 0.12$, $n = 7914$, $p < 0.01$), all other possible combinations of plot level interactions within all height classes, for black rhino, elephant and other browsers' were not significant. A list of 40 tree species, for which >100 individuals were sampled, found within the height class > 2.0 m, has been included, indicating percent contribution to the browse component of the elephant diet and dietary preference relative to the total number of species sampled within the height class ($n_{\text{individuals}} = 28\ 646$) (Table 2.2). This provides insight into which of the abundant taller tree species were targeted and avoided by elephant. However, the data from height class > 2.0 m were not analysed further.

For each of the six woody habitat types, we plotted the relative abundance of each woody species within the 0.51 – 2.0 m height as a proportion of the total number of individual trees sampled within that height class ($n_{\text{individuals}} = 9\ 894$) and ranked the species according to decreasing abundance (Fig. 2.2a-f). The percentage contribution of each woody species to the diet was plotted (retaining the same ranked order as the habitat type species distributions) for black rhino, elephant, and other browsers' to compare the diet selection with the forage species abundances 'as offered' to the herbivores (Fig. 2.2a-f). The data were Arcsine transformed to remove possible limits on the data imposed by the truncation of percentages. Zero values for woody species that did not contribute to the respective browsers diet were removed to reduce redundancy. We classed the data from the three lower lying habitat types (Riverine forest, Broadleaved woodland and Fineleaved woodland) into three abundance classes, 1 = Abundant (≥ 50 individuals sampled), 2 = Intermediate (10 - 49 individuals sampled) and 3 = Rare (< 10 individuals sampled). The three higher elevation, less widespread habitat types (Induced thicket, Thicket and Upland Forest) were excluded due to low sample size. A 2-Way ANOVA (Statistica v.7) was used to test for the effect of vegetation type and species abundance on browser preference. A posthoc Tukey HSD test was used to test for differences among specific group means.

Table 2.2: Utilization of woody species by elephant within the above 2.0 m height class: List of 40 woody species with >100 individuals sampled ($n_{\text{individuals}} = 28\,646$). We illustrate, per species, the dietary preference (Ele pref) and % contribution to the browse component of elephant diet (Ele % diet), relative to the total number of individual trees sampled. The list has been ordered by descending preference.

| Species | Total | % Relative Abundance | Ele pref | Ele % diet |
|----------------------------------|-------|----------------------|----------|------------|
| <i>Schotia brachypetala</i> | 345 | 1.20 | 0.76 | 2.12 |
| <i>Acacia robusta</i> | 589 | 2.06 | 0.69 | 3.48 |
| <i>Sclerocarya birrea</i> | 177 | 0.62 | 0.59 | 0.98 |
| <i>Scolopia mundii</i> | 126 | 0.44 | 0.56 | 0.69 |
| <i>Chaetachme aristata</i> | 120 | 0.42 | 0.56 | 0.65 |
| <i>Acacia gerrardii</i> | 656 | 2.29 | 0.49 | 3.40 |
| <i>Ziziphus mucronata</i> | 669 | 2.33 | 0.46 | 3.40 |
| <i>Acacia nilotica</i> | 1834 | 6.40 | 0.40 | 8.97 |
| <i>Berchemia zeyheri</i> | 460 | 1.61 | 0.40 | 2.25 |
| <i>Acacia burkei</i> | 515 | 1.80 | 0.39 | 2.49 |
| <i>Schotia capitata</i> | 124 | 0.43 | 0.36 | 0.59 |
| <i>Sideroxylon inerme</i> | 278 | 0.97 | 0.32 | 1.28 |
| <i>Acacia tortilis</i> | 381 | 1.33 | 0.31 | 1.74 |
| <i>Acacia nigrescens</i> | 496 | 1.73 | 0.29 | 2.23 |
| <i>Acacia karroo</i> | 1999 | 6.98 | 0.25 | 8.71 |
| <i>Tarchonanthus camphoratus</i> | 561 | 1.96 | 0.25 | 2.44 |
| <i>Acacia grandicornuta</i> | 836 | 2.92 | 0.19 | 3.46 |
| <i>Plectroniella armata</i> | 352 | 1.23 | 0.13 | 1.39 |
| <i>Gymnosporia heterophylla</i> | 335 | 1.17 | 0.11 | 1.30 |
| <i>Rhus pentheri</i> | 571 | 1.99 | 0.08 | 2.15 |
| <i>Combretum molle</i> | 451 | 1.57 | 0.08 | 1.70 |
| <i>Acalypha glabrata</i> | 337 | 1.18 | 0.03 | 1.22 |
| <i>Gymnosporia buxifolia</i> | 239 | 0.83 | 0.00 | 0.83 |
| <i>Canthium inerme</i> | 140 | 0.49 | -0.03 | 0.47 |
| <i>Acacia caffra</i> | 293 | 1.02 | -0.04 | 0.99 |
| <i>Micrococca capensis</i> | 118 | 0.41 | -0.04 | 0.39 |
| <i>Euclea divinorum</i> | 913 | 3.19 | -0.08 | 2.92 |
| <i>Brachylaena ilicifolia</i> | 474 | 1.65 | -0.11 | 1.47 |
| <i>Euclea racemosa</i> | 2608 | 9.10 | -0.13 | 7.93 |
| <i>Combretum apiculatum</i> | 146 | 0.51 | -0.13 | 0.44 |
| <i>Maytenus nemorosa</i> | 400 | 1.39 | -0.16 | 1.18 |
| <i>Dombeya rotundifolia</i> | 345 | 1.20 | -0.16 | 1.01 |
| <i>Calpurnia aurea</i> | 226 | 0.79 | -0.23 | 0.60 |
| <i>Euclea natalensis</i> | 170 | 0.59 | -0.31 | 0.41 |
| <i>Kraussia floribunda</i> | 162 | 0.57 | -0.33 | 0.38 |
| <i>Dichrostachys cinerea</i> | 2833 | 9.89 | -0.36 | 6.34 |
| <i>Cassine aethiopica</i> | 221 | 0.77 | -0.39 | 0.47 |
| <i>Gymnosporia senegalensis</i> | 740 | 2.58 | -0.39 | 1.56 |
| <i>Spirostachys africana</i> | 3396 | 11.86 | -0.49 | 5.99 |
| <i>Heteropyxis natalensis</i> | 102 | 0.35 | -0.82 | 0.07 |

The elephant preference index (Ele pref) is the deviance of observed from expected frequencies: (Ele pref = (observed browsed - expected browsed) / observed browsed)) (Williams 2005).

Habitat diversity and browser diet diversity indices were calculated per plot using the Shannon-Wiener diversity index (Shannon and Weaver 1949). This index was chosen because a higher value reflects both less evenness in abundance of species (in the vegetation or in the diet) and higher species richness, both of which are important to herbivore diet composition (Peet 1974; Krebs 1985; Begon et al. 1996).

$$H' = -\sum_{i=1}^s p_i \ln(p_i)$$

Values were reported as $e^{H'}$, where $e^{H'}$ is the base e raised to the power of the calculated diversity H' , S = number of species and p_i = proportion of the total sample belonging to the i^{th} species, high $e^{H'}$ values indicate high species heterogeneity (or wide diet breadth), and low H' values indicate a more homogeneous community (or narrow diet breadth). The relationship of diet diversity between browser groups across habitat types was analysed using a 2-Way ANOVA (Statistica v.7) with habitat diversity as a fixed factor. A posthoc Tukey HSD test was used to test for homogeneity among groups.

Niche overlap (Pianka 1973) (or in this case dietary species overlap) was calculated per habitat type and per plot, to represent the proportion of forage species overlap between species pairs of the three different browser groups, within the 0.51 – 2.0 m height class. The index is a pairwise measure of overlap

$$O_{jk} = O_{kj} = \frac{\sum_i^n P_{ij}P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}}$$

where O_{jk} and O_{kj} is the degree of overlap between the species pairs and P_{ij} and P_{ik} are the proportions of the i^{th} resource used by the j^{th} and k^{th} species respectively. Overlap was calculated separately for woody species utilization, within the six habitat types. We used the software package EcoSim v.7 (Gotelli and Entsminger 2008) (available online from <http://garyentsminger.com/ecosim.htm>). We used 1000 iterations to calculate the indices for each species pair within the six habitat types, where niche breadth was retained to preserve the degree of specialization of each species. We ran the calculations using the reshuffled zero states option (Gotelli and Entsminger 2008). We used the RA3 algorithm (Niche Breadth retained/ Zero States reshuffled), as this retains the amount of specialization, and detects non-random overlap patterns. Finally we used the abundance per woody species to weight the resource states, because species are not equally abundant or equally available to all species. The niche overlap index values range from 0 (no species used in common between two browsers) to 1.0 (the same species utilised in exactly the same proportions). The data were therefore Arcsine transformed to remove possible

limits on the data imposed by the truncation of percentages. The relationships between dietary overlap for the three species pairs across habitat types, were analysed using a 2-Way ANOVA (Statistica v.7). A posthoc Tukey HSD test was used to test for differences among specific group means.

2.3.3. Morphological and biochemical plant characteristics

We collected leaf and twig samples of 52 of the most abundant species within HiP in July 2007. Between 4 and 37 mature leaves (with negligible damage) were collected from a number of individuals per tree species at approximately 1.0 – 1.5 m above ground, at a location where the species was abundant. The location of each sample was recorded using a GPS. The leaves were photographed on a flat white surface, and the total leaf area and leaf perimeter, per leaf was measured with the software package Sigmascan Pro v.5. The specific leaf area (SLA) (g / cm^2) and the leaf fractal dimension (LFD) ($\text{leaf area cm}^2 / \text{leaf perimeter cm}$) were averaged from these measures. Next, the leaf samples were dried at 70 °C to a constant weight, weighed, and then ground using a laboratory mill to a mesh fraction < 1 mm. For the ground leaf samples, chemical analyses were carried out for contents of total N, total C, acid detergent fibre (ADF), neutral detergent fibre (NDF), and lignin. Total nitrogen (N) and carbon (C) were measured using a Carlo-Erba element analyser (Van Soest and Wine 1967). ADF, NDF and lignin were determined according to the stepwise extraction method described by Van Soest and Wine (1967). All chemical analyses done in duplicate, and the average of the two measurements was taken to represent each sample in the statistical analysis. Straight twigs, ranging in length from 6 – 26 cm, were collected approximately 1.0 – 1.5 m above ground from lateral branches that ranged between 2 – 25 cm in diameter. The twig length, start and end point diameters (cm) were measured, and the twig volume (cm^3) was calculated assuming a conical shape. Next, the twig samples were dried at 70 °C to a constant weight then weighted to calculate twig wood density (TWD) (g / cm^3). A database on additional morphological plant traits was assembled using Pooley (1993), Coates-Palgrave (2002) and online plant database resources (www.ars-grin.gov/cgi-bin, www.plantzafrica.com, www.worldagroforestrycentre.org) regarding spinescence (yes/no), leguminous (yes/no), deciduous vs. evergreen, maximum height (MaxHgt) (cm), general toxicity to herbivores (yes/no).

For those woody species that were analysed for chemical and morphological traits, and that occurred at least 50 times in the field plots, we calculated the preference index (PI) per browser per woody species: $\text{PI} = ((\text{observed browsed} - \text{expected browsed}) / \text{observed browsed})$ (Williams 2005) of all individual trees/shrubs that were browsed by elephant, black rhino or other browsers'. For this set of species ($n = 26$) we performed principal component analyses (PCA) (Statistica v.7)

to explore the multivariate relationships between morphological, nutritional and structural properties, and browser preference or avoidance. Plant species traits were added as active variables within the PCA while the black rhino, elephant and other browsers' preference values the woody species were added as passive variables. In addition linear regression analyses (Statistica v.7) were used to determine the level of significance between browser preference and plant trait variables associated along the SLA (digestibility) axis.

2.4. RESULTS

2.4.1. Utilization by browsers of the main habitat types

The following results should be viewed as first approximations and interpreted with extreme caution. More detailed studies are required that describe dietary composition for each of the browsers based on observations of actual feeding events.

The distribution of woody species within each habitat type followed the typical species abundance distribution also observed in other woody plant communities enriched by rarity (i.e. few dominant species and many rare) (Nekola and Brown 2007) (Fig. 2.2 a-f). The habitat SADs showed a continuous distribution of species from left (most abundant) to right (least abundant), therefore showing that each habitat type was adequately surveyed. The induced thicket, thicket and upland forest were higher in elevation and comprised 23 % of the vegetation (Table 2.1). This group of habitat types was less important as a forage resource for browsers, indicated by the less even contribution of species to the diet (all browser groups show a higher preference for rare species (Fig. 2.2 d-f)). However sample size was too low and not analysed further. The riverine forest, broadleaved woodland and fineleaved woodland habitat types formed the lower elevation vegetation and were proportionately more widespread throughout HiP, comprising 77 % of the vegetation (Table 2.1). These three habitat types formed the main forage resource, indicated by a large proportion of the woody species being utilized by all browsers within a narrow range of the habitat SAD (Fig. 2.2a - c). Black rhino (2-Way ANOVA: $F_{8,275} = 2.035$, $R^2 = 0.056$, $p = 0.043$) and other browsers' (2-Way ANOVA: $F_{8,275} = 3.34$, $R^2 = 0.090$, $p = 0.001$) show a significantly higher preference for rare woody species (i.e. actively selected rare species more than is expected from their abundance). For elephant this effect was not significant (2-Way ANOVA: $F_{8,275} = 1.01$, $R^2 = 0.029$, $p > 0.5$).

The thicket habitat had a significantly higher within plot diversity than any other habitat type (ANOVA: $F_{5,444} = 2.25$, $R^2 = 0.02$, $p < 0.05$). However diet diversity did not differ significantly across habitat types for each browser group (2-Way ANOVA with the per plot habitat diversity

scores as the covariate (H' Habitat): $F_{5,431} = 0.80$, $R^2 = 0.72$, $p > 0.05$) (Fig. 2.3a), i.e. diet diversity was not higher or lower across habitat types. However, there was a significant difference in diet diversity among the browser groups (2-Way ANOVA: $F_{2,431} = 148.01$, $R^2 = 0.72$, $p < 0.00$). Other browsers' diet diversity was significantly higher than that of either black rhino or elephant (Posthoc Tukey HSD test: $p < 0.05$) and diet diversity between black rhino and elephant was not significantly different (Posthoc Tukey HSD test: $p > 0.05$). This was not surprising because other browsers' comprise all data combined for giraffe, kudu, nyala, bushbuck, impala and common duiker, and the range in dietary species utilized would therefore be correspondingly wider.

Dietary overlap, per plot, across the six woody species habitats, did not differ significantly across habitat types for individual browser contrasts (2-Way ANOVA: $F_{5,301} = 0.31$, $R^2 = 0.15$, $p > 0.05$) (Fig. 2.3b). However dietary overlap between browser contrasts within each habitat type was significantly different (2-Way ANOVA: $F_{2,301} = 9.52$, $R^2 = 0.15$, $p < 0.00$). Elephant and other browsers' dietary overlap was significantly higher (mean overlap 0.35) than overlap between black rhino and elephant or black rhino and other browsers' (Posthoc Tukey HSD test: $p < 0.05$). Black rhino and elephant dietary overlap was the lowest of all three of the species pair combinations (mean overlap 0.12) which indicated that black rhino and elephant diet was composed of different species. Black rhino and other browsers' dietary overlap was intermediate (mean overlap of 0.20).

