Elephant versus other browsers' long-term influences on savanna woodland dynamics

Synergistic influences of elephant and other large mammalian herbivores on the structure and composition of woody plant communities in Hluhluwe-iMfolozi Park, South Africa

D.Phil. Thesis

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This thesis is dedicated to Julia and Alexandra

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ABSTRACT

Elephant versus other browsers' long-term influences on savanna woodland dynamics

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A crucial question in the debate about reintroducing elephant culling is whether the *long-term* effects of elephants and mesobrowsers on woodlands are similar. Sufficiently high biomass-densities of mesobrowsers may, following reduction or removal of elephants, continue to heavily impact earlier life-history stages of a similar suite of woody plants that elephant impacted, preventing these species from maturing. Thus a similar end-point for woodland structure and composition is achieved. No study exists in the literature where woody plant and habitat utilisation of the savanna browser guild has been determined in the same locality over the same period.

A review of 49 years of literature implied that the two groups impact the same core woody-species in the same habitats. Dietary and habitat utilisation of guild members was determined in Hluhluwe-iMfolozi Park, South Africa. A small suite (n = 8) of woody species formed the core diet of all guild members. Herbivores' densities were determined using a novel GIS approach; all members of the guild showed extensive overlap in habitat use. GPS collars and a GIS were then used to detect zones of different density of impala in the landscape, thus defining, for the first time, a natural fine-grain browsing gradient. Densities of woody seedlings were significantly less (average 48% reduction) in areas of high versus low impala density. A simple browse-browser model, incorporating, in a novel approach, functional groups of plant species, was parameterised from these results and an extensive review of the literature. Outputs suggest that over the long-term (100 years), impala will have a similar impact on woodland structure as elephant. An apparently strong synergistic effect between impala and elephant impact, suggests that reduction or removal of *either* impala *or* elephant will radically reduce long-term destruction of woodlands.

In smaller or medium sized reserves, where control of mesobrowser populations is practical, profitable and more acceptable than elephant culling, these findings imply a re-direction of management efforts. Management should consider the biomass-density of both groups, rather than just focus on the system's perceived 'keystone' species. Such principles may also apply to temperate and other systems.

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INTRODUCTION

Overview

Conservation of maximum biodiversity for posterity is the stated goal of all contracting parties to the Global Biodiversity Convention (WRI/IUCN/UNEP 1992) and of the National Parks of South Africa (Anon 1987). A central issue in African wildlife management is the effect elephants have on woodland vegetation directly and, through that, biodiversity in general. The direct effect of elephants on the growth and survival of different plant species of different sizes is compounded by the additional impact of other large mammalian herbivores, climate, fire, small mammals and insects. How the feeding of other herbivores influences the growth and survival of plants, and whether there is a synergistic effect between elephants and other herbivores is not thoroughly understood.

Based on the fact that some plants selected by elephants as food are also selected by other herbivores, it seems reasonable to assume that other herbivores impact on different size individuals of the same plant species. There is some suggestion in the literature that intermediate size herbivores can influence the composition (and therefore in the longer term the structure) of savanna systems. The overlap in habitat usage and plant species usage between elephants and other herbivores may act synergistically or antagonistically in affecting the growth and survival of plants. Such factors might be studied by use of exclosure experiments, but this approach is not without problems (e.g. difficulties in separating the effects of different herbivores, of fire, of plant competition and in maintaining barriers against elephant).

Where management is aimed at maintaining a desired state in the system (given structure and species composition), it is necessary that impacts from all sources are understood on a quantitative basis. To comprehend how elephants and other browsers influence the dynamics of savanna woodlands, a guild approach is necessary.

Background

As African elephants have been increasingly confined and concentrated, their destruction of trees has been spectacular in many reserves (Ben-Shahar 1993, Ben-Shahar 1998, Croze 1974a, Gadd 2002, Laws 1970, Leuthold 1977, Norton-Griffiths 1979, O'Connor *et al.* 2007, see Scholes & Mennell 2008 for summary). The perception that numbers of elephants and trees will stabilize only when woodlands have been converted to grassland (Buechner & Dawkins 1961, Lewis 1991), with an associated decline in biodiversity (Cumming *et al.* 1997, Fenton *et al.* 1998, Herremans 1995), has led to a resurgence of calls for elephant numbers to be reduced in many protected areas (Scholes & Mennell 2008), culminating in government policy in South Africa being changed in 2008 to re-allow elephant culling as a management tool, after a period of several years during which it was withdrawn as a management option (Anon 2008).

Opinion on the efficacy of culling elephants as a means of attaining a desired state in plant community structure and composition is divided. Those supporting culling as a management tool contend that elephants, because of their size, abundance and feeding

behaviour are keystone species and have an overriding effect (Bond 1993), and that therefore, a reduction in their numbers to a suitably low level will enable the system to be held in a desired state within upper and lower thresholds determined by climate and soils. An alternative view holds that other members of the browser guild, because of niche overlap and comparatively high biomass (Grunow 1980, Walker 1985), are similarly able to modify community structure because they impact smaller individuals of the same plant species. Proponents of this viewpoint hold that the equilibrium mix of woody species in any given savanna community, is determined by all of the guild together and that when a particular competitor (elephant) is removed, the remaining members of the guild will simply use the additional resources (or occupy the vacated niche space as a result of competitor release) and continue to impact on the vegetation. Therefore reduction in the numbers of a single member of the browser guild, in particular elephants, may have little effect on woody plant community composition *over the long-term* (Owen-Smith *et al.* 2006, Pickett *et al.* 2003).

The African elephant as a Keystone species

'Keystone' was first coined as a term by Paine (1966, 1969) describing marine community predators. He suggested that such species numbers and activities ensured "the integrity of the community and its unaltered persistence through time, that is, stability" (Paine 1969). The term has come to have the more general meaning of identifying species which "have a disproportionate effect on the persistence of all other species" (Bond 1993). Extinctions that have causes possibly unrelated to size of population are

characterised as deterministic (Schaffer 1981); removal or an excess of keystone species has been cited as a cause of deterministic extinctions, leading to loss of biodiversity. Convincing examples of keystone species and their having this effect have been identified in a number of aquatic environments (e.g. North Pacific sea otters' influence on sea urchin density and hence abundance of kelps and dependent species (Duggins 1980, Estes *et al.* 1978), effects of introduction of alien fish species (Fauth & Resetarits 1991), whelks relationship with lobsters and seaweeds (Barkai & McQuaid 1988)), but in only a few terrestrial systems (e.g. North American desert rodents' seed predation (Brown & Heske 1990)). Especially in terrestrial systems, anecdote, subjective explanations, little data and an absence of experimental support for hypotheses often characterise discussion of the possible role/existence of keystone species.

Nowhere is this more apparent than in relation to the African elephant, despite it being described as "the prime example of a keystone herbivore" (Bond 1993). Many of the numerous papers on deforestation by elephants describe the crucial role of other elements (e.g. giraffes and periodic burning (Pellew 1983c), fire (Dublin *et al.* 1990), fire and insects (Thompson 1975), fire, drought and disease (Shannon et al. 2008)), and none, as far as we are aware, demonstrate elephants as causing a reduction in biodiversity without the complicating influence of fire and/or other herbivores, or have shown elephants causing loss of biodiversity beyond the immediate locality i.e. at a regional level. Evidence that removal of (forest) elephants results in reduced plant biodiversity was "conspicuously absent" in datasets from Guinea (Hawthorne & Parren 2000). Additionally, an increasing literature points specifically to other browsers markedly

impacting woody vegetation. Giraffe (Birkett & Stevens-Wood 2005, Pellew 1983a, Pellew 1983b), impala (Belsky 1984, Prins & Van der Jeugd 1993), kudu (Barnes 2001), black rhino (Birkett & Stevens-Wood 2005), eland (Styles & Skinner 2000), non-elephant browsers in general (Sharam *et al.* 2006) and even dik-diks (Augustine & McNaughton 2004) have all been described to influence, variously, seedling establishment, seedling, sapling and mature tree growth and, thus, woodland growth/regeneration – mainly with regard to *Acacia* species. Some studies have demonstrated this influence over an extended period (e.g. Prins & Van der Jeugd 1993). Recently Guldemond & Van Aarde (2008) have identified a citation bias (Leimu & Koricheva 2005) in the literature that "..may have introduced a bias towards concluding that elephants have a negative impact on woody vegetation,..".

Owen-Smith (1987) prominently argued that pre-history evidence for elephants as a keystone species comes from the pattern of extinctions at the end of the Pleistocene, hypothesising that the elimination of elephants by man in Eurasia and America, but not in Africa, would have led to the conversion of mosaics of park-like woodlands to forests on the former land masses, but not the latter, leading to a loss of habitat diversity and hence biodiversity, thus explaining the otherwise puzzling difference in extinctions between these continents. It is, however, difficult to imagine human hunters of this period turning to such formidable and logistically demanding quarry as elephants, without having additionally hunted easier prey, such as mesoherbivores, to a lower density. Owen-Smith (1989) offered Hluhluwe Game Reserve in KwaZulu Natal, South Africa, as a modern-day test case of his hypothesis. Here, in the absence of elephants, woody vegetation was

increasing; the re-introduction of elephants in 1981 would, he predicted, reverse this trend. However thirty years later, with a sizeable (>0.5 per km2) and increasing (at ~ 7% p.a.) elephant population, but with a declining medium-sized browser (impala, giraffe, kudu and black rhino) population (Van Rensburg 2006), woody vegetation continues to increase (Van Rensburg 2008).

It would appear, therefore, that the available evidence suggests varied influences on woody vegetation, whilst not confirming elephants as a keystone species.

The concept of 'keystone species' itself is also not straight forward. Semantically, given the right circumstances, any species could have "a disproportionate effect". Additionally, the examples identified so far relate to stable systems with simplistic spatial dynamics where a species, the keystone species, has been added or removed creating a dramatic, short temporal (in evolutionary terms) effect. Finally, the notion that a complex, highly biodiverse system could be held hostage to one species, the keystone species, seems counter-intuitive to evolutionary theory – over evolutionary time such a system would be highly unlikely to survive as, a), if the keystone species disappears, the whole system is destabilised and, b), as other species in the system are held at low densities by the keystone species, their probability of survival over evolutionary time is remote (Schaffer 1981, Soule 1987). Thus the very existence of high biodiversity in the African savanna seems to argue against the viability of the 'keystone species' hypothesis in this system. Both media and scientific concentration on the keystone species hypothesis has unfortunately deflected debate away from the possible role of other herbivores in savanna

woody dynamics. Research which quantifies the relative role of elephants versus other herbivores is needed before the executive can make scientifically informed decisions on the management of African savanna systems.

Niche and competition

Grinnell (1917) was among the first to use the term 'niche', which became increasingly identified with "resource utilisation spectra" (Pianka 1976), through population biologists' theoretical (Levins 1968, MacArthur 1968, May 1974) and empirical work (Cody 1974, Pianka 1969, Pianka 1975, Schoener 1968, Schoener 1975). That interspecific niche overlap exists and varies under different conditions has been established amongst omnivores, carnivores and herbivores in a wide range of systems – tropical (Bagchi *et al.* 2003, Juarez & Marinho-Filho 2002, Leite *et al.* 1996), temperate (Bonesi *et al.* 2004, Kingery *et al.* 1996, Padial *et al.* 2002), arctic (Elmhagen *et al.* 2002, Ihl & Klein 2001), desert (Ilse & Hellgren 1995, Jones & Barmuta 2000) and, perhaps most extensively, in African savannas (Caro & Stoner 2003, Ferrar & Walker 1974, Field & Laws 1970, Fritz *et al.* 1996, Lamprey 1963, Loveridge & Macdonald 2003, Vesey-FitzGerald 1960), amongst others. The relevance of other browsers' influences on woody vegetation to the 'elephant problem' (Croze 1974b), will depend, in part, on the degree of habitat and diet overlap that exists between these two groups (Owen-Smith et al. 2006).

The above use of the phrase 'in part' relates to competition and niche theory. Theoretical competitors which are free to select their most favourable environment with complete

knowledge of resource availability (the 'ideal free distribution' concept (Fretwell 1972)), will, in reality, have their 'fundamental' niche (Hutchinson 1957) modified to produce the 'realised' niche (Hutchinson 1957, Vandermeer 1972); the difference between the two representing the effects of interspecific competition (and predation). However, overlap of niche only leads to competition when resources are sparse (Pianka 1976). It follows that marked overlap may actually be associated with reduced competition, leading Pianka (1972, see also Roughgarden & Feldman 1975) to propose his 'niche overlap hypothesis' – namely that "maximum tolerable overlap should be lower in intensely competitive situations than in environments with lower demand/supply ratios". Low levels of overlap between elephants and other browsers may thus, paradoxically, indicate heightened competition between the two groups. Whilst it is true that this 'ghost of competition past' (Connell 1980) might be alternatively simply explained as there having been no competition in the first place, this seems improbable when dealing with a guild of sympatric herbivores for whom the most nutritious plants available will remain the most preferred (Sinclair 1972, Stephens & Krebs 1986).

Reduced availability of prey will lead to prey switching (Dell'Arte *et al.* 2007, Ohizumi *et al.* 2000, Ostfeld 1982, Patterson *et al.* 1998, Steenhof & Kochert 1988), with niche breadth generally increasing as availability of resources decreases (Charnov 1973, Emlen 1968, Schoener 1971). Thus as resources become limiting, one would expect herbivores to select a different suite of plant species, although the most nutritious available will remain the most preferred (Sinclair 1972). However, the differing digestive strategy and size of elephants versus other browsers produces a corollary to these principles. Elephant

are non-ruminants, with most digestion occurring in the hind-gut (Van Hoven *et al.* 1981), and as such are adapted, compared to ruminants such as giraffe, kudu, nyala and impala (Smithers 1983), to process coarser forage at a rapid rate (Napier Bax & Sheldrick 1963). As larger animals, they can survive on relatively lower quality foods (Belovsky 1997, Demment & Van Soest 1985, Illius & Gordon 1992), consequent on the inter-relationships between body size, energy (Hungate et al. 1959) and protein turnover (Brody *et al.* 1934) and gut capacity (Illius & Gordon 1992) – the Jarman-Bell principle or body-size hypothesis (Bell 1971, Jarman 1974). Elephants' ability to cope with lower quality forage and ruminants' greater dependence on higher quality food (Owen-Smith & Novellie 1982) would be expected, especially when resources are limited (Beekman & Prins 1989, Demment & Van Soest 1985, Owen-Smith 2004), to cause separation in their diet choice. The degree to which the more specialist feeding requirements of ruminants (Belovsky 1981, Westoby 1974) will cause the latter, will vary with varying levels of resource depletion for different ungulates in different environments (Melton 1987).

Thus both ecological theory and the physiological realities of the differences between the two groups, support the following hypothesis: dietary overlap between elephants and other large browsers will decrease as the available forage decreases and/or total browser biomass density increases (i.e. competition increases).

Additionally, a primary indication of whether the browser guild uses the same resources or not and has the potential to act synergistically, is whether the population sizes of different guild members influence each other. A complication is that the differing

digestive strategy and size of elephants versus other browsers, not only influences differences between the two groups in how they impact woody species, but also shapes how they may influence each other's dynamics as well. In addition elephants and impala are mixed feeders who at times can subsist on a diet consisting of mostly grasses, herbs and forbes (Smithers 1983). The consequence of this, in terms of the impact on physiognomy and composition of woodlands, is that for these mixed feeders the limiting resource may not be trees, in which case the impact that they have may be heightened compared to a pure browser.

Perceptions

Whilst elephant plant usage and its effects are visually obvious due to the sheer size of the animal, the effects of smaller browsers are more cryptic. Indeed the argument that smaller browsers significantly impact savanna woodland structure may, to some, seem counter-intuitive. However, in arid/eutrophic savannas supporting high biomasses of both elephant and other browsers (East 1984), total biomass of smaller browsers may be comparable to that of elephants (e.g. in Hluhluwe-iMfolozi Park, South Africa, estimated total biomasses are: giraffe/black rhino/kudu/nyala/impala combined 3 million kg, elephant 1.4m kg (Van Rensburg 2006)). Even in the Kruger National Park, topical for its 'excessive' elephant population, non-elephant browsers' total biomass is a third of the elephants' biomass (SANParks 2007). Additionally, non-elephant browsers, due to their smaller size, will have higher energy requirements per unit mass (Demment & Van Soest 1985). The total energy they remove from the plant biomass is thus likely to be

proportionally higher. Smaller browsers also feed over a lower height range compared to elephants (du Toit 1990) and, where numerous enough, slow down seedling/sapling growth (Belsky 1984, Prins & Van der Jeugd 1993, Styles & Skinner 2000) making them more susceptible to fire for longer (Barnes 2001, Emslie 1999, Staver 2007). Thus, they can effectively 'trap' the browse species they most favour (the most palatable and nutritious) in a smaller size class – one less suited to the bulk-feeding elephant.

Thus, where their total biomass is of an appropriate magnitude, the role of smaller browsers in shaping savanna vegetation structure may be threefold. Directly, they consume, in energetic terms, proportionally more plant biomass than elephants and trap the most palatable species; indirectly, through resource competition, they thus displace elephants to utilise other species.

Savanna woodlands; a historical anomaly?

Over the period from ~ 1840 to 1920, large herbivore numbers were greatly reduced in ecological systems across Africa due to excessive hunting, disease (rinderpest, East Coast Fever and anthrax epidemics) and wars (large armies to feed; Boer war, Anglo/Zulu wars) (Skarpe et al. 2004). It is possible that the abundant savanna woodlands of Africa today, that considerable conservation effort is put into attempts to preserve, are in reality an anomaly consequent on the vastly reduced browsing presssure over that period (Moe *et al.* 2009, Rohde & Hoffman 2012, Skarpe *et al.* 2004). Early travellers' records before the effects of this period, although sparse, describe extensive grasslands with little

woodland in evidence. For instance, Baker in 1866 (Baker 1866) describing the Murchison Falls area writes "..the whole country was a wilderness of rank grass..", whilst Schweinfurth in 1888 (Schweinfurth *et al.* 1888), describing the same area, states "..the whole stretch of country is covered by grass…a ceaseless monotony envelops the traveller upon these marches, grass and isolated trees…" – and yet by 1932 aerial photographs showed the same area to be markedly wooded (Buechner & Dawkins 1961).

Thus not only, as outlined above, may elephants effect on savanna woodlands not be of an over-riding, keystone nature, but the decline of woodlands observed in many localities today may simply be a change in state in the system, from plant species mixes that arose during 100+ years of low large herbivore abundance, to that which prevails today in systems with full compliments of herbivore species.

Previous work

Despite considerable literature on the feeding ecology of a wide range of browsers in African savannas, the potential long-term role of non-elephant large browsers versus that of elephant on savanna woodland dynamics has only recently received empirical attention (e.g. Moe et al. 2009). A major stumbling block is the paucity of research conducted at the guild level in the same locality. Surprisingly few (n = 21) studies have researched plant use by elephant and at least one other browser in the same locality. Only six of these researched the overall diet, rather than use of just one particular plant species, and only one paper gives details of the entire guild's diet (see Chapter 1 for details). There is no published study that has determined simultaneous plant and habitat usage by the guild

in the same locality. This is a critical gap in the literature, as exposure of herbivores to different suites of plants in different localities would be expected to affect the degree to which particular woody species are utilized, preferred or avoided. Another problem is the scarcity of quantative, as opposed to qualitative, data on other browsers' impact on woody plant species.

The Study

To investigate the likely long-term influences of elephant versus that of other browsers on savanna woodland dynamics, Hluhluwe-iMfolozi Park, South Africa was choosen as the study site as it is a medium-sized reserve containing sizeable populations of both elephant and a wide range of non-elephant browsers, together with varied habitat types typical of the sub-region.

With the review of the literature of the past fifty years indicating the research direction needed, the overlap in both habitat and woody plant species usage between elephant and other browsers in the reserve was determined over two years. During the third year of field work a novel technique was used to assess, quantitatively, impact on woody species by other browsers. These findings, together with published data, were then used to explore, by means of modelling, the likely long-term (up to 100 years) impact of the two groups on savanna woodland structure and composition.

Specifically:

Study Objectives

(i) to review what is already known about overlap between elephant and other browsers in terms of habitat and plant species usage (Chapter 1),

(ii) to establish what overlap in plant species (Chapter 2) and habitat usage (Chapter 3) there is between elephant and other browsers in the study site (Hluhluwe-iMfolozi Park (HiP), South Africa),

(iii) to demonstrate, quantitatively, impact by a major non-elephant browser in HiP using an alternative to exclosures (Chapter 4),

(iv) to use this information to develop a predictive model of the long-term influences of elephant versus other browsers on the woodlands of HiP (Chapter 5).

Study Hypotheses

(i) An in-depth review of the literature will reveal a) extensive overlap between elephant and other browsers in habitat usage, and b) a central 'core', or staple diet, of woody species communal across the browser guild,

(ii) the browser guild in HiP will likewise show extensive habitat usage overlap and a staple, core diet communal to the guild,

(iii) mesobrowsers in HiP of high population biomass severely impact woody plant recruitment,

(iv) over the long-term, a) mesobrowsers of high population biomass exert, via their impact on recruitment, a major effect on savanna woodland structure, and b)

that therefore removal, or reduction in numbers, of elephants from the system may not have an overriding effect.

"*Single-species management blind to relationships of the larger, associated community is unlikely to preserve the suite of species and processes important in maintaining natural ecosystems*." (Paine 1995)

"*Predicting the effects of elephants, other browsers, fire and climatic variability on vegetation dynamics and habitat conditions requires reliable specification of how these factors interact within specific ecosystem contexts. At this stage we know little about processes governing the regeneration of savanna woodlands, except that many factors besides elephants potentially influence recruitment into the tall tree stage, with various contingencies involved.*" (Owen-Smith et al. 2006).

Note on the structure of this thesis

As the five central chapters are presented as papers published or submitted to journals, their content frequently includes analyses and discussion additional to the central theme of the thesis. Consequently, to aid the flow of this report, between each chapter there is a small 'linkage' paragraph outlining how the preceding chapter's findings have advanced the study's objectives, and what direction the succeeding chapter takes to the same end.

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CHAPTER 1

Are the long-term effects of mesobrowsers on woodland dynamics substitutive or additive to those of elephant?*

Abstract: The large spectrum of existing literature on browser-woodland dynamics, both from savanna and temperate biomes, converges towards concluding that all browsers importantly impact woody plants. In this context a crucial question in the current debate about reintroducing elephant culling, is whether the *long-term* effects of elephants and mesobrowsers are similar. If the two groups impact the same woody species in the same habitats, sufficiently high biomass-densities of mesobrowsers may, following removal of elephants, continue to heavily impact earlier life-history stages of the same suite of woody plants that elephant impacted, preventing these species from maturing. Thus, as existing mature trees die from natural causes and fade from the system, a similar end-point for woodland structure and composition is achieved. We reviewed 49 years of literature on the savanna browser guild, performing a meta-analysis on the disparate data on the guild's woody plant-species use (3,677 records) and habitat use (894 records). Mesobrowsers' and elephants' extensive overlap in habitat use and staple woody-species diet, together with evidence of their influencing each others' abundance and of their dietary separation increasing with resource depletion, implies that the two groups impact the same core woody-species in the same habitats. It therefore seems probable that high biomass-density mesobrowsers may have a long-term substitutive effect to that of elephant on woodland dynamics. Consequently management wanting a particular state of

savanna woodland, should consider the biomass-density of both groups, rather than just focus on the system's perceived keystone species. Such principles may also apply to temperate and other systems.

Key-words: browsers; woody plant use; niche overlap; biomass-density; competition; guild dynamics

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1. INTRODUCTION

A topical debate between wildlife managers and ecologists is the role of large herbivores in the top-down regulation of ecosystems (Moe *et al.* 2009), especially with regard to elephant *(Loxodonta africana)* versus mesobrowsers' influences on African savanna woodland dynamics. There is an extensive and heavily cited literature recording the impact of elephants on woody vegetation, principally in relation to mature tree mortality (e.g. Croze 1974, Laws 1970, Leuthold 1977, O'Connor *et al.* 2007, see Scholes & Mennell 2008 for summary). There are also numerous examples of savanna mesobrowsers impacting woody vegetation, mainly in relation to seedlings and sapling recruitment (e.g. impala (Moe *et al.* 2009, Prins & Van der Jeugd 1993), kudu (Barnes 2001), black rhino (Birkett & Stevens-Wood 2005), eland (Styles & Skinner 2000), dik-diks (Augustine & McNaughton 2004) and non-elephant browsers in general (Sharam *et al.* 2006)). Giraffe are recorded as slowing woody plants' progress through height classes (Pellew 1983), and causing mature tree mortality in over-browsed, small protected areas (Bond & Loffell 2001). It is thus now well established that all members of the savanna browsing guild importantly impact woody vegetation. It is equally well established that they do so utilizing different feeding height ranges (du Toit 1990) and plant parts (Jarman 1971, Lamprey 1963).

What is less well established, and is a critical management question in the context of the current debate about reintroducing elephant culling, is whether the *long-term* effects of elephants and mesobrowsers on woodland dynamics, controlling for their relative biomass-densities, are similar – are in fact their effects principally substitutive or

are they principally additive? The substitutive viewpoint holds that mesobrowsers, because of niche overlap and comparatively high biomass (Grunow 1980, Walker 1985), are able to modify community structure similarly to elephants because they impact smaller individuals of the same plant species. Thus when elephant are removed, mesobrowsers continue to impact earlier life-history stages of the same suite of woody plants that elephant impacted, over time the large mature trees, previously impacted principally only by elephant, die from natural causes and thus, if mesobrowser biomass-densities are high enough, mature individuals of these woody plants fade from the system – creating a similar end-point for woodland structure and composition to that widely recorded as the consequence of high elephant densities. Thus reduction in the numbers of a single member of the browser guild, even elephants, may not have an overriding effect on woody plant community composition over the long-term (Owen-Smith *et al.* 2006, Pickett *et al.* 2003). Alternatively mesobrowsers may impact different plant species to elephant. In this scenario their influences may be described as additive, with each group contributing a different long-term effect to woody plant community composition. Despite considerable literature on the feeding ecology of a wide range of browsers in African savannas, neither of these views has been examined in the light of existing data. We reviewed the extensive literature on the savanna browser guild to clarify their overlap in plant species and habitat use, and also sought evidence in support of some well established theories and concepts, discussed below, that are of direct relevance to the substitutive question.

