

Habitat partitioning, and an assessment of habitat suitability using presence data, of a large herbivore community on a Zimbabwean private wildlife reserve.

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Thesis presented in partial fulfilment of the requirements for the degree of Master of Forestry at the University of Stellenbosch

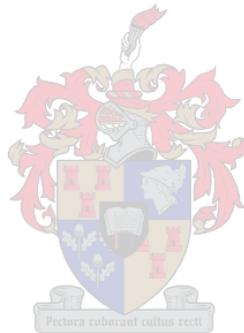


Promoter: Professor R.C. Bigalke

March 2003

Declaration

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it to any University for a degree.



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01/05/2003

Lochran Traill

Abstract

The factors determining habitat selection of large herbivores, on a private wildlife reserve in semi-arid southeastern Zimbabwe, were investigated. Gross vegetative structure, herbaceous composition and topographic features thought to determine herbivore distribution were measured. Seasonal variation in resource distribution was considered, and research therefore extended over an entire year. Herbivore distribution and ecological niche separation was explained through several important environmental variables, and potential for inter-specific competition inferred. Additionally, predictive habitat suitability models were designed for each of the grazing species in the critical dry season.

Herbivores showed a large degree of niche overlap in both the hot-wet season and the cool-dry season, when food resources were more plentiful. Niche separation between grazers was pronounced in the hot-dry season. Herbivore distribution was associated most closely with distance to water, grass sward height, time since burn, woody plant density and by the presence of predominant grasses, these being *Urochloa mossambicensis*, *Panicum maximum*, *Heteropogon contortus* and *Digitaria eriantha*. Ecological separation of herbivores by the grasses *P. maximum*, *H. contortus* and *D. eriantha* was more indicative of associated environmental variables than feeding niche separation.

A GIS-based analysis, using species presence data and quantitative coverages of environmental variables, produced maps of gradations of habitat suitability for grazing species during the dry season.

Results of both analyses were integrated and gave a better understanding of ecological separation, and possible competitive interactions, among the large herbivore community on Malilangwe Estate. Recommendations were made based on the interpretation of findings, within the context of available management options.

Opsomming

Die bepalende faktore van habitat seleksie by groot herbivore op 'n privaat wildreservaat in semi-dorre suidoos Zimbabwe is ondersoek. Globale plantegroei stuktuur, kruidagtige samestelling en topografiese eienskappe wat glo herbivore verspreiding bepaal, is gemeet. Seisoenale variasie in hulpbronverspreiding is in ag geneem en dus het navorsing oor 'n hele jaar gestrek. Herbivore verspreiding en ekologiese nisskeiding is verduidelik deur verskeie belangrike omgewingsveranderlikes en die potensiaal vir interspesifieke kompetisie is afgelei. Boonop is voorspellende habitat-geskiktheidsmodelle ontwerp vir elk van die weidingspesies in die krities droë seisoen.

Herbivore toon 'n hoë graad van nis oorvleueling in sowel die warm, nat seisoen as die koel, droë seisoen wanneer voedingsbronne meer volop is. Nis verdeling tussen weidiers was duidelik herkenbaar in die warm, droë seisoen. Herbivore verspreiding is meestal geassosieer met die afstand na die water, die grasveld hoogte, tydperk sedert 'n brand, digtheid van houtagtige plantsoorte en met die teenwoordigheid van die oorheersende grasse, *Urochloa mossambicensis*, *Panicum maximum*, *Heteropogon contortus* en *Digitaria eriantha*. Die ekologiese skeiding van herbivore deur die grasse *P. maximum*, *H. contortus* en *D. eriantha* het meer gedui op geassosieerde omgewingsveranderlikes as op skeiding van voedingsnise.

'n GIS-gebaseerde analise wat spesie-teenwoordigheidsdata en kwantitatiewe dekking van omgewingsveranderlikes gebruik, het klassifikasiekaarte geproduseer van habitatgeskiktheid vir weidiers tydens die droë seisoen.

Resultate van beide analyses is geïntegreer en het 'n beter begrip van ekologiese skeiding en moontlike kompeterende interaksies tussen die groot herbivore gemeenskap op Malilangwe Estate tot gevolg gehad. Aanbevelings is gemaak, gebaseer op die interpretasie van bevindinge, binne die konteks van beskikbare bestuursopsies.

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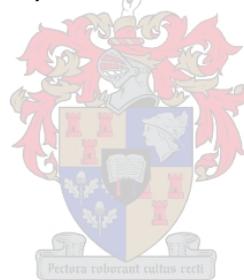
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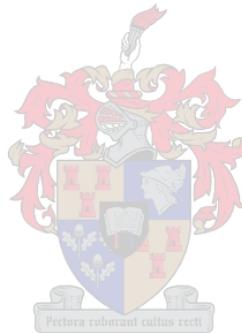
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Chapter 1: Introduction

This study is essentially about the effects that environmental parameters and competition have on the distribution and resultant habitat use of the large grazing herbivore community at Malilangwe Estate (ME hereafter), and how management can manipulate certain parameters to ensure a stable and productive community.