2.4.2. Morphological and biochemical plant characteristics

Three principal component axes were identified (PC I, PC II and PC III) together explaining 65 % of the total variation for continuous morphological traits (SLA, LFD, twig wood density (TWD) and MaxHgt), categorical morphological traits (deciduous (vs. evergreen), spinescent, leguminous and toxicity) and nutritional and fibre properties (N, C, ADF, NDF and Lignin) of the woody species sampled (Fig. 2.4a and c, Table 2.3)). The first principle axis (PC I) for 26 woody species for which we had a complete dataset for all the variables, showed that higher scores of species (Fig. 2.4a and c) represented an increase in SLA and N, but a decrease of fibre and structural components (C, NDF, ADF and lignin, which were all highly correlated to each other). Lower scores of species along the first axis therefore represented thicker leaves (and possibly lower growth rates) and higher chemical defence (tannins), and therefore lower palatability/digestibility for herbivores. Species with highly positive scores on this axes (high palatability species) *A. glabrata*, *Ehretia rigida* and *S. africana* (Fig. 2.4b and d, Table 2.3), were all potential dominants of gallery forests (upland or riverine). Species with opposite traits along this axis (thick, fibrous,

low N leaves) were *Euclea natalensis*, *Euclea divinorum* and *Cassine aethiopica* (Fig. 2.4b and d), which were all dominants of broadleaved shrublands.

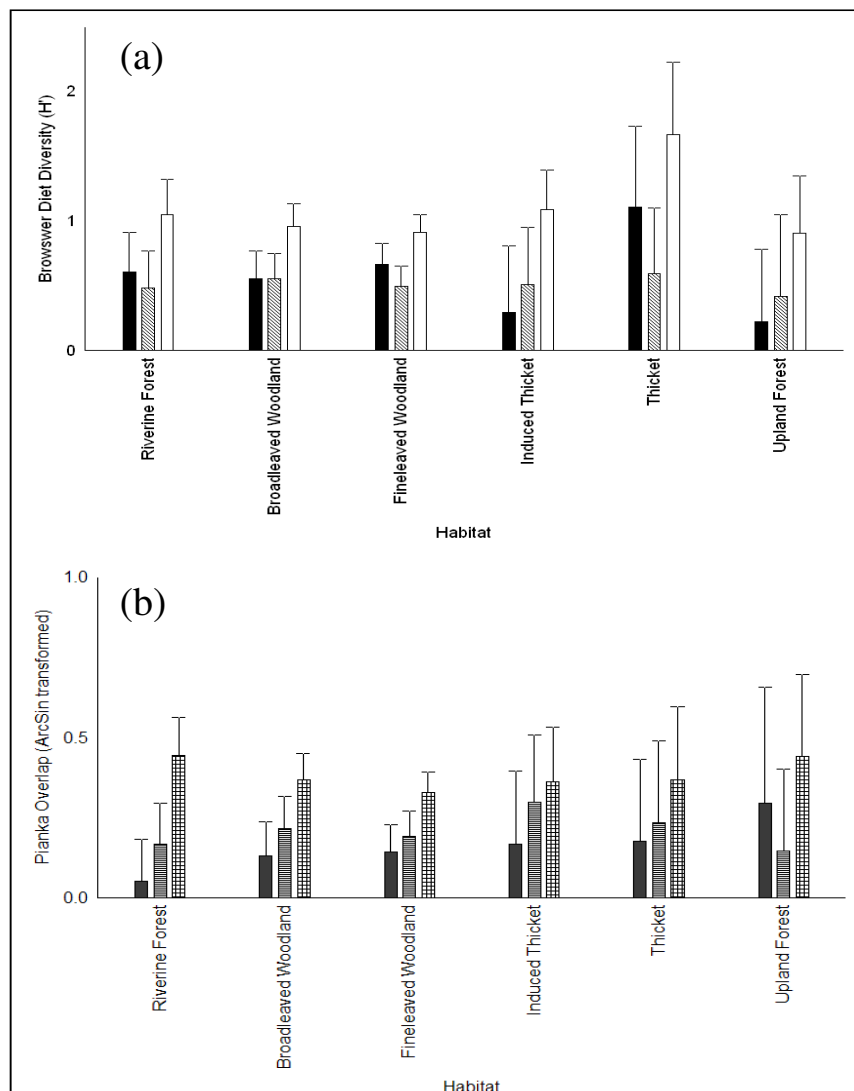


Figure 2.3: Resource partitioning among black rhino, elephant and a group of other browsers: (a) Shannon-Wiener index ($e^{H'}$) representing diet diversity between three browser groups; black rhino (solid black), elephant (diagonal lines) and other browsers' (solid white) across six main habitat types within HiP. Habitat types were ordered in ascending mean elevation from left to right. Between species diet diversity was significantly different, with other browsers' containing a significantly higher diet diversity than black rhino and elephant within the three lower elevation habitat types. Diet diversity did not differ across the six main habitat types. Error bars represent 95 % variance between plots. (b) Pianka's niche overlap representing the proportion of dietary overlap between three browser species pairs; black rhino and elephant overlap (solid grey), black rhino and other browsers' (horizontal lines) and elephant and other browsers' (square hatching) across the six main habitat types within HiP. Elephant and other browsers' dietary overlap were significantly higher than the other species pairs within the three lower elevation habitat types. Dietary overlap across the six habitat types was not significantly different. Error bars represent 95 % variance between plots.

The passive variables (black rhino, elephant and other browser species' woody species preference) were correlated positively with PC I and were located toward the high SLA (high digestibility), high N, position (Fig. 2.4a and c and Table 2.3). Additional linear regression analysis showed a significant negative effect of fibre properties, C ($F_{1,27} = 6.22$, $R^2 = 0.16$, $p < 0.05$), NDF ($F_{1,25} = 5.70$, $R^2 = 0.19$, $p < 0.05$), ADF ($F_{1,25} = 8.45$, $R^2 = 0.25$, $p < 0.05$) and lignin ($F_{1,25} = 6.45$, $R^2 = 0.20$, $p < 0.05$) on black rhino preference. Black rhino preference increased, although not significantly, with SLA ($F_{1,29} = 0.05$, $R^2 = 0.01$, $p = 0.59$) and N ($F_{1,27} = 6.22$, $R^2 = 0.07$, $p = 0.18$). Elephant preference was negatively affected by increasing fibre content, i.e. decreasing with increasing NDF ($F_{1,25} = 4.71$, $R^2 = 0.20$, $p < 0.05$), ADF ($F_{1,25} = 5.12$, $R^2 = 0.18$, $p < 0.05$) and lignin ($F_{1,25} = 9.06$, $R^2 = 0.26$, $p < 0.05$), but did not change significantly with C ($F_{1,27} = 0.67$, $R^2 = 0.03$, $p = 0.42$). Elephant preference was not significantly affected by SLA ($F_{1,29} = 0.46$, $R^2 = 0.00$, $p = 0.85$) or N ($F_{1,27} = 0.31$, $R^2 = 0.00$, $p = 0.91$). The preference of the other browsers' was negatively affected by increasing fibre content, i.e. significantly decreasing within increasing NDF ($F_{1,25} = 5.80$, $R^2 = 0.18$, $p < 0.05$), ADF ($F_{1,25} = 7.91$, $R^2 = 0.24$, $p < 0.05$) and lignin ($F_{1,25} = 7.88$, $R^2 = 0.25$, $p < 0.05$), but was not significantly affected by C ($F_{1,27} = 0.96$, $R^2 = 0.06$, $p = 0.25$). Other browsers' preference was significantly positively effected by increasing SLA ($F_{1,29} = 4.18$, $R^2 = 0.50$, $p < 0.01$) and N ($F_{1,27} = 9.95$, $R^2 = 0.65$, $p < 0.01$).

The second principle axis (PC II) shows that higher scores represented species with high LFD (i.e. fineleaved), which were spiny (physically defended) and were leguminous (*Acacia spp.* and *D. cinerea*) (Fig. 2.4a and b, Table 2.3). Lower scores along PC II corresponded to species with low LFD (broad leaved), that were generally not spiny (*H. pauciflorus*, *Dombeya rotundifolia*, *Diospyros dichrophylla* and *Kraussia floribunda*) and included species that contain higher levels of toxin (possibly alkaloids) (*S. africana* and *A. glabrata*). From the species abundance distribution curves (Fig. 2.2 a-f), we know that these species that were positively correlated along PC II were abundant and formed an important contribution to the browsers diet even though they were not highly preferred. Black rhino preference tended to be negative along PC II with high preference and contribution to the diet of woody species that contained toxins (*S. africana* contributed 17 % to the black rhino diet) (Fig. 2.4 a and c, Table 2.3).

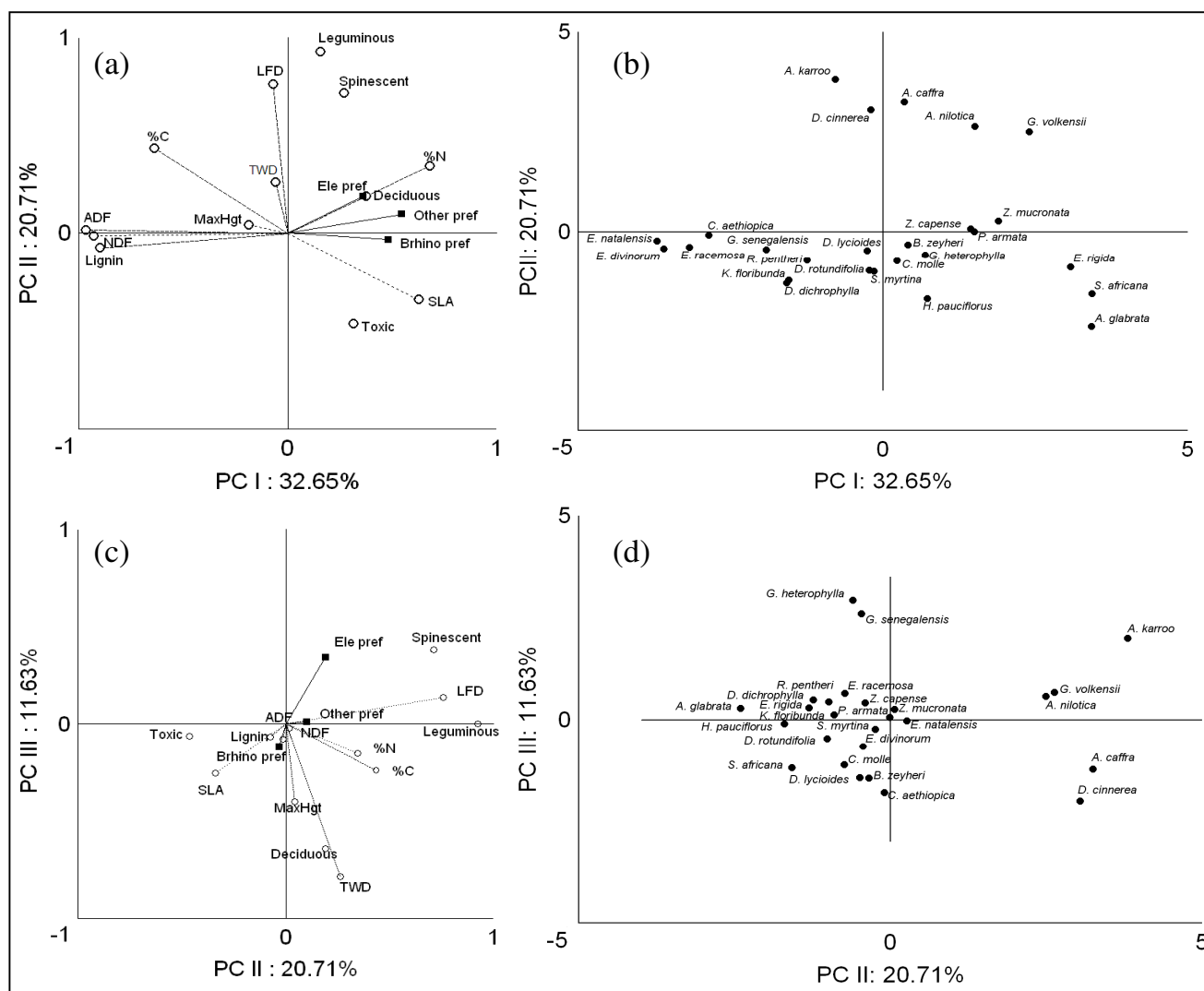


Figure 2.4: Browser preference in relation to chemical and morphological plant traits: Plots of axes PC I vs. PC II and PC II vs. PC III, representing morphological and chemical constituents of leaves for 26 indigenous abundant woody species found within HiP. Within plots (a) and (c), the first ordination axis represents the SLA (nutritional) axis from left to right, negative values represent woody species with high fibre content, low SLA and low % N, positive values represent high SLA, high % N and low fibre. Along the second ordination axis, positive values represent species that were fineleaved (high LFD), leguminous and spiny, negative values represent species that were broadleaved (low LFD) and have few physical defences. The third ordination axis (MaxHgt axis) is represented along the y-axis, where negative values comprise mostly deciduous woody species with high MaxHgt, high TWD and broad leaves and positive represent mostly evergreen species with lower MaxHgt, lower TWD and fine leaves. Plots (b) and (d) represent the individual woody species distributed within the corresponding ordination space to plots (a) and (c) respectively. Acronyms: SLA = Specific leaf area, MaxHgt = Maximum height, LFD = leaf fractal dimension, TWD = twig wood density, ADF = Acid detergent fibre, NDF = Neutral detergent fibre, % N = nitrogen content, % C = Carbon content. Plant species: *S. myrtina* = *Scutia myrtina* and *Z. capense* = *Zanthoxylum capense*, full names for all other species are included within the text.