Elephant are non-ruminants, with most digestion occurring in the hind-gut (Van Hoven *et al.* 1981), and as such are adapted, compared to ruminants such as giraffe, kudu, nyala and impala, to process coarser forage at a rapid rate (Napier Bax & Sheldrick 1963). Larger animals can survive on relatively lower quality foods in accordance with the Jarman-Bell principle (Bell 1971, Jarman 1974)), because of the inter-relationships between body size, energy (Hungate *et al.* 1959) and protein turnover (Brody *et al.* 1934) and gut capacity (Illius & Gordon 1992). Hence guild members closer in terms of their digestive strategy and/or body size should show greater dietary overlap.

Theory (Stephens & Krebs 1986) predicts that any animal will utilize the most nutritious food source available, and this has been demonstrated empirically in African herbivores (Sinclair 1972). For a guild of sympatric herbivores the most nutritious plants available are likely to be the most preferred across the guild, even though relative abundance of different plant species, competition and body-size/digestive strategy are likely to color such preferences. It follows that an extensive review of the woody plant diet of guild members is likely to reveal a central 'core', or staple diet, communal across the guild and comprised of the most nutritious and widespread plant species.

Niche overlap only leads to competition when resources are sparse (de Iongh *et al.* 2011, Pianka 1976). It follows that marked overlap may actually be associated with reduced competition, leading Pianka (1972) to propose his 'niche overlap hypothesis' – namely that "maximum tolerable overlap should be lower in intensely competitive situations than in environments with lower demand/supply ratios". Hence dietary overlap

between elephants and other browsers should decrease as the available forage decreases and/or total browser biomass-density increases (i.e. competition increases).

Where the same woody species are utilized within the browser guild, elephants may influence other browsers' numbers by reducing resources in the shrub layer, but mesobrowsers via their impact on seedlings and sapling may in time, where their total biomass is sufficient, reduce resource availability in larger plant-size classes and thus influence elephant abundance. Hence the literature would be expected to contain evidence of a community-level inverse correlation between the two groups abundance. However, at low to intermediate elephant densities, an increase in elephant density might facilitate food availability to other browsers by pollarding and the inducement of coppice growth in the shrub layer, or if completely different woody species are used by the two groups, by removal of competition between elephant food plants and those used by the rest of the guild.

With this background in mind, we reviewed the literature to determine the degree of actual and potential overlap in diet between elephants and the other members of the savanna browser guild, to determine if impacts were more likely to be substitutive or additive. In addition we examined the literature for evidence of competition between elephants and the rest of the browser guild.

2. METHODS

As the debate on reintroducing elephant culling is centered in southern Africa, we considered the prevalent browsers in the region - elephant, impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardalis*), black rhino (*Diceros bicornis*), kudu (*Tragelaphus strepsiceros*) and nyala (*Tragelaphus angasii*). We searched the literature from 1960 to 2009 for data on these species' habitat and woody plant species use (habitat: 192 data sources; plant: 161 data sources). We found surprisingly few (21) studies that have researched plant use by elephant and at least one other browser in the same locality. Only six of these researched the overall diet, rather than use of just one particular plant species, and only one paper gives details of the entire guild's diet. Consequently data relating to the guild's habitat and woody plant use is exceedingly disparate, and required additional analyses in an attempt to facilitate comparison of data from different studies in different localities.

Records on habitat use (894 records) and plant species use (3,677 records) are presented in the literature as i) preference indices, where the author has assessed use versus availability, comprising ~ 50% of records, or ii) percentage use (~ 30% of records) or iii) purely descriptive data (~ 20% of records), with the latter two approaches not assessing use versus availability. We standardized these measures of use into a semi-subjective ranking system (Table 1); this meta-analytical approach is similar to the methodology of a Cochrane Review (http://www3.interscience.wiley.com), a technique widely used in the medical field to analyze disparate data. The ranking system was then used in various combinations to assess overlap in plant species and habitat use amongst

the guild. Initially we analysed results for all members of the guild (both as separate animal species and combined as a guild) using i) all records, ii) only records based on preference indices, and iii) only records based on any method except preference indices (i.e. purely descriptive or percentage use). Unexpectedly, there were minimal differences in these three sets of results. Consequently we continued our analyses using the entire data set. Categories of use in our results relate to the ranking system as follows: plant species or habitat use described as 'well utilized' relates only to records that scored 2, 3, 4 or 5 in the ranking system, whilst 'utilized' relates only to records that scored 1, 2, 3, 4 or 5.

Importantly, exposure of herbivores to different suites of plants in different localities affects the degree to which particular woody species are utilized, preferred or avoided. To reduce, but clearly not remove, the influence of this effect on our results, we additionally i) grouped localities into broad habitat types (BHT) using White's Vegetation of Africa map (White 1983), ii) analysed woody diet overlap between pairs of herbivores using only plant species where both herbivores had record(s) in the literature, and iii) examined the overlap reported in the six specific studies that researched the overall diet of all or part of the guild in one locality. The pair-wise overlap was assessed by the percentage of plant species that one herbivore favoured that the second member of the pair also favoured – and similarly for avoidance. Favoured we defined as where the total records for that animal for that plant species consisted of > 50% of ranks 3, 4 or 5, and avoided where > 50% of total records were ranked 0, 1 or 2.

Due to the very large differences in the number of localities in which different members of the guild have been studied, a standard statistical meta-analysis of the published literature would be associated with sufficient uncertainty to preclude any firm conclusions. However, in terms of the objective of establishing whether impacts are likely to be substitutive or additive, some analysis is nevertheless possible. As for habitat use, a standard statistical meta-analysis was not appropriate when examining plant species use because of large differences in the number of studies for different members of the guild.

For habitat use, we used a variety of information (locality, authors' topographical, generalized vegetation type and specific plant species abundance descriptions) to assign a habitat type to a record.

3. RESULTS

3.1 Habitat Use

Elephants have been studied in many more habitat types, with a wide spread over the subcontinent, than the other browsers (Table 2). Habitat types most used by elephants were also most heavily used by other members of the guild (Table 2). Of the 35 studies where the habitat use of elephant and at least one other member of the guild has been

studied in the same locality, 86% reported overlap in habitat use between elephant and other members of the guild.

3.2 Plant Species Use

There were large differences in the number of studies for different members of the guild (Table 3). Of the 747 woody species recorded as being 'utilized' by any guild member, 10 species were used by all six of them, 19 by five, 33 by four, 47 by three, 98 by two and 540 by only one. If a species was cited frequently for one member of the guild, it was often, but not always, also cited frequently for all other members of the guild. The ten woody species recorded as being 'utilized' by the entire guild were also the most frequently cited for any one guild member. These species were, in descending order of use, *Dichrostachys cinerea, Acacia nilotica, Ziziphus mucronata, Sclerocarya birrea, Capparis tomentosa, Acacia karoo, Acacia caffra, Spirostachys africana, Euclea divinorum* and *Colophospermum mopane*. These frequently utilized species constitute the staple diet of the different guild members. Thus the larger sample size for elephant results in a longer list of less frequently recorded tree species used by elephants. Eight of the 30 most frequently utilized species were *Acacia* – amongst the most palatable (Cooper *et al.* 1988) and widespread (Midgley & Bond 2001, White 1983) plant species in savannas.

Despite the larger sample, elephants are not recorded as using all woody species utilized by other guild members (Table 4). However although elephant utilize high

percentages of other browsers' diets, the reverse does not appear to apply to the same extent. Similar results were obtained using only plant species where both herbivores' had record(s) in the literature (Table 5). High percentages of plants favoured by non-elephant members of the guild were also favoured by elephant (Table 5, first column), but plants favoured by elephant were not as frequently favoured by other members (Table 5, first row of data). The guild members which showed the most similarity to elephant in terms of favoured species were giraffe, black rhino and nyala, and the least impala. Kudu and impala showed very high percentages of similarity in favoured species (76% and 83%) and avoided species (74% and 78%) (Table 5, intersections of impala and kudu). Results in separate BHTs showed the same patterns.

Of the six studies reporting the complete woody diet of savanna browsers in one locality (Field & Ross 1975, Jarman 1971, Lamprey 1963, Makhabu 2005, Makhabu *et al.* 2006, Wiseman *et al.* 2004), only three provide sufficient data for detailed comparison. Lamprey determined overlap in diet for elephant, giraffe, black rhino and impala in Tarangire, Tanzania and obtained similar trends to those identified here – high percentages (> 50%) of plants utilized by non-elephant members of the guild were also utilized by elephant, but low percentages (<50%) of plants utilized by elephant were utilized by other guild members. However, Jarman who determined the overlap in diet between elephant, kudu, black rhino and impala in Kariba, Zimbabwe, and Makhabu who studied overlap between elephant, giraffe, kudu, and impala in Chobe, Botswana found low levels of overlap between other browsers and elephant. None of the six studies showed complete dietary overlap or separation between guild members.

3.3 Influence Of Abundance Of Each Group On The Other

Correlations between high non-elephant browser numbers and low elephant numbers were first reported by Fritz (1997). In a later extensive analysis of ungulate censuses from 31 ecosystems from East and southern Africa, Fritz et al. (2002) concluded that both mesobrowsers and mesomixed feeders were significantly affected by elephant and, in particular, that "…megaherbivores, and particularly elephants, appear to compete with mesomixed feeders and mesobrowsers." Valeix et al. (2007) reported decreases in the number of non-elephant browsers as elephant numbers increased, and in a later study using a data set over a longer period, in which the combined effects of elephants and rainfall were investigated, Valeix et al. (2008) recorded both declines in other browser numbers and reductions in their rate of population increase, leading them to suggested the existence of a negative influence of elephants on other browsers. In one instance mesobrowser and elephant numbers increased together over a short period (Rutina *et al.* 2005). Decreases in elephant numbers with a simultaneous increase in other browsers (Van der Jeugd & Prins 2000), have also been reported.

4. DISCUSSION

The high overlap in habitat use and staple woody-species diet between mesobrowsers and elephants, implies that the two groups impact the same core woody-species in the same habitats, and that impacts by elephants and mesobrowsers are likely to be substitutive under low elephant densities. However the occurrence in the diet of species not utilized by other members of the guild suggests that there may also be additive impacts of lower intensity.

The inverse correlation between the two groups' abundance reported in the literature (Fritz 1997, Fritz *et al.* 2002, Valeix *et al.* 2007, Van der Jeugd & Prins 2000), indicates that competition occurs between elephants and the other members of the guild. Pianka's 'niche overlap hypothesis' suggests that as competition increases niche overlap should decrease. The published literature does not provide any detail on the level of competition within the guild at the time that data were collected. However, the three studies of Lamprey (1963) in Tarangire where there was relatively high overlap, and Jarman (1971) and Makhabu (2005), in Kariba and Chobe respectively, where overlap was very low, and the reverse trend in herbivore abundance that can be inferred from comments by the authors, suggest that separation might occur between elephants and other members as competition increases. If this is correct it appears that impacts may initially be substitutive, but may become additive as resources are depleted. It is also possible that elephant-induced vegetation changes have modified the vulnerability of herbivores to their predators and that indirect competitive effects (Holt 1977) may be occurring. This is however unlikely, as simultaneous increases in predator numbers have not been reported (e.g. Loveridge & Macdonald 2002, Rasmussen 1997). Lagendijk *et al.*

(2012) recently found that resource specificity and browsing pressure by nyala increased in the absence of elephant, impling interference competition with competitive release.

The management relevance of substitutive effects becomes apparent when total population biomass of mesobrowsers, versus that of elephant, is considered. Although elephant plant use and its effects are visually obvious due to the sheer size of the animal, the effects of other browsers are more cryptic. In arid/eutrophic savannas supporting high biomasses of both elephant and other browsers (East 1984), total biomass of other large browsers may be comparable to that of elephants e.g. in the Kruger National Park, South Africa, topical for its 'excessive' elephant population, the total biomass of non-elephant browsers' is a third of the elephants' biomass (SANParks 2007). In smaller protected areas where elephant numbers are kept lower through contraception or hunting, the proportion can be much higher e.g. in Hluhluwe-iMfolozi Park, South Africa, estimated total biomass of other browsers is 3 million kg, and of elephant 1.4m kg (K.Z.N.Wildlife 2008). In such circumstance it seems highly probable that the effect mesobrowsers are having on the early life-history stages of the same woody species, and over the same habitats, that elephant are impacting at later life-history stages, is highly relevant to managers wanting to reach or maintain a specific desired state of savanna woodland over the long-term. Plant biomass consumed is not, however, straightforwardly linked to population biomass; mesobrowsers and elephants exhibit different relative consumption effects. Elephants, as large hind-gut fermenters, are adapted to process large quantities of poor quality forage, whilst mesobrowsers, due to their smaller size, will have higher

energy requirements per unit mass (Demment & Van Soest 1985), and thus the total energy they remove from the plant biomass is likely to be proportionally higher.

Both the Jarman-Bell principle and considerations of digestive strategy, outlined in the introduction, were supported; there was similarity in both species favoured and avoided between elephant and giraffe, both megaherbivores (Owen-Smith 1988), and between elephant and black rhino, two very large non-ruminants, and kudu and impala, two ruminants of similar size, showed the most overlap of any pair (Table 5). This finding is also of relevance to management, as it highlights to what extent, based on size and digestive strategy, different members of the guild are likely to overlap in plant species use and thus have potential substitutive effects. A logical, but as far as we are aware, unexplored corollary of these principles, is that where heavy competition exists between elephants and mesobrowsers for their mutually preferred woody species, elephants would be expected to ease this competition by, at least in part, including less palatable species which, due to their size/digestive abilities, they can process but mesobrowsers cannot. This implies that impact by elephants on these exclusively used woody species may in part be due to competitive displacement caused by mesobrowsers, in turn implying that reduction in the latter's numbers would, in time, alleviate impact on these exclusively used woody species as elephant returned to the central core of plant species preferred across the guild. Woolnough and du Toit (2001), studying vertical zonation between giraffe and smaller browsers, concluded that '..smaller members of ungulate guilds competitively displace the larger ones from shared feeding sites when resources become restricted.' In this way elephants and other savanna browser guild

members have additive effects on systems structure and composition when competition is high.

4.1 Conclusions

The literature review revealed a marked gap in the current state of knowledge, pertaining to mesobrowsers' and elephants' use of woody plant species in the same locality. Without such data, the precise effects of the substitutive and additive impacts of elephants and mesobrowsers on any particular system cannot be described.

Nevertheless, the two groups' overlap in woody species use where it has been studied in one locale, their widespread correspondence in staple diet and evidence of their influencing each others' abundance, all indicate a substitutive effect between elephants and mesobrowsers on woody vegetation structure and composition. In addition, the data on species used exclusively by elephants and other browsers implies a possible weak additive effect, which might occur as resources become scarce and competition between guild members is increased. The comparable biomass-densities of the two groups in many locations, translates these findings from an interesting concept to one of management relevance over the long-term. If elephants are removed or heavily reduced in number to save or restore woodlands, management may well find that comparable biomass-density mesobrowsers prevent the regeneration of the same woodland species

and thus, following death of the existing mature trees from natural causes, such woodlands fade from the system.

Others have investigated the role of elephant versus non-elephant browsers in savanna woodland dynamics in specific locations (e.g. Skarpe *et al.* 2004), and in relation to specific woody species (e.g. Moe *et al.* 2009). However, as far as we are aware, this is the first time that the widespread congruence in staple diet between the two groups has been revealed, and the implications of this finding in terms of browser-woodland dynamics explored.

Although savannas have an unusually diverse range of browsers, and thus are likely to have a high degree of redundancy in the system, management of systems' structure and composition, and biodiversity in general, by managing guilds rather than perceived keystone species, may also be applicable in temperate and other systems.

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Table 1. Ranking system used to standardize the varied measures of diet and habitat use present in the literature. Percentage use = the percentage of the entire diet or habitat use formed by that plant species or habitat type.

Rank (this paper)	Description of use	Percentage use	Preference index
0	absent	0%	totally avoided
1	very low	1% to 20%	heavily avoided
2	low	21% to 40%	mildly avoided
3	medium	41% to 60%	neutral selection
4	medium to high	61% to 80%	mildly selected
5	very high	81% to 100%	heavily selected

Table 2. Habitat use by the guild. Results for each habitat are expressed as percentages of the total number of records of occurrence in all habitats for that herbivore. Habitats are ranked on the basis of descending number of records for elephant and show 'well utilised' types (those ranked 2, 3, 4, or 5). Habitat types that were reported as heavily avoided or showed very low use (i.e. those ranked 1) are not included in the table. Numbers of records: elephant 231, giraffe 94, kudu 109, black rhino 53, nyala 8 and impala 104.

Habitat type	Elephant	Giraffe	Kudu	Black Rh.	Nyala	Impala
Acacia woodland	21.9	35.4	27.6	35.6	62.5	24.4
Riparian woodland	13.3	13.6	10.2	5.5	12.5	9.8
Mopane woodland	11.4	3.9	22.6	1.4		12.2
Baikaea woodland	9.5	2.7	5.8			4.9
Combretum woodland	9.0	2.0	3.0	4.2		9.6
Miombo woodland	5.7	2.7	8.6			9.6
Other woodland	5.2	1.4	7.5	4.2	12.5	2.3
Floodplain grassland	5.2					2.3
Commiphora woodland	4.6	9.2	4.4	8.2		7.0
General thicket	3.3	6.6	1.5	4.2	12.5	1.2
Acacia shrublands	2.8	9.2	4.4	9.5		3.5
Grassland	2.8	6.6	1.5	8.2		8.4
Swamp	2.8			5.5		
Wooded Grassland	2.4	6.8	3.0	13.5		4.9

Table 3. Number of sources in the literature containing diet information, number of diet records and total number of plant species recorded as being eaten.

Animal species	Number of papers, theses or reports	Number of diet records	Number of plant species eaten
Elephant	110	1571	704
Giraffe	29	486	178
Kudu	25	522	142
Black rhino	15	366	188
Nyala	3	154	64
Impala	35	578	203

Table 4. Percentage of woody species recorded as 'utilised' (ranks 1, 2, 3, 4 or 5) by the guild member in each row that are also 'utilised' by the guild member in the particular column. The numbers in brackets are the number of woody species recorded as 'utilised' by that herbivore.

	Elephant	Giraffe	Kudu	Bl. rhino	Nyala	Impala
Elephant (704)	X	16	15	16	5	15
Giraffe (178)	66	X	30	27	10	36
Kudu (142)	76	35	X	33	18	59
Black rhino (188)	60	23	25	X	17	32
Nyala (64)	58	27	41	50	X	48
Impala (203)	50	29	44	30	15	X

Table 5. Overlap in cited species favoured and avoided, between herbivore pairs. The first line in each box of the matrix gives percentages (%, %) of plant species used by both species that the herbivore in that row 'favours' that the herbivore heading that column 'favours' and 'avoids', respectively. The second line gives the percentage of plant species used by both that the herbivore in that row 'avoids' that the herbivore heading that column 'favours' and 'avoids', respectively. A species was defined as 'favoured' if >50 % of records for that herbivore for that plant species consisted of ranks 3, 4 or 5 and ' avoided' when > 50% of the records were ranks 0, 1 or 2. Records relating to plant species where neither herbivore in the pair exhibited 'favour' or 'avoidance' were ignored; consequently the sum of percentage figures in each line in each box is < 100%. Figures in parentheses are the number of plant species for which there are records in the literature for both members of each herbivore pair.

	Elephant	Giraffe	Kudu	Bl. rhino	Nyala	Impala
Elephant	X	43, 51 11, 87 (179)	28, 66 18, 72 (136)	45, 39 14, 75 (160)	54, 41 53, 35 (49)	24, 67 16, 78 (171)
Giraffe	73, 12 55, 42	X	48, 37 15, 84 (168)	44, 52 45, 52 (162)	64, 37 31, 62 (77)	31, 57 24, 72 (233)
Kudu	76, 17 68, 17	57, 28 23, 68	X	49, 47 58, 32 (119)	66, 26 20, 74 (66)	76, 19 22, 74 (213)
Bl. rhino	66, 18 39, 53	15, 83 15, 81	30, 64 22, 70	X	24, 69 57, 39 (58)	31, 65 27, 67 (175)
Nyala	62, 28 63, 25	15, 78 5, 91	48, 43 10, 88	46, 52 74, 19	X	60, 41 24, 71 (82)
Impala	73, 19 62, 27	54, 36 16, 80	83, 10 19, 78	33, 65 44, 50	68, 29 24, 70	X

Linkage paragraph, Chapter 1 to 2

The review of the literature from the past fifty years showed that elephant and other members of the browser guild heavily overlap in their usage of habitat types. It also revealed their communal use of a central core, or staple, diet, in terms of overlap in woody plant species usage. These findings were developed in terms of their implications for the long-term substitutive/synergistic effect of mesobrowsers, versus elephant, on woodland dynamics. The next stage in the project was now to verify whether these findings applied empirically to the browser guild at the study site, Hluhluwe-iMfolozi Park, South Africa – a typical southern African savanna woodland reserve, with a full complement of browsers (and predators).

CHAPTER 2

Overlap and seasonal shifts in use of woody plant species amongst a guild of savanna browsers*

Abstract: To clarify the potential influence of different browsers in the same guild on woody vegetation, dietary overlap and separation between elephant, giraffe, kudu, nyala and impala was assessed in Hluhluwe-iMfolozi Park, South Africa. Woody species browsed, browsing heights, plant-parts browsed and browsing versus grazing were recorded over 2 y by direct observation. We obtained 3068 browse records. Niche breadth (Levin's measure) and overlap (Schoener's index) in species browsed and browsing heights were calculated. Annual and seasonal differences in these measurements, plant-part use and browsing versus grazing were assessed. Elephant utilised the largest number (n = 78) of different woody plant species. Overlap in species browsed was lower between elephant and other browsers than amongst the latter. Seasonal rainfall influenced the range of woody plants utilised, niche breadth in terms of species browsed and browsing versus grazing. Marked resource depletion caused elephant, contrary to theoretical predictions, to narrow niche breadth in terms of species browsed. However, resource depletion rarely had a significant effect on interspecific overlap in species browsed or overlap in browsing heights, on actual browsing heights or plant-parts utilised. A small suite (n = 8) of woody species formed the core diet of all

guild members, implying the potential for synergistic impacts by guild members on these species and for competition between populations of different guild members.

Key words: elephant, giraffe, impact, impala, kudu, niche, nyala, woodland dynamics

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INTRODUCTION

A topical debate is the role of large herbivores in the top-down regulation of ecosystems (Moe *et al.* 2009). There exists a considerable literature on herbivores modifying habitat by impacting vegetation. However, studies addressing the impact of entire guilds on the broader vegetation and complete habitats are rare (Heroldova 1996, Hulme 1994, Makhabu 2005, Olofsson *et al.* 2004). Research assessing the long-term impact of altering the numbers of one member of a species pair (Albon *et al.* 2007, Hobbs *et al.* 1996) or of part of a guild (Flecker 1997, Madhusudan 2004) is also very uncommon. Yet consideration of various concepts of niche partitioning in herbivore guilds, suggests that focusing on entire guilds, rather than supposed keystone species, may be a better approach.

A prime example is the role of the African elephant (*Loxodonta africana* (Blumenbach)), versus that of other browsers, in savanna woodland dynamics. As African elephant populations have increased, habitat modification has been observed (Scholes & Mennell 2008). Some observers maintain that elephant and tree populations will stabilize only when woodlands have been converted to grassland (Lewis 1991), with an associated decline in diversity (Cumming *et al.* 1997). Others contend that other browsers, because of niche overlap (Walker 1985), may similarly modify woodland structure by impacting smaller individuals of the same plant species. In that case, reducing a single browser species, even elephant, may have little effect on community composition over the long term (Owen-Smith *et al.* 2006, Pickett *et al.* 2003).

Although elephants are widely described as a keystone species (Bond 1993), a substantial, but less quoted, literature describes other savanna browsers impacting woody

vegetation. We reviewed the literature from 1960 to 2009 and found surprisingly few (21) studies that have researched plant usage by elephant and at least one other browser in the same locality. Only one paper (Makhabu 2005) gives details of the entire guild's diet. The respective roles of different sympatric browsers in woodland dynamics are therefore unclear.

Elephant are non-ruminants, with most digestion occurring in the hind-gut (Van Hoven *et al.* 1981), and as such are adapted, compared to ruminants such as giraffe, kudu, nyala and impala, to process coarser forage at a rapid rate (Napier Bax & Sheldrick 1963). As larger animals, they can also survive on relatively lower-quality foods (the Jarman-Bell principle (Bell 1971, Jarman 1974). Thus elephant would be expected to have a broader diet and show a greater increase in diet breadth with increasing forage depletion (Beekman & Prins 1989, Owen-Smith 1988), compared to smaller, ruminant browsers. Degree of dietary overlap could also be explained in terms of resource competition. Niche overlap leads to competition only when resources are limiting (Pianka 1976), suggesting that overlap should be lower in intensely competitive situations (Pianka 1972). Low levels of overlap between different groups may thus, paradoxically, indicate heightened competition between the two groups. Competition has been used to explain feeding-height separation amongst African browsing ruminants (Woolnough & du Toit 2001).

This study examined dietary resource partitioning between elephant, giraffe, kudu, nyala and impala. We hypothesised that (1) overlap between different guild members, in both woody species use and plant parts browsed, would be greatest between those of similar size and/or digestive strategy, (2) overlap in browsing heights would be

greatest between similarly sized herbivores, (3) variation in annual and seasonal rainfall, via its effect on resource availability, would influence these overlaps, and (4) mixed feeders would browse more in the dry season.

METHODS

Study site

We conducted the study from September 2006 to October 2008 in Hluhluwe–iMfolozi Park (HiP), KwaZulu–Natal, South Africa (28°00′–28°26′ S; 31°43′–32°09′ E). HiP is a 900-km² fenced nature reserve, situated in the foothills of the first escarpment on the west side of the Zululand coastal plain (Whateley & Porter 1983). Mean annual rainfall and altitude decrease from Hluhluwe in the north (990 mm and 450 m asl), to iMfolozi in the south (635 mm and 60 m asl), with April to September being the dry season (Balfour & Howison 2001). During the study the second dry season was noticeably drier than the first, with the height of the second dry season (July-September) particularly dry (first year: wet season 569 mm, dry season 253 mm, July-September 51 mm; second year: wet season 577 mm, dry season 167 mm, July-September 19 mm). Terrain varies between valleys, hills and plains. The soils are mainly derived from sandstone, shale and dolerite intrusions and are generally eutrophic (Balfour & Howison 2001). In Hluhluwe during June and July (coldest months) the mean daily minimum temperature recorded over the study period was 12°C, and during January and February (hottest months) 31°C.