ME is a large, privately-owned wildlife reserve in the southeast lowveld region of Zimbabwe that primarily caters for the photographic tourist, as well as select hunting clients. The estate is owned by a Trust, the Malilangwe Trust, which has recently made substantial financial investments into the large herbivore community (through species introductions) with the objective of restoring the estate to its 'pristine' wildlife state, or as best this can be realized.

Some of the large herbivore species re-introduced include rare, ecologically sensitive (IUCN 1990) and economically valuable individuals (Goodman P.S. pers. comm.). These are: white rhino *Ceratotherium simum* (rare and economically valuable), sable antelope *Hippotragus niger* (rare, ecologically sensitive and economically valuable) and buffalo *Syncerus caffer* (economically valuable). Management at ME hope to maintain viable populations of all their large herbivores, but particularly the rare and valuable species, given the investment made. Before management can achieve this objective however, they require an understanding of the habitat preferences of, and potential for competition among, the large herbivore community, with particular relevance to the grazing species (Goodman pers. comm.).

An understanding of the relationships between large African herbivores and their habitat has been the basis of wildlife management for decades (Ben-Shahar & Skinner 1988; Dorgeloh 1998; Ferrar & Walker 1974; Melton 1978; Pienaar 1974) and is essential to the effective conservation of a species or community (Ferrar & Walker 1974; Pienaar 1974). Previous studies have achieved a better understanding of large African herbivore communities, *viz.* habitat preferences of species and the competitive interactions among them, through the quantitative description of species niches and their placement within a community hyper-volume (Fabricius & Mentis 1990; Ferrar & Walker 1974; Melton 1978), based on the Hutchinsonian concept of niche (Hutchinson

1957). His definition perceives the species niche as an n -dimensional hyper-volume, where the dimensions are equivalent to the environmental pressures, and can be quantified through the use of descriptive multivariate statistics (Green 1971).

Thus, this study set out to understand the large grazing herbivore community at ME by defining the species niches within a community hyper-volume and through the use of a descriptive multivariate technique; preferably one that had been successfully used in similar studies, with similar objectives and study species. Discriminant function analysis was used here, after Ferrar & Walker (1974) and Melton (1987) and essentially orders species locations within the community hyper-volume according to the combined influence of several independent environmental variables (Green 1971). An understanding of those environmental variables that serve to ecologically separate species (Ferrar & Walker 1974) may allow anthropogenic manipulation of one or more environmental variables to the benefit of certain animal species.

The study also attempts an assessment of suitability of habitat for each of the species comprising the grazing guild during the critical dry season, based on work done by Hirzel (2001), and a geographic information systems model developed by Hirzel *et al.* (2001). The development of habitat suitability maps allows for a more accurate assessment of species carrying capacities, and further analysis of maps allows for prediction of competitive overlap between similar species.

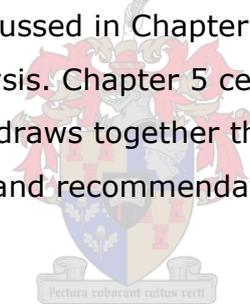
Management 'tools' are considered throughout the study and are the basis of discussion and recommendations. Tools available to management include fire, surface water control and harvesting (Bothma 1989; Trollope 1990). The habitat variables time-since-burn, distance-to-water and woody density are thus given particular attention in the interpretation of results, as these are the environmental variables that management can potentially manipulate. Potential for interspecific competition is considered and forms the basis of recommended species off-takes.

Ecologically relevant theory that forms the basis of this study is described in the following Chapter. Essentially, all individuals of each species were assumed to select the most suitable habitat, given the constraints, and data collected from individuals of each species was averaged and assumed to be an accurate indication of suitable and preferred habitat for that species.

Partitioning of resources among species was assumed to occur, primarily as a means of reducing interspecific competition, after Dekker *et al.* (1996), Sinclair (1975) and Putman (1996). Resources were assumed to be limiting during the critical period (here the hot dry season) after Sinclair (1975) and interspecific competition was thought to *potentially* occur. Furthermore species niche shifts were also assumed to *potentially* occur, forcing species to adopt their essential realized niches (Schoener 1982), i.e. species utilize those resources to which they are best adapted, thereby reducing interspecific competition.

Density-dependent effects were assumed at the outset of the study to be minimal, but the potential effects of increased intraspecific competition i.e. niche expansion and the resultant interspecific perturbations, are discussed in detail, particularly given that droughts will occur at some point in the future.

The theories of habitat selection, ecological separation, competition (including the concept of niche) and facilitation are reviewed in the following chapter. The study area is discussed in Chapter 3, and the fourth Chapter involves the discriminant analysis. Chapter 5 centres on the habitat suitability analysis and the final Chapter draws together the results of the two analyses and includes final conclusions and recommendations.