Table 2.3: Browser preference in relation to the three main ordination axes: Showing, per species the dietary preference (pref) and % diet contribution (% diet) for black rhino (Brhino), elephant (Ele) and a group of other browsers relative tot the total number of individual trees sampled (n individuals = 9 894). Scores of species along the three ordination axes and vector values including; average specific leaf area (SLA), leaf fractal dimension (LFD), nitrogen (N), carbon (C), neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin, twig wood density (TWD), maximum tree height (MaxHgt), spinescence, leguminous, deciduous and toxic.

| Species | Total # Individuals sampled | Principal component (PC) scores | | | Browser preference and dietary contribution per species | | | | | | Vector values for principle component analysis | | | | | | | | | | | | |
|---------------------------------|-----------------------------------|------------------------------------|-------------------|--------------------|--|----------------|---------------|-------------|-----------------|---------------|--|--|-----|------|------|------|--------|--------------------------|---------------|------------|------------|-----------|-------|
| | | PC I (32.65%) | PC II (20.71%) | PC III (11.63%) | Brhino % diet | Brhino pref | Ele % diet | Ele pref | Other % diet | Other pref | SLA (g/cm ²) | LFD (area cm ² / perimeter cm) | N | C | NDF | ADF | Lignin | TWD (g/cm ³) | MaxHgt (m) | Spinescent | Leguminous | Deciduous | Toxic |
| <i>Spirostachys africana</i> | 564 | 3.4 | -1.6 | -1.2 | 17.5 | 2.6 | 5.6 | 0.1 | 3.5 | -0.3 | 118.1 | 2.0 | 1.9 | 44.9 | 23.7 | 15.5 | 3.7 | 1.0 | 10.0 | no | no | deciduous | yes |
| <i>Acalypha glabrata</i> | 238 | 3.4 | -2.4 | 0.3 | 0.9 | -0.7 | 5.6 | 1.1 | 5.2 | 0.9 | 179.2 | 1.9 | 1.9 | 43.9 | 27.1 | 22.1 | 4.9 | 0.9 | 5.0 | no | no | evergreen | yes |
| <i>Ehretia rigida</i> | 114 | 3.1 | -0.9 | 0.1 | 2.3 | 0.7 | 0.2 | -0.9 | 1.2 | 0.0 | 126.1 | 2.0 | 2.6 | 44.6 | 29.8 | 20.9 | 6.1 | 0.7 | 6.0 | no | no | deciduous | no |
| <i>Gardenia volkensii</i> | 82 | 2.4 | 2.5 | 0.6 | 3.0 | 1.7 | 3.4 | 2.1 | 2.2 | 1.2 | 72.2 | 4.4 | 2.1 | 45.8 | 30.5 | 24.6 | 4.1 | 0.9 | 7.0 | yes | yes | deciduous | no |
| <i>Ziziphus mucronata</i> | 99 | 1.9 | 0.3 | 0.0 | 0.9 | 0.1 | 0.2 | -0.8 | 1.5 | 0.8 | 116.7 | 1.4 | 2.7 | 47.7 | 38.3 | 30.0 | 9.9 | 0.8 | 10.0 | yes | no | deciduous | no |
| <i>Acacia nilotica</i> | 333 | 1.5 | 2.6 | 0.7 | 1.9 | -0.2 | 5.2 | 1.2 | 2.4 | 0.1 | 74.4 | 3.5 | 1.7 | 52.0 | 23.1 | 22.0 | 4.6 | 1.1 | 6.0 | yes | yes | evergreen | no |
| <i>Plectroniella armata</i> | 181 | 1.5 | 0.0 | 0.1 | 1.5 | 0.0 | 1.1 | -0.3 | 2.0 | 0.3 | 126.7 | 1.8 | 1.6 | 48.5 | 30.9 | 28.6 | 11.9 | 0.9 | 7.0 | yes | no | deciduous | no |
| <i>Zanthoxylum capense</i> | 76 | 1.4 | 0.1 | 0.3 | 1.1 | 0.2 | 0.5 | -0.5 | 1.8 | 0.9 | 140.1 | 2.8 | 2.4 | 45.8 | 37.5 | 31.0 | 12.5 | 0.9 | 15.0 | yes | no | evergreen | no |
| <i>Hippobromus pauciflorus</i> | 130 | 0.7 | -1.7 | -0.1 | 1.5 | 0.5 | 1.9 | 0.9 | 1.1 | 0.2 | 133.4 | 2.3 | 1.7 | 47.6 | 41.4 | 33.3 | 14.8 | 1.0 | 4.0 | no | no | evergreen | yes |
| <i>Gymnosporia heterophylla</i> | 126 | 0.7 | -0.6 | 2.9 | 1.1 | -0.1 | 2.2 | 0.7 | 0.7 | -0.5 | 59.2 | 2.0 | 1.3 | 43.6 | 37.7 | 31.2 | 8.6 | 0.6 | 6.0 | yes | no | evergreen | no |
| <i>Berchemia zeyheri</i> | 122 | 0.4 | -0.3 | -1.5 | 0.8 | 0.0 | 0.6 | -0.2 | 1.1 | 0.4 | 103.9 | 2.8 | 2.0 | 46.4 | 39.7 | 36.6 | 16.4 | 1.0 | 12.0 | no | no | deciduous | no |
| <i>Acacia caffra</i> | 139 | 0.4 | 3.3 | -1.2 | 0.9 | -0.4 | 1.6 | 0.0 | 1.8 | 0.2 | 70.7 | 3.5 | 2.8 | 51.8 | 41.6 | 35.8 | 15.8 | 1.0 | 12.0 | yes | yes | deciduous | no |
| <i>Combretum molle</i> | 199 | 0.2 | -0.7 | -1.1 | 0.9 | -0.6 | 3.8 | 0.7 | 3.2 | 0.4 | 92.6 | 0.8 | 1.5 | 49.9 | 37.6 | 32.5 | 9.2 | 0.9 | 12.0 | no | no | deciduous | no |
| <i>Dombeya rotundifolia</i> | 151 | -0.1 | -1.0 | -0.5 | 2.5 | 0.6 | 1.9 | 0.2 | 1.3 | -0.1 | 85.6 | 1.0 | 1.4 | 47.1 | 41.9 | 34.9 | 18.4 | 1.0 | 5.0 | no | no | deciduous | no |
| <i>Dichrostachys cinerea</i> | 1614 | -0.2 | 3.1 | -2.0 | 13.0 | -0.3 | 9.5 | -0.5 | 19.8 | 0.1 | 127.7 | 5.2 | 1.8 | 49.9 | 47.4 | 42.0 | 19.7 | 1.4 | 7.0 | yes | yes | deciduous | no |
| <i>Scutia myrtina</i> | 51 | -0.2 | -1.0 | 0.4 | 0.6 | 0.1 | 0.6 | 0.3 | 0.9 | 0.8 | 83.3 | 1.7 | 2.0 | 46.4 | 44.1 | 34.9 | 14.9 | 0.7 | 15.0 | no | no | evergreen | no |
| <i>Diospyros lycioides</i> | 367 | -0.2 | -0.5 | -1.4 | 1.3 | -0.7 | 0.3 | -0.9 | 1.6 | -0.6 | 120.8 | 2.7 | 1.8 | 47.2 | 41.6 | 39.5 | 26.5 | 1.1 | 7.0 | no | no | deciduous | no |
| <i>Acacia karroo</i> | 597 | -0.8 | 3.8 | 2.0 | 8.7 | 0.2 | 11.3 | 0.5 | 10.6 | 0.4 | 65.7 | 9.2 | 2.1 | 49.8 | 43.2 | 41.3 | 21.7 | 0.8 | 7.0 | yes | yes | evergreen | no |
| <i>Rhus pentheri</i> | 239 | -1.2 | -0.7 | 0.6 | 2.6 | 0.2 | 3.0 | 0.3 | 1.8 | -0.2 | 120.3 | 3.3 | 1.6 | 48.8 | 46.4 | 44.6 | 24.2 | 0.8 | 6.0 | no | no | evergreen | no |
| <i>Kraussia floribunda</i> | 173 | -1.5 | -1.2 | 0.5 | 1.3 | -0.3 | 1.3 | -0.3 | 1.6 | -0.1 | 113.0 | 1.3 | 1.4 | 49.6 | 42.2 | 41.1 | 33.3 | 0.8 | 6.0 | no | no | evergreen | no |
| <i>Diospyros dichrophylla</i> | 157 | -1.6 | -1.3 | 0.3 | 3.0 | 0.6 | 0.6 | -0.7 | 1.8 | -0.1 | 83.3 | 2.7 | 1.6 | 50.0 | 45.4 | 46.7 | 27.0 | 0.8 | 10.0 | no | no | evergreen | yes |
| <i>Gymnosporia senegalensis</i> | 516 | -1.9 | -0.5 | 2.6 | 1.1 | -0.8 | 3.9 | -0.2 | 2.9 | -0.4 | 57.0 | 1.7 | 1.1 | 47.1 | 50.4 | 50.3 | 22.3 | 0.6 | 4.0 | yes | no | evergreen | no |
| <i>Cassine aethiopica</i> | 53 | -2.9 | -0.1 | -1.8 | 0.2 | 0.9 | 0.0 | -1.0 | 0.1 | -0.4 | 56.1 | 2.7 | 1.1 | 49.6 | 54.8 | 51.6 | 23.6 | 1.1 | 15.0 | no | no | deciduous | no |
| <i>Euclea racemosa</i> | 858 | -3.2 | -0.4 | 0.4 | 1.3 | -0.8 | 4.2 | -0.3 | 3.9 | -0.3 | 58.9 | 3.3 | 1.0 | 50.2 | 50.9 | 51.1 | 27.3 | 0.8 | 12.0 | no | no | evergreen | no |
| <i>Euclea divinorum</i> | 315 | -3.6 | -0.4 | -0.7 | 0.6 | -0.8 | 2.2 | -0.2 | 0.8 | -0.7 | 63.5 | 2.1 | 1.2 | 50.0 | 57.9 | 58.4 | 27.8 | 1.2 | 8.0 | no | no | evergreen | no |
| <i>Euclea natalensis</i> | 108 | -3.7 | -0.2 | -0.2 | 0.2 | -0.8 | 0.6 | -0.4 | 0.7 | -0.4 | 51.8 | 2.0 | 1.2 | 53.1 | 55.0 | 50.1 | 30.8 | 1.0 | 10.0 | no | no | evergreen | no |

The browser preference index (pref) is the deviance of observed from expected frequencies: (pref = (observed browsed - expected browsed) / observed browsed)) (Williams 2005).

The third principle axis represented an increase in properties related to MaxHgt, i.e. taller species that were mostly deciduous, with higher total TWD; with *Combretum molle*, *A. caffra*, *D. lycioides*, *Berchemia zeyheri*, *Cassine aethiopica* and *D. cinerea* positively correlated with PC III (Fig. 2.4c and d, Table 2.3). Differentiation among the browser preferences occurs along the third axis, where elephant preference was positively correlated with shorter, evergreen, spinescent species with lighter TWD (*A. karroo*, *Acacia nilotica* and *Gardenia volkensii*). Black rhino and other browsers' preference continued to be aligned with the SLA (digestibility traits), although black rhino tend toward species that contained high levels of toxin.

2.5. DISCUSSION

Mechanisms for resource partitioning that determine the coexistence of a diverse guild of browsers include the vertical and horizontal stratification of the forage resource (e.g. canopy height and architecture, species heterogeneity and abundance, chemical composition and morphological woody traits) and interspecific differences related to body size (e.g. metabolic morphology, tolerance for lower quality forage and metabolic adaptations to mitigate the effect of toxins) (Jarman and Sinclair 1979; Owen-Smith and Cooper 1987; du Toit and Owen-Smith 1989; Skarpe et al. 2000; du Toit 2003; Palmer et al. 2003; Cromsigt and Olff 2006; Fornara and du Toit 2008). The capacity of fragmented conservation areas to support populations of large herbivores is limited because available resources and maximum productivity are ultimately restricted by boundary fences and neighbouring agricultural communities (Owen-Smith 1988; Ritchie and Olff 1999; Chapin et al. 2000). Therefore direct management of the natural systems is essential to sustaining viable populations within these diverse communities (Owen-Smith 1988; Chapin et al. 2000).

The large browsers of HiP depended highly on common, abundant woody species that were mostly found in fineleaved and broadleaved woodlands. However in addition they highly preferred several rare species found in all habitat types throughout HiP. Browsers require a mixed diet in order to assist in detoxification of plant chemical deterrents and to obtain a nutritionally balanced diet (Owen-Smith and Cooper 1987; Provenza 1995; Skarpe et al. 2000; Provenza 2003; Shaw et al. 2006). Iason (1999) presents data on how lower quality diets need longer retention time for adequate digestion and nutrient extraction. By adding relatively small quantities of high nutritional quality forage to the diet, time required for nutrient extraction is lowered and therefore the diet becomes more balanced between bulk lower quality forage and high quality nutrient rich species (Demment and van Soest 1985). Therefore, the high woody species diversity found in HiP may be very important to sustain the current high levels of browsers, especially critically endangered black rhino. Black rhino populations in East Africa show very slow rates of recovery

despite intensive protection which may be attributable to low vegetation diversity as found in Ngorongoro (Moehlman et al. 1996).

In our study, the highest dietary overlap was found between elephant and other browser species' and the lowest dietary overlap was found between elephant and black rhino indicating a mostly separated diet. So, although on a between-plots level the utilisation of sites was positively correlated between elephant and black rhino, within-plot the two main browsers strongly partitioned resources. Understanding diet overlap between black rhino and elephant was an important outcome of this study, given the critically endangered status of black rhino (Slotow et al. 2001; IUCN 2008) and the potential negative impact that a large population of elephant can inflict on the vegetation (Fritz et al. 1996; Makhabu et al. 2006). Therefore, our findings highlight the potential negative impact from the growing elephant population on important black rhino forage resources, i.e. by causing shifts in the woodland composition, specifically the rare higher quality species that are a critical component of black rhino diet (Oloo et al. 1994), this should be monitored within the three lower elevation habitat types (i.e. riverine forest, broadleaved woodland and fineleaved woodlands). Elephant damage to woody species within the height class >2.0 m (i.e. above the forage height of black rhino and antelope) indicated that elephant utilized the full spectrum of forage available, positively selecting for some species (*Schotia brachypetala*, *Acacia robusta* and *Sclerocarya birrea* being most preferred) and negatively selecting for others (*Gymnosporia senegalensis*, *S. africana* and *Heteropyxis natalensis* being least preferred). It is interesting to note that the most preferred species of black rhino (*S. africana*) is one of the least preferred forage species of elephant; so it is unlikely that elephant facilitate black rhino foraging by making *S. africana* more accessible by breakage. The results pertaining to diet overlap between the various browsers are specific to HiP and the ability to extrapolate to other areas may be limited.

Factors that determine acceptability of foliage to herbivores include morphological features (e.g. SLA, LFD, MaxHgt and spinescence), digestibility (e.g. proteins and fibre) and chemical defences (e.g. phenolics, condensed tannins and other secondary plant metabolites) (Demment and van Soest 1985; Owen-Smith and Cooper 1987; Iason and van Wieren 1999; Iason and Villalba 2006). Plant morphological and chemical adaptations to herbivory, and conversely herbivore adaptations to cope with plant traits, are reflected in the nutrient and digestibility properties (Iason and van Wieren 1999; Iason and Villalba 2006). Plants allocate resources to rapid growth or defence mechanisms depending on the availability of resources relative to loss of resources from herbivory (Skarpe et al. 2000) and the availability of resources (Coley et al. 1985). Herbivores select food and feeding habitats in order to maximize intake rate of nutrients and digestible

energy, while avoiding chemical and structural deterrents (Owen-Smith and Cooper 1987; Skarpe et al. 2000; Iason and Villalba 2006). The most effective plant defence is often dependent on environmental conditions, which causes a variety of defence mechanisms to co-occur in the same region (Belovsky and Schmitz 1994).

Of the four trait-based plant ecological strategies described by Westoby (2002) we were able to assess two (SLA and MaxHgt) with respect to their importance to browser preference, high SLA (i.e. thin leaves, low fibre content and high N content) was preferred by all browsers. In the PCA analyses of morphological and chemical woody species properties, we found that the first ordination axis corresponded to higher SLA, lower fibre and higher N contents. From a herbivore perspective, plant species with lower scores on this axis are more digestible, but herbivores may need more time to collect enough leaf material from these species (Iason and van Wieren 1999; Iason and Villalba 2006)). From a plant's perspective, these traits contribute to a higher relative growth rate (Poorter et al. 1990; Poorter and Bergkotte 1992; Wright et al. 2004). The second ordination axis distinguishes between fineleaved and broadleaved species. The species that correspond positively along PC II are generally abundant and form an important contribution to the browsers diet, even though they are not highly preferred. This substantiates findings within the literature that more abundant forage species are lower in quality and have more physical morphological defences to reduce herbivory (Demment and van Soest 1985; Owen-Smith and Cooper 1987; Skarpe et al. 2000). The third ordination axis (MaxHgt) was found to be independent of the SLA axis (Westoby et al. 2002), and browser preference was intermediate tending towards shorter species (i.e. lower MaxHgt, low LFD and low TWD), especially by elephant. Elephant and other browsers' in HiP prefer fast growing, high SLA, low fibre, high leaf N species, with fine leaves, short stature, and light wood. Black rhino prefer high SLA, low fibre, high leaf N species, but tend toward species with broad leaves, denser wood with some preferred species showing higher levels of toxin (milky latex of the Euphorbiaceae) (Pooley 1993; Coates Palgrave 2002). Therefore there is a strong species-level niche differentiation among browsers, probably based on interspecies differences among browsers in detoxification mechanisms.