The majority of HiP is savanna, classified as Northern Zululand Sourveld and Zululand Lowveld, with areas of Scarp Forest in Hlhuhluwe (Mucina & Rutherford 2006). The vegetation of the park is characterised by fine-leaved *Acacia* savanna with a continuous grass layer and a fairly open tree canopy. Hluhluwe is typified by *Acacia nilotica* (Pooley 2003) woodlands, *Acacia karoo–Dichrostachys cinerea* thicket, *Euclea divinorum* woodlands and, at higher altitudes, *Celtis africana* forest communities; in iMfolozi *Acacia nigrescens* woodlands, *Acacia tortilis* woodlands and *Spirostachys africanus* woodlands predominate (Whateley & Porter 1983). The *A. nilotica* woodlands and *A. karroo–D. cinerea* communities that dominate Hluhluwe are allied with dense, tall grass swards, consisting primarily of species of the tribe Andropogoneae such as *Themeda triandra* and *Cymbopogon excavatus*.

The principal browsers, and their current estimated average densities, are elephant 0.56 km^{-2}, giraffe (*Giraffa camelopardalis* (Linnaeus)) 0.89 km^{-2}, black rhino (*Diceros bicornis* (Lichtenstein)) 0.35 km^{-2}, kudu (*Tragelaphus strepsiceros* (Pallas)) 1.3 km^{-2}, nyala (*Tragelaphus angasii* (Gray)) 7.3 km^{-2} and impala (*Aepyceros melampus* (Lichtenstein)) 26.1 km^{-2} (K.Z.N. Wildlife 2008, unpubl. data).

Data collection

We drove at 20 km h^{-1} on a fixed route through a representative sample of the different vegetation types, using the reserve's road network, for 5 d once a month. When study animals were seen, the vehicle was stopped. One observer then recorded the number of

animals, their sex, their main activity and the percentage of animals grazing versus browsing. The other observer noted, by simple instantaneous visual scan, which individual plants were being browsed. We then visited on foot each of the individual plants that were observed to have been utilised and recorded the plant species, height browsed at, height of the plant and plant parts consumed. For 88% of observations animals browsed over a height range, rather than one point, and hence the highest and lowest points were recorded.

Data analysis

We analysed the data in terms of 'browsing records', where a particular herbivore browsing from a particular individual plant formed one record, irrespective of how many bites were taken from that plant. Data were analysed across the whole study period, by year and by separate seasons (Schooley 1994).

To assess whether the data collected on plant species browsed by herbivores recorded the full range of their use of different woody species, the number of browsing events were plotted against the cumulative number of different plant species browsed, to establish whether an asymptote was reached.

For each herbivore species, the proportion contributed by each plant species to the total observed browsing of that herbivore was calculated. Using these proportions, herbivore niche breadth, in terms of woody plant species used, was assessed using Levins' measure (Levins 1968),

$$B = 1 \Big/ \sum_{s=1}^{n} P_s^2$$

where B is the niche breadth, P_s is the proportion of all browsing events on plant species s and n is the number of plant species browsed by that herbivore. This was standardised using the procedure of Hurlbert (1978),

$$Bs = (B - 1) / (n - 1)$$

where Bs is the standardised niche breadth, B is the niche breadth and n is the number of plant species eaten at least once by at least one of the herbivore species studied. On the standardised scale, one represents the complete generalist feeder that feeds without preference, while zero represents the complete specialist that feeds exclusively on one species and ignores all others.

Overlap of browsed woody species between all pairwise combinations of herbivores in the guild was assessed using Schoener's index (Schoener 1974). Where there is no use of the same resources this index is zero, and where completely identical resources are used to the same extent it is one; overlap is generally considered significant where the index ≥ 0.6 (Wallace 1981). Schoener's index for overlap of browsed-species was:

$$O_{ab} = 1 - \frac{1}{2} \sum_{s=1}^{n} \left| P_{sa} - P_{sb} \right|$$

where O_{ab} is the overlap between herbivore species a and b. P_{sa} is the proportion of all browsing events on plant species s by herbivore species a, P_{sb} similarly for herbivore species b and n is the number of plant species browsed by either herbivore species. Spearman rank correlations, based on these same proportions, were determined as an additional measure of diet similarity between herbivores. To assess potential problems in calculating Schoener's index values due to variation in sample sizes amongst the guild, the index was also calculated using a random subsample of 60 browse records per herbivore per season.

To determine overlap in browsing height between all pairwise combinations of herbivores, average feeding height (defined as the average of the highest and lowest browsing levels) for each browse record were classed into 20-cm intervals and these intervals replaced plant species in the above Schoener's index.

The Wilcoxon rank-sum test was applied to test the difference between the wet- and dry-season overlaps in plant species and browsing height by comparing the $\left|P_{sa} - P_{sb}\right|$ part of the overlap index equation.

Regressing all average feeding heights on all tree heights revealed no correlation. Therefore in analysing herbivore browsing heights, it was assumed they were independent of plant species. To determine whether herbivore species browsed at significantly different overall average heights (i.e. the average of the average feeding heights) to one another, after Fisher's F test showed that the majority of variances were not equal, the robust ANOVA in S-PLUS was applied and followed by multiple pairwise comparisons using the robust Dunnett's test – both tests assuming unequal variances

(Crawley 2002). Seasonal differences in the overall average feeding height, the average upper and the average lower feeding height at which individual herbivore species fed were analysed using the standard two-sample t-test (equal variances) or Welch's modified two-sample t-test (unequal variances).

Interspecific, intraspecific and seasonal differences in various other aspects of the herbivore foraging strategies were tested using Pearson's chi-squared test with Yates's continuity correction (Crawley 2002).

Estimates of the relative abundance of different woody species in the study area were derived from the 2007 Elephant Impact Study carried out by HiP reserve scientists. This study recorded all woody plant species, their stem numbers and diameters within 180 transects spread throughout a representative sample of the reserve's different vegetation types. We calculated the total basal area for each woody plant species across all the transects, and then expressed this as a proportion of the total basal area of all woody species across all transects.

All statistical procedures were carried out in S-PLUS 2000 (Mathsoft, Lucent Technologies, Inc., Murray Hill, U.S.A.).

RESULTS

Woody plant species browsed

We obtained a total of 3068 browse records (Table 1). Only eight records of black rhino feeding were obtained, so this browser species was not included in the analysis.

Asymptotes of the cumulative number of different plant species browsed against number of observations were approached between 40 and 70 records for all herbivores in all seasons, except for nyala in the 2008 dry season.

A total of 133 woody species, from a potential of at least 223 listed for HiP, were observed browsed by at least one of the five herbivore species during the study period. However, few woody species accounted for more than 10% of the total browsing records for each herbivore in each season, with a small suite of these woody species forming the staple or core diet of the entire guild (Table 1). Elephant utilised the greatest number of different woody species (Table 2), and utilised higher percentages of species utilised by other guild members, than other guild members utilised of elephant woody diet (Table 3).

Acacia karoo had the highest number of browsing events by elephant and giraffe, with both herbivores increasing use of it in the dry season. *Sclerocarya birrea* was the second most used species by elephant, especially in the wet seasons, but was used little by other members of the guild. *Dichrostachys cinerea*, *Ziziphus mucronata* and, to a lesser extent, *Maytenus heterophylla*, were important for all members of the guild. *Spirostachys africana* was another important food source for all members of the guild, except for elephant. The genus *Acacia* was used more in terms of browsing events than any other (Table 1).

With the design of the study, some random variation between season and year in the number of plant species recorded as utilised would be expected. However whilst there were minimal inter-seasonal changes by giraffe and impala, there was a marked increase in the number of woody species utilised by elephant in the dry season in both years, whilst kudu and nyala did so only in the more severe dry season (Table 2).

In terms of plant species browsed elephant occupied the widest niche of the guild in both wet seasons, and narrowed this niche during the second, considerably drier, dry season (Figure 1). Over both dry seasons the browsed-species niche of giraffe decreased, whilst that of kudu and nyala increased during the severe second dry season. As plots for nyala did not reach an asymptote, further data collection would probably have revealed an even broader niche.

Elephant did not show a significant (Schoener's index ≥ 0.6) or high (Schoener's index ≥ 0.5) overlap with other herbivores in species browsed. High or significant overlaps in species browsed were found, to varying extents, between herbivore pairs excluding elephant (wet season 2007: giraffe/kudu 0.52, giraffe/impala 0.64, kudu/impala 0.54; dry season 2007: giraffe/impala 0.52; wet season 2008: giraffe/impala 0.51; dry season 2008: kudu/impala 0.53, nyala/impala 0.50). Schoener's index results were generally supported by the corresponding Spearman rank correlations; however, there was a positive correlation between species browsed by elephant and giraffe over the wet and dry season of 2008. Although there were no significant differences ($P > 0.05$, Wilcoxon rank-sum test) in dietary overlap between the wet and dry seasons of 2007, in 2008, with its harsher dry season, highly significant increases ($P < 0.005$, Wilcoxon rank-sum test) in overlap between elephant and kudu and between kudu and nyala were found. Schoener's index based on the random subsample of 60 browse records closely matched that based on the full data set – higher overlaps were again found between non-elephant pairs and > 90% of the index values varied from those of the full data set by < 0.1. As would be expected from sampling theory, the vast majority (> 90%) of this minor variation was in the direction of reduced overlap.

Comparison of the estimated abundance of woody species in the reserve with observed browsing events, suggests potential impact will be high on certain species (e.g. *Capparis tomentosa*, Table 4) and low on others (e.g. *Euclea racemosa*, Table 4).

Browsing heights

Elephant and giraffe showed a wider range of average feeding heights than did kudu, nyala and impala during all four seasons (Figure 2). Pairwise analysis of overall average feeding heights showed that each herbivore species fed at a significantly different ($P < 0.05$, Dunnett method) average height compared to other members of the guild, except impala and nyala, where there was no significant difference ($P > 0.05$, Dunnett method) in feeding heights in any of the four seasons, and elephant and giraffe, where feeding heights during the wet and dry season of 2007 did not differ significantly ($P > 0.05$, Dunnett method) (wet season 2007, $F_{4,607} = 134$; dry 2007, $F_{4,751} = 216$; wet 2008, $F_{4,725} = 239$; dry 2008, $F_{4,918} = 191$). Similarly, Schoener's index for overlap in browsing heights showed significant overlap between impala and nyala in all four seasons (wet 2007: 0.77, dry 2007: 0.72, wet 2008: 0.80, dry 2008: 0.74), whilst for elephant and giraffe there was significant overlap in both the wet and dry season of 2008 (0.62, 0.65) and the dry season of 2007 (0.71). There was also significant overlap between elephant and kudu in the wet season of 2007 (0.62).

There were no significant seasonal differences ($P > 0.05$, Wilcoxon rank-sum test) in the Schoener's index for overlap in browsing heights for any herbivore pair, in either

year. There were no significant seasonal differences in the overall average feeding height ($P > 0.05$, standard two-sample t-test or Welch modified two-sample t-test, as appropriate), or the average upper or average lower feeding height at which individual herbivore species fed in either year, with the exception of elephant. Elephant fed at a significantly lower overall average feeding height in the dry season (average = 1.85 m) of 2008 compared to the preceding wet season (average = 2.52 m; $t = 5.3$, $P < 0.005$ (two-tailed), $df = 299$), and at significantly lower average upper (2.32 m versus 3.17 m; $P < 0.005$) and average lower (1.46 m versus 1.84 m; $P < 0.05$) feeding heights.

Plant parts and mixed feeding

Browsing technique varied amongst the guild members. Elephant favoured breaking off leafy branches or stripping leaves (70% and 23%, respectively, of the total observed browsing events for elephant over the study period), giraffe stripped leaves (67%), kudu bit off branch ends or shoots (53% and 33% respectively), nyala bit off shoots, mature leaves or branch ends (44%, 29% and 22% respectively), and impala bit off shoots and mature leaves (57% and 31% respectively). Kudu foraging showed significantly higher taking of branch ends compared to nyala ($\chi^2 = 21.1$, $df = 1$, $P < 0.0001$). Nyala showed a significantly higher usage of branch ends amongst the males versus the females ($\chi^2 = 4.51$, $df = 1$, $P = 0.034$). Impala, alone, showed significant changes in plant part usage between wet and dry seasons in both years; there was a significantly lower usage of mature leaves (first year: $\chi^2 = 6.12$, $df = 1$, $P = 0.014$; second year: $\chi^2 = 14.4$, $df = 1$, $P =$

0.0001) and higher usage of shoots (first year: $\chi^2 = 4.12$, df = 1, P = 0.043; second year: $\chi^2 = 9.61$, df = 1, P = 0.0019) in the wet seasons compared to the dry seasons.

Amongst the mixed feeders in the guild, elephant and impala showed a highly significant increase in the percentage of browsing versus grazing feeding-observations in both dry seasons, compared to the preceding wet season (elephant, first year: $\chi^2 = 41.8$, df = 1, P < 0.0001, second year: $\chi^2 = 43.2$, df = 1, P = < 0.0001; impala, first year: $\chi^2 = 61.9$, df = 1, P < 0.0001; second year: $\chi^2 = 34.7$, df = 1, P < 0.0001). Nyala, however, showed a significant decrease in the relative frequency of browsing to grazing in the first dry season ($\chi^2 = 12.0$, df = 1, P = 0.0005), but a significant increase in the second dry season ($\chi^2 = 34.5$, df = 1, P < 0.0001). Elephant and nyala, but not impala, increased the percentage of browsing versus grazing in the drier, second dry season significantly more than in the wetter, first dry season (elephant: $\chi^2 = 211$, df = 1, P < 0.0001; nyala: $\chi^2 = 19.5$, df = 1, P < 0.0001). However, both impala and nyala still grazed substantially more than browsed in both seasons, whilst elephant browsed more than grazed in both dry years.

In both years, the percentage of animal activity observations that were recorded as feeding significantly increased in the dry versus wet season (year one: wet = 58%, dry = 78%, $\chi^2 = 127$, df = 1, P < 0.0001; year two: wet = 68%, dry = 79%, $\chi^2 = 30.3$, df = 1, P = 0.0001).

DISCUSSION

Selection of woody species

Overlap in species browsed was greater amongst the non-elephant browsers than that between elephant and other browsers. Elephant showed the most overlap with giraffe, a fellow megaherbivore (Owen-Smith 1988), generally the broadest species browsed niche and utilised a higher percentage of plant species utilised by other guild members, than vice versa. These results agree with the predictions arising from differences in body-size and from differing digestive systems, as discussed in the introduction. They also agree with the few relevant studies in the literature. Jarman (1971) studying dietary overlap in Kariba, Zimbabwe, and Makhabu (2005) studying overlap in Chobe, Botswana, both found greater overlap amongst non-elephant browsers than that between elephant and other browsers. Field & Ross (1975), working in Kidepo Valley, found high levels of overlap (64%) in diet between giraffe and elephant, as did Lamprey (1963) in Tarangire (77%-86%). Our review of the literature from 1960 to 2009 showed that elephant utilised the widest range of woody species and shared higher percentages of diet with other browsers than vice versa.

Makhabu (2005), who also used Schoener's Index to assess woody diet overlap amongst the guild, found lower levels of overlap between elephant and other browsers (ranging from 0.2 to 0.32) than this study, even though the suite of plants browsed was considerably smaller (35 woody species versus 133). Jarman (1971), although calculating dietary overlap differently, also found 'considerable separation between [elephant, black rhino, kudu and impala] in the plants upon which each was most dependent'. Both authors describe resource limitation at their sites – the latter studying the guild after the construction of the Kariba dam had markedly compressed its range, the former along the

Chobe riverfront, an area of very high browser densities (Mosugelo *et al.* 2002). In contrast, Lamprey (1963) found high overlap between elephant and other browsers (elephant utilising between 71% and 77% of other browsers' diet), whilst studying the guild in Tarangire in the early 1960s when browse would probably have been plentiful. Current browse availability in HiP probably lies midway between these extremes – as does the degree of overlap between elephant and other browsers. Thus there appears to be a continuum with increasing levels of resource depletion being associated with decreasing dietary overlap between elephant and other browsers – agreeing with the niche overlap hypothesis of Pianka (1972).

An unexpected finding, in terms of the body-size hypothesis and, for elephant, digestive tract type, was the marked dry-season decrease in the browsed-species niche breadth of giraffe and elephant. Greater mobility of these species may be the explanation. Home ranges for both elephant and giraffe are considerably greater than those for smaller herbivores (du Toit 1990b). They are also, by virtue of their size, less susceptible to predation (Owen-Smith 1988) and consequently less restricted by dense undergrowth which may conceal predators (Grand 2002). Elephant and giraffe might therefore be expected to mitigate resource depletion more successfully than smaller herbivores, by concentrating their foraging in whatever part of their larger range provides the best forage, relatively independent of predators. This appeared to be the case, with the relevant dry-season diet of both elephant and giraffe having a considerably higher percentage contribution from *Acacia karoo* – a species principally available in the north-eastern part of the study area, which is characterised by thicker undergrowth.

Interspecific variation in plant utilisation might also relate to plant chemical defences (Owen-Smith 1993). Rapidly absorbed toxins such as alkaloids may influence hindgut fermenters, such as elephant, more than ruminants, which may be more affected by compounds hindering digestion (Palo 1987). For example, *Spirostachys africana*, poisonous to man, has previously been reported as avoided by elephant (Bowland & Yeaton 1997) but favoured by impala (Rodgers 1976), kudu (Hirst 1975) and nyala (Vincent *et al.* 1968) – as was the case in this study.

Arid/eutrophic savannas typically support high biomasses of both elephant and other browsers (East 1984) and HiP is no exception – indeed, the estimated total biomass of other large browsers exceeds that of elephant (3000 Mg versus 1400 Mg). Thus the heavy utilisation by the entire guild of a relatively small suite of woody species, whilst at least 90 (40%) of available species were ignored, suggests that the guild as a whole may impact these core species. This suggests the potential for interspecific competition in the guild, in turn implying the potential for guild members to influence the population size of other guild members. Keystone species are species defined as having a disproportionate effect on the ecosystem compared to their biomass. It may be that amongst the savanna browser guild impact is proportional to total biomass and that, therefore, the high profile impact of elephant is purely a reflection of its high total biomass in many areas.

Browsing heights

That different-sized herbivores browse at different heights, thus reducing niche overlap, is well established (du Toit 1990a). Similar mean browsing heights, and high Schoener's index values, between the comparably sized nyala and impala and, to a lesser extent, between giraffe and elephant, were therefore expected. Only elephant adjusted feeding height in response to resource availability. Giraffe may have reduced the available forage in the higher branches, competitively displacing elephant lower, but still above nyala and impala. Woolnough & du Toit (2001) concluded that when resources are restricted smaller ungulates competitively displace larger ones from shared feeding sites.

Plant parts and mixed feeding

Plant parts browsed differed amongst the guild broadly as predicted by both the body-size hypothesis and variation in digestive systems. The large, non-ruminant elephant fed mainly on leafy branches, containing a high proportion of relatively indigestible (Gordon & Illius 1996) woody matter, whilst impala, the smallest ruminant, fed mainly on nutritious shoots or leaves. Kudu showed the highest use of branch-ends (a resource that contains some wood, but also nutritious young leaves and/or buds), nyala, between kudu and impala in size, less usage and impala the lowest. Nyala, a markedly sexually dimorphic species, showed greater branch-end usage by males versus females. Plant parts browsed were not, except for impala, influenced by resource availability.

As grass ages the concentration of protein decreases whilst relatively indigestible crude fibre increases (McDonald *et al.* 1987). Browse, although generally a lower-quality

food than young grass (Codron *et al.* 2007), thus becomes more attractive as the dry season advances (Williamson 1975), explaining the increase in browsing versus grazing feeding observations for elephant and impala in both dry seasons. Flushes of green grass follow dry-season burning (Scholes & Walker 1982); the attractiveness of newly burnt areas to large herbivores is widely recognized (Rowe-Rowe 1982). However elephant were not observed utilising grass flushes and would be unlikely to be physically able to harvest such short grass. Thus in the dry season elephant rely heavily on browse, whilst grass flushes form an important part of impala and nyala diet – as reflected in the dry-season feeding-observations for elephant being predominantly browsing, whilst those for impala and nyala were predominantly grazing (Meissner *et al.* 1996). The impact of impala and nyala on woody vegetation during the dry season is likely, therefore, to be reduced by the availability of grass flushes.

The increase in 'feeding' observations in the dry versus wet seasons probably reflects the lower quality of dry-season forage, requiring proportionately greater time spent foraging to satisfy metabolic requirements.

CONCLUSIONS

Overlap in plant species browsed was less between elephant and the rest of the guild than amongst the latter. Seasonal and annual variation in resource availability influenced herbivore choice and range of woody plants utilised. However, variation in resource availability rarely had a significant effect on interspecific overlap in plant species browsed, on overlap in browsing heights, on browsing heights themselves or on plant

parts utilised. Elephant, contrary to theoretical predictions, decreased their niche breadth of plant species browsed in response to marked resource depletion.

A relatively small suite of species formed the core diet of all guild members, implying that there is the potential for synergistic impacts by guild members on these species and for competition between populations of different guild members. This strongly suggests that management, concerned about the long-term dynamics of savanna woodland, should consider the entire guild, rather than exclusively manage elephant.

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Figure 1. Seasonal standardized niche breadth of woody species browsed, shown by Levins' niche-breadth index, standardized to a scale of 0-1 following Hurlbert (1978). Wet (black) and dry (open) seasons are shown, with, for each herbivore, the first two columns representing the first year, the second two the second year of the study in Hluhluwe-iMfolozi Park.

Figure 2. Location and variation in heights browsed by members of the browser guild in Hluhluwe-iMfolozi Park during the wet (cross hatched) and dry (open) seasons. The box plots are based on average feeding heights (the average of the highest and lowest browsing levels) from browse records. The first pair of boxes for each herbivore represent data from the first year; the second pair from the second year. The lines within the boxes are sample medians and the 25^{th} and 75^{th} quartiles are respectively shown by the lower and upper box ends. The lines outside the boxes extend to the minimum and maximum values within the next 25^{th} quartile and the symbols beyond represent outlying observations.

Table 1. Frequency of browsing events on different woody species by guild members in Hluhluwe-iMfolozi Park. The values show the use of each plant species by each herbivore, expressed as a percentage of the total records for that herbivore over the two wet or two dry seasons. Only plant species that contributed ≥ 10% to the browsing of at least one herbivore species in one season are named. The penultimate row shows the total number of browse records obtained for each herbivore over the wet or dry seasons. The last row shows the number of plant species that formed the top 80% of browsing records (B.R.) for each herbivore. Nomenclature follows Pooley (2003).

	Elephant		Giraffe		Kudu		Nyala		Impala	
Plant species	wet	dry	wet	dry	wet	dry	wet	dry	wet	dry
Acacia grandicornuta	5	2	2	1	2	2	7		10	5
Acacia karoo	11	18	25	35	1	4	2	3	3	10
Acacia nilotica	5	2	9	5	6	2	1	1	8	7
Acacia tortillis	1		7	8	3	4			11	12
Acalypha sonderiana							11	1		
Berchemia zeyheri	2	2	3	3	2	3	11	9	1	1
Capparis tomentosa	1	1	1	1		2	2	6	1	5
Dichrostachys cinerea	3	10	12	4	14	11	9	5	17	6
Maytenus heterophylla	5	4	2	3	1	10	16	9	6	8
Phoenix reclinata	6	1								
Sclerocarya birrea	12	6	1		2				1	
Spirostachys africana	2	1	4	3	1	13	6	1	9	10
Strychnos spinosa				1	7	2				
Tarchonanthus camphoratus		1		1	1	3		9	1	4
Ziziphus mucronata	7	3	13	6	27	14	6	8	11	4
Number of browse records	183	300	290	324	110	134	109	104	688	826
Number of species top 80% B.R.	15	18	9	11	8	12	10	12	10	13

Table 2. Utilisation of different woody plant species by the browser guild in Hluhluwe-iMfolozi Park. The number of different woody species utilised, by season, by the guild and by each herbivore species are shown, together with the total number of different woody species utilised by each herbivore species over the study period.

Season	Total by guild	Elephant	Giraffe	Kudu	Nyala	Impala
Wet 2007	70	28	22	19	26	35
Dry 2007	79	41	25	16	19	34
Wet 2008	59	31	28	16	13	34
Dry 2008	81	42	28	28	26	37
Total by each herbivore species		78	49	46	47	65

Table 3. Overlap in utilisation of woody plant species amongst the browser guild in Hluhluwe-iMfolozi Park. The figures show the percentage of plant species used by the herbivore in a row, that the herbivore in the column also utilised (e.g. elephant utilised 61% of the plant species utilised by giraffe, but giraffe utilised only 40% of the plant species utilised by elephant).

	Elephant	Giraffe	Kudu	Nyala	Impala
Elephant	X	40	35	38	37
Giraffe	61	X	67	55	67
Kudu	59	74	X	61	72
Nyala	63	58	58	X	69
Impala	58	52	49	49	X

Table 4. Woody plant species potentially subject to high or low impact from the browser guild in Hluhluwe-iMfolozi Park. The first column shows plant species that contributed ≥ 5% to the observed browsing of at least one herbivore species (shown in parentheses) and have low estimated proportional abundance in the reserve (second column), whilst the third column shows plant species that did not contribute ≥ 5% to the browsing of at least one herbivore species and have high estimated abundance in the reserve (fourth column). Estimated abundance is expressed as the proportion of the total basal area of all woody species sampled during the 2007 Elephant Impact Study in Hluhluwe-iMfolozi Park.