Chapter 2: Theoretical background

2.1 Introduction

It is necessary here to introduce the theoretical background of this study. This primarily serves to put the research into a biological context, and explain the underlying assumptions. At no point does this study set out to test any of the mentioned theories; the research is rather done within the framework of current theory, and pertains to management-oriented goals.

Mention is thus given to the theories of habitat selection, ecological separation, competition and facilitation. These processes are given separate mention, and relevant literature is succinctly reviewed. There is no hierarchical approach given to each of the relevant theories.

Also discussed is adaptive management within an ecological context. Adaptive management and particularly the tools used to achieve this, forms the basis of discussion and final recommendations.

A review of each herbivore species is not included here as relevant literature pertaining to each species is discussed in the final Chapter.

2.2 Habitat selection and ecological separation

A species has varying needs, of which finding a suitable place to live, and in which to find food and shelter, is the most important. Finding a suitable place to live differs for species, but is usually defined by the physical environment; factors including topography, soil type, vegetation structure and type (Ben-Shahar 1995; De Santo 1978). Thus, *habitat* is generally understood to be the *living place of an organism or community, characterized by its physical or biotic properties* (De Santo 1978; Fretwell & Lucas 1970; Hutto 1985; Melton 1987).

Habitat selection implies "the choice by an organism of a particular habitat in preference to others" (Allaby 1998). It is the relative suitability of different habitats that gives rise to habitat selection, as individuals that select relatively poor habitats are selected against in the evolutionary process (Fretwell & Lucas

1970; Melton 1987). The suitability of habitat varies in terms of benefits, such as food availability, and costs, such as predation (Melton 1987). Benefits and costs vary for species, which view the environment from different perspectives. An abundance of one resource is likely to favour one or more similar species, but not another species. The same could be said for costs, such as predation.

The underlying assumption of habitat selection theory is that habitats occur as patches and organisms make choices about how to allocate their time among those patches (Hutto 1985; Rosenzweig 1985). Furthermore, the arising differential habitat selection is one of the principal relationships which permit species to co-exist (Rosenzweig 1981). These assumptions form the backbone of this study, and are discussed further in explaining ideal free distribution theory:

Ideal free distribution: Fretwell & Lucas (1970) developed this theory to describe a particular way in which bird populations might distribute themselves over the available living places. In order to understand habitat distribution, Fretwell & Lucas first defined the factors affecting the distribution of a species within an environment. These are:

- Habitat selection: habitat distribution among a species is usually based on habitat selection, at least some individuals being exposed to a variety of habitats of which just one is chosen for residence. This selection can be considered a behavioural phenomenon, involving stimuli and responses. The evolution of selective behaviour is due to the processes of natural selection in response to varying environmental factors.
- Habitat suitability: individuals that choose relatively poor habitats are selected against (in the evolutionary process), assuming that habitats range from good to bad. The suitability of habitat is determined by several factors, such as resource availability and predators. Thus, the relative suitabilities of the different habitats give rise to habitat selection, which in turn determines the habitat distribution.

The influence of some of these factors is also density dependent, thus the suitability of a habitat from an individual's perspective is influenced by the density of other individuals from the same species already present (example of birds used by Fretwell & Lucas).

The ideal free distribution then is based on the below two assumptions:

- Habitat suitability assumptions: suitability always decreases with density, and thus maximum suitability occurs when density equals zero. This ignores ALLEE'S principle (Allee *et al.* 1949, unseen, as quoted in Fretwell & Lucas 1970). This principle states that survival and reproductive rates increase with population size up to some maximum. Further increase in population size leads to a decrease in survival and reproduction.
- Species assumptions: all individuals occur in the habitat most suitable to them, and all individuals within a habitat have identical expected success rates.

These two assumptions together assert that *each individual will go to the habitat of highest suitability*. Such choices ultimately determine a distribution: the ideal free distribution. The ideal free distribution is an assumption of the habitat suitability analysis, using *Biomapper* (see Chapter 5).

Habitat selection among African herbivores: habitat selection is primarily hierarchical in approach (Eltringham 1979; Rushworth 1992; Smith 1996). Hutto (1985) notes that birds appear to initially assess the general features of the landscape *viz.* the type of terrain, gross vegetational features such as open grassland, shrubby areas, types and extent of forest and homogenous or patchy vegetational distribution. Once within a broad general area, the birds respond to more specific features of habitats, such as the structural configuration of vegetation.

Habitat selection among herbivores, similarly, occurs at four hierarchical orders (Rushworth 1992), these being:

1. The geographical range,
2. home range within the geographical range,
3. utilization or avoidance of different habitat components,
4. Actual food preference within the home range.

This hierarchy is approximate to the regional systems, landscapes, plant communities and micro patches of Senft, Coughenour, Baily, Rittenhouse, Sala & Swift (1981) in relation to large herbivore habitat selection.