The coexistence of species that compete for the same class of resource can partly be explained by interspecific differences related to body size (Cromsigt and Olff 2006). Differences in body size create variation in availability of the forage resource (Ritchie and Olff 1999; du Toit 2003). Our study clearly illustrates the principle that larger herbivores utilize lower quality forage at a coarser scale (low diet diversity) than smaller herbivores (high diet diversity and high dietary overlap with larger species) (Ritchie and Olff 1999). Dietary species overlap between different sized browsers can be higher due to the vertical partitioning in use of the forage resource (du Toit 2003;

Makhabu 2005). Similar sized browsers (in this case mega-browsers >1000 kg) dietary overlap was low, which may indicate past competitive pressures resulting in differential use of the available forage species (Lawlor 1980). Black rhino compete with other smaller browser within the < 2 m height class. We found that black rhino claim an exclusive niche by utilizing abundant forage species with poisoned latex (*S. africana* and *A. glabrata*) (Hitchins 1969; Emslie and Adcock 1990; Pooley 1993; Emslie 1999; Coates Palgrave 2002), but perhaps with the repercussion of having to select a wide range of other species to facilitate detoxification (Owen-Smith and Cooper 1987; Skarpe et al. 2000; Iason and Villalba 2006). This would suggest that black rhino need a habitat with a high tree diversity (Oloo et al. 1994) in order to compete successfully for resources with other browsers'. Black rhino diet composition is different to the diet composition of other browsers', in that other herbivores generally select a diet that limits intake of species with high levels of toxin, or at least includes small amounts of species containing toxins together with biochemically complimentary species that diminish the effects of toxin (Provenza 1995, 2003; Shaw et al. 2006). Generalist browsers may also switch resources enhancing their competitive advantage over specialist browsers e.g. elephant utilize graminoid species in the wet season and switch to a more fibrous browse diet in the dry season (Owen-Smith 1988). Black rhino conversely are specialist browsers that do not adapt to unsuitable habitats (McKinney and Lockwood 1999), and have no alternative forage resource to switch to, although it has been documented that small succulent forbs form part of their diet during the wet season (Oloo et al. 1994; Emslie 1999). This poses a problem for the black rhino who utilize the browse forage resource within the same height range as the small to medium antelope species. How can the black rhino successfully compete for forage? We propose that black rhino have different strategic and metabolic mechanisms to eliminate toxins or their effects. Black rhino utilize abundant woody species (such as *S. africana* and *A. glabrata*) with high secondary plant compounds. Black rhino also have a wide diet breadth utilizing many of the rarer woody species (Oloo et al. 1994; Emslie 1999), thereby countering the effects of the toxin through mixing abundant (but toxic) forage with many high nutritional quality species that are biochemically complimentary, and which mitigate the effects of the toxin (Freeland and Janzen 1974; Provenza 1995; Iason and van Wieren 1999; Provenza 2003).

Elephant are mega-browsers (body size of > 1000 kg) whose populations are not depressed by predation (in contrast to medium sized browsers, in this case other browsers') (Owen-Smith 1988), or by natural density dependent processes (e.g. nutritional stress) (Gough and Kerley 2007; Woolley et al. 2008). Elephant are gregarious mixed feeders who utilize the browse forage resource within the fine-leaved and broadleaved woodlands approximately equal to the relative abundance and diversity, and are known as the largest contributor to structural and compositional

alteration of vegetation (Fritz et al. 1996; Makhabu et al. 2006). Black rhino mega-browsers, but in contrast to elephant, are solitary, at most being accompanied by a single calf, and are highly selective browsers (Owen-Smith 1988). Therefore we expected lower diet diversity as they show strong selection for specific species, both within the abundant and rarely occurring woody species (highly preferred species are used more than would be expected in relation to their abundance causing a deviation above the community SAD e.g. highly preferred *S. africana*). Black rhino are one of the most critically endangered (Slotow et al. 2001; IUCN 2008) of the mega browser species, the survival of which has become tenuous and Africa wide conservation groups are searching for suitable areas to establish founder populations through translocation from founder populations (Emslie and Brooks 1999). Threats to key founder populations need to be carefully managed and monitored, and the unchecked expansion of the elephant population has been identified as a potential threat to the survival of black rhino (Oloo et al. 1994; Emslie and Brooks 1999). The carrying capacity of small enclosed protected areas is very limited and the local mismanagement of herbivore populations can lead to overpopulation which threatens the integrity of spatial vegetation heterogeneity and species diversity (Fritz 2002; Makhabu 2006). Species abundance distributions can be used to detect degradation of a community (Hill and Hamer 1998). Therefore if the population of elephants exceeds the carrying capacity of HiP, the SAD for highly impacted habitat types will indicate a log-series distribution in place of the log normal distribution (Hill and Hamer 1998) which is currently observed, i.e. indicating that impact from elephants on these habitats is not currently above carrying capacity.

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3. THE EFFECT OF THE INVASIVE WEED *CHROMOLAENA ODORATA* ON THE CRITICALLY ENDANGERED BLACK RHINO IN HLUHLUWE-IMFOLOZI PARK, SOUTH AFRICA

Ruth A. Howison, Mariska te Beest, Rob Slotow & Han Olff

3.1. ABSTRACT

African savannas are fragmented by agriculture and urbanisation, and threatened by invasion of exotic species. Black rhino (*Diceros bicornis*) are critically endangered and their declining global population is directly affected by these threats. The black rhino population in Hluhluwe-iMfolozi Park (HiP), South Africa, has been declining since 1993, possibly due to the invasion of an exotic plant *Chromolaena odorata*. We assessed changes in the overall spatial distribution of the black rhino population between two discrete time periods then calculated core home ranges for black rhino with 30 or more sightings. Using GIS we related changes in distribution and home range area to the temporal expansion of *C. odorata*. Finally we assessed the woody species composition and utilisation by black rhino along random vegetation transects across the *C. odorata* prevalence gradient. We found a shift in the distribution of the black rhino population toward the south between 1998 and 2004 and indigenous vegetation types invaded by *C. odorata* were used significantly less over this period. Core home ranges did not change in size over time, however home ranges in the north contain a significantly higher proportion of *C. odorata* than in the southern home ranges. *Spirostachys africana* contributed a large proportion of the diet and was highly preferred, but the local presence of *C. odorata* significantly reduced utilization of this food source. We conclude that the invasion of *C. odorata* negatively impacts forage species utilization, leading to a spatial reorganization of the black rhino population. This may explain the recent decline in the population. Therefore, biotic homogenization through the introduction of invasive species can contribute to the extirpation of endangered species.

3.2. INTRODUCTION

Expanding human populations in African savannas are currently causing many species to become critically endangered, especially through habitat loss and overexploitation of populations (Oloff et al. 2002; Wessels et al. 2003; Western 2003). The black rhino (*Diceros bicornis minor*) is one of these critically endangered species whose global population has declined from several hundred thousand individuals, to 3700 individuals (Sherriffs 2007; IUCN 2008). The species is now limited predominantly to small enclosed wildlife sanctuaries and conservancies where intensive law enforcement and management can be effectively implemented (IUCN 2008). These small conservation areas require careful management to maintain suitable habitat for black rhino, and the populations should be monitored closely to maintain a critical balance between ecological carrying capacity and maximum population growth for sustainable harvesting to form new populations (Emslie 1999). Black rhino populations are facing many challenges, especially poaching (Western 1987; Mills et al. 2006), habitat deterioration (Emslie 1999; Reid et al. 2007), disease (Birkett 2002; Mills et al. 2006) and interspecific competition (Birkett 2002; Mills et al. 2006). South Africa is one of only four African countries in which successful black rhino conservation has been achieved (IUCN 2008). The black rhino population of Hluhluwe-iMfolozi Park (HiP), categorised as an A1 key population (Brooks 1993), is essential to the global metapopulation management of the species as a donor population (Slotow et al. 2001). After Kruger Park, it holds the second largest population of this species globally (Smit 2003). However, of great concern is the decline in numbers from 429 individuals in 1993 (Reid et al. 2007) to 264 individuals in 2004 (EKZNW unpublished data).

Invasive alien species are increasingly seen as a threat to all aspects of biodiversity, including endangered species (Mooney and Drake 1986; Leslie and Spotila 2001; Keane and Crawley 2002; Turpie 2003; Strayer et al. 2006). Human activities have broken traditional dispersal barriers between the major bioregions of the earth, leading to large exchanges of plant species between continents that had separate flora before (Mooney and Drake 1986). *Chromolaena odorata*, a species that has invaded grasslands, savannas and forests of Asia, Africa and the Pacific is among the worst 100 invasive species (ISSG 2008), replacing indigenous vegetation with exotic monocultures, thus altering the habitat to a degree that threatens the diversity of resident flora and fauna (Witkowski 2001; Mgobozi et al. 2008). In the long term, species in a community may shift towards communities that are resistant to the effects of the invader (Levine et al. 2004; Parker and Hay 2005; Strayer et al. 2006). However, these changes may result in irreversible ecological and economic consequences (e.g. elimination of native species) (Leslie and Spotila 2001; Strayer et al.

2006). Few studies have shown the true impacts of invasive species on endangered herbivore species, especially for large mammals (McKinney and Lockwood 1999; Leslie and Spotila 2001; Gaston and Fuller 2007). A thorough knowledge of invasive plant species ecology is therefore required to ascertain the level of risk the invader poses to indigenous species, and especially threatened indigenous species (Mooney and Drake 1986; Leslie and Spotila 2001; Strayer et al. 2006).

Originating from Central America and the Caribbean (McFadyen and Skarratt 1996; von Senger et al. 2000; Kriticos et al. 2004; Raimundo et al. 2007), *Chromolaena odorata* is a species that has now invaded the tropical regions of Asia, Africa and the islands of the Pacific, and worldwide is among the worst 100 invasive species (ISSG 2008). It replaces indigenous vegetation with exotic monocultures, thus altering the habitat to a degree that threatens the diversity of resident flora and fauna (Witkowski 2001; Mgobozi et al. 2008). In the long term, species in ecological communities may shift towards communities that are resistant to the effects of the invader (Levine et al. 2004; Parker and Hay 2005; Strayer et al. 2006). However, these changes may result in irreversible ecological and economic consequences (e.g. extinction of native species) (Leslie and Spotila 2001; Strayer et al. 2006). A thorough knowledge of invasive species ecology, including their impacts, is therefore required to ascertain the level of risk the invader poses to indigenous species, and especially threatened indigenous species (Mooney and Drake 1986; Leslie and Spotila 2001; Strayer et al. 2006).

Chromolaena odorata has invaded the east coast of KwaZulu-Natal, South Africa (Goodall and Erasmus 1996; Richardson and Van Wilgen 2004; Raimundo et al. 2007) over the past six decades. The species has spread alarmingly quickly, and forms dense thickets which exclude natural vegetation (Leslie and Spotila 2001; Witkowski 2001; Richardson and Van Wilgen 2004; Mgobozi et al. 2008), and forms a barrier to mammals such as large ungulates (pers. obs.). *C. odorata* preferentially invades riverine areas (Leslie and Spotila 2001), which are important to black rhino for browse and shelter (Emslie 1999). The steady expansion of *C. odorata* has been mapped within Hluhluwe-iMfolozi Park from when it was first detected in 1961 until 2001 (MacDonald 1978; Howison, O. et al. unpublished data). The main spread of the plant has been concentrated towards the northern part of the park (Howison, O. et al. unpublished data) while the southern areas have remained relatively free of *C. odorata* (EKZNW unpublished data), possibly due to lower rainfall (Balfour and Howison 2001). MacDonald (1983) predicted that this exotic plant would pose the most serious threat to the maintenance of natural vegetation in HiP, a concern that now appears justified (Witkowski 2001).

In this paper, we assess the possible negative effect of the expansion of the exotic invasive *C. odorata* on the black rhino population of HiP. First, we evaluate the population trends and spatial distribution of the rhinos. Secondly, we investigate the spatial reorganisation of the black rhino through the calculation of home ranges from individual sightings, which are compared in location and size between two time periods (before and during the major expansion of *C. odorata* through HiP) for male and female rhino. Finally, we explore shifts in black rhino foraging preference and selection due to *C. odorata* invasion through diet observations along transects, where browsing by black rhino could be uniquely identified from other browsers’.

3.3. METHODS

3.3.1. Study site

HiP is an 890 km² fenced game reserve situated in the north-eastern KwaZulu-Natal, South Africa. The park is divided into five management sections, Makhamsa and Nqumeni (north) and Masinda, Mbuzane and Makhamsa (south) (Fig. 3.1a). The mean annual rainfall declines from 985 mm in the north to 650 mm in the south and is positively correlated with elevation (Balfour and Howison 2001) (Fig. 3.1b). The highest elevation (584 m) is at the northwest of the Hluhluwe section with a steady south-eastward decline in elevation towards the confluence of the black and white Umfolozi rivers (38 m) (Fig. 3.1c) (Whateley and Porter 1983; Schulze 2003; Crooms and Olf 2008). As a consequence of the variation in elevation and rainfall, vegetation is heterogeneous with vegetation types ranging from open grasslands to closed *Acacia* and broad-leaved woodlands (Whateley and Porter 1983; Archibald et al. 2005). Daily temperatures range from a minimum of 13 °C in the cooler and drier winter season (May-October) to a maximum of 35 °C in the warmer and wetter summer (November – April) (MacDonald 1978; Brooks and MacDonald 1983). A specialized black rhino monitoring program is conducted within HiP where a mark and recapture technique is used. Marking of rhino include ear notching together with micro chipping, and use of natural uniquely identifiable body markings (MacDonald 1978; Hitchins 1990). Identikits and pedigrees are compiled for all uniquely identifiable rhino (Conway et al. 2001). Annual population estimates are derived from ongoing identification data that includes; births, sightings, introductions, removals and mortalities, using the Bayesian mark-recapture software package ‘RHINO’ (Emslie and Brooks 1999; Emslie 1999; Conway et al. 2001).