Woody species potentially subject to high impact	Estimated abundance	Woody species potentially subject to low impact	Estimated abundance
Capparis tomentosa (all)	0.0008	*Euclea racemosa*	0.08
Ehretia rigida (impala, kudu, nyala)	0.0003	*Sideroxylon inerme*	0.027
Hippobromus pauciflorus (elephant, nyala)	0.0005	*Pappea capensis*	0.013
Strychnos spinosum (kudu)	0.0005	*Schotia capitata*	0.011
Acalypha glabrata (nyala)	0.0013	*Olea woodiana*	0.01
Acalypha sonderiana (nyala)	0.002	*Combretum apiculatum*	0.01

Figure 1

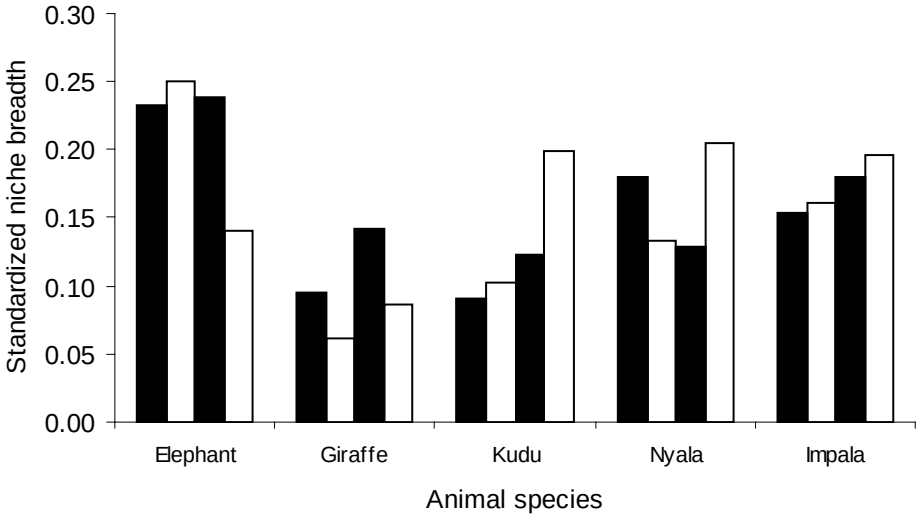
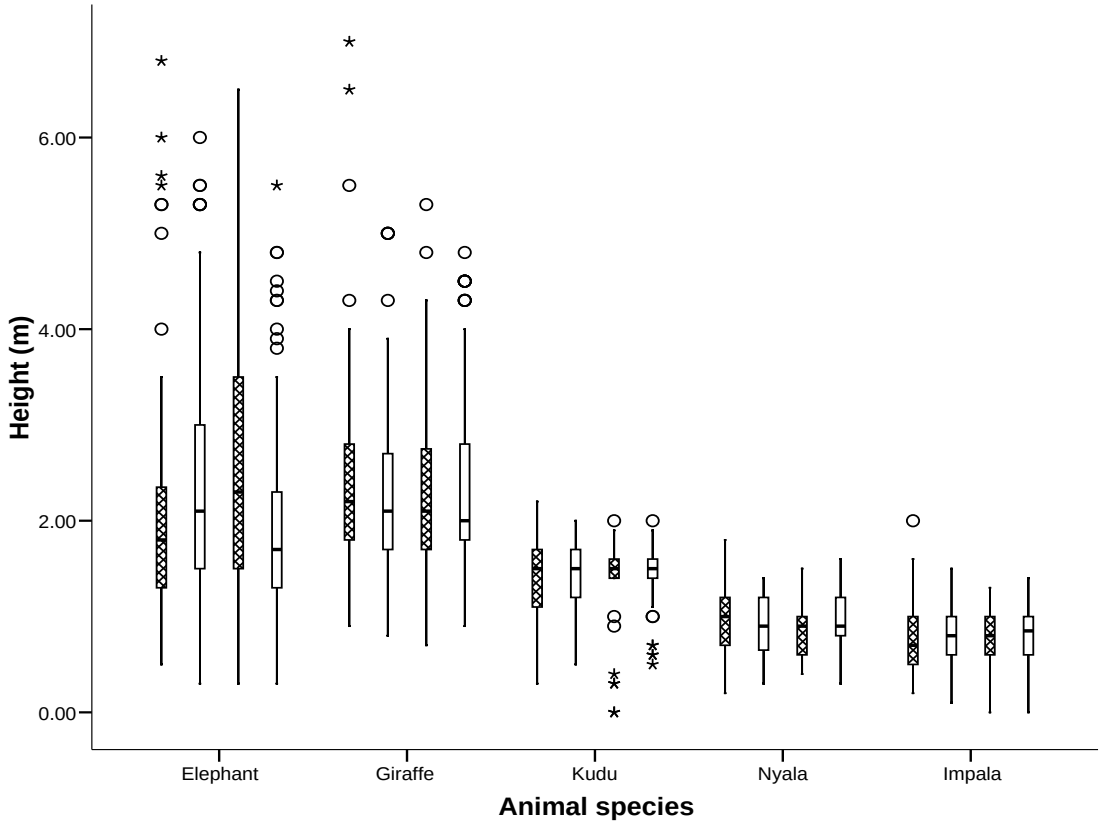

0.30
0.25
0.20
0.15
0.10
0.05
0.00
Standardized niche breadth
Elephant
Giraffe
Kudu
Nyala
Impala
Animal species

Figure 2


Height (m)
6.00
4.00
2.00
0.00
Elephant
Giraffe
Kudu
Nyala
Impala
Animal species

Linkage paragraph, Chapter 2 to 3

Thus my data confirmed, empirically, the existence of a core, staple diet across the browser guild at the study site, HiP. The next stage was to determine whether extensive overlap in habitat usage across the guild, as suggested by the literature review, also existed in HiP.

CHAPTER 3

Empirical assessment of theoretical influences of resource limitation on habitat usage by a guild*

Abstract: Resource depletion and associated increases in interspecific competition are likely to influence differential habitat usage amongst a guild. We empirically tested some prominent theoretical concepts using observed differences in seasonal habitat use amongst the savanna browser guild, for which the widespread increase in elephant numbers is a topical problem for management. Herbivores' locations were recorded over two years using repeated road transects and, for elephant, GPS/cell-phone collars. Densities were calculated using a novel GIS approach. Selectivity for (Manly's α, Ivlev's Electivity Index) vegetation types, and overlap (Schoener's Index, Morisita's Index of Similarity) in vegetation type usage were calculated. Resource depletion in the dry season resulted in all members of the guild increasing selectivity for vegetation types, but decreasing interspecific overlap. These effects were more marked over the second, more severe, dry season. We found support for the Niche Overlap Hypothesis and the Niche Compression Hypothesis, but not for Ideal Free Distribution Theory or Centrifugal Community Organization Theory. The Jarman-Bell Principle was generally supported, although unexpectedly during the severe dry season elephant showed the most selectivity, amongst the guild's mixed feeders, for vegetation type. The greater the resource depletion, the more relevant interspecific differences in habitat usage become in relation to the differential impacts of guild members.

Key Words: browsers, competition, elephant, GIS, niche, savanna, selectivity

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1. Introduction

As resources decrease and competition increases amongst a guild, interspecific differential use of available habitats may alter. The resultant alteration in levels of impact across the range of habitats is likely to influence biodiversity. However studies from the guild perspective are rare – whether assessing the impacts of entire guilds on their habitats (Makhabu 2005, Olofsson *et al.* 2004), or the consequences of altering the density of part of a guild (Flecker 1997, Madhusudan 2004). Yet there is a considerable theoretical literature on the relationship between interspecific competition and niche use. Here we summarize these theories, the bodies of which spawn hypotheses which offer testable predictions. We then test these predictions using the savanna browser guild as a topical case study. Elephant (*Loxodonta africana* (Blumenbach)) densities are increasing, except where there is heavy poaching, in all areas (Scholes & Mennell 2008). It is uncertain how this will affect elephant and other members of the guild's differential use of their habitats.

Niche overlap has been demonstrated for omnivores, carnivores and herbivores in a wide range of systems including tropical (Bagchi *et al.* 2003), temperate (Bonesi *et al.* 2004), arctic (Elmhagen *et al.* 2002), desert (Jones & Barmuta 2000) and, perhaps most extensively, in African savannas (Ferrar & Walker 1974, Fritz *et al.* 1996, Lamprey 1963, Loveridge & Macdonald 2003). However niche overlap leads to competition only when resources are sparse, and maximum tolerable overlap would be expected to be lower if there is intense competition (Pianka 1972, Pianka 1976). Ideal Free Distribution Theory (Fretwell & Lucas 1970) and Centrifugal Community Organization Theory (Rosenzweig 1981), suggest that interspecific niche overlap is reduced by competing individuals

increasing their niche breadth, by being less selective and utilising a wider range of resources. Conversely, the Niche Compression Hypothesis (MacArthur & Pianka 1966) suggests that niche overlap is reduced by reducing niche breadth, with competitors increasing selection and utilising a narrower range of resources.

The Jarman-Bell Principle (Bell 1971, Belovsky 1997, see also Demment & Van Soest 1985, Jarman 1974) predicts that larger animals can survive on relatively lower quality foods, because of the inter-relationships between body size, energy (Hungate *et al.* 1959) and protein turnover (Brody *et al.* 1934) and gut capacity (Illius & Gordon 1992). As a result of this wider food quality tolerance, larger herbivores would be expected to utilise a higher proportion of habitat types than smaller herbivores (Cromsigt *et al.* 2009). Elephant are non-ruminants, with most digestion occurring in the hind-gut (Van Hoven *et al.* 1981), and as such are adapted, compared to ruminants such as giraffe, kudu, nyala and impala, to process coarser forage at a rapid rate (Napier Bax & Sheldrick 1963).

These theories lead to the following hypotheses as to how resource limitation may influence habitat usage by the savanna browser guild: a) with increasing resource limitation i) interspecific habitat usage overlap will decrease (Niche Overlap Hypothesis), and ii) selectivity for habitat types may either decrease (Ideal Free Distribution Theory and Centrifugal Community Organization Theory) or increase (Niche Compression Hypothesis), b) larger herbivores will be less selective of habitat type than smaller herbivores (Jarman-Bell Principle) and c) elephant, as the largest member of the guild and its only non-ruminant, will be less selective of habitat type than other guild members (Jarman-Bell Principle and digestive strategy).

Community or vegetation type has been widely shown to be the principal influence on the habitat choice of large mammalian herbivores (Dekker *et al.* 1996, Ferrar & Walker 1974, Field & Laws 1970, Lamprey 1963). We assessed habitat usage, in terms of vegetation type usage, of elephant, giraffe (*Giraffa camelopardalis* (Linnaeus)), kudu (*Tragelaphus strepsiceros* (Pallas)), impala (*Aepyceros melampus* (Lichtenstein)) and nyala (*Tragelaphus angasii* (Gray)). We used observed differences in seasonal use to evaluate the described predictions from niche theory.

2. Methods

2.1 Study site

We conducted the study from September 2006 to October 2008 in Hluhluwe–iMfolozi Park (HiP), KwaZulu–Natal, South Africa (28°00′–28°26′ S; 31°43′–32°09′ E). HiP is a 900 km² completely fenced nature reserve, situated in the foothills of the first escarpment on the west side of the Zululand coastal plain (Whateley & Porter 1983). Mean annual rainfall and altitude decrease from Hluhluwe in the north (990mm and 450m a.s.l.), to iMfolozi in the south (635mm and 60m a.s.l.), with April to September being the dry season. During the study the second dry season was noticeably drier than the first, with the height of the second dry season (July-September) particularly dry (first year: wet season 569 mm, dry season 253 mm, July-September 51 mm; second year: wet season 577 mm, dry season 167 mm, July-September 19 mm). Terrain varies between valleys,

hills and plains. The soils are mainly derived from sandstone, shale, and dolerite intrusions and are generally eutrophic. In Hluhluwe during June and July (coldest months) the mean daily minimum temperature recorded over the study period was 12°C, and during January and February (hottest months) 31°C (Zululand Grass Project Weather Data, unpubl. data).

The national vegetation map of South Africa (Mucina & Rutherford 2006) recognizes three major vegetation types within HiP. These are Northern Zululand Sourveld (SVI22), Zululand Lowveld (SVI23) and Scarp Forest (FOz5). The vegetation is characterised by fine-leaved *Acacia* savanna with a continuous grass layer and a fairly open tree canopy. Hluhluwe is typified by *Acacia nilotica* woodlands, *Acacia karoo – Dichrostachys cinerea* thicket, *Euclea divinorum* woodlands and, at higher altitudes, *Celtis africana* forest communities. In the Corridor *A. nilotica* woodlands and *A. karroo – D. cinerea* thicket predominate; in iMfolozi *Acacia nigrescens* woodlands, *Acacia tortilis* woodlands, and *Spirostachys africanus* woodlands (Whateley & Porter 1983). The *A. nilotica* woodlands and *A. karroo – D. cinerea* communities that dominate Hluhluwe and the Corridor are allied with dense, tall grass swards, consisting primarily of species of the *Andropogoneae* tribe such as *Themeda triandra* and *Cymbopogon excavatus*.

HiP supports a large and diverse herbivore population. The principal browsers, and their current estimated average densities (K.Z.N.Wildlife 2008), are elephant 0.52 km^{-2} (increasing at 9% p.a.), giraffe 0.89 km^{-2}, black rhino (*Diceros bicornis* (Lichtenstein)) 0.35 km^{-2}, kudu 1.3 km^{-2}, nyala 7.3 km^{-2} and impala 26.1 km^{-2}.

2.2 Data collection

Management required a cheaper alternative to annual aerial censuses for monitoring population sizes amongst the browser guild. Previous use of Distance sampling (Buckland *et al.* 2001) to analyse ground census data had produced unrealistic population estimates. This was probably due to the assumptions inherent in Distance sampling being violated. Distance sampling assumes that sighting visibility falls off gradually as distance from the observer increases. The varied topography of HiP frequently results in visibility being abruptly cut off, leading to areas of dead ground where animals cannot be seen, between the observer and the limit of his vision. We therefore developed our own method, based on a GIS, for determining herbivores' densities by habitat type, from which management could extrapolate to monitor reserve-wide population sizes. Comparison of the population size estimates from our GIS method with those from previous aerial censuses was used to assess the accuracy of our approach.

We drove at 20 km h^{-1} on the same fixed route through a representative sample of the different vegetation types, using the reserve's road network, for 5 d once a month for two complete years (September 2006 to September 2008). When study animals were seen the vehicle was stopped, and the species and number of animals recorded. At each sighting location we recorded the longitude/latitude of the vehicle using a GPS (Garmin 12XL), the distance from the vehicle to the (approximate) centre of the herd using a laser rangefinder (Yardage Pro 1000) and the compass bearing from the vehicle to the herd, using the GPS that was recording the direction of travel. The position of the individual animal or herd was then determined trigonometrically and imported into a GIS (ArcGIS 9). To determine the area sampled all transects were slowly re-driven to obtain visibility

profiles, with observers recording manually on large scale maps maximum sighting distances on either side of the vehicle, together with the start and end of dead ground where this occurred.

Although elephant form an estimated one third of the reserve's browser biomass, their small numbers, comparative to the other browsers studied, results in comparatively few elephant sightings. Repeated transects relying on frequent sightings was therefore not an appropriate technique, and consequently an alternative approach was needed to determine elephant habitat usage. Over the study period six cow elephants, one in each of the reserve's six breeding herds, were fitted with G.P.S./cell-phone collars set to record and download the wearer's position every thirty minutes. These records were then also imported into the GIS.

2.3 Data analyses

Data were analysed across the whole study period, by year and by separate seasons (Schooley 1994).

2.3.1 Densities of each herbivore species in each vegetation type

A simplified vegetation map with nine types was constructed from the Whateley and Porter (1983) vegetation map, with 30 types, by merging those with similar structure and composition. The resulting types were *Celtis, Harpephyllum, Euclea racemosa* scarp forest, *Acacia robusta, Ficus* riparian woodland and forest, *Olea europa, Commiphora harveyi* dry forest, *Euclea divinorum* broad-leafed thicket, *Spirostachus africana, Euclea*

racemosa, *Acacia grandicornuta* closed woodland, *Acacia*, *Dichrostachys cineria* fine-leafed thicket, *A. nigrescens, A. tortilis, A. nilotica, A. burkei*, *Commiphora apiculatum* open woodland, *A. karoo, A. caffra, D. cineria* wooded grassland, and *Themeda triandra, Cymbopogon excavatus* invaded grassland.

We compared sighting distances at the height of summer (Dec, Jan, Feb) and late winter (Aug, Sept, Oct) to establish if there were differences in sighting distances in the two seasons. There was no significant difference. Histograms of sighting distance versus numbers seen showed that the maximum effective sighting distance (~ 200m), and that the drop-off in the probability of sighting (between 30m and 40m), was the same for all species. The visibility profiles were then used to construct a single polygon in the GIS of the total area sampled. This was validated using the 3,108 sighting records to ensure that none occurred outside of the area surveyed. Using the intersection features of ArcGIS, the vegetation layer and the sampled area polygon, the area sampled by vegetation type was determined. Densities per vegetation type were then calculated from the number of animals sighted in each type, averaged over the six month period for each of the four seasonal periods.

Densities for elephant were determined from their collar data. A concurrent study on the social behaviour of the six breeding herds in HiP showed that, over the period of this study, each collared cow remained with her herd and that membership of each herd varied little (Bodasing 2011). During the height of the dry season breeding herds coalesced, typically into two large herds, with, again, the collared cows remaining with their core breeding herd within the larger dry season herd. Thus movements of each collared cow can be taken as representative of their respective breeding herd. Overlaying

the GPS downloads (n = 187,254) onto the GIS vegetation layer enabled the proportion of time spent in each vegetation type by each collared elephant to be calculated. Average numbers of elephants in each of the six herds for each of the four seasons where then used to weight these proportions. Knowing the total number of elephants in the reserve and total area of each vegetation type, these weighted proportions were used to produce densities for elephant by vegetation type across the reserve.

The different methods used to determine densities per vegetation type for elephant versus other browsers, means one cannot directly compare the actual densities across these two groups. However, comparison of the *proportional* usage of different vegetation types by elephant versus other browsers is valid.

2.3.2 Vegetation types: preferences and overlaps

Krebs (1999) recommends Manly's α preference index (Manly *et al.* 1972) as a simple measure of preference derived from probability theory, that includes all the biological factors that may affect capture and encounter rates of prey, including availability.

Manly's α (Constant Prey Populations) may be adapted for habitat usage to:

$$\alpha_i = \frac{p_i}{P_i}\left(\frac{1}{\sum(p_j/P_j)}\right)$$

where α_i = Manly's α (preference index) for habitat type *i*

p_i, p_j = proportion of the overall habitat usage that usage of habitat type *i* or *j* forms (*i* and *j* = 1, 2, 3,…..n)

P_i, P_j = proportion of habitat type *i* or *j* in the environment

n = number of habitat types

If α_i is > than (1/n) then habitat type *i* is preferred; if < than (1/n) habitat type *i* is avoided.

Seasonal differences in vegetation type preferences by the guild were assessed by calculating, and comparing, the sum of absolute values away from the neutral value for Manly's Alpha (here 0.111) for the entire guild, and for each herbivore species, in each season. As obligate browsers (kudu and giraffe) experience different resource limitation between seasons compared to mixed feeders (impala, nyala and elephant), herbivores were grouped into obligate browsers or mixed feeders to assess the predictions of the Jarman-Bell Principle. Weights of herbivores are the average of adult male and female, taken from Estes (1991).

As an additional measure of preference Ivlev's Electivity Index (1961), recommended by Lechowitz (1982), was calculated as:

$$E_i = (p_i - P_i)/(p_i + P_i)$$

where *Ei* = Ivlev's Electivity Index for habitat i

p_i = proportion of the overall habitat usage that usage of habitat type *i* forms

P_i = proportion of habitat type *i* in the environment

If *Ei* = 0, then no selection occurs. The closer *Ei* is to +1, the greater the preference; *Ei* of -1 represents complete avoidance.

Overlap of vegetation type usage between all pair-wise combinations of herbivores in the guild was assessed using Schoener's Index (Schoener 1974), recommended by Abrams (1980) as a measure meeting the required criteria of an overlap measure. Where there is no use of the same resources this index is zero, and where completely identical resources are used to the same extent it is one; overlap is generally considered significant where the index ≥ 0.6 (Wallace 1981). Schoener's index for overlap of habitat usage was:

$$S_{ab} = 1 - \frac{1}{2}\sum_{i=1}^{n} \left| p_{ai} - p_{bi} \right|$$

where S_{ab} = Schoener's Index for overlap of habitat usage between herbivore species *a* and *b*

p_{ai} = proportion of the overall habitat usage that usage of habitat type *i* by herbivore species *a* forms

p_{bi} = similarly for herbivore species *b*

n = number of habitat types

Seasonal differences in overlap of vegetation type usage were assessed by applying the Wilcoxon rank-sum test to the wet and dry seasons $\left| P_{ai} - P_{bi} \right|$ part of Schoener's index equation.

Schoener's index is relatively unaffected by sample size. It is shown in Appendix B to be identical to Renkonen' Index (Percentage Similarity) (1938), another recommended measure of overlap (Krebs 1999).

As an additional measure of overlap Morisita's Index of Similarity (1959), recommended by Wolda (1981) as "the best overall measure of similarity for ecological use" but one affected by very small sample size (Krebs 1999), was calculated as:

$$M_{ab} = \frac{2\sum X_{ai}X_{bi}}{(\lambda_1 + \lambda_2)N_a N_b}$$

where M_{ab} = Morisita's index of similarity of habitat usage between herbivore species *a* and *b*

X_{ai} = number of individuals of herbivore species *a* in habitat type *i*

X_{bi} = number of individuals of herbivore species *b* in habitat type *i*

$N_a = \Sigma X_a$ = total number of individuals of herbivore species *a*

$N_b = \Sigma X_b$ = total number of individuals of herbivore species *b*

and

$$\lambda_1 = \frac{\sum[X_{ai}(X_{ai} - 1)]}{N_a(N_a - 1)}$$

$$\lambda_2 = \frac{\sum[X_{bi}(X_{bi} - 1)]}{N_b(N_b - 1)}$$

The Morisita Index of similarity varies from 0 (no similarity) to 1.0 (complete similarity).

All statistical procedures were carried out in S-PLUS (MathSoft 1999).

3. Results

Over the study period we obtained 3,108 sighting records (totalling 27,947 animals). Data obtained on black rhino were too limited to form part of the analyses. Population estimates derived from aerial censuses were available for impala (23,500) and for giraffe (800). Estimates derived from our GIS approach (impala: 23,600; giraffe: 900) compared favourably with these.

In the wet season the guild's members utilised a wide range of woodland vegetation types, with grassland, scarp forest and riparian communities generally avoided (Table 1 and 2). However, in the dry season there was a noticeable shift to these latter three vegetation types, with elephant and giraffe particularly preferring scarp forest and impala and nyala (and, to a lesser extent, kudu) riparian communities (Table 1 and 2). The guild's reduced usage in the dry season of closed, open and grassed woodland was striking (Table 2). Impala heavily preferred dry forest and nyala broad leaved thicket in both seasons.

The sum of absolute values away from the neutral value for Manly's Alpha for the entire guild was higher in both dry seasons (3.97, 5.16) compared to the preceding wet seasons (3.12, 3.68), indicating greater selection (whether avoidance or preference) of vegetation types occurred in the dry season. The higher value in the second dry season and the noticeably larger difference between the wet and dry season of the second year (1.48) compared to the first year (0.85), indicated greater selection was occurring in the severer, drier second dry season. Larger herbivores, within the category of obligate browser or mixed feeder, were generally less selective of habitat type than smaller

herbivores (Table 3). However over the first, less severe, dry season elephant showed a comparable degree of selectivity to the much smaller nyala, whilst over the second, severe dry season elephant were the most selective mixed feeder. Similarly, amongst the obligate browsers, giraffe showed a comparable degree of selectivity to the smaller kudu over the second, severe dry season. Manly's Alpha results were supported by Ivlev's Electivity Index results. The two indices closely agreed with each other (Appendix A), with 6% of results differing (marginally) in terms of showing a preference or avoidance.

Overlap was significant (Schoener's Index ≥ 0.6) for all herbivore pairs in both wet seasons and for 95% of herbivore pairs in both dry seasons (Table 4). 80% of overlap values were lower in the dry season compared to the preceding wet season in both years. Significant seasonal reduction in overlap ($p < 0.05$, Wilcoxon rank-sum test) was shown by only one herbivore pair in the first year, but by three herbivore pairs in the second year with its severer dry season. Similarly, across the guild as a whole significant seasonal reduction in overlap ($p < 0.05$, Wilcoxon rank-sum test) occurred between the wet and dry season in the second year, but not in the first. Schoener's Index results were supported by Morisita's Index of Similarity results. The relative values of the two indices amongst the guild were similar and showed similar seasonal shifts (Table 4).

4. Discussion

The similarity of our population estimates to those derived from aerial censuses, suggests our novel GIS approach to determining herbivore densities gives consistent values.

Additionally, the finding of extensive utilisation of woodland vegetation types by the guild's different members is in agreement with previous work on the habitat usage of elephant (Laws 1970), giraffe (Dagg & Foster 1976), impala (Jarman 1972), kudu (Grunow 1980), nyala (Anderson 1978), and black rhino (Tatman *et al.* 2000). This widely reported preference is probably because woodlands have both a physiognomy that maximises the availability of food to browsers and mixed feeders of different sizes, and are likely to have a high nutritional status because of rapidly growing early successional species, resulting from browsing, fire and wind disturbance. Increased usage of riparian habitats during the dry season has been specifically demonstrated by others for elephant (Mosugelo *et al.* 2002), giraffe (Pellew 1984), impala (Jarman 1972), kudu (Simpson & Cowrie 1967), and black rhino (Oloo *et al.* 1994); it corresponds to the dry season movement down the cateena that has been demonstrated for grazing ungulates (Bell 1970) and elephants (de Knegt *et al.* 2008). Whilst impala, nyala and, to a lesser extent, kudu showed this shift here, elephant and giraffe did not but, rather, showed a dry season shift to scarp forests. This vegetation type only occurs in the considerably wetter north of the reserve and presumably retains, similar to riparian habitats, higher plant nutrient values through the dry season compared to other vegetation types.

The extensive overlap in vegetation type usage found amongst the guild implies that different guild members will broadly impact the same vegetation types. Pianka's Niche Overlap Hypothesis was supported – in both dry seasons most guild members showed a decrease in interspecific overlap, whilst significant reductions in overlap were more numerous in the second, severer dry season, during which, uniquely, overlap across the guild as a whole also significantly declined. Thus interspecific habitat usage overlap

decreased with increasing resource limitation. The Niche Compression Hypothesis was also supported – selectivity for vegetation types increased in both dry seasons, with this effect also more pronounced in the more severe of the two dry seasons, again implying a direct relationship with increasing resource limitation and, thus, competition. Shrader *et al*. (2012), working in nearby Ithala Game Reserve, also found that elephant increased selectivity for vegetation types over the dry season. Conversely, the predictions of the Ideal Free Distribution Theory and Centrifugal Community Organization Theory, that selectivity decreases with increasing resource depletion, were not supported. Thus from the perspective of management, the greater the resource depletion (e.g. following increases in elephant density), the more relevant interspecific differences in habitat usage become in relation to guild members' differential impacts.