The geographic range is the area within which a species or population occurs. It may be represented on a map and easily interpreted (Rushworth 1992).

Home range is the area within which an animal normally lives (Allaby 1998; Smith 1996). Animals generally confine their activities to one or several circumscribed areas in the course of a year and mostly, their entire lifetime (Leuthold 1977). Thus home range may be further defined as the area over which an animal normally travels in pursuit of its routine activities (Leuthold 1977). It may be defended in part or in whole and may overlap with home ranges of individuals of the same species.

Home ranges do not have fixed boundaries and are seldom rigid in use, size and establishment (Senft *et al.* 1981). Possession of a home range confers certain advantages; the animal becomes familiar with the local area, forage availability, shelter and cover (Eltringham 1979).

Utilization by herbivores of some habitats and avoidance of others follows the above-mentioned theory of habitat selection, *viz.* that animals will seek out their preferred habitat type. To herbivores, a suitable habitat must provide water, minerals, shelter from climatic extremes, cover from predators and food (Melton 1987). Different species rate these factors according to their own needs (Jarman & Sinclair 1979) although, according to Pienaar (1974), vegetation structure and composition is the all-important factor in herbivore biology and habitat preference.

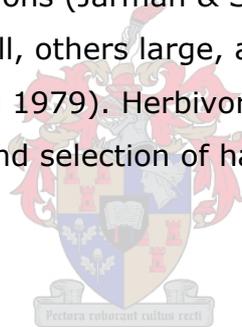
Many studies have been done recently on the habitat preferences of African herbivores, including Ben-Shahar (1995), Dekker, Van Rooyen & Bothma (1996), Evans (1979), Ferrar & Walker (1974), Melton (1978), and Mwangi & Western (1998). These have shown that vegetation structure/composition, and topography are the main determinants of habitat utilization among African herbivores, along with competitive interactions (Melton 1987).

Since different species assess the environment according to their own scale of importance (Jarman & Sinclair 1979), partitioning of resources occurs, known as *habitat partitioning* (Dekker *et al.* 1996) or *ecological separation* (Jarman & Sinclair 1979; Leuthold 1977). Lamprey (1963) demonstrated ecological separation by observing that: "*each species of large herbivore in a community depends upon separate resources because of different spatial and temporal distribution, plant species choice and forage height.*"

Food preference is the most refined level of selection among (grazing) herbivores. It is at this level that grazing animals select different plant species, plant parts and at different heights, thereby reducing competition (Jarman & Sinclair 1979). The works of Gwynne (Gwynne & Bell 1968; Sinclair & Gwynne 1972) in East Africa showed that, to a grazing herbivore: *“grass is a heterogeneous collection of parts as distinct and distinguishable in value as those of a shrub or tree. At any one time, the parts of one grass plant differ more than the average quality of whole plants of different species.”* Thus, differential selection arises.

In reality, there may often be competitive overlap for plant species choice among herbivores, usually to the advantage of bulk grazing species (Collinson & Goodman 1982). Ultimately however, and in response to the seasonal and spatial differences between plant communities in species composition, production, and food quality, evolution has produced an ungulate community that differs in size and adaptations (Jarman & Sinclair 1979; Putman 1996). Some grazing animals are small, others large, and many differ in adaptations of the mouth and gut (Eltringham 1979). Herbivore physiology thus also plays a large part in food preference and selection of habitat (Owen-Smith 1985).

2.3 Competition



Individuals within a species population interact with individuals of their own species and those of other species. If the effects of this interaction are mutually negative, the relationship is termed *competition* (Begon, Mortimer & Thompson 1996; Smith 1996). Competition is further defined as: *“an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of the competing individuals concerned”* (Begon, Harper & Townsend 1990). If this competition takes place among individuals of different species it is termed *interspecific competition*. If among individuals of the same species, then: *intraspecific competition*. These concepts are now discussed in greater detail.

2.3.1 Intraspecific competition

This supposes competition between individuals of the same species, almost always within a population. It is defined by the following characteristics (after Begon *et al.* 1990, Begon *et al.* 1996):

1. The ultimate effect of competition is a decreased contribution of individuals to the next generation. Intraspecific competition acts directly (more or less) on either survivorship or fecundity, or on both,
2. the resource for which the individuals are competing must be in limited supply,
3. the competing individuals are inherently equivalent,
4. The effect of competition on any individual is greater, the greater number of individuals there are, and therefore the effects are density-dependent.
All density-dependent effects do share a tendency to regulate population size.

Regulation here refers to the ability to decrease the size of populations above a certain level, but to allow an increase in the size of populations below that level. This equilibrium level is referred to as the *carrying capacity* (K) of the population. In reality, however, individuals of a population are affected by a wealth of factors, of which intraspecific competition is only one, and resources not only affect density, but respond to density as well. Intraspecific competition does not hold natural populations to a predictable and unchanging K but may act upon a wide range of starting densities and bring them to a narrower range of final densities (Smith 1996). Furthermore, the intensity of intraspecific competition experienced by an individual is not really determined by the density of the population as a whole. An individual is rather affected by the extent to which it is crowded and inhibited by its immediate neighbours (Begon *et al.* 1996; Sinclair 1985). Density-dependent *effects* are the result of a density-dependent factor, acting through a density-dependent process.