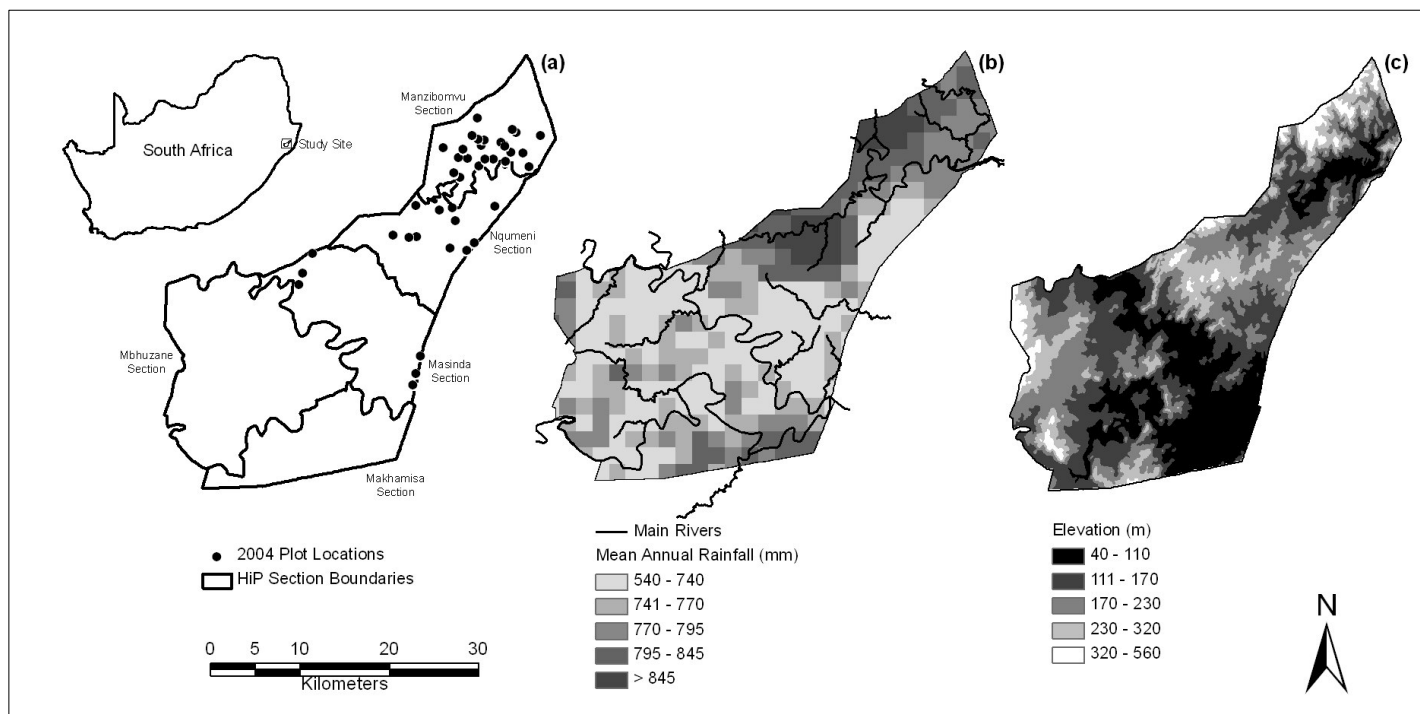


Figure 3.1: Geographic context of the study site. (a) The location of Hluhluwe-iMfolozi Park within South Africa, the five management sections of the Park; Manzibomvu and Nqumeni (north), Masinda, Mbhuzane and Makhamsa (south) and the location of the browser impact plots sampled in 2004. (b) Major rivers and mean annual rainfall of Hluhluwe-iMfolozi Park, (Schulze 2003). Average rainfall ranges from 980mm p.a. in the north to 540mm p.a. in the south. Most of the rainfall is received between October and March each year. (c) Elevation of Hluhluwe-iMfolozi Park (NASA 2004), ranging from 584 m in the north to 38 m in the south east.

3.3.2. Spatial redistribution of black rhino

To map the spatial redistribution of black rhino within HiP we used spatially explicit black rhino sighting data collected in HiP by field rangers whilst conducting their daily security patrols of the Park. Sighting data were collected from 1991 – 1999 on 1:50 000 topographic paper maps with a 1 km² Lo31 grid superimposed (minimum resolution for data analysis of 1 km²). From the year 2000 onwards the data were collected with higher spatial precision (50 m) using GPS. All coordinates of black rhino sightings were plotted on a map and validated against original records; sightings that could not be corrected/verified were discarded. The sighting data were then divided into two time periods, 1991 – 1997 and 1998 – 2004, representing two time periods in *C. odorata* invasion before and during its major expansion (Howison, O. et al. unpublished data). An observed sighting density raster was calculated using the point density tool (Arc Info 9.x, ESRI), for each of the time periods, at a 1 km² resolution.

A sampling effort bias emerged from the observed sighting data, with sighting density decreasing with distance from field ranger outpost. To correct for the resulting spatial variation in sampling effort, we calculated an index for sighting density distribution, for the two time periods based on the observed vs. expected values, which we termed 'observer-bias-corrected sighting index' (CSI) as follows: To calculate the expected sighting density we created a point map of ranger outposts in a GIS. Using spatial analyst (Arc Info 9.x, ESRI), we used the Euclidian distance tool to calculate a 1 km² resolution raster where each cell represents the linear distance between all ranger outposts, in all directions, contained within the boundary of HiP. We created a point map which placed a point in the centre of each 1km² pixels (termed centroid). Using the Hawth's Tools (Beyer 2004), we intercepted the centroids with the observed sighting density raster and with Euclidean distance raster, to create an attribute table with two fields; 1) observed sighting density and 2) distance from outpost. We then plotted the observed sighting density against distance from ranger outpost, for each of the two time periods. To predict the expected sighting density from the distance from ranger outpost we fitted second order quadratic polynomials through the data; 1991 – 1997 ($y = -0.0364x + 0.525$, $R^2 = 0.79$) and 1998 – 2004 ($y = -0.0423x + 0.6132$, $R^2 = 0.79$). We modelled the expected rhino density spatially by using the raster calculator (Arc Info 9.x, ESRI) and the derived quadratic equations, where x = distance from ranger outpost, and y = the expected sighting density, for each of the time periods. Using the raster calculator, we spatially represented the observer-bias-corrected sighting index (CSI) for each time period as $CSI = \log_{10}((\text{observed}/\text{expected} + 0.1))$. To assess the change in distribution of black rhino, in relation to the vegetation communities over time, we subtracted the CSI calculated for 1998-2004 from the CSI calculated for 1991-1997; using zonal statistics (Arc Info 9.x, ESRI) we appended the mean CSI value per vegetation type polygon.

Stepwise linear regression (Statistica v7.x) was used to model effect of elevation, rainfall and mean fire frequency on the changes in black rhino sightings (corrected for sighting effort) per vegetation type. Using a GIS we calculated the average change in CSI per vegetation type and then, using zonal statistics (Arc Info 9.x, ESRI) calculated the mean annual rainfall (Schulze 2003), mean elevation (NASA 2004) and mean fire frequency (calculated from digitized fire records (1: 50 000) dating back to 1955 (EKZNW unpublished data) per vegetation polygon (Whateley and Porter 1983; EKZNW unpublished data).

To assess the relationship between the changes in spatial distribution of black rhino with the expansion of *C. odorata* over time, we calculated the vegetation types preferentially invaded by *C. odorata*. The presence of *C. odorata* per 0.25 km², was mapped within the Park in 1978, 1980, 1981, 1982, 1983, 1987, 1998, 2000 and 2001 (Fig. 3.2). Using a GIS we calculated the

percentage of each vegetation type invaded by *C. odorata*. To detect differences in vulnerability to invasion by *C. odorata*, per vegetation type we calculated Manly's selection index (MSI), where $MSI = ((\text{Area } C. \text{ odorata present per veg type} / \text{total area of veg type}) / (\text{total area of veg type} / \text{total area of HiP}) / (\text{sum of selection indices of all veg types}))$ (Manly et al. 2002). Stepwise linear regression was used to model effect of rainfall, elevation and fire frequency, for susceptibility of the vegetation types to invasion. Using zonal statistics (Arc Info 9.x, ESRI) we appended the mean MSI value to the vegetation type polygons. Finally the average CSI was correlated with the average MSI per vegetation type.

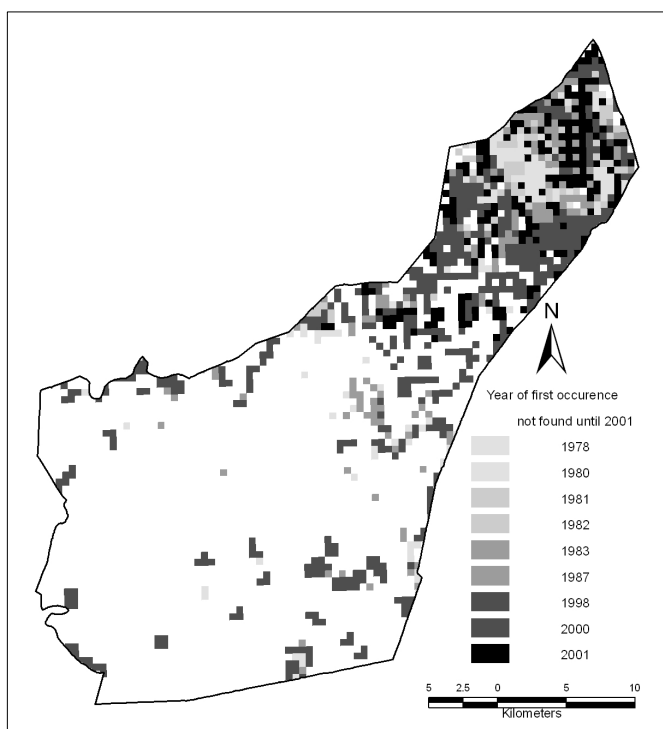


Figure 3.2: Year of first occurrence of *C. odorata* per grid cell (0.25 km^2), representing the expansion of *C. odorata* (1978 – 2001) (Sources: north: Howison, O. et al. unpublished data; south: EKZNW unpublished data). The map indicates that spatially some areas of the park have been heavily invaded in the north while the southern areas have remained relatively free of invasion.

3.3.3. Changes in home range

Changes in home ranges of rhino over time were explored using Kernel home ranges (Hooge and Eichenlaub 2000) for individuals with 30 or more sightings (Seaman and Powell 1996; Reid et al. 2007). Home ranges were then calculated for 37 black rhino in time period one (1991-1997) and 30 black rhino in time period two (1998-2004). We divided the black rhino population for each time period into northern (individuals found in Manzibomvu and Nqumeni) and southern (individuals found in Masinda, Mbuzane and Makhamsa) management sections. This was done to separate individuals found in high prevalence *C. odorata* areas (north) from individuals found in low prevalence *C. odorata* areas (south). Pearson's Chi-square test was used to test for differences among the number of rhino found with 30 or more sightings between the north and south sections and between time period one and time period two. Using movement analysis tools (Arc View 3.x) (Hooge and Eichenlaub 2000), we calculated the average kernel home range size for all black rhino, for 95 % and 50 % home range kernels, within each time period. Using zonal statistics (Arc Info 9.x) we extracted the mean annual rainfall per home range kernel polygon. Using a 2-way ANOVA, we tested for effect of time period (1991 – 1997 and 1998 – 2004), section (north and south of HiP), and sex (male and female) on change in overall home range area, change in home range area containing *C. odorata* and change in area without *C. odorata* present. In addition we tested for differences in average rainfall experienced by male and female home ranges over time and between the northern and southern sections of HiP using a 2-way ANOVA.

3.3.4. Changes in diet choice

To assess diet preference of black rhino, we sampled vegetation within 40 (50 x 4 m) plots, evenly distributed within *C. odorata* prevalence areas (Fig. 3.1a) (Walker 1976; Balfour 2003). Sampling was conducted in June and July of 2004. Starting from a random point, a 50 m line transect was laid out in a north easterly direction. The location of the start and end points of the transects were recorded with a GPS. Within 2 m either side of the line, all trees 0.5 - 2.0 m were assessed, as this is the preferred height range of black rhino (Hitchins 1969; Emslie 1999). For each individual tree, we noted species and the height of the tree was measured (ground to top of living material). Black rhino browse was identified by the characteristic, neatly bitten off branches cut at a 45° angle (Emslie 1999). The prevalence of *C. odorata* cover within each plot was estimated by eye, and was assessed from the zero point of the 50 m centre line and categorised as follows; 0 = 0 % , 1 = 1 – 25 % , 2 = 26 – 50 % , 3 = 51 – 75 % , 4 = 76 – 100 %. Individual trees measured were categorised as either browsed or not browsed by black rhino. A spreadsheet was produced where the number of trees browsed, not browsed, and total number of trees measured per tree species,

was calculated. The abundance of each tree species was calculated ($\text{abundance} = n_{\text{species}} / n_{\text{all trees}}$), and an expected number of individual trees browsed per species could then be calculated ($\text{expected browsed} = n_{\text{browsed}} * \text{abundance}$). A preference index (PI) per species was calculated: $\text{PI} = ((\text{observed browsed} - \text{expected browsed}) / \text{observed browsed})$ (Williams 2005). Species were then ranked in descending order of preference to establish a preferred dietary species list for black rhino. Data for tree species with $n < 50$ were excluded from the analysis due to low sample size. We calculated the number of individual trees per species that were browsed or not browsed per plot. Using Spearman's rank order correlation (Statistica v7.x), between browsing (0 = no, 1 = yes) and the *C. odorata* density class per plot, we tested 16 dietary species for the effect of increasing *C. odorata* prevalence on species utilization by black rhino.

3.4. RESULTS

3.4.1. Spatial redistribution of black rhino

The population size of black rhino increased from the early 1990s until 1997 when the population was estimated to be 409, however thereafter there has been a steady decline in number where in 2004 a population estimate of 264 animals was determined (Fig. 3.3a). The presence of *C. odorata* has strongly increased in the north since the early 1990s, and by 2001 28 % of the 0.25 km² grid cells HiP had already been invaded (Fig. 3.3b).

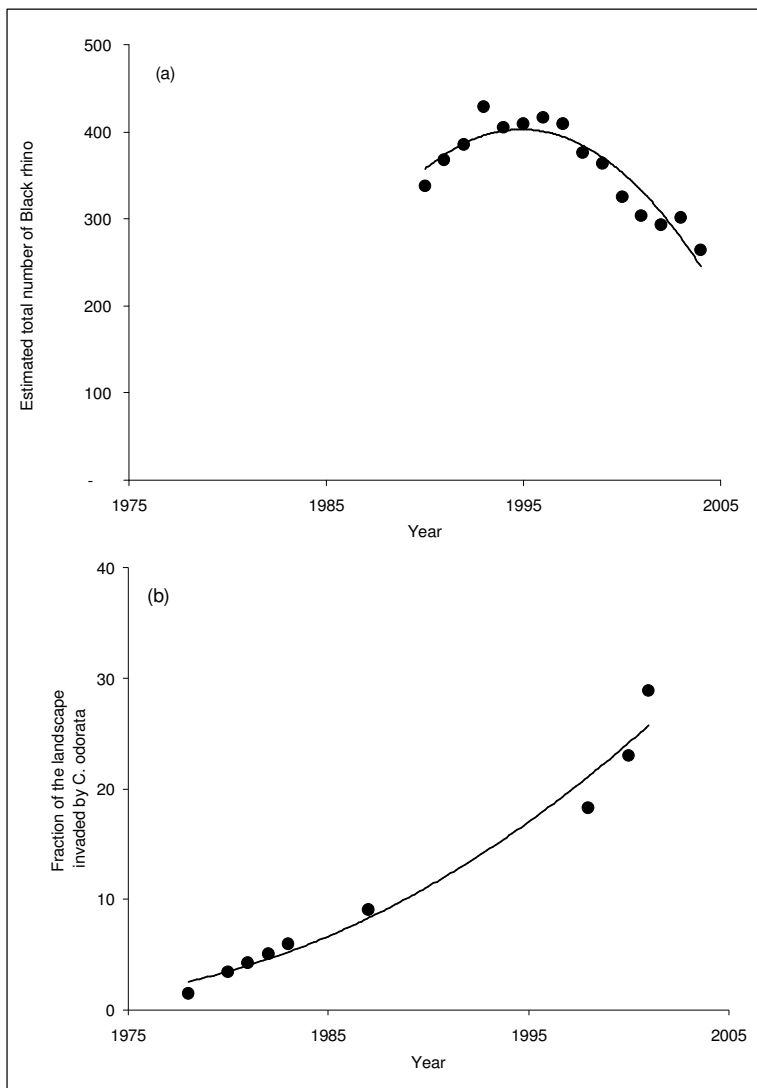


Figure 3.3: Effect of *C. odorata* invasion on black rhino population size. (a) Black rhino census results from 1991 – 2004. (b) Cumulative distribution of *C. odorata* (1978 – 2001), within HiP, showing that *C. odorata* is present in 28 % of the park.