The Jarman-Bell Principle was generally supported, with smaller herbivores showing decreased diversity of habitat use (i.e. increased selectivity) compared to larger herbivores. These findings directly support Cromsigt *et al.* (2009) who, working on the savanna grazing guild in HiP, found that larger ruminant grazers were more evenly distributed than smaller ruminants and had a more diverse use of habitats. However the dry season selectivity of elephant, and to a lesser extent giraffe, did not support the Jarman-Bell principle, as these largest members of the guild showed comparable or, under marked resource limitation conditions, greater selectivity than smaller guild members. The explanation for both species may be their greater mobility. Home ranges for both giraffe and elephant are markedly greater than those for smaller herbivores (du Toit 1990). By virtue of their size they are also less susceptible to predation (Owen-Smith 1988), and consequently less restricted by dense undergrowth which may conceal

predators (Grand 2002). Dense undergrowth also supports higher densities of ticks; it has been suggested that larger ungulates may be better able to tolerate the metabolic cost of tick infestation than smaller ungulates (Gallivan & Horak 1997). Giraffe are also heavily attended by the tick-removing oxpecker (Hart *et al.* 1990). Elephant and giraffe might therefore be expected to alleviate resource depletion more successfully than smaller herbivores, by concentrating their foraging in whatever part of their larger range provides the best forage, relatively independent of predators or ticks. This appeared to be the case, with the relevant dry seasons' range of both elephant and giraffe being concentrated in the north-eastern part of the study area, which is characterised by thicker undergrowth and stands of *Acacia karoo* – a woody species heavily favoured by both herbivores (O'Kane *et al.* 2011). Elephant are also known to communicate over long distances (Poole *et al.* 1988), and thus the disparate but related herds that combine in the dry season (Bodasing 2008, Wittemyer *et al.* 2007) might inform one another where the best forage is to be found. The manner in which the smaller members of the guild were apparently unable to capitalise on these superior resources, emphasises that factors other than efficiency in acquiring food sources of high nutritional value, as suggested by Optimal Foraging Theory (Stephens & Krebs 1986), may also influence habitat and food selection. For instance, the Giving Up Density Theories (Brown 1988) suggest that both niche breadth and niche overlap may be influenced by factors such as predation. Hopcraft *et al.* (2012) found that niche size, in terms of spatial distribution, of smaller grazers was, compared to larger grazers, limited by predation. Additionally it is noteworthy that although the Jarman-Bell Principle is widely accepted, some recent empirical evidence

(Clauss & Hummel 2005, Franz *et al.* 2011, Weckerly 2009) questions this theoretically derived concept.

Conclusions

Amongst the savanna browser guild we found that with increasing resource depletion interspecific overlap in habitat usage decreased, whilst selectivity for habitat types increased. Smaller members of the guild generally showed greater selectivity for habitat types, but exceptions, noticeably elephant under marked resource depletion, were found.

These principles may apply to other guilds and in other systems. However, the savanna browser guild has an unusually diverse range of browsers, and is thus likely to have a high degree of redundancy in the system, translating into heightened competitive effects amongst the guild. Guilds lacking these characteristics are likely to respond to resource limitation, in terms of the shifts in habitat usage overlap and selectivity discussed here, in a more muted manner.

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Table 1. Densities by vegetation type. Densities in each vegetation type are shown for each member of the guild, in different wet (w) and dry (d) seasons (S), in numbers per square kilometre.

Herbivore	S	Broad leafed thicket	Closed woodl'd	Dry forest	Fine leafed thicket	Invaded grassl'd	Open woodl'd	Riparian	Scarp forest	Wooded grassl'd
Elephant	w07	0.7	0.4	0.6	0.4	0.2	0.5	0.5	0.4	0.5
Elephant	w08	0.1	0.6	0.7	0.2	0.1	0.5	0.5	0.1	0.6
Giraffe	w07	0.8	0.9	0.1	0.9	0	0.8	0.4	0	0.6
Giraffe	w08	2.7	0.3	1.0	1.6	0	1.7	0.3	0	1.5
Kudu	w07	0	0.7	0.6	0.3	0	0.7	0.1	0	1.0
Kudu	w08	0	0.1	1.2	0.2	0	0.8	0.2	0	0.5
Nyala	w07	7.0	2.2	1.3	0.7	0.8	1.7	1.3	2.4	2.1
Nyala	w08	4.7	3.0	0.7	1.6	0.2	2.0	0.1	1.1	1.5
Impala	w07	5.6	42.0	56.2	4.9	1.2	35.3	17.4	0	14.5
Impala	w08	2.0	33.3	35.3	2.8	5.3	40.1	10.5	1.1	19.0
Elephant	d07	1.3	0.2	0.3	1.0	0.4	0.4	0.7	1.1	0.4
Elephant	d08	1.1	0.3	0.4	0.8	0.6	0.4	0.7	1.6	0.5
Giraffe	d07	0.8	0.9	0.2	1.2	3.2	1.5	0.9	2.2	0.7
Giraffe	d08	0	0.6	0.8	1.7	3.2	0.9	0.5	2.0	0.8
Kudu	d07	0	0.4	0	0	0	0.7	0.2	0	0.8
Kudu	d08	0	0.9	1.0	0.2	1.0	0.8	0	0	0.6
Nyala	d07	5.3	2.5	0.7	1.2	0	2.8	3.2	0	1.4
Nyala	d08	1.8	3.1	0.4	0.8	0	1.8	2.1	0.6	1.5
Impala	d07	1.4	36.0	63.4	4.8	1.2	31.7	33.3	0	12.1
Impala	d08	5.6	38.9	40.1	3.9	2.8	32.4	32.5	0	8.4

Table 2. Selection for vegetation types. Manly's Alpha (Constant Prey Populations) Preference Index values (Appendix 1) are used to demonstrate selection by each member of the guild, in different wet (w) and dry (d) seasons (S). With nine variants of vegetation type, the index indicates neutral selection at 0.11. Heavy preference (++) was taken as index value > 0.25, preference (+) 0.15 to 0.25, neutral or mild preference/avoidance (n) > 0.09 and < 0.15, avoidance (-) 0.09 to 0.05 and heavily avoided (--) as < 0.05.

Herbivore	S	Broad leafed thicket	Closed woodl'd	Dry forest	Fine leafed thicket	Invaded Grassl'd	Open woodl'd	Riparian	Scarp forest	Wooded grassl'd
Elephant	w07	+	n	+	n	- -	n	n	-	n
Elephant	w08	-	+	n	- -	- -	+	+	-	+
Giraffe	w07	+	+	- -	+	- -	+	-	- -	n
Giraffe	w08	+ +	- -	n	+	- -	+	- -	- -	+
Kudu	w07	- -	+	+	-	- -	+	- -	- -	+ +
Kudu	w08	- -	-	+ +	-	- -	+ +	-	- -	+
Nyala	w07	+ +	n	-	- -	- -	-	-	n	n
Nyala	w08	+ +	+	- -	n	- -	n	- -	-	n
Impala	w07	- -	+	+ +	- -	- -	+	n	- -	-
Impala	w08	- -	+	+	- -	- -	+ +	-	- -	n
Elephant	d07	+ +	- -	- -	-	-	-	n	+ +	-
Elephant	d08	+	- -	-	- -	n	- -	-	+ +	- -
Giraffe	d07	-	-	- -	n	+ +	n	-	+	-
Giraffe	d08	- -	- -	-	- -	+ +	- -	- -	+ +	- -
Kudu	d07	- -	+	- -	- -	- -	+ +	n	- -	+ +
Kudu	d08	- -	-	+ +	- -	+ +	- -	n	- -	- -
Nyala	d07	+ +	n	- -	-	- -	+	+	- -	-
Nyala	d08	+ +	n	-	- -	- -	- -	+	+	- -
Impala	d07	- -	+	+ +	- -	- -	+	+	- -	-
Impala	d08	-	n	+ +	- -	-	- -	+	- -	- -

Table 3. Selectivity for vegetation types by guild members. The absolute values away from the neutral value for Manly's Alpha (here 0.111) are shown. The higher the value, the greater the degree of selectivity. Values are shown for each of the four seasons studied, for both wet and dry seasons and for all seasons combined. Weights (kg) are the average of adult male and female, taken from Estes (1991).

	Herbivore	Weight	Wet 2007	Dry 2007	Wet 2008	Dry 2008	Both wet	Both dry	All
Obligate grazers	Kudu	214	0.85	1.11	0.98	1.25	1.83	2.36	4.19
	Giraffe	900	0.66	0.53	0.76	1.23	1.42	1.76	3.18
Mixed feeders	Impala	53	0.84	0.9	0.82	0.93	1.66	1.83	3.49
	Nyala	86	0.52	0.72	0.64	0.8	1.16	1.52	2.68
	Elephant	4000	0.25	0.71	0.49	0.95	0.74	1.66	2.4

Table 4. Overlap in vegetation type use amongst guild members. Schoener's Index and Morisita's Index are shown for each herbivore species pair in each of the four seasons.

	Schoener's Index				Morisita's Index			
Species pair	Wet 07	Dry 07	Wet 08	Dry 08	Wet 07	Dry 07	Wet 08	Dry 08
Elephant/giraffe	0.85	0.77	0.77	0.80	0.97	0.93	0.92	0.93
Elephant/kudu	0.82*	0.58*	0.78	0.71	0.96	0.82	0.94	0.91
Elephant/nyala	0.85	0.77	0.82	0.79	0.96	0.92	0.97	0.91
Elephant/impala	0.80	0.62	0.86*	0.65*	0.96	0.82	0.97	0.85
Giraffe/kudu	0.81	0.72	0.80	0.70	0.94	0.90	0.96	0.87
Giraffe/nyala	0.79	0.83	0.77	0.69	0.94	0.98	0.90	0.84
Giraffe/impala	0.78	0.76	0.70*	0.60*	0.94	0.93	0.90	0.78
Kudu/nyala	0.83	0.76	0.84*	0.67*	0.96	0.93	0.98	0.87
Kudu/impala	0.76	0.75	0.85	0.84	0.91	0.91	0.97	0.97
Nyala/impala	0.73	0.85	0.76	0.81	0.90	0.97	0.92	0.95

For Schoener's Index, values ≥ 0.6 are considered significant.

* Schoener's Indices which showed a significant change ($p < 0.05$, Wilcoxon rank sum test) from the wet to the corresponding dry season.

Appendix A

Selection of vegetation types by the guild's different members. Results for Manly's Alpha (preference index) (M.α) and Ivlev's Electivity Index (I.E.I.) are shown for each herbivore in each of the four seasons. For Manly's α, >0.11 indicates +ve selection, 0.11 neutral selection and <0.11 negative selection; for Ivlev's Electivity Index, >0 indicates +ve selection (to a maximum of nearly 1), 0 neutral selection and <0 negative selection (-1 complete avoidance). Result pairs in bold are those results where the direction of selection differed between the two indices. S. = season, w = wet and d = dry.

			Habitat								
Species	S.	Pref. Index	Broad leafed thicket	Closed woodl'd	Dry forest	Fine leafed thicket	Invaded Grassl'd	Open woodl'd	Riparian	Scarp forest	Wooded grassl'd
Elephant	w07	M. α	0.17	0.1	0.15	0.1	0.04	0.12	0.12	0.09	0.12
		I.E.I.	0.18	-0.09	0.14	-0.08	-0.53	0.02	0.04	-0.13	0.02
Elephant	d07	M. α	0.28	0.03	0.03	**0.08**	0.05	0.07	0.11	0.3	0.06
		I.E.I.	0.59	-0.42	-0.45	**0.06**	-0.22	-0.03	0.22	0.62	-0.1
Elephant	w08	M. α	0.07	0.18	**0.14**	0.04	0.02	0.18	0.16	0.07	0.15
		I.E.I.	-0.34	0.13	**-0.02**	-0.53	-0.73	0.11	0.06	-0.37	0.01
Elephant	d08	M. α	0.22	0.01	0.05	0.03	**0.13**	0.01	**0.07**	0.46	0.02
		I.E.I.	0.47	-0.18	-0.31	-0.07	**-0.15**	-0.02	**0.16**	0.62	-0.05
Giraffe	w07	M. α	0.18	0.19	0.02	0.2	0	0.19	0.09	0	**0.13**
		I.E.I.	0.05	0.09	-0.77	0.11	-1	0.08	-0.27	-1	**-0.13**
Giraffe	d07	M. α	0.07	0.07	0.02	0.11	0.27	0.13	0.08	0.19	0.06
		I.E.I.	-0.22	-0.15	-0.68	0.03	0.46	0.13	-0.15	0.31	-0.28
Giraffe	w08	M. α	0.3	0.03	0.11	0.17	0	0.18	0.03	0	0.17
		I.E.I.	0.36	-0.65	-0.13	0.1	-1	0.13	-0.61	-1	0.08
Giraffe	d08	M. α	0	0.01	0.06	0.04	0.45	0.01	0.03	0.39	0.01
		I.E.I.	-1	-0.21	-0.11	-0.08	0.53	-0.04	-0.34	0.34	-0.1
Kudu	w07	M. α	0	0.21	**0.16**	0.09	0	0.2	0.04	0	0.3
		I.E.I.	-1	0.08	**-0.05**	-0.32	-1	0.04	-0.64	-1	0.25
Kudu	d07	M. α	0	**0.21**	0	0	0	0.31	**0.11**	0	0.37
		I.E.I.	-1	**-0.02**	-1	-1	-1	0.17	**-0.32**	-1	0.26
Kudu	w08	M. α	0	0.05	0.41	0.08	0	0.26	0.05	0	0.16
		I.E.I.	-1	-0.55	0.44	-0.35	-1	0.23	-0.5	-1	0
Kudu	d08	M. α	0	**0.07**	0.31	0.02	0.54	0.02	0.1	0	0.04
		I.E.I.	-1	**0.2**	0.23	-0.45	0.23	-0.32	-0.02	-1	-0.04
Nyala	w07	M. α	0.36	0.11	0.07	0.04	0.04	0.09	0.07	0.12	0.11
		I.E.I.	0.59	0.1	-0.15	-0.43	-0.36	-0.04	-0.17	0.14	0.08
Nyala	d07	M. α	0.31	0.14	0.04	0.07	0	0.16	0.19	0	0.08
		I.E.I.	0.42	0.06	-0.53	-0.27	-1	0.12	0.2	-1	-0.22
Nyala	w08	M. α	0.32	0.2	0.04	0.11	0.01	0.13	0.01	0.08	0.1
		I.E.I.	0.43	0.23	-0.48	-0.09	-0.81	0.03	-0.92	-0.25	-0.11
Nyala	d08	M. α	0.34	0.11	0.06	0.03	0	**0.02**	0.2	0.19	0.04
		I.E.I.	0.04	0.3	-0.58	-0.38	-1	**0.02**	0.1	0.35	-0.05
Impala	w07	M. α	0.03	0.24	0.32	0.03	0.01	0.2	0.1	0	0.08
		I.E.I.	-0.64	0.24	0.37	-0.68	-0.91	0.15	-0.2	-1	-0.28
Impala	d07	M. α	0.01	0.2	0.34	0.03	0.01	0.17	0.18	0	0.07
		I.E.I.	-0.89	0.19	0.45	-0.67	-0.91	0.13	0.16	-1	-0.33
Impala	w08	M. α	0.01	0.22	0.24	0.02	0.04	0.27	0.07	0.01	**0.13**
		I.E.I.	-0.86	0.13	0.16	-0.81	-0.66	0.22	-0.42	-0.92	**-0.15**
Impala	d08	M. α	0.08	0.11	0.44	0.01	0.05	0.04	0.25	0	0.02
		I.E.I.	-0.61	0.25	0.26	-0.72	-0.79	-0.74	0.16	-1	-0.47

Appendix B

Theorem: Schoener's index (see text) is identical to Renkonen's Index.

Proof :

$$\sum_{i=1}^{n}\left|p_{ai}-p_{bi}\right| = \sum_{i=1}^{n}\left(\max(\%p_{ai},\%p_{bi})-\min(\%p_{ai},\%p_{bi})\right)$$

$$=\left(\sum_{i=1}^{n}\max(\%p_{ai},\%p_{bi})-\sum_{i=1}^{n}\min(\%p_{ai},\%p_{bi})\right)$$

therefore:

$$1-\frac{1}{2}\sum_{i=1}^{n}\left|p_{ai}-p_{bi}\right| = 1-(1/2)*\left(\sum_{i=1}^{n}\max(\%p_{ai},\%p_{bi})-\sum_{i=1}^{n}\min(\%p_{ai},\%p_{bi})\right)$$

If $1-(1/2)*\left(\sum_{i=1}^{n}\max(\%p_{ai},\%p_{bi})-\sum_{i=1}^{n}\min(\%p_{ai},\%p_{bi})\right) = \sum_{i=1}^{n}\min(\%p_{ai},\%p_{bi})$ ------(1)

Then $\sum_{i=1}^{n}\min(\%p_{ai},\%p_{bi})+\sum_{i=1}^{n}\max(\%p_{ai},\%p_{bi}) = 2$

Which is obviously true and thus (1) is also true.

Linkage paragraph, Chapter 3 to 4

My field studies in HiP confirmed, as suggested by the literature review, that a communal, core diet exists across the browser guild and that members extensively overlap in habitat usage. These findings were used to emphasise the potential for synergistic impacts by guild members on these woody species and that management, rather than exclusively managing elephant, should consider the entire guild. The next stage was to demonstrate, in a quantitative fashion, that woody species '*use*' by a high population-biomass mesobrowser in HiP actually translated into significant '*impact*'. An additional challenge here was to do so by a method other than using exclosures – a technique which seems to utterly dominate the field, but which appears to have numerous potential short comings.

CHAPTER 4

Heavy impact on seedlings by the impala suggests a central role in woodland dynamics*

Abstract: Research has increasingly established that mesoherbivores influence the regeneration of woody plants. However the relationship between mesoherbivore density and degree of impact, and the spatial component of this impact, has not been well established. Using a novel sampling design, we assessed in iMfolozi Park, South Africa, the impact of impala (*Aepyceros melampus*) across the full complement of woody species within the home range, evaluating its spatial component and relationship to impala density. We used four GPS collars, in separate breeding herds, and a GIS to detect zones of different density of impala in the landscape, thus defining a fine-grain browsing gradient. We assessed impact on woody recruits (≤ 0.5 m height) across this gradient by means of 1600 random 1 × 1-m quadrats. Densities of woody seedlings, and mean percentage of remaining canopy, were significantly less in areas of high impala density versus low-density areas. There was a significant correlation between increasing impala density and decreasing density of favoured woody recruits. We propose a hypothesis of impala-induced patch dynamics. It seems likely that the ubiquitous impala may create and sustain a shifting mosaic of patches, and thus function as a key determinant of landscape heterogeneity.

Key Words: guilds, keystone, patch dynamics, savanna, seedlings

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INTRODUCTION

A topical debate amongst ecologists is the role of large herbivores in the top-down regulation of ecosystems (Moe *et al.* 2009). It is now well established that mesobrowsers influence the regeneration of woody plants (e.g. in temperate biomes: cervids (Ward *et al.* 2008), beavers (Rosell *et al.* 2005); in savanna biomes: impala (Prins & Van der Jeugd 1993), kudu (Barnes 2001), dik-dik (Augustine & McNaughton 2004), black rhino (Birkett & Stevens-Wood 2005), eland (Styles & Skinner 2000), and non-elephant browsers in general (Sharam *et al.* 2006)). Savanna biomes are structurally heterogeneous (Ben-Shahar 1996) and the impacts of browsers are unlikely to be evenly distributed across the landscape (Levick & Rogers 2008). However, although patch-dynamics have been inferred in savanna systems (Gillson 2004, Moustakas *et al.* 2009), the effects of variation in the spatial distribution of a browser's impacts on woody vegetation have not been studied in any depth. Mourik *et al* (2007) showed that fire and browsers maintain woody patches by impeding tree recruitment at patch boundaries, and Levick & Rogers (2008) showed, by use of exclosures, that browser impacts are focused on certain patch and species types. Moreover, despite increasing recognition of the role that mesobrowsers play in woodland dynamics (Moe *et al.* 2009), the spatial component of their impact, as opposed to that of browsers in general, has not been directly investigated. This variation in impact is thought to be important in maintaining diversity (Noss 1990).

Where home-ranges of different browser species overlap, separating the species-specific impacts on woody vegetation becomes difficult (Guldemond & van Aarde 2009). Three broad approaches have been used: visual separation based on characteristic markings left by different browsers on plants (Barnes 2001, Sharam *et al.* 2006),

correlating episodic growth of woodlands with population collapses of specific browser species (Prins & Van der Jeugd 1993) and, most commonly, the use of exclosures that exclude particular browser species (Augustine & McNaughton 2004, Belsky 1984, Goheen *et al.* 2004, Moe *et al.* 2009). Results from exclosure experiments may be confounded by a wide variety of factors. Small mammals (Goheen *et al.* 2004), termites (Braak 1995), grasshoppers (Gandar 1982), lepidoptera (Frost 1985) and invertebrates in general (Hagenah *et al.* 2009) have all been shown to impact woody vegetation, in some cases more heavily than large mammals. Exclusion of large mammals may result in increases in both small-mammal (Keesing 1998) and invertebrate abundance (Shaw *et al.* 2002). Interspecific competition between woody plants (Riginos & Young 2007), between grasses and woody plants (Seymour 2008) and facilitation between woody plants (Russell & Fowler 2004) may further complicate exclosure results, as may trampling by large mammals (Munoz *et al.* 2009), large herbivores influencing one another's presence (Young *et al.* 2005) and elephants breaching exclosures (Gaugris *et al.* 2008). Furthermore, where exclosures are erected on areas already impacted by herbivores, they monitor the recovery phase and not necessarily landscape-level effects (Bergström & Edenius 2003). Alternative approaches to studying impacts by browsers are therefore useful.

The impala is the quintessential southern African savanna/lowveld mesobrowser (Smithers 1983). Here we describe a novel sampling design, not utilizing exclosures, devised to determine the impact of impala on the recruitment of woody species within their home-ranges. We hypothesized that impact on woody plant recruits is greatest in

areas of an impala herd's home-range in which the greatest number of impala spend the most time, and on those woody species that are well utilized.

METHODS

Study site

The study ran from November 2008 to July 2009 in the iMfolozi section of Hluhluwe-iMfolozi Park (HiP), KwaZulu–Natal, South Africa (28°00′–28°26′ S; 31°43′–32°09′ E). HiP is a 900-km², completely fenced nature reserve, situated in the foothills of the first escarpment on the west side of the Zululand coastal plain (Whateley & Porter 1983). The majority of HiP is savanna, classified as Northern Zululand Sourveld and Zululand Lowveld (Mucina & Rutherford 2006). Mean annual rainfall in iMfolozi is 635 mm, with April to September being the dry season (Balfour & Howison 2001). Terrain varies between valleys, hills and plains. The soils are mainly derived from sandstone, shale and dolerite intrusions and are generally eutrophic (Balfour & Howison 2001). iMfolozi is typified by *Acacia nigrescens, A. tortilis* and *Spirostachys africana* woodlands (Whateley & Porter 1983). About 50% of iMfolozi is covered by open woodland (*A. nigrescens/A. tortilis, A. nilotica, A. burkei* and *Combretum apiculatum*), with closed woodland (dominated by *S. africana/Euclea racemosa* and *A. grandicornuta* (Pooley 2003) in roughly equal percentages) covering about 25% of the terrain. The principal browsers in HiP, and their current estimated crude densities (KZN Wildlife, unpubl.), are elephant

Loxodonta africana Blumenbach (0.56 km^{-2}), giraffe *Giraffa camelopardalis* Linnaeus (0.89 km^{-2}), black rhino *Diceros bicornis* Lichtenstein (0.35 km^{-2}), kudu *Tragelaphus strepsiceros* Pallas (1.3 km^{-2}), nyala *Tragelaphus angasii* Gray (7.3 km^{-2}) and impala *Aepyceros melampus* Lichtenstein (26.1 km^{-2}).

Sampling design

We used GPS collars to detect zones of different density of impala in the landscape and to thus define a fine-grain browsing gradient. At the start of the study period, four female impala in different breeding herds were fitted with GPS collars. These transmitted, via the mobile telephone network, the co-ordinates of the wearer every 6 h.

Impala breeding herds in iMfolozi were observed to remain spatially distinct during the study period; mixing of herds was observed only after the study ended, at the height of the dry season. Monthly field observations, utilizing the VHF-transmitting facility built into the collars, showed that all collared individuals stayed within their original herd over the study period. Numbers of adults in each of the four herds showed little variation over the study period (± < 15%). GPS locations showed, utilising a GIS (ArcGIS 9 by ESRI), that home ranges for all four collared individuals changed little in either size or location of core and peripheral areas over the study period. This demonstration of stability in herd membership and size and fidelity to area of home ranges agrees with previous findings on impala breeding herds (Jarman 1970, Murray 1982). Thus the movements of each collared individual can be taken to represent the movements of its herd, which, over the period of the study, was stable in size, spatially distinct from other herds and occupied a home range that varied little in size or location.

Overlaying the GPS downloads after the 9 mo of data collection onto the GIS vegetation layer for the reserve, showed that open and closed woodland, two similar vegetation types, were the most commonly occupied vegetation types. For each of the collared individuals' home ranges, 50% and 95% kernels were determined using Hawths Tools (hawthorne@spatialecology.com) and its Fixed Kernel Density Estimator. As the area of the 50% kernel was much smaller than that of the fringing (95%-50%) kernel, a core area of high occupancy (the 50% kernel), and an outer band of lower occupancy (95% kernel minus the 50% kernel) were defined. Densities of impala in each of these areas were then calculated. This was achieved by taking the number of GPS downloads in an area, multiplied by the average number of impala in that herd, divided by the area (ha) and all divided again by the number of days that the relevant collar functioned. This produced a value for impala density expressed as the number of impala per unit time per unit area. The 50% and 95%-50% kernels and the two different vegetation types thus provided four sites within each of the home ranges (area of high impala density versus area of low impala density, in open woodland and in closed woodland). However, for one of the four collars, home range fell entirely within only open woodland, giving two sites (area of high impala density versus area of low impala density in open woodland).