Territoriality is an important and widespread form of asymmetric intraspecific competition. The term is usually used for cases in which there is active interference, such that an exclusive area is defended against intruders by a recognizable pattern of interference (Begon *et al.* 1990; Smith 1996). The most important consequence of territoriality is population regulation, or more

particularly, the regulation of the number of territory holders. Among large mammals, territory size may differ from year to year, thus if resources are abundant, the territories are likely to be small, and if resources are less abundant, so territories are likely to be large (Smith 1996). Probably the most important benefit an individual of a species gains from holding territory is an increased food intake (Begon *et al.* 1990).

As a result of contest competition among males of a species for space, some individuals secure optimal territories, while others are denied territory (Smith 1996; Walker & Goodman 1983). Thus a portion of the population does not reproduce as they are excluded from suitable breeding sites. They make up a surplus breeding population, or a floating reserve, that would reproduce should a territory become available to them (Smith 1996).

Home range is a term not to be confused with territory. As mentioned above, home ranges do not have fixed boundaries and are seldom rigid in use, size and establishment (Smith 1996).

Note: an important assumption of this study is that intraspecific competition forces some individuals to seek food at the extremes of that particular species niche (Begon *et al.* 1996; Smith 1996). Therefore a partial niche expansion will possibly occur with an increase in intraspecific competition. Intraspecific competition encourages expansion of the resource base, while interspecific competition narrows the range (Putman 1996).

2.3.2 Interspecific competition

Interspecific competition involves the seeking of a resource in short supply by individuals of two or more species, and that results in reductions of each other's survival, growth or fecundity (Begon *et al.* 1996; Pimm & Rosenzweig 1981). The effects of interspecific competition are usually density dependent.

Interspecific competition may be one of two kinds, *interference* and *exploitative* (Begon *et al.* 1996, Smith 1996). Individuals of different species that utilize the same resource experience exploitative competition. Prior utilization by one species reduces the availability for another, the outcome being determined by how effectively each of the competitors utilizes the resources. Interference competition involves a direct interaction between the

competitors in which one interferes with access to a resource by another, usually in some form of aggressive behaviour.

Competitive exclusion is based on the theoretical assumption that if one species in a competitive situation grows rapidly enough to prevent the population increase of another, it can reduce that population to extinction or exclude it from the area (Smith 1996). Hardin (1960) wrote that "*complete competitors cannot co-exist. Two competing species with identical ecological requirements cannot occupy the same area.*" However, two different species cannot have identical requirements, and in reality, two or more species can compete for an essential resource without being complete competitors (Smith 1996). In natural situations, competition is spread over a number of resources. A high competitive interaction for one resource may be counterbalanced by low competitive interactions for other resources. This gives rise to *diffuse competition* as proposed by MacArthur (1972) i.e. minimal competitive inhibitions on several gradients among several species, can for some individual species be equivalent to strong competitive interaction for one resource from a single competing species. Thus, diffuse competition may in theory exclude a species or greatly reduce its numbers through competitive interactions with a specific combination of other species.

In addition to the utilization of scarce resources, Pielou (1974) lists the following set of conditions necessary for competitive exclusion to take place:

1. competitors must remain genetically unchanged,
2. immigrants from areas with different conditions cannot move into the population of losing species,
3. environmental conditions must remain constant, and
4. Competition must continue for a long enough period for equilibrium to be reached.

In the absence of any of these requirements, species usually co-exist (Smith 1996).

Coexistence: classic competition theory (see the Lotka-Volterra model, as cited in Schoener 1982) assumes a stable environment and continuous competition. In reality, however, interspecific competition is most probably discontinuous

because of variable environments, and coexistence of different species is allowed. In variable environments, resource levels vary between superabundance and scarcity. Periods of resource scarcity create ecological crises that can result in intense interspecific competition and act as a major selective force on competing species (Smith 1996).

Resource partitioning suggests that species sharing the same habitat co-exist by utilizing different resources (Dekker *et al.* 1996; Dunbar 1978; Ferrar & Walker 1974; Melton 1978; Melton 1987; Rushworth 1992). Animals consume different sizes and types of food, or feed at different times or in different areas. This partitioning of resources, also known as differential resource utilization is often regarded as an outcome of interspecific competition, Leuthold (1977) defining separation as the mechanisms that reduce interspecific competition and thus prevent possible competitive exclusion.