The spatial distribution of the black rhino sightings before the main expansion of *C. odorata* (1991-1997), and during the expansion (1998-2004), showed strong spatial heterogeneity. However, the spatial distribution was associated with the distribution of ranger posts from which the surveys were started, calling for the correction for sampling effort, as outlined in the methods, and used henceforth (Fig. 3.4a and Fig. 3.4b). There were strong spatial differences in the changes between the two periods. In particular northern and central regions of the park showed a decline in sightings, while sightings in particular parts of the south increased (Fig. 3.4c).

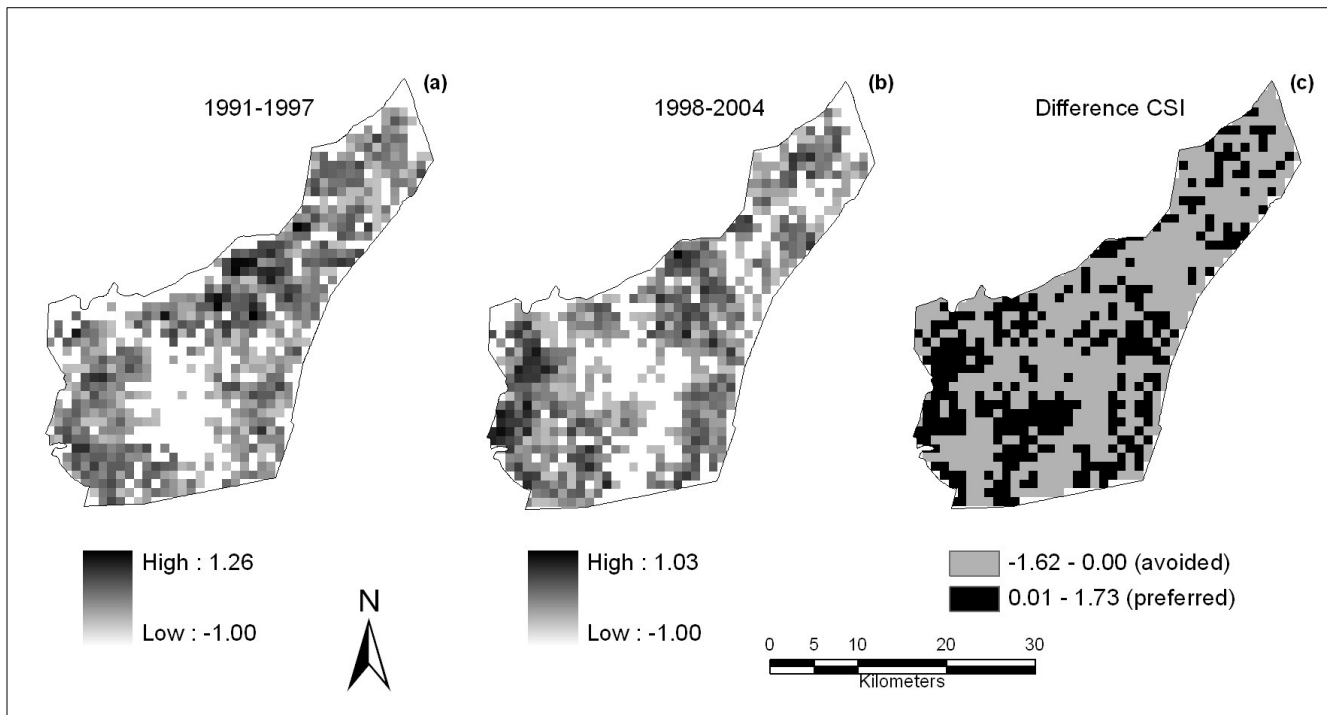


Figure 3.4: Spatial representation of the 'corrected sighting index' ($CSI = \text{Log}_{10}(\text{Obs}/\text{Exp}+0.1)$) which represents the change in spatial distribution of black rhino (corrected for observer bias) for: (a) 1991-1997; (b) 1998-2004; and (c) Difference in CSI, which represents the change in distribution of black rhino over time, with areas that have become avoided (negative values) and areas that have become preferred (positive values)

The increase of *C. odorata* was localized at first: the invasion started in drainage lines at high rainfall in the north, gradually spreading to lower rainfall regions in the south (Fig. 3.2). By relating Manly's 'selection index (MSI) of the 'habitat selection' of *C. odorata* in 2004 for the different main vegetation types mapped for the area by Whateley and Porter (1983) to the average rainfall of each vegetation type (average over all polygons of that type), we found that the preference of *C. odorata* for a different vegetation type exponentially increased with average rainfall (Linear regression: $F_{1,30} = 63.58$, $R^2 = 0.67$, $p < 0.001$). Howison, O. et al. (unpublished data) found that vegetation types initially susceptible to the invasion of *C. odorata* were at higher elevation and higher rainfall. Subsequent to the initial exponential invasion, the higher propagule pressure within highly invaded communities, allowed *C. odorata* to move into adjacent, less susceptible vegetation types in lower rainfall regions (through increased competitive advantage) (Richardson and Pysek 2006; Dawson et al. 2009; Howison, O. et al. unpublished data). Fire

frequency did not significantly affect susceptibility of vegetation type to invasion (Linear regression: $F_{1,30} = 3.07$, $R^2 = 0.09$, $p > 0.05$).

We find a significant negative effect of *C. odorata* invasion (MSI per vegetation type) on rhino distribution (CSI per vegetation type) (Linear regression: $F_{1,30} = 19.56$, $R^2 = 0.39$, $p < 0.001$) (Fig. 3.5). All vegetation communities with a high MSI for *C. odorata* have a low CSI for black rhino, indicating that those vegetation types were actively avoided by black rhino. Within the vegetation communities with a low MSI, some were preferred (high CSI) or avoided (low CSI) vegetation communities. This is expected because there are communities which they did not prefer or were inaccessible due to topological characteristics. Therefore, the change in distribution from time period one (1991-1997) to time period two (1998-2004), represented by average CSI per vegetation type, shows that black rhino avoided areas where *C. odorata* preferentially invaded.

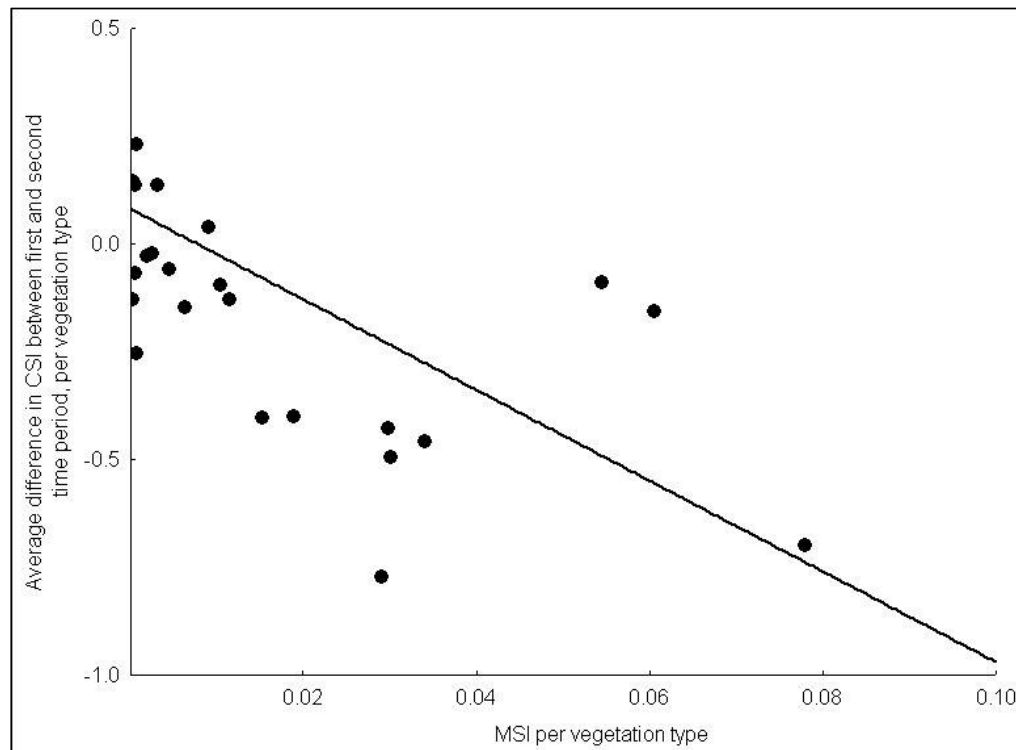


Figure 3.5: Sensitivity (Manly's selection index (MSI)) of vegetation types to invasion by *C. odorata* (high MSI = sensitive vegetation type) in relation to change in distribution of black rhino across vegetation types from time period one (1991-1997) to time period two (1998-2004), represented by average corrected sighting index (CSI) (high CSI = preferred vegetation types), showing that black rhino have begun to avoid vegetation communities that are preferentially invaded by *C. odorata* (i.e. all vegetation communities that have a high Manly's selection index for *C. odorata* are avoided by black rhino).

3.4.2. Changes in home range

Of the 37 black rhino individuals observed from period one (1991 – 1997), with 30 or more sightings, 22 individuals were found in the north and 15 individuals were found in the south of the Park (Table 3.1). During period two (1998 – 2004) a significant shift in the spatial distribution of rhino (with 30 or more sightings) had occurred, black rhino were concentrated in the southern part of the Park and the total number of black rhino found decreased to 30. Seven individuals (i.e. a decrease of 15 individuals) in the north and 23 (i.e. an increase of eight individuals) in the south (Pearson's Chi-Square: $\chi^2 (1, N = 67) = 8.81, p < 0.01$) (Table 3.1).

No significant change in size was found for averaged 50 % home range kernels between time period 1 and time period 2, between north and south or for male and female black rhino (2-Way ANOVA: $F_{1,59} = 0.85, R^2 = 0.09, p = 0.55$) (Fig. 3.6a). Only one male rhino was found with ≥ 30 sightings in the north in the second time period (Fig. 3.6a - d), therefore the confidence interval around the mean of male rhino in the second time period is quite wide. Average rainfall experienced by home ranges in the north was significantly higher than in the south (2-Way ANOVA: $F_{1,56} = 5.98, R^2 = 0.36, p < 0.001$), and both male and female black rhino generally moved out of the high rainfall (high *C. odorata* prevalence) areas and were now concentrated more to the south (Table 3.1). The area of home ranges containing *C. odorata* are significantly larger in the north than in the south (2-Way ANOVA: $F_{1,59} = 9.39, R^2 = 0.47, p < 0.001$), with approximately half the female home range containing *C. odorata* (Fig. 3.6c). There was a significant increase in area containing *C. odorata* within the male black rhino home ranges over time (2-Way ANOVA: $F_{1,25} = 18.06, p < 0.05$) (Fig. 3.6c), however this result is driven by a single male rhino found within the northern section in the second time period. Home range areas without *C. odorata* present are significantly smaller in the north than in the south (2-Way ANOVA: $F_{1,59} = 2.54, R^2 = 0.14, p < 0.05$) (Fig. 3.6d), showing that area available for rhino occupation within the north (without *C. odorata*) was limited.

Table 3.1: Change in number and sex ratio, of male and female black rhino, from time period one to time period two in the north and south of HiP, showing a significant shift in rhino distribution from the north to the south of HiP. See text for statistical analyses.

| Time Period | North | | | South | | |
|-------------|--------|------|-------|--------|------|-------|
| | Female | Male | Total | Female | Male | Total |
| 1991–1997 | 13 | 9 | 22 | 7 | 8 | 15 |
| 1998–2004 | 6 | 1 | 7 | 12 | 11 | 23 |

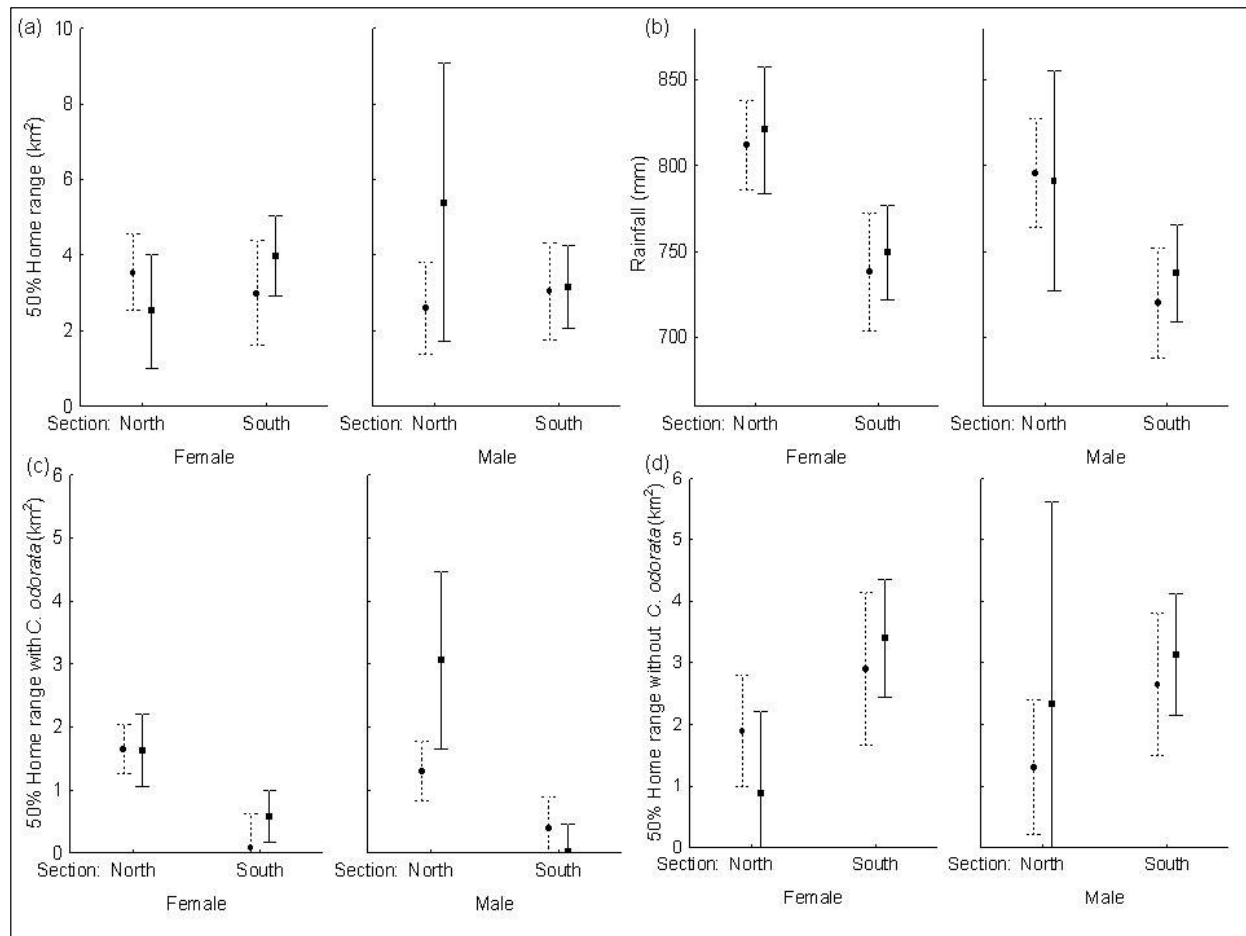


Figure 3.6: Presence of *C. odorata* and average annual rainfall within black rhino home ranges (50 % kernels), from time period 1(1991 – 1997, dashed error bar) to period two (1998 – 2004, solid error bar), for male and female black rhino. Error bars denote 95 % confidence intervals. (a) Change in home range size from period one to period two showing that the average 50 % kernel home range for both male and female rhino for both time periods falls between 2 and 6 km². (b) Mean annual rainfall (Schulze 2003) of home ranges in the north and south of the Park, rainfall is significantly lower moving from the north to the south of HiP, the distribution of home ranges along the rainfall gradient did not significantly change over time. (c) The portion of home ranges containing *C. odorata* were significantly larger in the north than in the south, there was no significant change in area over time with *C. odorata* present for female rhino, there was a significant increase in *C. odorata* present within the northern male rhino, however this result is driven by a single male rhino found within the northern section in the 2nd time period. (d) The portion of 50 % kernel home ranges without *C. odorata*, average home range areas in the north were significantly smaller than in the south. See text for statistical analyses.