Impact on woody recruits by other browsers

Additionally we determined densities, by vegetation type, for all the reserve's principal browsers in the same local region of the reserve as the four impala home ranges. This was achieved by monthly repeated road and foot transects, over a 2-y period immediately prior to this study. We also estimated the comparative abundance of impala, nyala and

kudu within each home-range study site, using those transect counts falling within the overlap of home-range and transect area (as determined in the GIS). Furthermore we determined, over the same period, feeding heights of the principal browsers and which woody plant species they utilized and to what extent (O'Kane *et al.* 2011).

Impact on woody recruits by each principal browser species prevalent in HiP other than impala, within the site areas, was considered to be minimal for the following reasons: (1) Elephant. Although elephant biomass densities (closed woodland: 1500 kg km^{-2}; open woodland: 1250 kg km^{-2}) were similar to those of impala (closed woodland: 1500 kg km^{-2}; open woodland: 1600 kg km^{-2}), we determined that there was no significant overlap (Schoener's Index 0.16 to 0.35 (O'Kane *et al.* 2011)) between elephant and impala feeding height in any season. Less than 6% of elephant feeding records were in the height range $\leq$ 0.5 m, compared to 47% of impala's. Boundja & Midgley (2010), also working in HiP, concluded that elephants had little impact on woody saplings < 1 m in height. Various authors have similarly reported minimal feeding by elephants on woody plants below 1 m (Augustine & McNaughton 2004, Croze 1974, Dublin *et al.* 1990, Stokke & du Toit 2000), whilst smaller browsers commonly utilizing woody recruits is equally well established (Augustine & McNaughton 1998, Belsky 1984, Hobbs 1996). When elephants do feed on seedlings, the damage caused (tearing marks and uprooting) is very characteristic (Sharam *et al.* 2006); we found no evidence of such feeding within the sites. We also determined that there was no significant overlap (Schoener's Index = 0.32-0.39) between elephant and impala in woody plant species utilized; Makhabu (2005) also found no significant overlap (Schoener's Index = 0.22-0.24) in woody species utilized by the two herbivores. (2) Kudu and nyala. Both species

utilized woody recruits, with nyala showing significant overlap in feeding height with impala in all seasons. However, kudu and nyala densities by vegetation type and estimated abundance within each impala home range were consistently <10% of those of impala (Table 1). (3) Giraffe. There was no significant overlap (Schoener's Index = 0.07-0.11) between giraffe and impala in feeding height in any season. Giraffe very rarely feed below 0.5 m (< 0.5% of woody feeding records), agreeing with the findings of others (du Toit 1990). (4) The black rhino makes a very distinctive 45° bite mark on vegetation (Emslie 1999), and thus its potential role in woody impact could be confidently excluded during data collection.

For these reasons, it was argued that variation in impact on woody recruits across sites in the same vegetation type would be principally due to variation in impala density.

Data collection

Density of woody recruits. - We defined woody recruits as recruits of woody plant species ≤ 0.5 m height. Within each site, woody recruits were sampled in 100 randomly located 1 × 1-m quadrats, giving 400 quadrats within each home-range. In each quadrat, the numbers of woody recruits were counted and, for each recruit, the plant species, whether it had been browsed and an estimate of the percentage of canopy remaining were recorded. For the fourth collar, 200 quadrats were sampled in each of the two sites (area of high impala density versus area of low impala density in open woodland). Sampling was undertaken in the early part of the dry season (July) when impact of browsing by

impala, after a full wet season (November-March) and 4 mo of dry season (April-July), would be most apparent.

Data analysis

Differences in density of woody recruits. - The null hypothesis was that there was no difference in the mean density of woody recruits, or the mean percentage of their remaining canopy, between areas of high impala density versus areas of low impala density. Fisher's F test was used to determine whether variances in means were significantly different, with the standard two-sample t-test (equal variances) or Welch's modified two-sample t-test (unequal variances)(Crawley 2005) then used to test the null hypothesis. P-values ≤ 0.05 resulted in rejection of the null hypothesis, i.e. represented significant differences between areas of high impala density versus areas of low impala density. Differences in number of recruits and number of quadrats with no woody plants were analysed by constructing contingency tables, and then testing the null hypothesis using Pearson's Chi-squared test with Yates' continuity correction (Crawley 2005). To assess impact on different height classes of recruits, the densities of recruits in 100-mm classes in areas of high impala density versus areas of low impala density were calculated and plotted (with 95% CIs).

Influence of impala density on density of woody recruits. – To explore the relationship between density of impala and density of woody recruits, we used a generalized linear model having counts of recruits as the response variable (thus requiring a Poisson link), and impala density (continuous), woodland type (categorical) and interactions as

explanatory variables. All statistical procedures were carried out in S-PLUS (Mathsoft 1999. Lucent Technologies, Inc., Murray Hill, USA).

RESULTS

Density of recruits was significantly lower in areas of high impala density (mean = 0.61 m^{-2}) than in areas of low impala density (mean = 1.04 m^{-2}: $t = 6.92$, $P < 0.001$ (two-tailed), df = 1598). Percentage of remaining canopy of recruits was also significantly lower in areas of high impala density (mean = 48.7%) than in areas of low impala density (mean = 63.3%: $t = 9.44$, $P < 0.001$ (two-tailed), df = 1632). Statistically more empty quadrats where found in areas of high, versus low, impala density ($\chi^2 = 6.3$, df = 1, $P = 0.012$). The average reduction in numbers of recruits going from areas of low to high impala density was 48% (range = 32%-75%). Of recruits that showed greater impact in areas of high versus low impala density, 74% were amongst the top 20 woody species previously determined as the most utilized by impala. Differences in recruit density between areas of high versus low impala density were especially marked in the 0-200mm height range, with these differences apparently carried through to larger recruit height classes (Figure 1).

The generalized linear model showed a highly significant regression between increasing density of impala and decreasing density of recruits of the 20 woody species previously determined as the most utilized by impala (slope = -2.59, SE = 0.696, $t = 3.72$, $P < 0.001$, df = 1599). The slope of this regression was significantly greater in closed woodland compared to open woodland (Table 2). Although there was a correlation

between increasing density of impala and decreasing density of all recruits, this was not significant (P = 0.088).

DISCUSSION

Our results strongly suggest that impala breeding herds significantly impact woody recruits in iMfolozi Park. Moe *et al.* (2009) recently demonstrated, using an exclosure experiment, that ungulate browsing reduces woody seedling survival along the Chobe riverfront, with impala strongly inferred as the cause. Prins & van der Jeugd (1993) convincingly related similar-aged stands of *Acacia* woodlands in East Africa to anthrax-induced impala population crashes. Our study thus further emphasizes the role of non-elephant browsers of high population-biomass in controlling savanna woodland dynamics. We showed a positive relationship between increasing density of impala and greater impact on woody recruits. The strong correspondence between impacted woody species and those previously recorded as utilized by impala, strengthens the validity of our findings. As far as we are aware, this is the first time GPS collars, combined with herd monitoring, have been used to determine fine-grain, quantifiable ungulate densities across home ranges that have been related to woody impact.

Over the 9-mo period (March-November) of their exclosure experiment, which monitored four woody species, Moe *et al*. (2009) reported a reduction in mean seedling survival due to ungulate browsing of ~50%. Although the two studies had different approaches, this value compares favourably with the mean 48% reduction in numbers of recruits reported here, quantitatively emphasizing the heavy mortality impala may inflict

on young woody plants. Stability of home ranges may imply that in a reserve such as HiP, where the high impala population presumably translates into a mosaic of adjacent home ranges across the entire landscape, areas currently impacted will continue to be so. That the slope of the correlation between increasing density of impala and decreasing density of recruits was significantly greater in closed woodland compared to open woodland, suggests that increasing impala density impacts recruits more severely in closed woodland. This may be because less grass is available in closed woodland, forcing impala to browse more.

However, two caveats should be born in mind. We have, as have Moe *et al*. (2009) and Prins & van der Jeugd (1993), demonstrated a correlation between impala and marked impact on woody recruits, not proven a causal relationship between the two. Secondly, other mesobrowsers (e.g. the larger kudu) although markedly less prevalent than impala, are likely to contribute to impact on woody recruits in a manner related to their localised total biomass.

The smaller the plant utilized the greater the proportion of the canopy removed when a bite is taken; for example a single bite from a small seedling by an impala removes nearly all of the leaves (and cotyledons if present) or uproots the seedling totally (pers. obs.), and the resultant impact is high. This is probably the explanation for the marked difference in plant density within the smaller height classes between areas of high versus low impala density.

A hypothesis of impala-induced patch dynamics

Optimal foraging theory (Stephens & Krebs 1986) suggests that, at least initially, core areas of home ranges should occur where resources are highest within the home range. Subsequently, however, browsing lowers density of woody recruits in the core compared to the area surrounding it, in proportion to the density of impala. Further our data indicate that the core areas in each home range have been stable over at least the period of the study. Impact on seedlings, as would be expected, is translated to higher size classes. Thus, if the core persists for long enough, a patch of woody species at relatively low densities will be created not only in the < 0.5-m-height layer, but also in the larger classes. Although other variables will also influence shifts in home range, it seems likely that as woody recruit density declines, the core should shift into the current area of high woody recruit density and low impala density. This might occur suddenly at some threshold, or gradually over a period of time. Thus, dependent on core persistence, patch dynamics (MacArthur & Pianka 1966) are established, whereby high- and low-density patches of woody species occur at the scale of the core(s). In this way a shifting mosaic of patches might be created and sustained by impala browsing. Similar proposals have been made for grazers affecting the structural heterogeneity of grasslands (Farnsworth *et al.* 2002, Verweij *et al.* 2006).

CONCLUSIONS

Impala appear to have a markedly negative effect on woody species recruitment. This impact was patchy and increased with increasing density of impala. A potential shifting mosaic of high- and low-density patches of recruits and older trees, may be induced by

the effects of impala feeding in restricted home ranges of high fidelity. Thus impala may function as a key determinant of landscape heterogeneity. Although the elephant is often perceived by management as a keystone species and hence of over-riding importance in woodland dynamics, our findings further highlight the role of other herbivores of high population-biomass in the long-term structure and composition of savanna woodlands. Indeed, it seems possible that long-term impact caused by different species within the browser guild may be proportionate to their population biomass, and thus the prominent impact of elephant may merely be a manifestation of its high total biomass in many areas.

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Fig. 1. Impact on different height classes of woody plants ≤ 0.5 m in iMfolozi Park. Variation between areas of high (filled) and low (open) impala density in terms of the density of woody plants ≤ 0.5 m m^{-2} is shown, with error bars displaying 95% CIs.

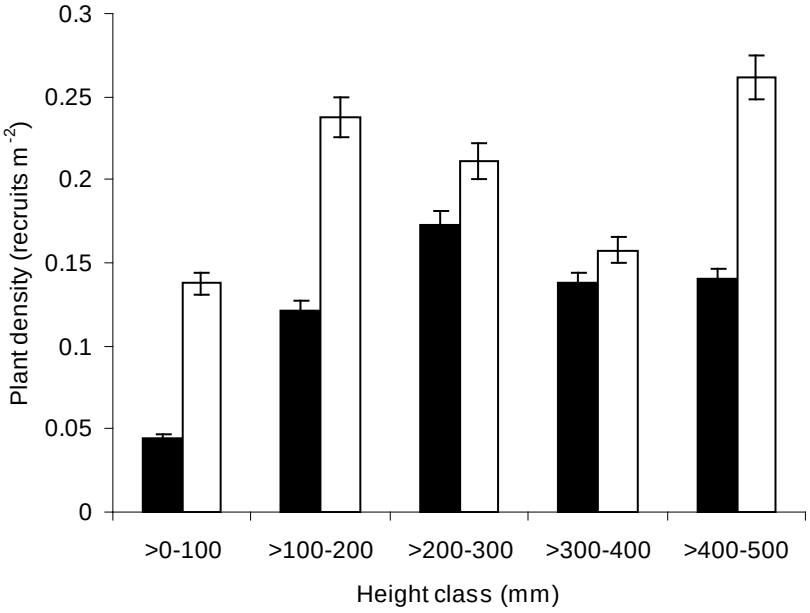
Table 1. Comparative prevalence of kudu, nyala and impala in the localized study area in iMfolozi Park. Densities of these herbivores (numbers km^{-2}) in closed and open woodland vegetation types, derived from 2 y of road transects in the localized study area, are shown for wet and dry seasons. Additionally, estimates of abundance of these herbivores within each of the four separate impala home ranges assessed (home ranges a, b, c and d) are shown. These estimates are the total number of road transect counts occurring within the area of overlap between home-range and transect area.

Herbivore	Season	Density in closed woodland	Density in open woodland	Home range a overlap abundance	Home range b overlap abundance	Home range c overlap abundance	Home range d overlap abundance
Kudu	Wet	0.4	0.7	37	18	27	49
Kudu	Dry	0.7	0.7				
Nyala	Wet	2.6	1.8	15	32	0	115
Nyala	Dry	2.8	2.3				
Impala	Wet	37.7	37.7	2948	2140	1951	1665
Impala	Dry	37.5	32.0				

Table 2. Output of a generalized linear model of woody recruits versus density of impala in iMfolozi Park. The model (df = 1599) has counts of woody recruits (response variable) against density of impala (continuous explanatory variable), type of woodland (categorical explanatory variable) and interactions.

	Estimate	SE	t value	P value
(Intercept)	0.21	0.07	2.84	0.005
Density of impala	-4.56	1.18	3.86	< 0.001
Open woodland	-0.49	0.11	4.67	< 0.001
Density of impala:open woodland	3.84	1.46	2.62	0.009

Figure 1


0.3
0.25
0.2
0.15
0.1
0.05
0
Plant density (recruits m-2)
>0-100
>100-200
>200-300
>300-400
>400-500
Height class (mm)

Linkage paragraph, Chapter 4 to 5

At this juncture in the project, the existence of a communal, core diet of woody species and extensive overlap in habitat usage, both suggested by the literature review, has been empirically confirmed for the browser guild at the study site. The markedly negative impact a high population-biomass mesobrowser (impala) has on woody species recruitment, has also been quantitatively demonstrated. Study objectives and hypotheses i) to iii), as outlined in the introduction to this report (p. 16), have thus been achieved/supported. The next stage is to use these findings, both in terms of their logic and actual results, to help develop a model describing likely long-term woodland dynamics.

CHAPTER 5

Model calls into question keystone role of elephant in long-term woodland dynamics, suggesting redirection of management efforts*

Abstract: The impact of the African elephant on savanna woodlands is well documented. Recent research has increasingly emphasized the influence smaller mammalian browsers have on woody plants, especially at the recruitment stage. However, the potential long-term influences of mesobrowsers versus those of elephant on woodland dynamics have not been explored. This may be a critical omission especially in relation to management policies in southern African savannas, where the few efforts to control browser populations to preserve existing woodlands are typically directed at elephant management. We describe the development of a simple browse-browser model, parameterised from an extensive review of the literature and our own data, including quantitative assessment of impala impact, from the study site, iMfolozi Park, South Africa. As there is a paucity of species-specific demographic data on savanna woody species, we modelled, in a novel approach, functional groups of plant species typical of *Acacia* woodlands. Outputs of the model suggest that over the long-term (100 years), low to moderate densities of impala will have a similar impact on woodland structure, in terms of density of adult trees, as low to moderate densities of elephant. Further, the outputs highlight the apparently strong synergistic effect impala and elephant impacts

combined have on woodland dynamics, suggesting that reduction or removal of *either* impala *or* elephant will radically reduce long-term destruction of savanna woodlands. Recorded changes in adult tree numbers in iMfolozi broadly supported the model's outputs. In smaller or medium sized reserves, where control of mesobrowser populations is practical, profitable and more acceptable than elephant culling, these findings imply a re-direction of management efforts.

Key Words: culling, functional groups, herbivory, impact, long-term, woody plants

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Introduction

Keystone species are species having a disproportionate effect on their ecosystem compared to their biomass (Bond 1993). The African elephant (*Loxodonta africana* (Blumenbach)) has widely been described as the prime example of a keystone herbivore (Scholes & Mennell 2008). However, as the total population-biomass of elephants in many areas is comparatively high, it could be argued that their effect may in fact be proportionate to their biomass (O'Kane *et al.* 2011b). Research findings are increasingly emphasising the impact on ecosystems of both smaller mammalian (Goheen *et al.* 2004, Joubert *et al.* 2008, Moe *et al.* 2009) and invertebrate herbivores (Braak 1995, Hagenah *et al.* 2009). These considerations raise the possibility that herbivore influences on their ecosystem, especially over the long-term, are essentially a function of total population-biomass, rather than any perceived keystone effect. This is an important consideration for management, especially in smaller reserves where control of smaller browsers, rather than just megaherbivores (Owen-Smith 1988) such as elephant, is practical.

The structure and productivity of savanna systems is controlled by dynamic and complex interactions between soil, climate and disturbances – most notably fire and herbivory (Scholes & Walker 1982). In a recent review of savanna woody plant dynamics, Midgley *et al.* (2010) conclude that fire and herbivory acting together strongly limit recruitment, but that some herbivores acting alone, notably elephant and impala (*Aepyceros melampus* (Lichtenstein)), can have greater effects than fire alone on population sizes of woody plants. These various factors are difficult to manipulate and isolate experimentally at temporal and spatial scales relevant to ecosystem dynamics;

they are, however, conducive to evaluation with simulation models (House *et al.* 2003). However, development of savanna tree-herbivore interaction models has been frustrated by a shortage of data for models (Hawkes 2000), with little being known about height or diameter growth of savanna trees (Baxter & Getz 2008a, Wiegand *et al.* 2008), or the quantitative effect of high population-biomass smaller browsers, such as impala, on recruitment and release (Midgley & Bond 2001). An additional problem is the disparate nature of data relating to habitat and woody plant use by the browser guild. In a review of the literature from 1960 to 2009 (O'Kane *et al.* 2011a) we found surprisingly few (n = 21) studies that have researched plant use by elephant and at least one other browser in the same locality. Only six of these researched the overall diet, rather than use of just one particular plant species, and only one paper gives details of the entire guild's diet (Makhabu 2005). This is a critical gap in the literature, as exposure of herbivores to different suites of plants in different localities would be expected to affect the degree to which particular woody species are utilized, preferred or avoided.

In view of the current state of the literature we considered it timely to redress some of these gaps in our knowledge, and to then model the long-term effects of elephant versus those of impala on savanna woodland structure. Over two years and in different seasons, we determined at our study site, iMfolozi Park, South Africa, the woody species (O'Kane *et al.* 2011b) and habitat use (O'Kane *et al.*, in prep.) of elephant versus that of impala, and the quantitative impact of impala on seedlings (O'Kane *et al.* 2012). Armed with these data, together with parameterisation from an extensive search of the literature, including some recently published quantitative data on impala impact (Moe *et al.* 2009), we constructed a model to determine the plausibility of two hypotheses. These were that,

over the long-term, i) smaller mammalian browsers of high population-biomass exert, via their impact on recruitment, a major effect on savanna woodland structure, and ii) that therefore removal of elephants from the system will not have an overriding effect. We are interested in the relative role of the two groups of herbivores when at densities typically found in managed reserves; few would dispute the devastating impact of extreme densities of elephant or mesobrowsers. We recognise the simplicity of the model and that it portrays a crude approximation to reality. However it does allow us to manipulate elephant versus another browser's impact in isolation, and thus illuminate how different densities of the two groups might inter-relate in their long-term influence on savanna woodlands. The aim is not to attempt to describe what woodlands would look like in x years with y herbivore densities, but rather to throw light on the underlying browser-plant dynamics (Hawkes 2000).

Methods

Study area

iMfolozi Park lies in the southern section of Hluhluwe–iMfolozi Park, KwaZulu–Natal, South Africa (28°00′–28°26′ S; 31°43′–32°09′ E), a 900-km² fenced nature reserve, situated in the foothills of the first escarpment on the west side of the Zululand coastal plain (Whateley & Porter 1983). Twenty five year mean annual rainfall is 635 mm, with April to September being the dry season (Balfour & Howison 2001). Terrain varies between valleys, hills and plains. The soils are mainly derived from sandstone, shale and

dolerite intrusions and are generally eutrophic (Balfour & Howison 2001). The majority of iMfolozi Park is savanna, classified as Zululand Lowveld (Mucina & Rutherford 2006), with the vegetation characterised by fine-leaved *Acacia* savanna with a continuous grass layer and a fairly open tree canopy. *Acacia nigrescens* woodlands, *Acacia tortilis* woodlands and *Spirostachys africana* (Pooley 2003) woodlands predominate (Whateley & Porter 1983).

The principal browsers, and their current estimated average densities, are elephant 0.56 km^{-2}, giraffe (*Giraffa camelopardalis* (Linnaeus)) 0.89 km^{-2}, black rhino (*Diceros bicornis* (Lichtenstein)) 0.35 km^{-2}, kudu (*Tragelaphus strepsiceros* (Pallas)) 1.3 km^{-2}, nyala (*Tragelaphus angasii* (Gray)) 7.3 km^{-2} and impala 26.1 km^{-2} (K.Z.N. Wildlife, unpubl. data).

'*Acacia* woodland dynamics' model (Fig. 1)

Assumptions

We made a number of biologically realistic and conservative assumptions about the conditions under which the model operates.

Acacia woodlands. We determined, by monthly driven and walked transects over a two year period (O'Kane *et al.*, in prep.), that elephant and impala (and mesobrowsers in general) communally and heavily utilise *Acacia* woodlands in iMfolozi, supporting an extensive literature on these herbivores' habitat preferences. We defined '*Acacia* woodlands' by selecting appropriate sub-classes from an extensive survey (Whateley & Porter 1983) of iMfolozi's woody vegetation communities. Within these sub-classes we identified the most prevalent woody plant species using a database analysis of > 110,000

woody vegetation records, obtained from walked transects carried out in the reserve from 1999 to 2007. We ascribed to each of these prevalent woody species broad characteristics of recruitment, growth and utilisation. Recruitment characteristics were obtained by comparing, in the 1999 to 2007 transect records, numbers of recruits versus numbers of adult trees. Utilisation characteristics were derived from over 3,000 direct feeding observations in the reserve (O'Kane *et al.* 2011b). Growth characteristics, where available, were obtained from an extensive review of the literature. Each prevalent woody species was thus broadly categorised as of either low, medium or high recruitment, growth and utilisation, thus giving 'functional' groupings prevalent in *Acacia* woodlands in iMfolozi (Table 1). By modelling these broad functional groups (Blaum *et al.* 2011, Schmidt *et al.* 2011), rather than specific plant species, the aim was to produce model outputs likely to be of more general application.

Tree size classes. We chose to define tree size classes by height, which is strongly related to canopy diameter (Wiegand *et al.* 2008), which in turn is strongly related to stem diameter (Riginos 2009) and stem diameter is strongly related to woody biomass (Okello *et al.* 2001). We defined seedlings as woody recruits ≤ 0.5 m height and adult trees as > 3 m (Baxter & Getz 2008b, Ben-Shahar 1996, Dublin *et al.* 1990). Saplings are utilised by both elephant and impala, but it is unclear under what circumstances mammalian herbivory either hinders (Rooke & Bergstrom 2007), promotes (Riginos & Young 2007, Tsumele *et al.* 2007) or has no single coherent effect (Danell *et al.* 1994, Fornara & du Toit 2008) on recruitment of saplings into adult size classes . Inclusion of a sapling size class in the model would therefore have confounded attempts to assess the

underlying dynamics of elephant impact on adult trees versus, or combined with, impala impact on seedlings.

Elephant and impala. We determined in the study area (O'Kane *et al.* 2011b) that < 6% of elephant woody feeding records were in the height range ≤ 0.5 m, compared to 47% of impalas. Boundja and Midgley (2010), also working in iMfolozi Park, concluded that elephants had little impact on woody plants < 1 m in height. Various authors have similarly reported minimal feeding by elephants on woody plants below 1m (Augustine & McNaughton 2004, Croze 1974b, Dublin *et al.* 1990, Stokke & du Toit 2000), whilst smaller browsers commonly utilizing woody recruits is equally well established (Augustine & McNaughton 1998, Belsky 1984, Hobbs 1996). When elephants do feed on seedlings, the damage caused (tearing marks and uprooting) is very characteristic (Sharam *et al.* 2006); we found scant evidence of such feeding within our study area. We determined (O'Kane *et al.* 2011b) that impala feed from ground level up to a maximum height of ~ 1.5 m, agreeing with others (Augustine & McNaughton 1998, Belsky 1984, Hobbs 1996). We thus model impala, but not elephant, impacting seedlings, and elephant, but not impala, impacting adult trees.

Carrying capacities. Analysis of the 1999 to 2007 transect records relating to our '*Acacia* woodlands' gave a maximum seedling density of ~ 4,000 seedlings ha^{-1}. Ben-Shahar (1996), the only reference we found giving natural seedling densities in the field, recorded 1,344 *Colophospermum mopane* seedlings ha^{-1}. Maximum adult tree (>3 m height) density derived from the iMfolozi transects was ~ 1,300 trees ha^{-1}. If one takes a typical adult *Acacia* as having a canopy of 10 m (pers. obs.), this produces a theoretical

maximum density of purely adult trees of 1,000 ha^{-1}. We thus chose to set carrying capacities in our model at 4,000 ha^{-1} for seedlings and 1,000 ha^{-1} for adult trees.

Constants and variables

We reviewed 106 sources in the literature (Appendix 1a), obtaining a biologically realistic range of recruitment, growth and elephant inflicted mortality for savanna woody species. This range was then applied to our functional groupings (Table 1). Where values for these parameters specific to the prevalent woody species were identified in the literature, these were applied to the model. For impala inflicted mortality we used the results of O'Kane et al. (2012), Moe et al. (2009), Ben-Shahar (1996), Dube et al. (2009), Sief El Din & Obeid (1971) and Iponga et al. (2009). As the values for seedling recruitment rate in the model include seedling first year survival, we did not incorporate a separate rate for seedling natural mortality. Natural mortality rate for adult trees was a constant parameter taken from the results of Croze (1974a), Pellew (1983) and Dublin et al. (1990). Initial seedling and adult tree densities were taken from Dublin et al. (1990).

Test conditions

For each functional group the model was run over a 100 year period. To isolate the individual effect of elephant, impala impact was set at zero and all other rates were held constant while elephant impact was varied within realistic ranges, and vice-versa to isolate the individual effect of impala. To determine their synergistic effects, elephant and impala impact were then varied together, again within realistic ranges. The model calculates the density (ha^{-1}) of adult trees against time and, by comparison of relative

changes in the density of different functional groups, highlights likely long-term changes in savanna woodlands under different densities (and hence impact levels) of elephant versus impala. The rate equations in the model are given in Appendix 2.