The theoretical basis of resource partitioning is largely based on work done by MacArthur & Levins (1967). If a theoretical species A utilizes a range of different sized food items, the utilization is likely to be in the shape of a bell-shaped curve on a graph, with food as the ordinate and fitness as the abscissa. Most individuals feed about the optimum. As population size increases, so the range of food taken may increase assuming that intraspecific competition forces some individuals to select food at two extremes. If a second species B is now allowed to enter the area, its resource use curve will show considerable overlap. Selective pressure from interspecific competition forces both species A and B to narrow their range of resource use. Thus they will diverge, reducing direct interspecific competition and allowing coexistence. A third species C is now allowed to invade this resource gradient, between the curves of A and B. This is assuming that A and B are relatively rare and below carrying capacity, and that resources are abundant. Competition will then force these species to become more specialized in their resource utilization and thus space themselves more narrowly on the resource gradient.

To summarise, Begon *et al.* (1996, after research by Davidson 1978) list four important points characterizing interspecific competition:

1. Species from distantly related taxa can compete with one another for a limited resource.

2. Competition need not lead to exclusion: species can co-exist.
3. Coexisting species tend to differ in at least one respect in the way they utilize the limited resource, and species that utilize the resource identically, tend to exclude one another from a site.
4. The nature of a species, and the manner in which it utilizes the resource, can itself respond to the species' competitive milieu.

It is necessary here to discuss a closely associated concept, that of the niche:

2.3.2.1 Niche

Smith (1996) categorizes the concept of niche under competition, and thus follows here. The concept of niche was apparently first proposed by Grinnell (1928, unseen, as cited in Smith 1996), who suggested that the niche be regarded as a subdivision of the environment occupied by a species. This is really the habitat of the species (De Santo 1978; Melton 1987).

Elton (1927, unseen, as cited in Smith 1996) considered the niche to be the fundamental role of the organism in the community i.e. what it does and its relation to its food and enemies. This theory actually implies the occupational status of the species in the community (Smith 1996).

The definition that links niche to competition was proposed by Hutchinson (1957). The *Hutchinsonian concept of niche* suggests that an organism's niche consists of many biotic and abiotic variables, each of which can be considered a point in a multidimensional space. This space is termed the *hyper-volume*. A large number of environmental variables comprise the dimensions (n -difficult to visualize and impossible to graph (Smith 1996)), of the hyper-volume that would be the species niche, thus n -dimensional hyper-volume.

Whittaker and Levin (1975) defined niche as the way a species population fits into a given community. Therefore a niche is part of the whole set of relationships of the species to the environment (Whittaker & Levin 1975).

The *niche* concept focuses on ways the species relates to other species within the same community. For example, a hawk and an owl that feed on the same prey differ in niche along a time axis *viz.* the hawk feeds diurnally, the owl; nocturnally.

The environmental relationships of a species form a complex whole, usually with no sharp distinction between niche and habitat, or between habitat and

area. An environmental variable may be involved at all three levels (Whittaker & Levin 1975). The fact that niche, habitat and area are usually continuous does not reduce the importance of these concepts.

Fundamental niche: of a species assumes the absence of competition (Begon *et al.* 1996; Putman 1996). A species free from the interference of another could occupy the full hyper-volume or range of variables to which it is adapted. Thus, competitive relationships usually force the species to constrict a portion of the fundamental niche it could potentially occupy. The conditions under which organisms usually exist pertain to realized niche.

Realized niche: under superior competitive pressure a species may be forced to retreat to that portion of the fundamental niche hyper-volume to which it is most highly adapted. This is the realized niche (Begon *et al.* 1996; Putman 1996; Rushworth 1992). Competitors are nearly always part of the species environment (Schoener 1982) and so most research conducted in community ecology pertains to the realized niche.

Competition is assumed to occur when a resource is in short supply (Melton 1987; Sinclair 1975), and is mostly perceived through an overlap of niches between species (Ferrar & Walker 1974). Smith (1996), however, adds that considerable niche overlap between species does not necessarily imply high competitive interaction, the reverse possibly being true. Extensive niche overlap may indicate that little competition exists and that resources are abundant. High niche overlap or an absence of overlap may also reflect other environmental and behavioural influences and not interspecific competition at all (Putman 1996; Smith 1996).

Niche overlap is usually considered within one or two dimensions. In reality, a niche involves many different resources: food, shelter, water availability etc (Smith 1996; Whittaker & Levin 1975). Species may overlap on one gradient but not on another (Smith 1996).

Niche change: If, hypothetically, a community comprising species with broad niches is invaded by competitors, intense competition may force the original occupants to compress their utilization of space and confine their foraging and other activities to those patches of habitat providing optimal resources (Smith

1996). Competition that results in the contraction of habitat is termed *niche compression*. If the experienced interspecific competition is reduced, a species may expand its niche by utilizing habitat previously unavailable, a process known as *ecological release* (Begon *et al.* 1990; Smith 1996).

Niche shift is the process whereby two competing populations reduce interspecific competition by the adoption of changed behavioural and feeding patterns (Putman 1996).