3.4.3. Changes in diet choice

Within the study site, 16 woody species were browsed by black rhino; five species were positively selected for, and formed part of the preferred diet of black rhino, while the remaining 11 species were browsed, but had lower utilization than was expected given their relative abundance (Table 3.2). *Spirostachys africana* contributed a large proportion to the diet, and, in line with previous

studies (Emslie 1999), was most preferred. In addition, we found reduced utilization of *S. africana* by black rhino in plots with increasing prevalence of *C. odorata* (Spearman's rank order correlation: $r_s = -0.22$, $p < 0.05$) (Fig. 3.7). Although not significant, the results for the remaining forage species were useful in understanding how black rhino are affected by increased prevalence of *C. odorata*. Utilization of the remaining four positively selected species was not found above 26 – 50 % *C. odorata* prevalence, with the exception of *Rhus pentheri* which had some utilization within the 51 – 75 % prevalence category (Table 3.2). Within the negatively selected species, we recorded utilization of *Acacia robusta* within the *C. odorata* prevalence class 76 – 99 %, *Kraussia floribunda* and *Euclea divinorum* within 26 – 50 % prevalence category and *Gymnosporia buxifolia* within the 1 – 25 % prevalence category. For all other species minimal utilization were recorded. Therefore, we found that black rhino avoid their preferred forage species with increasing prevalence of *C. odorata*.

Table 3.2: List of dietary species for black rhino, in order of preference (Species with n<50 have been removed from the analyses). Species are ordered in descending order of preference.

| Species | Total | Relative abundance | Preference index | Utilization description |
|---------------------------------|-------------|--------------------|------------------|--|
| <i>Spirostachys africana</i> | 313 | 0.055 | 6.424 | Utilization reduced with increased presence of <i>C. odorata</i> (P<0.05), with no utilization above 51 – 75% prevalence |
| <i>Plectroniella armata</i> | 81 | 0.014 | 4.625 | No utilization above 26 – 50% <i>C. odorata</i> prevalence |
| <i>Ziziphus mucronata</i> | 65 | 0.012 | 1.103 | No utilization above 26 – 50% <i>C. odorata</i> prevalence |
| <i>Rhus pentheri</i> | 178 | 0.032 | 0.792 | No utilization above 26 – 50% <i>C. odorata</i> prevalence |
| <i>Diospyros lycioides</i> | 115 | 0.02 | 0.189 | No utilization above 26 – 50% <i>C. odorata</i> prevalence |
| <i>Kraussia floribunda</i> | 78 | 0.014 | -0.416 | No utilization above 26 – 50% <i>C. odorata</i> prevalence |
| <i>Acacia robusta</i> | 80 | 0.014 | -0.43 | Utilization found only in 76 – 100% <i>C. odorata</i> prevalence |
| <i>Berchemia zeyheri</i> | 104 | 0.018 | -0.562 | Minimal utilization |
| <i>Euclea divinorum</i> | 220 | 0.039 | -0.586 | No utilization above 26 – 50% <i>C. odorata</i> prevalence |
| <i>Gymnosporia buxifolia</i> | 117 | 0.021 | -0.611 | Utilization found only in 1 – 25% <i>C. odorata</i> prevalence |
| <i>Acacia caffra</i> | 118 | 0.021 | -0.614 | Minimal utilization |
| <i>Acacia nilotica</i> | 251 | 0.044 | -0.637 | Minimal utilization |
| <i>Euclea racemosa</i> | 723 | 0.128 | -0.685 | Minimal utilization |
| <i>Dombeya rotundifolia</i> | 171 | 0.03 | -0.734 | Minimal utilization |
| <i>Dichrostachys cinerea</i> | 1042 | 0.184 | -0.738 | Minimal utilization |
| <i>Acacia karroo</i> | 368 | 0.065 | -0.752 | Minimal utilization |
| <i>Gymnosporia senegalensis</i> | 221 | 0.039 | -1 | Not utilized |
| <i>Cassine aethiopica</i> | 85 | 0.015 | -1 | Not utilized |
| <i>Combretum molle</i> | 78 | 0.014 | -1 | Not utilized |
| <i>Tricalysia sonderiana</i> | 63 | 0.011 | -1 | Not utilized |
| <i>Euclea natalensis</i> | 60 | 0.011 | -1 | Not utilized |
| <i>Acalypha glabrata</i> | 54 | 0.01 | -1 | Not utilized |
| <i>Maytenus nemorosa</i> | 54 | 0.01 | -1 | Not utilized |
| <i>Rhoicissus tridentata</i> | 50 | 0.009 | -1 | Not utilized |
| Total n sampled | 5650 | | | |

Preference index calculates the proportion of deviance of observed from expected frequencies; (PI = (observed browsed - expected browsed) / observed browsed)) (Williams 2005).

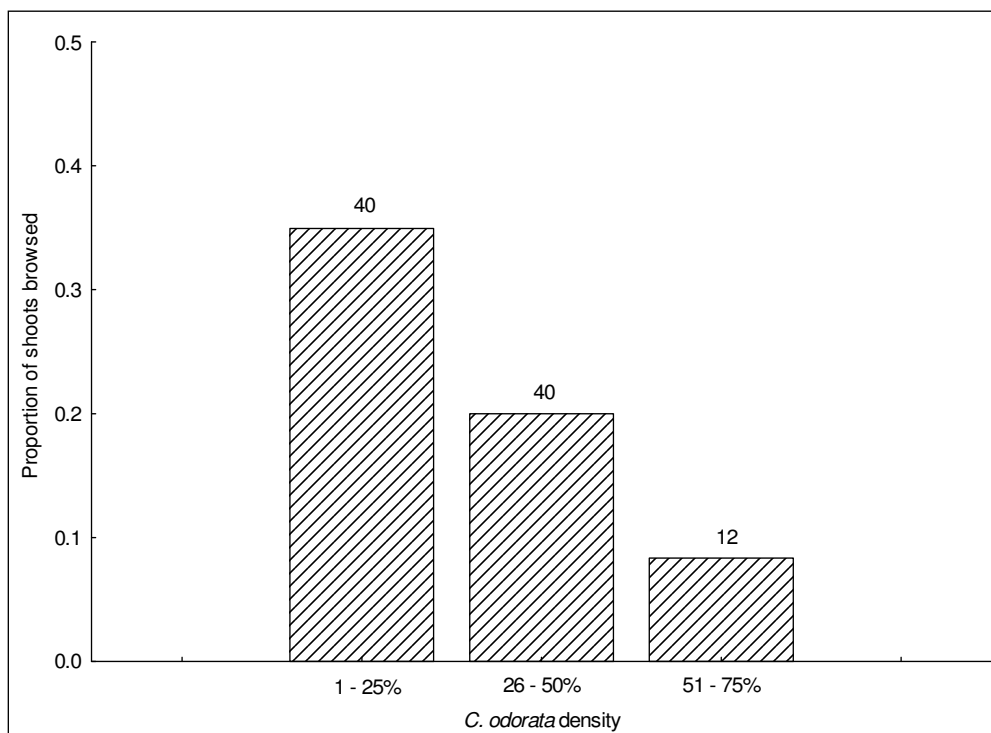


Figure 3.7: Effect of *C. odorata* invasion on selection of *S. africana*, the preferred forage species, by black rhino. Spearman's rank order correlation: $r_s = -0.22$, $p < 0.05$. Numerical value above bars represents n individuals sampled within *C. odorata* density categories.

3.5. DISCUSSION

The invasive plant *C. odorata* expanded into 28 % of the total area of HiP over a 23 year period (Howison, O. et al. unpublished data; this study). The expansion occurred throughout all vegetation types within the northern section of the Park (Howison, O. et al. unpublished data), with particular preference for vegetation found at high elevation and with higher annual rainfall (Kriticos et al. 2004; this study). The rapid rate and large spatial extent of invasion requires active management at the park wide scale, as the implications include loss of diversity within plant communities and negative impacts to habitat for both invertebrates and vertebrates (Leslie and Spotila 2001; Richardson and Van Wilgen 2004; Strayer et al. 2006; Mgobozi et al. 2008). Currently, large-scale manual control efforts are indeed aimed at eradicating *C. odorata* from HiP (Wadge 2007).

Spatial changes in the distribution of black rhino sightings over time showed a decrease in the central and northern regions, while sightings within the southern region increased. Home range analyses also showed a shift in the number of black rhino with >30 sightings from the northern to the southern regions. The average rainfall for home range is significantly higher in the north than

in the south, however this is because the northern part of the park is higher in elevation and receives a significantly higher proportion of rainfall annually (Balfour and Howison 2001). The vegetation types within the northern region are more susceptible to the invasion of *C. odorata* (Kriticos et al. 2004; Howison, O. et al. unpublished data; this study). Our results showed that a significantly larger portion of the northern home ranges contains *C. odorata* than in the southern home ranges. *C. odorata* forms dense impenetrable thickets (Leslie and Spotila 2001; Mgobozi et al. 2008) and we suggest that these thickets form barriers to black rhino. This has reduced areas for rhino occupation in the northern region of HiP and has caused shifts in the spatial organization of the population towards the southern region where *C. odorata* is less prevalent. A possible cause for the shift in distribution of rhino from north to south is habitat that would have been available for black rhino range expansion had been invaded by the less preferred *C. odorata* and therefore avoided by black rhino. Exotic species are known to alter physical resources such as living space or habitat (Richardson and Van Wilgen 2004).

Selection of the most important and most highly selected woody forage species (*S. africana*) was significantly less with increasing presence of *C. odorata*. Emslie (1999) reports similar findings where he observed swards of tall grass prevented access to palatable woody browse within the preferred height range of black rhino. Increasing prevalence of *C. odorata* negatively impacted the selection of almost all other preferred woody forage species where very little utilization was observed above 26 – 50 % prevalence. Howison, O. et al. (unpublished data) found that the *C. odorata* expansion had reached a phase where vulnerable vegetation types were saturated with *C. odorata* and that the southward expansion of the invasive plant was invading less susceptible vegetation types through propagule pressure (Richardson and Pysek 2006; Dawson et al. 2009), therefore further reducing area for black rhino occupation.

Subsequent to this study large areas have been manually cleared of *C. odorata* (Wadge 2007). This has coincided with a dry period since 2004 (SA Weather Bureau, unpublished data). At present the clearing operation has been effective, with large areas recovering from the invasion (pers. obs.). However, long term rainfall data indicates cyclic rainfall patterns of wet and dry periods (Balfour and Howison 2001). Should a wetter weather cycle return, we predict that reinvasion will occur in previously vulnerable areas (Leslie and Spotila 2001; Witkowski 2001; Kriticos et al. 2004; Richardson and Van Wilgen 2004) through seed dispersal from pockets of vegetation where the plant still persists inside and outside the Park (Richardson and Pysek 2006; Dawson et al. 2009; Howison, O. et al. unpublished data). Therefore the current level of intensive *C. odorata* clearing within HiP should continue (Wadge 2007).

It is important that population harvesting off-take does not result in declining source populations. An important aim of the black rhino expansion program is to keep the population at a level of maximum sustainable yield (Hearne and Swart 1991; Emslie and Brooks 1999). Cromsigt et al. (2002) predicted that black rhino populations should be held at around 10-15 % below equilibrium density to have maximal population growth rate. For HiP, this would mean keeping the population at around 350 - 380 animals, if we assume equilibrium density of around 420 (Cromsigt et al. 2002) animals. What actually happened in practice is that off take was much higher (Cromsigt et al. 2002), consequently between 2001 until 2004 the population was kept lower than 10-15 % below equilibrium density (ranging from 22 – 37 % below equilibrium density) (EKZNW unpublished data), which resulted in a reduced growth rate (Cromsigt et al. 2002). The high removal in itself requires further investigation as an important explanation for the decline in black rhino numbers in HiP. The population is far from equilibrium density resulting in below optimal growth rate and partly explains why the rhino population in HiP is slow to recover from high off takes (Cromsigt pers. comm.). Further, as we show in this study invasion of important black rhino habitat by *C. odorata* is a crucial additional factor that limits population recovery.

Black rhino are specifically threatened by biotic homogenization, whereby local biota are replaced by non-indigenous species, usually introduced by humans (McKinney and Lockwood 1999). Other studies also suggest that black rhino are large animals that cannot easily disperse; they are selective within their use of their habitat, are negatively affected by human activity (Western 1987; McKinney and Lockwood 1999; Reid et al. 2007) and are highly sensitive to habitat deterioration (Emslie 1999; Reid et al. 2007). It is therefore critical that managers implement strict population monitoring programmes to provide data for detecting and understanding decline of populations (Emslie and Brooks 1999; Emslie 1999). In our study we highlight vegetation types that are vulnerable to invasion by *C. odorata* and black rhino actively move out of these areas. Once these areas are saturated with the invasive species, previously less vulnerable vegetation communities become at risk of being invaded (Richardson and Pysek 2006; Dawson et al. 2009) which further reduce the area available for black rhino. Currently, within HiP, the dry period (since 2004) together with large scale fire has brought the invasive species under control, however should a wetter cycle return, control efforts should be focused within the vulnerable vegetation communities (i.e. higher lying, higher rainfall vegetation types and water catchments).

Management of non-indigenous species is a crucial aspect of maintaining native biodiversity and normal ecosystem functions (Byers et al. 2002). The encroachment of invasive species within the natural environment leads to habitat loss through the replacement of many endemic species with a

few widespread species (McKinney and Lockwood 1999; McKinney 2004; Cassey et al. 2008). Species that are highly threatened with global or regional extinction exhibit extinction biasing traits i.e. k-selected traits (large size, low fecundity), small population size, high specialization with respect to habitat requirements, slow population dispersal mechanisms and poor adaptation to human activities (McKinney and Lockwood 1999; Gaston and Fuller 2007). Biotic homogenization excludes specialized rare species by promoting habitat formation suitable for more generalist species that can adapt to the physical and environmental changes and expand their geographic range (McKinney and Lockwood 1999; Gaston and Fuller 2007). Metapopulation management of endangered species can be used alleviate problems such as slow dispersal mechanisms through population harvesting for translocation of founder groups to colonize new suitable areas (Hearne and Swart 1991; McKinney and Lockwood 1999; Crooms et al. 2002; Gaston and Fuller 2007; Linklater and Swaisgood 2008). Fragmented populations of endangered species spread the risk of specific threats (e.g. genetic isolation, disease, environmental extremes and habitat destruction) over many populations (McKinney and Lockwood 1999; Gaston and Fuller 2007; Linklater and Swaisgood 2008) and are therefore essential to their long term persistence (Harrison and Quinn 1989).