Model validation

The model's structure, logic and parameters are based on empirical values in the literature or, where these are not published, biologically realistic and conservative assumptions detailed above.

Additionally, appropriate outputs of the model are compared with recorded changes in iMfolozi Park. Elephant, only reintroduced into the study area in 1981, are increasing their numbers at ~ 7% p.a., whilst impala, present since shortly after the park's creation in 1895, are stable or decreasing slightly (K.Z.N. Wildlife, unpubl. data). Over the period of the extensive walked transects (1999 to 2007) elephant density rose from 0.29 km^{-2} to 0.52 km^{-2}, an increase of 67%. Comparison with the extensive literature on elephant densities throughout Africa (105 sources, Appendix 1b), suggests these figures represent a rise from a very low density to a low density. Above densities of 0.5 km^{-2} elephants are postulated to impact woodlands (Cumming *et al.* 1997). The literature on impala densities (33 sources, Appendix 1c) suggests their prevalent density of 26 km^{-2} may be characterised as medium. Thus over the 1999 – 2007 period elephant impact probably rose to a low level, whilst impala impact remained at a medium level. The outputs and predictions of the model, for this change from only impala impact to a combination of impala and elephant impact, are compared with recorded changes in adult tree densities in the *Acacia* woodlands of iMfolozi Park from 1999 to 2007.

Results

Predictions of the model

In the absence of any herbivores, functional groups with medium or high recruitment rates approach carrying capacity over a matter of decades. Low recruitment groups do not, and are still continuing to rise towards carrying capacity at the modelling end-point of 100 years. The very low recruitment group, exemplified in iMfolozi by *Sclerocarya birrea*, achieves a stable state but at densities markedly below carrying capacity (Fig. 2). In the absence of other browsers, elephant at low densities have a marginal effect on functional groups with medium or high recruitment rates, but a marked effect on low recruitment groups. At medium densities these effects are more marked, with low recruitment groups approaching extinction (Fig. 2a).

In the absence of elephants, impala at low and at medium densities have a similar effect to that of elephant on the functional groups both herbivores utilise, with low recruitment groups again the most affected (Fig. 2b). The model therefore suggests that the structure of *Acacia* woodland, in terms of overall densities of adult trees, will be similar at the 100 year end-point whether impact is solely by elephant or solely by impala. However the composition, in terms of the relative density of different woody species, will vary according to which species are exclusively impacted by elephant or impala (Fig. 2a and 2b).

When elephant and impala impact are combined, the model predicts markedly severe effects (Fig. 2c). Even low densities of elephant combined with medium densities of impala, result in functional groups with high or medium recruitment stabilising at considerably lower densities than is the case with either herbivore acting alone. Low recruitment groups are severely affected and are predicted to be in steep decline towards extinction. Combining medium densities of elephant with medium densities of impala has a striking effect, with all functional groups, irrespective of recruitment or growth characteristics, at or approaching extinction, thus allowing un-impacted woody species to assume dominance.

Validation of the model's predictions in iMfolozi Park

Moving from a situation of only impala (medium) impact to combined elephant (low) and impala (medium) impact, the model predicts certain changes to the structure and composition of *Acacia* woodlands in iMfolozi Park (Fig. 3a). Comparison of these predicted changes with actual changes in numbers of adult tree over the 1999 – 2007 period (Fig. 3b), suggests that the model, in these circumstances, is supported. Two anomalies stand out: *Dichrostachys cinerea*, predicted to decline, has increased, whilst *Euclea racemosa*, predicted to be unchanged, has increased in density.

Discussion

Our model suggests that impala exert, via their impact on the seedlings of woody species, a major long-term effect on *Acacia* woodlands in iMfolozi Park. Prins & Van der Jeugd (1993), working in Lake Manyara National Park, Tanzania, convincingly related even-aged stands of *Acacia* woodland to collapses in local impala populations, caused by episodic anthrax and rinderpest epidemics. Using exclosure experiments in the riparian woodlands of Chobe, northern Botswana, Moe et al.(2009) concluded that impala control woodland regeneration '..after elephants have killed the big trees'. Other smaller browsers at high density have also been shown, generally by exclosure experiments, to heavily impact recruitment of woody plants (e.g. dik-diks (Augustine & McNaughton 2004), kudu (Barnes 2001), and non-elephant browsers in general (Sharam *et al.* 2006)). It seems likely, therefore, that any smaller mammalian browser of high population-biomass will have a major long-term effect on savanna woodland structure, thus supporting our first hypothesis.

However our second hypothesis, that therefore removal of elephants from the system will not have an overriding effect, was not supported. Due to the synergistic effect of elephant and impala impact suggested by our model, removal of elephants is likely to radically reduce long-term impact on savanna woodlands. Critically, though, the converse situation of removing impala whilst leaving elephant is likely, the model suggests, to cause a similarly marked reduction in long-term impact. Scogings et al. (2012), using exclosure experiments in the Kruger National Park, South Africa, showed that over a short period (5 years) elephant exclusion alone had no effect on density of woody vegetation, but exclusion of all browsers did result in a significant increase in density of woody vegetation. Lagendijk et al. (2011), also using exclosures, found that excluding

both elephant and nyala in combination enhanced recruitment of woody species, indicating that forest regeneration is impacted by both mega- and mesoherbivores. These findings directly support our model's suggestion that *both* elephant and smaller browsers are required to markedly affect woodland dynamics.

The model was particularly sensitive to recruitment rates, supporting others' findings that woodlands appear to be far more sensitive to impact on seedlings than impact on mature trees (Dublin *et al.* 1990, Norton-Griffiths 1979). The model also highlights, as would be expected, that high growth rates enable plants to escape the impact of impala rather than that of elephant. The model's predictions for changes to *Acacia* woodland in iMfolozi Park were broadly supported by available transect data. Anomalies between the two can probably be explained by omissions in our model, driven by our aim to simplify in order to highlight elephant/impala impacts. The unpredicted increase in the density of *Euclea racemosa*, a highly unpalatable plant (Hattas *et al.* 2011), is most likely due to a competitive advantage gained by the species as other woody species declined in density; we did not model inter-specific competitive effects (Sea & Hanan 2012). The unpredicted increase in *Dichrostachys cinerea* probably relates to incorporating in the model growth rates, taken from the general literature, inappropriately low for the situation in iMfolozi, where the plant behaves like an alien invasive species. Nor did we attempt to account for pulsed recruitment in the model, offering a possible explanation for the generally lower densities of *Spirostachys africana* predicted by the model than are found in iMfolozi, where dense stands of the species appear to be even-aged (pers. obs.). The effects of fire were also not modelled. Fire affects *Acacia* seedlings and saplings considerably more than adult trees (Midgley &

Bond 2001, Schutz *et al.* 2011, Staver *et al.* 2011), and thus inclusion of it in the model would be expected to compound impact on the size classes impala, rather than elephant, impact, thus increasing the central role of seedling dynamics in woodland structure and composition.

As far as we are aware, this is the first time that savanna woody plants have been placed into functional groups, these groups realistically parameterised and the effect of plants' differing characteristics on long-term community composition explored. This approach emphasises how the behaviour of different functional groups of plants varies under the same level of impact, due to different recruitment and growth characteristics, in turn influencing community composition. It also highlights how interspecific variation in browsers' utilisation of woody species results in differential woody community composition.

Our findings suggest major implications for management. Where management aims to conserve woodlands over the long-term, reduction in mesobrowser biomass may be just as effective as reduction in elephant biomass. The latter is unpopular with tourists, often the major revenue generators, and considered morally repugnant by many (see Scholes & Mennell 2008). Culling of prevalent mesobrowsers, such as impala, is more acceptable to tourists, and, through hunting licences and meat sales, can generate substantial revenues. Such strategies are being implemented at the study site (pers. comm.), where impala meat is also distributed free to the low income rural families surrounding the reserve, thus improving relations with a burgeoning local population eager for land.

However, management attempts to preserve dense woodlands may themselves be misguided. Dense woodlands are probably a temporary, unstable state that arose following the decimation of browser populations, in the late 19th and early 20th centuries, through hunting and the rinderpest pandemic (Rohde & Hoffman 2012, Skarpe *et al.* 2004). Our model supports suggestions by others (Moe *et al.* 2009) that maintenance of dense woodlands requires decimation of both mesobrowser and elephant populations, which is an impractical policy at the landscape scale.

CONCLUSIONS

Our model suggests that smaller mammalian browsers of high population-biomass exert, via their impact on recruitment of woody species, a major effect on the long-term dynamics of savanna woodlands. This effect appears to be synergistic with the more established effect of elephant, suggesting management of mesobrowsers may alleviate pressures on both woodlands and elephant.

Characterising the African elephant as the quintessential keystone species may be misguided, exaggerating its influence on woodland dynamics (Prins & Van der Jeugd 1993). Its prominent influence in many locales may merely be a consequence of its localised high population-biomass, rather than any disproportionate effect. The keystone herbivore in an ecosystem is probably merely the herbivore with the greatest population-biomass, whether megaherbivore, mesoherbivore, rodent (Goheen *et al.* 2004) or invertebrate (Hagenah *et al.* 2009, Okullo & Moe 2012).

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Fig. 1. *Acacia* woodland dynamics model. The structure of the model used to assess the long-term dynamics of *Acacia* woodlands in iMfolozi Park is shown. Rectangular boxes contain levels (number of seedlings or number of adult trees). The underlying equations in the model are given in Appendix 2.

Fig. 2. Outputs of the *Acacia* woodland model for iMfolozi Park. The density of adult trees predicted by the model at the 100 y end-point, are shown for each functional group of woody plant species modelled (see Table 1 for functional groupings). The filled columns are the model's outputs with no herbivore impact. Columns with no associated arrows represent functional groups that were at, or approaching, a steady state, in terms of adult tree density, at the modelling end-point. Arrows on top of columns show functional groups that did not reach a stable state, but rather were either clearly increasing (upward arrows), decreasing (downward arrows) or marginally increasing (upward arrow heads only), at the modelling end-point. a) The striped columns show outputs with low elephant density and the open columns with medium elephant density; b) striped columns low impala density, open columns medium impala density; c) striped and open columns show medium impala density combined with low and medium elephant density, respectively.

Fig. 3. Predicted and actual changes in *Acacia* woodlands, iMfolozi Park. a) The density of adult trees predicted by the model at the 100 y end-point, and b) the total number of trees (≥ 3m height) counted over walked transects (n = 102). The open columns are the model's outputs (3a) with medium impala density only, approximating the situation in

iMfolozi in 1999 (3b), whilst the striped columns are the model's outputs (3a) with medium impala density combined with low elephant density, approximating the situation in iMfolozi in 2007 (3b). See Table 1 for codes for the functional groups and the corresponding representative plant species in iMfolozi. Differences in numbers of adult trees counted in 1999 versus in 2007 (Fig. 3b), were significantly different ($p < 0.05$) for all plant species, except *Spirostachys africana* ($p = 0.61$, Pearson's chi-square test with Yates' continuity correction), representative of functional group F.

Table 1. Functional groupings of woody plant species prevalent in *Acacia* woodlands of iMfolozi Park. Each prevalent woody species was assigned (see text for method) to a broad category of recruitment (recr.), growth and utilisation rate. The actual rates used in the '*Acacia* woodland' model, derived from the literature, are given in the final three columns. Units: recruitment rate is the number of seedlings per adult tree per annum, including first year survival; growth rate is the rate per annum from the model's seedling class into the adult class; impact rates are the percentage of, for elephant (ele), adult trees killed per annum, and, for impala (imp), the percentage of seedlings killed per annum. The first percentage given in brackets is the impact rate used to simulate low density, the second medium density of the respective herbivore. Code = the letter used to identify that functional group or representative plant species in the bar charts. Plant nomenclature after Pooley (2003).

Functional group			Code	Representative species	Rates used in model		
Recr.	Growth	Utilisation			Recr.	Growth	Impact
High	medium	high	A	*Dichrostachys cinerea*	2.5	0.06	ele (2%,7%) imp (10%,30%)
Medium	high	high	B	*Acacia karroo*	1.7	0.18	ele (2%,7%) imp (10%,30%)
Medium	low	medium	C	*Maytenus heterophylla*	1.7	0.04	ele (1%,2%) imp (5%,10%)
Low	medium	high	D	*Ziziphus mucronata*	0.3	0.06	ele (2%,7%) imp (10%,30%)
Low	medium	not utilised	E	*Euclea racemosa*	0.6	0.06	ele (0%) imp (0%)
Low	Low	high; imp only	F	*Spirostachys africana*	0.4	0.018	ele (0%) imp (10%,30%)
Low	medium	high; ele only	G	*Sclerocarya birrea*	0.1	0.06	ele (2%,7%) imp (0%)

Figure 1

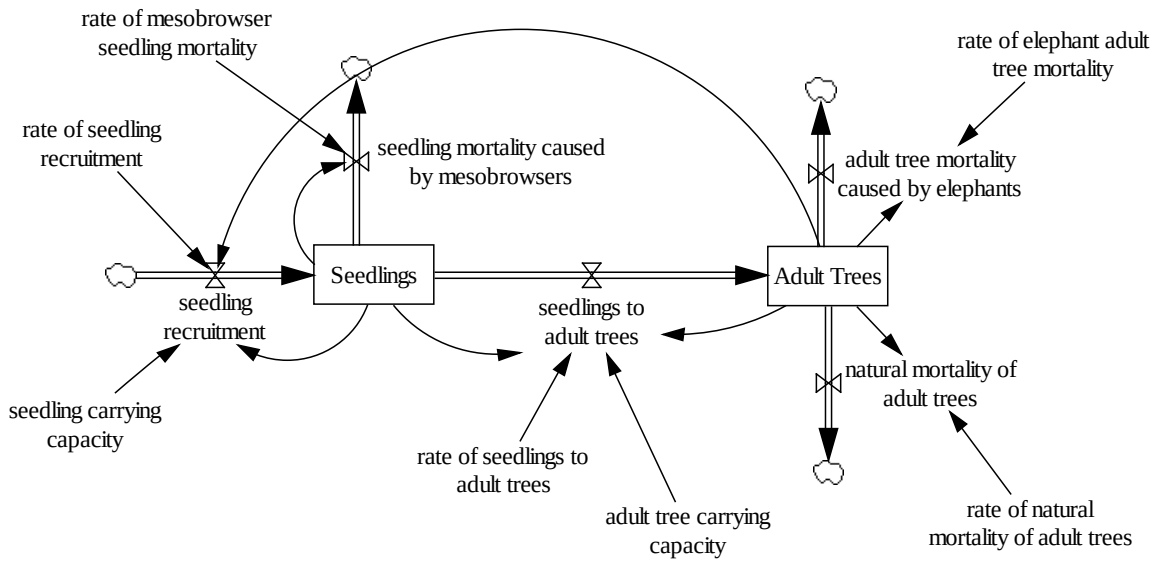

rate of mesobrowser seedling mortality
rate of elephant adult tree mortality
rate of seedling recruitment
seedling mortality caused by mesobrowsers
adult tree mortality caused by elephants
Seedlings
Adult Trees
seedling recruitment
seedlings to adult trees
natural mortality of adult trees
seedling carrying capacity
rate of seedlings to adult trees
adult tree carrying capacity
rate of natural mortality of adult trees

Figure 2a

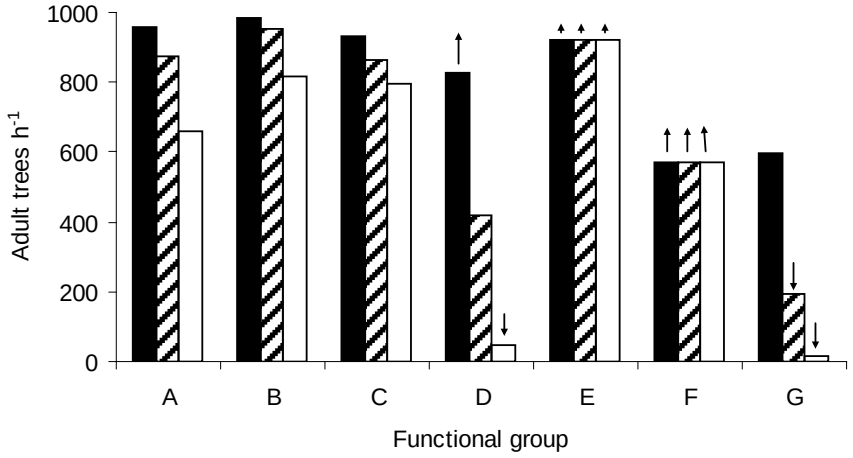


Figure 2b

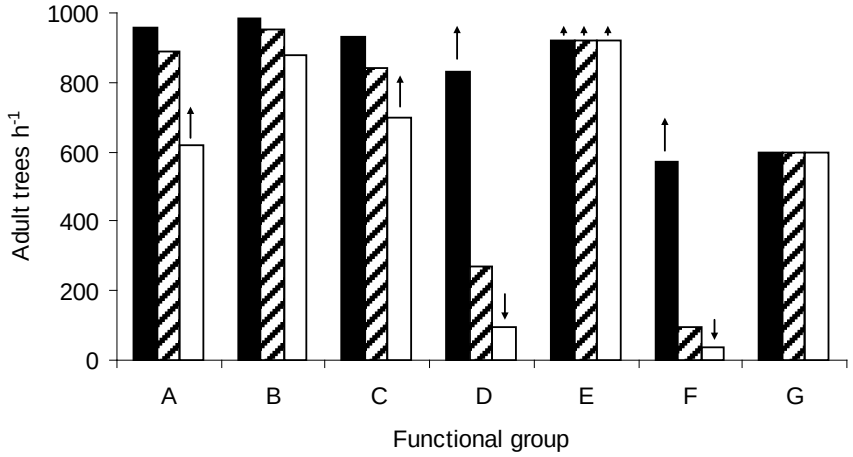


Figure 2c

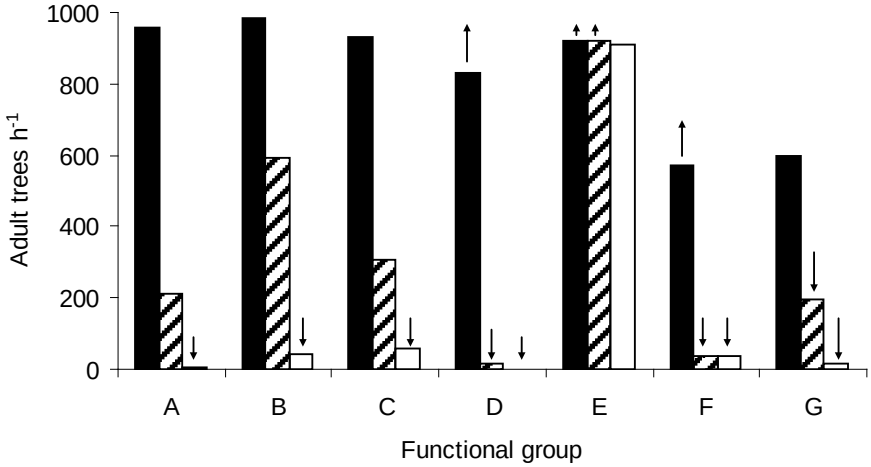


Figure 3a

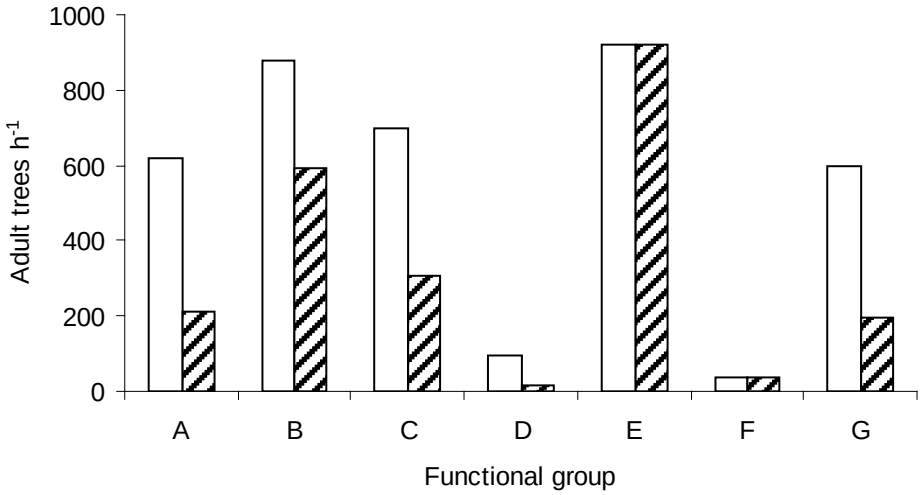
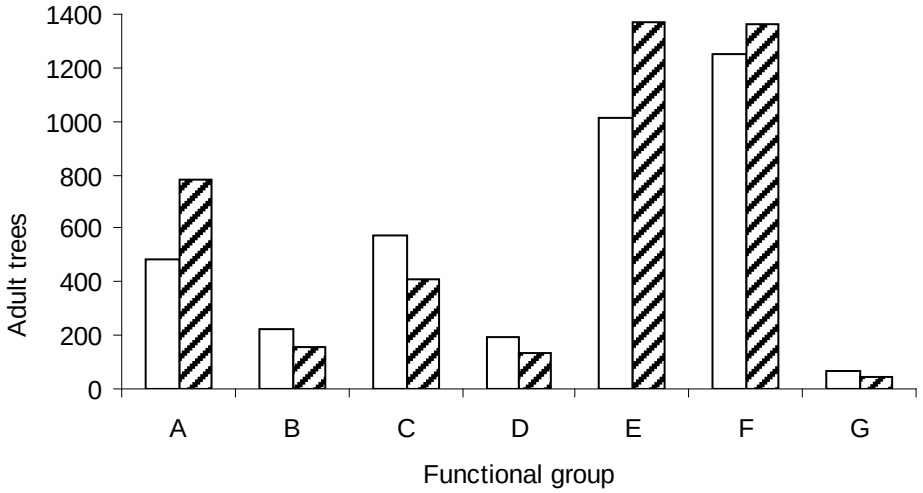


Figure 3b



Appendix 1a. Literature sources for recruitment, growth and elephant impact rates used in the *Acacia* woodlands model.

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Appendix 2. Equations for the *Acacia* woodlands model.

1) Adult tree mortality caused by elephants = (adult trees) x (rate of elephant adult tree mortality)

2) Adult Trees = $\int$ (seedlings to adult trees – adult tree mortality caused by elephants – natural mortality of adult trees)

3) Natural mortality of adult trees = (adult trees) x (rate of natural mortality of adult trees)

4) Seedling mortality caused by mesobrowsers = (seedlings) x (rate of mesobrowser seedling mortality)

5) Seedling recruitment = (rate of seedling recruitment x adult trees x 0.1) x (1 – seedlings/seedling carrying capacity)

6) Seedlings = $\int$ (seedling recruitment – seedling mortality caused by mesobrowsers – seedlings to adult trees)

7) Seedlings to adult trees = (seedlings x rate of seedlings to adult trees) x (1 – adult trees/adult tree carrying capacity)

8) Time steps = 1 year, initial time for simulations = 0, final time for simulations = 100 years.

SUMMARY

The study was devised to determine whether the long-term effects of elephants and mesobrowsers on woodlands are likely to be similar. This is a critical question in the ongoing debate on the reintroduction of elephant culling in southern Africa. With an extensive literature review indicating the research direction needed, the overlap in both habitat and woody plant species usage between elephant and other browsers was determined, over two years, in Hluhluwe-iMfolozi Park, South Africa - a medium-sized reserve containing sizeable populations of both elephant and a wide range of non-elephant browsers. During the third year GPS collars were used to assess, quantitatively, impact on woody species by a prevalent mesobrowser. These findings, together with published data, were then used to explore, by means of modelling, the likely long-term (up to 100 years) impact of the two groups on savanna woodland structure and composition. Here the study's ecological and methodological findings are summarised, together with its implications for conservation management. The summary finishes with consideration of future research and conclusions.

Ecological findings

Chapter 1. The review of 49 years of literature on the African savanna browser guild, revealed surprisingly few (n = 21) studies that have researched woody plant use by elephant and at least one other browser in the same locality. Only one paper gives details of the diet of the entire guild in the same locality. This disparate nature of the published

data necessitated a meta-analysis, which revealed extensive overlap between mesobrowsers and elephant in habitat use (an established finding), and the existence of a staple diet of woody-species communal across the guild (a novel finding). Together with evidence of the two groups influencing each others' abundance and of their dietary separation increasing with resource depletion, these findings imply that the two groups impact the same core woody-species in the same habitats. This in turn suggests that mesobrowsers at high population biomass may have a long-term substitutive effect to that of elephant on woodland dynamics, with additional additive effects relating to woody species exclusively used by mesobrowsers. The review's findings lent indirect support to a number of well established theories: i) Optimal Foraging Theory (Stephens & Krebs 1986)(a communal diet of favoured woody-species across the guild), ii) Niche Overlap Hypothesis (Pianka 1972)(dietary separation increasing with competition), and iii) the Jarman-Bell Principle (Bell 1971, Jarman 1974)(guild members closer in size showing greater dietary overlap).

Chapter 2. At the study site, Hluhluwe-iMfolozi Park, a small suite (n = 8) of woody species formed the core diet of all guild members, supporting the review's findings. Seasonal and annual variation in resource availability influenced herbivore choice and range of woody plants utilised. Overlap in woody-species browsed was lower between elephant and other browsers than amongst the latter, with elephant utilising the largest number of different woody-species, thus supporting the Jarman-Bell Principle and/or theories of digestive strategy (Napier Bax & Sheldrick 1963). Plant parts browsed also differed amongst the guild broadly as predicted by both the Jarman-Bell Principle and

variation in digestive systems. However resource depletion caused elephant, contrary to these theories' predictions, to narrow niche breadth in terms of species browsed. Elephants' greater range and relative indifference to predators appeared to offer the likeliest proximal explanation for this unexpected finding. Resource depletion rarely had a significant effect on interspecific overlap in species browsed or overlap in browsing heights, on actual browsing heights or plant-parts utilised. Consequently Pianka's Niche Overlap Hypothesis was not supported by these empirical data within the Park, but comparison with others' findings did suggest, where the contrast in resource depletion is marked, a continuum of increasing levels of resource depletion being associated with decreasing dietary overlap, thus supporting the Niche Overlap Hypothesis.