2.3.3 Facilitation.

Gwynne & Bell (1968) and Bell (1970) noted a process of facilitation at work among grazers in the Serengeti. Essentially this is a process whereby a species modifies a habitat to the extent that another species is then able to 'invade' and benefit (Allaby 1998; Begon *et al.* 1996). Gwynne and Bell (1968) in a study done on herbivores in east Africa showed that zebra (*Equus burchelli*) initiated the process through trampling and feeding selection of grass stems. This opened up the herb layer, stimulated grass growth and increased the proportion of leaf availability. Topi's (*Damaliscalus korrigum*) and wildebeest followed as the height of the grass sward is now more to their liking, and grazed the grass to such an extent that the proportion of dicotyledonous vegetation increased. This was then advantageous to Thomson's gazelle (*Gazella thomsonii*), which followed.

Facilitation may possibly occur at an environment like ME when bulk grazing species such as zebra and buffalo open up the sward (and shorten it) to the advantage of species such as wildebeest and warthog (pers. obs.).

2.4 Adaptive management

Adaptive management implies the application of wildlife management tools to achieve goal-oriented objectives (Trollope 1990). Management objectives are relevant to the wildlife area in question.

Management of enclosed wildlife areas is, in most cases, extremely complex (Trollope 1990). Because of this complexity, sound, ecologically-based objectives need to be set, implemented and monitored in order to obtain results (Tainton 1999). This is where the term *adaptive* is relevant, since long-term

monitoring may show that specific goals are not being met, or the tools of management are shown to be deleterious in certain aspects, and thus adaptation is required. Adaptive management is defined by Walker & Goodman (1983) as “*using information produced or developed as a result of management activities in the formulation of future management policy.*” If this is done as a simple feed-back, it is referred to as *passive adaptive management*. *Active adaptive management* involves the deliberate manipulation of the system to gain particular information. This is not usually practical within a wildlife reserve, particularly given financial constraints, and therefore passive management is usually practiced, this being so at Malilangwe Estate.

The main tools available to wildlife managers are fire, water provision and game cropping (Owen-Smith 1996; Tainton 1999; Trollope 1990). Rotational resting of veld and the control of bush encroachment are discussed within the context of the burning programme. The abovementioned tools are now elaborated on:

2.4.1 Water provision

Water provision is a powerful management tool, that may be effectively used to achieve objectives, but also can be detrimental when inappropriately used (Owen-Smith 1996). All ecosystem components are affected by the placement and supply of water within a wildlife area (Clegg, S. 1999). Soil, as well as botanical, structure and composition close to water is altered through an associated increase in animal trampling, utilisation and defecation. Changes in vegetation structure and composition then alter the quality and availability of forage and cover for animal species (Clegg, S. 1999). This may be advantageous to some animal populations, but detrimental to others (Goodman 1982), and thus depending on the objectives of the area in question, water placement needs to be carefully planned and implemented. This is particularly pertinent in areas such as Malilangwe, where wildlife use is non-consumptive, and thus sustainability of the supporting resources and habitat condition is crucial (Owen-Smith 1996). Fortunately, at Malilangwe Estate, M.Sc. level research has been done on the provision of perennial water (see Clegg, S. 1999), and the recommendations of her study are discussed later.

The purpose of this study is not to determine water placement or possible detrimental effects, but rather the effect that permanent water has on the

utilization of habitat by herbivores, and the possible ecological implications of this. Recommendations take the ecological implications of perennial water placement into account. The water requirements of the study species and the implications of water provision are elaborated on here.

Water requirements of study species: Water dependency is related to a species physiological and behavioural adaptation to coping without water, and the moisture content of an animal's forage (Taylor 1969; Western 1975). Goodman (1982) broadly classifies game as *water dependent* and *water independent*. Eland (scientific names and list of study species given on page 42) are classified as water independent, *viz.* can go without water for long periods of time (time period not specified in literature). Water dependent species, i.e. those species that require water regularly, can be further divided in to two groups according to the distances that these species are capable of ranging from permanent surface water (Tainton 1999). For *non-mobile water dependent* species, densities significantly decline beyond 5-6 km from water. These species include impala, nyala, waterbuck and warthog. *Mobile water dependent species* require regular drinking water but are able to range fairly far from water sources, i.e. distances up to 10 km. These are buffalo, elephant, sable antelope, wildebeest, white rhino and zebra.



Ecological implications of water provision: firstly, perennial water position affects herbivore distribution since most large herbivores are dependent on water (Owen-Smith 1996). Veld utilisation is in turn directly related to herbivore distribution. Thus, if water points are placed far apart and herbivore stocking rates are moderate; the intensity of vegetation utilisation declines as distance from water increases, resulting in a zone of attenuating impact (a *piosphere*) around water points (Lange 1969, unseen, as cited in Clegg, S. 1999).