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4. GENERAL DISCUSSION

Previous studies on African community level plant-herbivore interactions generally focus either on vegetation responses to herbivores (Wiseman et al. 2004; Kurokawa and Nakashizuka 2008), or on resource partitioning of co-existing species facilitated by graduated body size (McNaughton and Georgiadis 1986; Owen-Smith 1988; Prins and Olff 1998; Arsenault and Owen-Smith 2002; Cromsigt and Olff 2006). I approached the plant-herbivore interaction at the community level both from the plant's and the herbivore's perspective. Specifically, I investigated how overall plant diversity influences browser diet diversity and dietary overlap. I looked more closely at which plant traits are most important to browsers by assigning these traits along the major plant ecological dimensions described by Westoby (2002), using these analyses I was able to identify mechanisms that facilitate resource partitioning among browsers at the plant species level. Finally, I assessed the impact of an aggressive exotic invasive plant species *Chromolaena odorata* (Witkowski 2001) on the critically endangered black rhino (*Diceros bicornis*) (IUCN 2008) habitat use and diet selection.

I identified seven habitat types (characterized by vegetation structure). Six habitats (excluding grasslands) were used to analyze the most important forage resources for a diverse guild of browsers. The vegetation impact surveys were conducted in the late dry season for the study area, therefore representing the period of greatest nutritional stress and greatest potential for competition for resources among co-occurring species (Gordon and Illius 1989; de Boer and Prins 1990). Herbivores species that successfully co-occur, do so primarily through vertical partitioning of the forage resource as a consequence of differences in body size (Schoener 1974; Voeten and Prins 1999) and metabolic adaptations which allow them to utilize plant species that are morphologically and chemically defended to minimize resource loss through herbivory (Gordon and Illius 1989; Iason and van Wieren 1999; Voeten and Prins 1999). A herbivore's diet is typically made up of abundantly available forage species (Freeland and Janzen 1974; Owen-Smith and Novellie 1982; Provenza 1995; Shaw et al. 2006). Forage species that are abundantly available often have traits that make them less digestible, and intake must therefore include rarer (higher quality) species that require more search energy (Owen-Smith and Novellie 1982; Demment and van Soest 1985; Iason and Villalba 2006). These rarer more digestible species improve digestibility of the bulk forage and to help mitigate the postingestive effects of toxicity (caused by plant secondary metabolites) (Demment and van Soest 1985; Provenza 1995). I calculated habitat type diversity using the Shannon-Wiener diversity index (Shannon and Weaver 1949) and diet composition diversity of black rhino (*Diceros bicornis*), elephant (*Loxodonta africana*) and a group of 'other' browsers (comprising: giraffe (*Giraffa*

camelopardalis), kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*), bushbuck (*Tragelaphus scriptus*), impala (*Aepyceros melampus*) and common duiker (*Silvicapra grimmia*)). I found that habitat diversity did not influence browser diet composition diversity between habitat types. However the diet diversity between browsers was different, where the diet composition diversity of the group of other browsers was significantly higher than for either black rhino or elephant. This was not surprising because other browsers' comprised a group of six different species of browsers, which have different forage species preferences, diet composition and metabolic adaptations that facilitate resource partitioning (Owen-Smith 1988; Estes 1991; du Toit 2003). Furthermore, I found that black rhino tended to have a few highly preferred species, causing a positive deviation from the community SAD (e.g. *Spirostachys africana*, and many of the rarer species), further supporting the evidence shown by Emslie (1999) that black rhino are highly selective browsers depending on a wide range of species. Elephant and other browser utilization of the abundant browse species was closely related to the available abundance indicating that these were more generalist browsers; however they show a higher preference for rarer species (other browsers' more so than elephant).

My study has highlighted new strategic and metabolic mechanisms whereby black rhino claim an exclusive niche to successfully compete with other browsers' that utilize the available browse within the same height range (Chapter 2). Black rhino showed wide diet breadth, preferring abundant but toxic forage species, and adding many rare higher quality forage species that are biochemically complimentary within their diet. I propose that black rhino use this strategy together with unique detoxification pathways to mitigate the effects of toxins (Jenkins and Wright 1988; Dearing and Cork 1999; Provenza 2003). Further research is required to investigate diet mixing by black rhino. What species, and in what quantities, does a black rhino typically consume in a day? Are there spatial and temporal strategies involved where black rhino utilize feeding patches that contain bulk lower quality (higher toxin) patches mixed with shorter periods (and high search costs) in patches of higher quality species?

Dietary species overlap calculations (Pianka 1973) indicated that overlap between elephant and other browsers' and between black rhino and other browser interactions were higher than between black rhino and elephant. These results, together with the woody species preference indices, showed that elephant and black rhino have diets that comprise different species, with highly preferred species for black rhino being of intermediate preference or even avoided by elephant and visa versa. In my study we showed that the three lower elevation habitats (Riverine Forests, Fineleaved and Broadleaved Woodlands representing 75 % of HiP) form the accessible forage resource for browser species, and the three higher lying habitat types (Induced Thicket, Thicket

and Upland Forest) are less important. However some of the rare species that occurred within these habitats were utilized and preferred by browsers. From a strategic management perspective the three lower elevation habitats form the realized area available for the browser community. However, carrying capacity calculations based on the quantity of suitable available browse do not predict habitat selection for browsers where behavioural constraints (territoriality) or habitat topography may interfere with the assumption of free distribution utilization (Morgan et al. 2009). Therefore when upper limits for populations of species are set, these limits need to take into account the behavioural ecology of the species (Morgan et al. 2009), because critical population management decisions are based on these upper limits (Hearne and Swart 1991; Cromsigt et al. 2002), such as population growth performance and off takes for species conservation (Hearne and Swart 1991; Cromsigt et al. 2002; Morgan et al. 2009). Conservation objectives include the protection of natural vegetation as well as the faunal assemblages they support (Conway et al. 2001), overestimating the carrying capacity of the conservation area can lead to overstocking and ultimately degradation of the natural vegetation communities (Skarpe et al. 2000; Makhabu et al. 2006). Changes in vegetation composition occur over time and as a consequence of elevation, rainfall, soil composition, fire return interval, higher CO₂ levels related to climate change, large scale invasion of exotic invasive plant species and changes in herbivore population densities (McKinney and Lockwood 1999; Bond and Midgley 2000; Skarpe et al. 2000; Archibald et al. 2005). Periodic assessments of the vegetation composition are required to identify possible negative impacts on vegetation heterogeneity and the consequent negative effects this may have on herbivore dietary species (Hill and Hamer 1998).

Herbivores partition available forage resources through specialized diet selection facilitated by physical and metabolic adaptations originating from competition for food (Belovsky 1997). Much of the literature pertaining to mammalian foraging deals with allometric differentiation (Jarman and Sinclair 1979; Demment and van Soest 1985; Owen-Smith 1988; du Toit and Owen-Smith 1989; Belovsky 1997; Ritchie and Olff 1999; Cromsigt and Olff 2006). Body size and associated metabolic adaptations are used to explain the co-existence of large and small herbivores within the same community (Demment and van Soest 1985; McNaughton and Georgiadis 1986; Belovsky 1997). Larger herbivores with lower metabolic needs are able to utilize abundant lower quality forage (Belovsky 1997; Ritchie and Olff 1999). Smaller herbivores with higher metabolic needs require less abundant higher quality forage (Belovsky 1997; Ritchie and Olff 1999) and may more finely define their dietary intake through specialized mouth morphology selecting specific plant parts that are higher in nutrient value than other more physically or chemically defended plant parts (Jarman and Sinclair 1979). However there is still much to be learned about how herbivores who utilize forage within the same height range (despite differences in body size)

co-exist. In my study I show that resource partitioning is strongly determined at the individual plant level (chapter two). Metabolic and strategic mechanisms allow certain herbivores to become specialized in utilizing forage species that are toxic to other herbivores (Belovsky 1997; Feng et al. 2009), because of unique toxin eliminating digestive pathways (Provenza 1995) or by increasing diet breadth to include rarer higher quality forage species that are biochemically complimentary and assist to mitigate the toxic effects (Freeland and Janzen 1974; Westoby 1978; Oloo et al. 1994; Dearing and Cork 1999).

Individual plant traits are the result of long-term selection pressures to prevailing environmental conditions and community assembly and filtering rules (Skarpe et al. 2000; Westoby et al. 2002). Several plant traits determine the palatability to herbivores (digestibility and defence properties including; specific leaf area, nitrogen, fibre, lignin, secondary plant metabolites, spinescence, leguminous) and accessibility (structural properties including; maximum height, density of wood, leaf lifespan (deciduous, evergreen), leaf fractal dimension) (Owen-Smith and Cooper 1987; Westoby 1998; Skarpe et al. 2000; Westoby et al. 2002; Iason and Villalba 2006) of the herbivore forage resource. Westoby (1998 and 2002) describe four plant ecological strategies that describe the variation among vascular plants. I related two of these dimensions, specific leaf area – leaf lifespan (SLA-LL) (properties that represent turnover of plant parts, which are highly correlated to digestibility) and maximum height (light interception and structural properties) to browser preference for individual plant traits (Westoby 1998; Iason and van Wieren 1999; Westoby et al. 2002). I showed that browser preference was highly correlated to the SLA-LL axis, towards the high SLA, low LL, low fibre and high nitrogen content. The maximum height axis did not appear to be as important to browsers as the SLA-LL axis, with generally intermediate preference for plant species that strongly represented this axis. However, there was a tendency of preference towards the lower maximum height and lower leaf size position (tall trees escape the majority of browsers with the exception of elephant and giraffe and other climbing herbivores (Birkett 2002; Westoby et al. 2002)). Resource partitioning related to vertical height, dietary preference, dietary composition and metabolic adaptations to diet quality determine mechanisms whereby a guild of herbivores coexists (Owen-Smith and Cooper 1987; Iason and van Wieren 1999; du Toit 2003; Iason and Villalba 2006). There are many more species that belong within the browser guild for which these mechanisms have not been described in relation to each other (e.g. giraffe, kudu, nyala, bushbuck, impala and common duiker). Further research within this field will aid managers in strategic planning to conserve maximum biodiversity within a limited extent (Ceballos and Brown 1995; Chapin et al. 2000).

The integrity of natural biodiversity is threatened by biological invasions by altering species composition which decreases regional scale biological distinctiveness – a process called biotic homogenization (McKinney and Lockwood 1999; McKinney 2004; Cassey et al. 2008). In the long term, the composition of ecological communities may shift towards species that are resistant to the effects of the invader (Levine et al. 2004; Strayer et al. 2006), however these changes may result in irreversible ecological and economic consequences (e.g. extirpation of native species) (Leslie and Spotila 2001; Strayer et al. 2006). Almost one third (28 %) of HiP has now been invaded by an aggressive exotic invasive plant species, *Chromolaena odorata*. This is a great concern, as this Park hosts one of the largest population of the critically endangered black rhino (*Diceros bicornis*) (Slotow et al. 2001). In chapter three I used sophisticated GIS analyses to calculate the change in distribution of black rhino within two discrete time periods, and using statistical models related this change in distribution to the 32 vegetation types (finer scale classification within the seven habitat types) identified within the Park. The GIS and statistical analyses were then used to calculate the most susceptible vegetation communities to the invasion of *C. odorata*, and then I related the invasion to the changes in distribution of black rhino per vegetation type. I found that black rhino have actively moved out of areas preferentially invaded by *C. odorata*. Of concern is the decline in population numbers of black rhino (Reid et al. 2007). Crooms (2002) show that high population off-takes reduce population growth, and this together the invasion of *C. odorata*, through the formation of physical barriers that reduce habitat quality and limit access to preferred forage and water, contribute to the slow recovery of the population. The large scale manual clearing program to remove *C. odorata* from HiP (post 2004) has been successful (EKZNW unpublished data), largely due to a period of lower rainfall (SA Weather Bureau, unpublished data; pers. obs.). Further research is required to assess the positive or negative effects this has had on the spatial organization of the black rhino population, given the vulnerability of the vegetation to reinvasion should a wetter cycle return (Leslie and Spotila 2001; Witkowski 2001; Kriticos et al. 2004; Richardson and Van Wilgen 2004; ISSG 2008). The process of biotic homogenization (in this case expansive invasion of *C. odorata*) may exclude specialist browsers (McKinney and Lockwood 1999; Gaston and Fuller 2007), (e.g. black rhino, bushbuck, red and blue duiker), by promoting habitat formation for more generalist and mixed grazer/browser species (e.g. impala and elephant) who not only survive the ecological changes but may expand their ranges (McKinney and Lockwood 1999; Gaston and Fuller 2007).

Protected areas are recognized as the most important core ‘units’ for in situ conservation. The information contained in the World Database on Protected Areas (WDPA) records over 100 000 sites, covering more than 11.5 % of the Earth’s land area (Chape et al. 2005). Human induced fragmentation of natural habitat has caused most populations of ungulates to become isolated

from each other (Hastings and Harrison 1994; Chapin et al. 2000). These populations must now be managed as metapopulations (Hastings and Harrison 1994; Hanski et al. 1995). Black rhino are critically endangered and current management is focused on maximum production within the larger populations (Hearne and Swart 1991; Emslie and Brooks 1999). Excess animals are translocated from high density populations to other areas suitable for the establishment of new herds (Hearne and Swart 1991; Cromsigt et al. 2002). Our study highlights important considerations when evaluating an area for black rhino suitability. Firstly, a high heterogeneity of forage species is required (Oloo et al. 1994) for black rhino to successfully utilize their preferred bulk diet comprising members of the Euphorbiaceae (Emslie 1999). Second black rhino are sensitive to habitat degradation brought about by the invasion of prime habitat by exotic invasive species (McKinney and Lockwood 1999). This invasion may have contributed to the slow recovery of the rhino population which, in addition, has been heavily harvested in recent years (Cromsigt et al. 2002; EKZNW unpublished data). Further research is required to understand how population recovery rate is affected by high removal rate from the population. Local management of the black rhino population within HiP, one of the largest populations of black rhino (Linklater and Swaisgood 2008), has included high removal rates in recent years (EKZNW unpublished data), and it is necessary to investigate the effects this will have on spatial organization of the population and recent decline in black rhino numbers. Metapopulation management is centred on the assumption that populations of species exist in fragmented patches which may or may not be connected, and the populations exist in a balance between extinction and colonization (Hastings and Harrison 1994; Hanski and Gilpin 1998). Management strategies include translocation of animals between populations and harvesting from larger populations (which are kept 10 – 15 % below carrying capacity to facilitate maximum population growth (Hearne and Swart 1991; Cromsigt et al. 2002)), to form founder groups to colonize new suitable areas, which spreads the risk of demographic and environmental stochastic events among many populations e.g. environmental extremes, genetic differentiation through isolation, habitat destruction and disease (Hastings and Harrison 1994; Ceballos and Brown 1995; Hanski and Gilpin 1998; Linklater and Swaisgood 2008). The Afrotropical Region (otherwise known as the Ethiopian Region) which includes all of sub-Saharan Africa and the island of Madagascar contain the most diverse assemblage of mammals (52 families, 17 endemic) and 23 % of all described species (Crosskey and White 1977; Cole et al. 1994). Human induced fragmentation of the landscape threatens the integrity of these populations by removing the natural corridors between them; therefore, populations must be manually manipulated to simulate previous spatial dispersal and colonization patterns (Cole et al. 1994; Ceballos and Brown 1995; Chapin et al. 2000).

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