Chapter 3. At the study site, herbivores' selectivity for vegetation types conformed to the well documented habitat preferences of the different guild members. All members of the guild showed extensive overlap in habitat use. Increasing resource depletion in the dry season resulted in all members of the guild increasing selectivity for vegetation types, but decreasing interspecific overlap. These findings provided support for the Niche Compression Hypothesis (MacArthur & Pianka 1966) and the Niche Overlap Hypothesis, respectively. The contrast between resource depletion at the study site causing a widespread decrease in interspecific overlap in habitat use, but rarely having an effect on interspecific overlap in woody-species browsed or browsing heights, emphasises the importance of considering different aspects of a niche before commenting on any possible niche shifts. As Pianka remarked (1976), an ecological niche consists of the '..resource utilization spectra..' of an organism.

Chapter 4. In iMfolozi Park, densities of woody seedlings, and mean percentage of remaining canopy, were significantly less in areas of high impala density versus low-density areas. The average reduction in numbers of recruits going from areas of low to high impala density was 48% (range = 32%-75%). There was a significant correlation between increasing impala density and decreasing density of favoured woody recruits. It seems likely that the ubiquitous impala may create and sustain a shifting mosaic of patches, and thus function as a key determinant of landscape heterogeneity.

Chapter 5. The simple browse-browser model suggested that over the long-term (100 years), low to moderate densities of impala will have a similar impact on woodland structure, in terms of density of adult trees, as low to moderate densities of elephant. The outputs also highlighted the apparently strong synergistic effect impala and elephant impacts combined have on woodland dynamics, suggesting that reduction or removal of *either* impala *or* elephant will radically reduce long-term destruction of savanna woodlands. Recorded changes in adult tree numbers in iMfolozi broadly supported the model's outputs.

Methodological findings

Dealing with > 4,500 records on the guild's plant and habitat usage, gathered over ~ 50 years at a wide variety of study sites, represented a formidable methodological challenge. This was especially so as the paucity of records gathered in the same locality at the same

time prevented a standard statistical analysis. The meta-analytical approach used, however, lends itself to both dealing with such a large and disparate data set, and to enabling qualified objective conclusions, in the absence of any hard statistical analysis, to be drawn at different levels of the data set.

Determining the co-ordinates of herbivores sighted during repeated road transects, and then using these data in a GIS programme to determine habitat usage, represented a novel approach to determining animals' density by habitat type. This arose out of the requirement at the study site to develop an annual census method that: i) was more cost effective than aerial censuses, and ii) an alternative to the Distance programme which does not account for abrupt cut-offs in visibility within habitat types, a frequent topographical feature in HiP, and requires a level of I.T. training not available to basic staff. Once the area sampled and the total area in the reserve for each habitat type has been determined, as is the case at the study site, the GIS approach produces a cheap and accessible framework for annual censuses. All that is required is for an observer to drive carefully the same transects, record the numbers of each herbivore species seen by habitat type and then scale up these totals. Recognition of habitat type is a skill embedded in the local, rural staff employed. This same GIS approach to herbivore censuses has successfully been employed in the nearby Ithala Game Reserve, which also suffers from pronounced cut-offs in visibility. The population estimates produced by the technique in Ithala closely match those generated by both aerial and ground transects, which were continued over the first two years of the GIS approach to assess its validity.

Although GPS collar use has in recent years been widely combined with GIS programmes to determine and analyse animals' home-range, habitat usage and daily

activities, the project's use of these two technologies to determine and define a fine-grain browsing gradient was, apparently, unique. The development of this methodology was driven by the desire to assess impact by browsers by means other than using exclosure experiments, which dominate the field and yet may suffer from various practical and theoretical limitations. This aim was achieved. However, compared to the relative simplicity of the 'set up and leave' nature of exclosures, the method was comparatively expensive (GPS collars, radio-telemetry equipment), time consuming (monthly tracking of herds, 1,600 impact quadrats) and depended on extensive other research (two years of transects and feeding observations). It seems likely, therefore, that using this methodology elsewhere will only be appropriate in specialized circumstances.

Implications for conservation management

Findings from the literature review implied that elephant and mesoherbivores impact the same core woody-species in the same habitats. Field work at the study site confirmed extensive overlap in habitat use across the guild, and that a small suite of woody species form the core diet of all guild members, strongly suggesting the potential for synergistic impacts by guild members on these woody species and for competition between populations of different guild members. Quantitative assessment of impact by impala, a prevalent mesobrowser, on woody species at the study site, revealed the marked effect mesobrowsers at high biomass-density have on woody recruitment.

Combining these findings, together with extensive parameterisation from the literature, in a simple browser-woodlands model suggests that, over the long-term, low to

moderate densities of impala will have a similar impact on woodland structure as low to moderate densities of elephant. Moreover, the model's outputs highlight an apparently strong synergistic effect impala and elephant impacts combined have on woodland dynamics, suggesting that reduction or removal of *either* impala *or* elephant will markedly reduce long-term destruction of savanna woodlands.

Across the southern African region, management attempts over past decades to control declining woodlands have often been characterised by control of elephant populations alone. Although in recent years research has increasingly highlighted the role of mesobrowsers in woodland dynamics, this message has rarely translated into a re-direction of management's efforts. This is unfortunate as in smaller and medium sized reserves, where control of mesobrowser populations is practical, culling of antelope could be highly profitable and is clearly more acceptable to revenue providers, and society at large, than culling of elephant. Such sized reserves are an increasingly popular model for game reserves, especially in South Africa. It is perhaps worth remarking that where the message has been taken up, and mesobrowsers/the guild as a whole are managed, management is staffed by a younger generation, typically with a formal scientific background rather than an informal agricultural one.

Caveats, however, exist to these implications for management of savanna woodlands. Neither this research nor that of others has proven that mesobrowsers play a significant role in woodland dynamics; the evidence is correlative. Proving this role is difficult (see 'Future research') and evidence over the coming decades is likely to be circumstantial.

The broader message for conservation is that management of guilds as a whole, rather than focusing on one perceived 'keystone' species, may be a more appropriate policy. A 'keystone' species may be designated such purely on the basis of its size and obviousness of impact, whilst smaller members of the guild, but ones of comparable or greater population biomass, may in fact have a similar or greater effect. Such effects may be immediate or of a long-term nature in terms of humans perceiving the effect – as appears to be the likely case with mesobrowsers and their influence on adult tree density. Whilst the concept of considering different members of a guild in terms of their total population biomass, rather than individual size, seems entirely logical, it is one relatively novel to management of mammalian herbivore guilds. Nor should management ignore possible interactions between different mammalian savanna guilds (Maclean *et al.* 2011), or the wider ramification of possible changes to food-web 'biostructure' (Lewis 2009).

The broader picture

Although the topic of this thesis is about elephant versus other browsers' influences on woody vegetation, and consequently how they might be managed, this cannot be seen in isolation from other ecosystem processes. Savanna ecosystem dynamics involve complex and varied processes and it is appropriate to consider the most prominent of these in this summary.

Fire. Fire has been described as a large, or mega, generalist herbivore (Bond 1997). It influences plant communities through episodic, large-scale destruction of plant biomass and, where intense enough, by actually killing plants. Widespread evidence (see

Scholes & Walker 1982 for summary) that exclusion of fire leads to increases in biomass of woody plants, has lead many to the conclusion that fire is vital in savannas to prevent progression to forest states of vegetation. Others, however, have shown that in arid environments excluding fire leads to a denser variant of savanna, rather than inevitable forest (van Wilgen & Scholes 1997). Midgley *et al.* (2010), reviewing the role of fire and herbivory on woody vegetation, concluded that the two generally act synergistically but that herbivory alone, noticeably that of elephant and impala, can have greater effects than fire alone. Hluhluwe-iMfolozi, with its widely different annual rainfall north to south, provides an interesting example of these varying influences of fire in one locality. To the north, in Hluhluwe, the high annual rainfall (~ 1000mm p.a.) leads to large fuel loads resulting in intense and widespread fires. Yet to the south, in iMfolozi, the lower rainfall (~ 600mm p.a.) leads to lower fuel loads, which are further reduced by the locally high density of grazers and mixed feeders. Consequently control of woody vegetation in Hluhluwe is dominated by fire, whilst in iMfolozi by herbivory (Staver *et al.* 2011).

Global and local drivers of increasing woody vegetation. Increased levels of $C0_2$ and higher annual rainfalls, both associated with the phenomenon of global warming, are postulated to be factors encouraging woody encroachment globally. Bond and Midgley (2000) suggested that the C_4 metabolic pathway of woody plants, versus the C_3 pathway of grasses, is favoured by increased levels of CO_2 in the atmosphere. Kgope *et al.* (2010) has recently provided direct empirical support for this in African savannas by demonstrating, under laboratory conditions, greater growth rates of woody plants (*Acacia karoo*) versus those of grasses (*Themeda triandra*) in response to increased CO_2 levels. Sankaran *et al.* (2005), in a review of over 850 locations across Africa, concluded that

650mm p.a. of rainfall represents a pivotal threshold in the relationship between woody encroachment and rainfall. Below this level woody cover is held in check, in a stable manner, by water availability and is further reduced by disturbances, such as fire, herbivory and man. However above this level it seems woody encroachment is unstable and will inevitably proceed to full woody cover – unless modified by disturbances. Local drivers of woody encroachment in African savannas principally relate to the reduction or absence of browsers (Rohde & Hoffman 2012). As has been discussed elsewhere in the thesis, the very existence of substantial savanna woodlands may be an historical anomaly consequent on the widespread reduction in the browser population during the late 19th and early 20th centuries. Principle causes of this reduction were disease (rinderpest, anthrax and East Coast fever) and hunting (Skarpe *et al.* 2004).

Ecosystem flux and patch dynamics. The savanna landscape may be regarded as a biological and physical mosaic influenced by fluxes of energy, materials and organisms (Pickett *et al.* 2003). Heterogeneity, both biotic and abiotic, within this mosaic is accounted for by patch dynamics – whether on a coarse scale(e.g. tectonic shift, climate and geology (Venter *et al.* 2003)), a medium scale (e.g. fire, wind, flood (Dale *et al.* 1999), rainfall patterns (Mills *et al.* 1995)) or a fine scale (e.g. herbivory (Levick & Rogers 2008, Mourik *et al.* 2007)). Heterogeneity is an important cause of ecological systems' productivity and richness and, hence, the functioning of ecological systems (Pickett *et al.* 2003). Species coexistence and the structure of ecosystems and their assemblages have been shown to be extensively caused and facilitated by patch dynamics (Fisher 1993, Rogers 1997). The recognition of the importance of patch dynamics and

landscape heterogeneity has led, in recent years, to a move away from excessive management promoting landscape homogeneity (Mills *et al.* 2003).

Water distribution. Together with fire and culling, water provision stands as the main managerial intervention available to African savanna managers (Gaylard *et al.* 2003). Establishment of widespread artificial water-points in the Kruger National Park, during the last century, was intended to minimize the influence of drought on herbivore populations (Pienaar 1983). However, this provision of water probably reduced herbivore diversity by extending the range of common species and hence associated predators, resulting in a decline of rarer herbivores (Owen-Smith 1996). It is also possible that the expansion in elephant range associated with artificial water provision may have reduced the structural heterogeneity of the woody vegetation (Gaylard *et al.* 2003). Consequently, management's viewpoint has shifted away from provision of artificial water-points (Gaylard *et al.* 2003).

Cascade effects of management strategies. Past experiences of the effects of intervention caution against a too proactive approach in the management of savanna ecosystems. The Kruger National Park is the prime example of the dangers of over management. For example, efficient anti-poaching operations in the Park over the 1930s to the 1970s, together with artificial water provision (discussed above), led to an increase in lion and spotted hyena numbers through an increase in resident herbivores. These increases, especially in the latter, probably led to the extinction in the Park of the subordinate brown hyena (Mills & Funston 2003). Water provision and manipulation, excessive burning, fencing, culling and disease control were the tools of management in the Park (Pienaar 1983) and, combined, it is regarded they represented excessive control

and shifted the ecosystem towards habit homogeneity (Mills *et al.* 2003). Going forward, the Park's management, in a model likely to be appropriate for conservation in general, have embraced an adaptive management programme that aims to utilise the latest and best information, as it becomes available, to continuously redefine 'thresholds of potential concern' (TPCs). The essence of this approach is to recognise the innate resilience of the ecosystem to shock, whilst keeping the system within desired states and avoiding irreversible threshold effects (Mills *et al.* 2003).

Future research

The postulated role of mesobrowsers, at population biomasses comparable to that of elephant, is important for the practical, long-term management of savanna woodlands. It is also important in terms of ecological theory and how that relates, over short versus the long-term, to 'keystone' species theory, inter-specific competition within a guild and the impact of a guild on its environment. Although the thesis has concentrated on the savanna browser guild, in terms of the differential management of mesobrowsers versus elephant, these theoretical considerations are probably relevant to other mammalian herbivore guilds and, possibly, guilds in other ecological systems and at other trophic levels. For these reasons it is desirable that the project's findings are confirmed or refuted by future research.

Obtaining data at other sites on whether the savanna browser guild does, in the same locality, show considerable overlap in habitat usage and communally utilise a central, core diet of woody species, is straight forward and could be accomplished as

additional tasks during censuses and other, general field-work. Proving that mesobrowsers have a central role in the long-term dynamics of savanna woodlands is, however, difficult. This would require, ideally, a large area containing the same flora and fauna, having the same topography, soil and climate, which could then be divided into separate areas, secure over the long-term, with i) no mammalian browsers and ii) just mesobrowsers. This is most unlikely to happen and, consequently, 'proof' of mesobrowsers' postulated long-term impact is likely to be more circumstantial. For instance it may be observed, over the long-term, that in reserves lacking elephant but with sizeable mesobrowser populations, woodlands do indeed decline compared to un-impacted areas. Entirely anecdotal but at Tala Game Reserve, a small reserve in South Africa which has had no elephant but a wide range of mesobrowsers for several decades, staff have commented on an apparent lack of younger trees in their woodlands (pers. comm.).

Proving the postulated inter-specific competition within the browser guild is also problematic. This would require multiple replicates of experimental areas where the effects of elephant removal (leaving just mesobrowsers), versus mesobrowser removal (leaving just elephant) on herbivore population dynamics could be assessed. Under these experimental conditions the remaining group would be expected, as resource availability increases, to increase in population biomass. The size of the animals involved and their associated home-ranges are likely to make such multiply replicated field experiments impractical, although techniques do exist for dealing with unreplicated perturbations (e.g. Before-After-Control-Impacts-Pairs design (Stewart-Oaten *et al.* 1992)). Again, 'proof' is likely to come over time as the body of evidence, small at present and discussed in

Chapter 1, for competitive effects (influences on each others' population size, overlap in resources use) builds up across the continent. Proving competition in the field is, in general, notoriously difficult (e.g. Bonesi *et al.* 2004, Connell 1980, Dublin *et al.* 1990, Sinclair 1985, Valeix *et al.* 2007).

Conclusions

The study set out to verify a number of hypotheses. These and whether they were supported by the study's findings may be summarised:

(i) An in-depth review of the literature will reveal a) extensive overlap between elephant and other browsers in habitat usage, and b) a central 'core', or staple diet, of woody species communal across the browser guild. The literature review confirmed extensive overlap in habitat usage, whilst the existence of a communal woody diet across the guild was strongly suggested within the limits of the meta-analysis performed.

(ii) The browser guild in HiP will likewise show extensive habitat usage overlap and a staple, core diet communal to the guild. Both these hypotheses were directly supported by the study's field work.

(iii) Mesobrowsers in HiP of high population biomass severely impact woody plant recruitment. This hypothesis was also directly supported by the study's field work.

(iv) Over the long-term a) mesobrowsers of high population biomass exert, via their impact on recruitment, a major effect on savanna woodland structure, and b) that therefore removal, or reduction in numbers, of elephants from the system may not have an overriding effect. The logic implied by the findings of the literature review and the project's field work supported both parts of this hypothesis. However, whilst the project's model also provided indirect support for part a), it did not do so for part b). Rather, the model's outputs suggest that removal, or reduction in numbers, of elephant will have an overriding effect on long-term savanna woodland dynamics, consequent on the apparently synergistic impact of elephant and mesobrowsers. Crucially, however, this synergy also appears to imply that removal, or reduction in numbers, of mesobrowsers from the system will have a similar overriding effect.

The project's hypotheses were thus broadly supported, although with important qualifications.

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APPENDIX

Four additional topics of interest to the project are included below. These were not included in the main body of the thesis to maintain its coherence.

A). Effects of savanna mammalian browsers on the different life-stages of woody plants, with emphasis on *Acacias*; a mini-review

Seedling germination:

Miller (1995) recorded that ingestion by animals increased germination of seeds. Encroachment of *Acacias* into pastoral areas has in part been suggested as due to increased rates of seed germination after passage through cattle (Moleele & Perkins 1998); similarly, rarity of recruitment of *Acacias* has been attributed to absence of large herbivores and the beneficial scarifying effect their digestion has on the hard seed coat during digestion (Ward & Rohner 1997). However, extensive seed mortality after ingestion by cattle has been recorded (Donaldson 1969) and ingestion by cows did not improve *A. albida* germination rates (Hauser 1994), calling into question the effect of herbivores' digestion on seedling germination (Midgley & Bond 2001).

Seedlings/recruitment:

Pellew (1983) suggested that influences on the regeneration of *Acacia*, rather than studies on their adult mortality, were needed. Belsky (1984) demonstrated the role of smaller

ungulate browsers (smaller than elephant or giraffe) on recruitment using exclosure plots, whilst Prins & Van der Jeugd (1993) related even-aged stands of *Acacia* to episodic recruitment opportunities, consequent on anthrax-induced impala population crashes. Midgley & Bond (2001) commented that the "lack of small and intermediate size-classes noted in many savannas...probably due to a chronic lack of escape opportunities rather than seed/seedling limitation". Scogings & Mopipi (2008) studied *A. karroo* seedlings following experimental clipping, finding that compensatory or over-compensatory regrowth only occurred when water was added and grass removed (i.e. abundant resources with removal of competition). In Kenya Goheen et al. (2004) noted that rodents/invertebrates had a greater effect than meso- or megaherbivores on seedling survival, commenting on the "...negligible direct impacts of large mammalian herbivores on seedling survival." However in Botswana Moe et al. (2009), also using an exclosure experiment, found that ungulates markedly reduced seedling survival (mean reduction ~ 50%), and that seedling survival was negatively correlated to local density of impala.

Saplings/medium size classes:

Du Toit et al. (1990) recorded that compensatory shoot regrowth in *A. nigrescens* and *A. tortilis*, even with severe browsing (i.e. pruning), more than compensated for herbivory. However, they noted that pruning has a different effect from severe defoliation (i.e. beneficial versus detrimental). They concluded, however, that the benefits of concentrated browsing appear to be short lived – "preliminary evidence indicates that severe selective browsing ultimately leads to replacement of *A. nigrescens* by less palatable and productive species." Fornara and Du Toit (2007) concluded that *A.*

nigrescens responded to heavy browsing with tolerance (high regrowth abilities) and resistance (close thorn spacing), but at the expense of reproductive success.

In an exclosure experiment, Riginos & Young (2007) showed browsers (elephant, giraffe and Grant's gazelle) had a positive effect on sapling (>15cm, <70cm in height) growth - over two years total stem length (= main stem plus main branches) increased on average 25% more in the presence of these browsers. However Rooke & Bergstrom (2007) found mean growth in tree height over the growing season was increasingly reduced with increasing leaf and shoot tip removal (i.e. simulated browsing). Simulating herbivory by clipping twigs of saplings (1.5-2metres height) in the dry season, and measuring resprouts 7 months later, Tsumele et al. (2007) found *A. nilotica* over-compensated in terms of resprout biomass, *A. karroo* fully compensated and *A. rehmanniana* under-compensated.

Studying 1 to 4m trees, Fornara & du Toit (2008) noted that heavily browsed trees produced fewer pods and had narrower canopies, but found no evidence of heavy browsing affecting community dominance: "…resilient-spinescent woody plants can maintain community dominance even under conditions of chronic ungulate browsing". Noumi et al. (2010), working in Tunisia, concluded: "Browsing by livestock seems to be a negative factor affecting the general structure of the *A. tortilis* populations (reduced density, canopy cover and canopy diameter) but a positive factor in terms of regeneration (higher abundance of young trees in browsed (versus unbrowsed) areas)."

Interestingly, in a review of the effects of browsing by moose on woody plants in North America, Danell et al. (1994) concluded that there was no single coherent response.

Adult trees:

The damage elephants, especially at high density, can cause to mature trees is well established in the literature, whether by extensive removal of large branches, ring-barking or pushing trees over (Ben-Shahar 1993, Ben-Shahar 1998, Croze 1974, Gadd 2002, Laws 1970b, Leuthold 1977, Norton-Griffiths 1979, for summary see Scholes & Mennell 2008). Giraffe effects on adult trees are less clearly understood. Pellew (1984) found that up to 85% utilisation of new shoots on *A. xanthophloea* did not result in lowered plant productivity (at least over the short-term), whilst others (du Toit *et al.* 1990) have found that *A. tortilis* and *A. nigrescens* showed rapid regrowth to compensate for even heavy browsing by giraffe. However, in some locations giraffe have had a markedly negative effect on *Acacia* populations (Bond & Loffell 2001).

Sexually mature trees:

Reproductive trees (taken as >1.3m height for *A. drepanolobium* byGoheen et al., and >1m height by Fornara and du Toit) have been shown to have their reproduction suppressed by mammalian herbivory (Fornara & Du Toit 2007, Fornara & du Toit 2008, Goheen *et al.* 2007).

Summary

The current state of knowledge on the effects of savanna mammalian browsers on woody plants ranges from the well established to the apparently contradictory. Whilst the detrimental effects of elephants at high density on adult trees is widely recorded, browser

influences on saplings/medium size classes are variously reported as beneficial or detrimental, with longer-term influences on reproductive success further complicating the situation. It seems likely that such wide variation is consequent on the browsing technique (pruning, leaf stripping, leaf biting or branch removal), the amount of biomass removed, the plant species and its nutritional status. It is unclear whether mammalian digestion aids or hinders seeds' germination. Mesoherbivores, principally impala, appear to have a markedly negative effect on *Acacia* seedlings and hence recruitment.

B). Coarse estimate of impala versus elephant forage consumption, based on weight of impala stomach contents, goat and elephant literature

Whilst estimates of the weight of elephants' daily forage consumption appear in the literature (Laws 1970a), those of impala do not. Goats, a mixed feeder of similar size to impala, consume on semiarid lands 48.4g/kg$^{\wedge 0.75}$ per 24 hours, with a mean retention time through the rumen of 26-31 hours (Garcia et al. 1995). Applying this same formula to a 60kg adult male impala, gives a consumption rate of 2kg per 24hrs, implying upwards of 3kg of forage in the rumen. We determined the total (wet) weight of the stomach contents (by dissection of the rumen, reticulum, abomasums, omasum and ventral blind sac within two hours of death) of 32 (male) impala, shot (for local meat sales) near to and in the same vegetation type as the collared impala. The average wet weight of impala stomach contents was 3.25kg – implying impala rumination operates at a similar rate to that of

goats. It seems reasonable, therefore, to estimate average impala (i.e. averaged across all age groups and sexes) forage consumption as 1.5kg per 24hrs.

Laws (1970a) gives elephant daily forage consumption as 300kg for large bulls and 170kg for non-pregnant adult females. An estimated average of 140kg per 24 hrs seems reasonable. Using these figures and HiP population numbers for impala (24,000) and elephant (500), gives an estimated total forage consumption per 24hrs of 70,000kg for elephant and 36,000kg for impala. Although these estimates are clearly extremely coarse, and do not address seasonal variation in browse versus grass consumption, they make the point that similar orders of magnitude of forage are probably being consumed in HiP by elephant versus impala. Since impala consume more nutritious growth stages/plant parts and, as ruminants, extract more energy from forage than hindgut fermenters such as elephant, they are probably extracting, per unit weight of forage, more energy from the system than elephants. Additionally, other non-elephant browsers, although not at such high densities as impala, form a considerable additional browser biomass in the reserve.

C). Utilisation of hooked versus straight spined *Acacia*

Acacia, which are widely utilised by the guild (Fornara & du Toit 2008), defend themselves from herbivory with spines (Owen-Smith & Cooper 1987). It has been suggested (Dunham 1980, Hempson 2004) that thorn shape influences the effectiveness

of this defence, and hence herbivores' potential impact on different *Acacia*. During feeding observations we recorded the browsing technique used by guild members in relation to the type of spine, or thorn, present on the different *Acacia* species utilised.

Giraffe showed a significantly lower percentage use of stripping on hooked, versus straight, spined *Acacia* (χ^2-test, $P < 0.005$). Impala showed significantly higher percentage of small bites, versus medium or large bites, on hooked versus straight spined *Acacia* (χ^2-test, $P < 0.005$), whilst elephant, kudu and nyala showed no difference in branch end use between the two *Acacia* thorn types (χ^2-test, $P > 0.05$). Black rhino's second most preferred plant in HiP is the hooked *Acacia tortillis* (Emslie 1999). The hooked Acacia in the reserve were *Acacia tortillis*, *A. nigrescens*, *A. ataxacantha*, *A. burkei*, *A. luederitzii* and *A. senegal*.

Hooked, versus straight, thorns thus appear to be more effective in reducing the potential impact giraffe and impala may have on *Acacia*. Cooper and Owen-Smith (1986) similarly found hooked thorns more effective against smaller, selective browsers such as impala. This seems to be a well accepted fact by the local rural population, who use the Zulu word 'um-bambampala' for *Acacia nigrescens*, a prevalent hooked *Acacia*, which broadly translates as 'if impala gets his lip hooked, he won't escape'.

D). Smaller browsers' utilisation of trees pushed over by elephant

Elephants push over large trees and snap or uproot smaller trees (Midgley et al. 2005). Where the tree survives, mesoherbivores may benefit from this behaviour as it has been shown to cause increased shoot abundance at lower levels in the canopy (Makhabu et al. 2006), as well as an improvement in browse quality (Kohi *et al.* 2011). We noted when mesoherbivores were feeding on trees that had clearly been pushed over by elephant. Only 3.5% of all mesoherbivore feeding records (n = 2559) occurred on such trees, suggesting that in HiP elephant facilitation of mesoherbivore browsing in this fashion is minimal.

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