Herbivore impact determines the characteristics of grass cover, fire intensity and the structure of woody plant communities, thus habitat diversity (Tainton 1999). Piosphere size and characteristics are determined by such variables as herbivore population density and community structure, distance between perennial water points, vegetation type and structure, soil type, age of water point and rainfall patterns etc (Clegg, S. 1999). Tainton (1999)

represented how distance to water determines habitat diversity diagrammatically and this is given below:

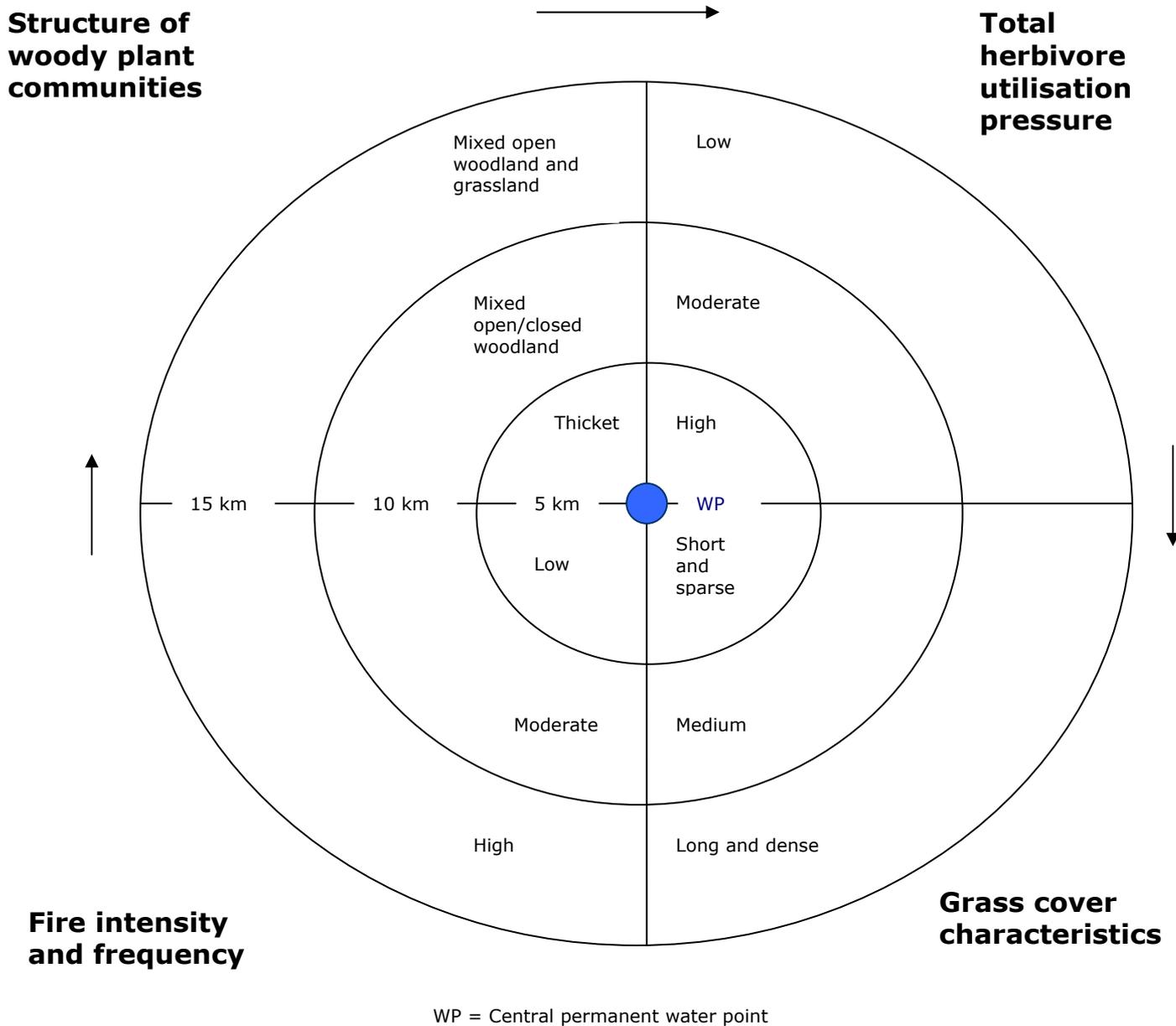


Figure 1: Diagrammatic illustration of how distance to water is an important determinant of habitat diversity within an area, after Tainton (1999).

Owen-Smith (1996) listed some critical ecological principles associated with water provision, following case studies on differently managed National Parks within southern Africa:

1. Surface water availability forms the primary limitation on the distribution of large herbivore populations in semi-arid environments.
2. Species that pre-dominate in biomass, notably elephant, buffalo, wildebeest and zebra, are most affected by water distribution.
3. Some ungulate species can survive for long periods without drinking water, except during severe droughts.
4. Abundant water points favour common ungulates at the expense of rarer species, through predator-mediated interactions and vegetation impacts.
5. Excessively close spacing between water points exacerbates starvation induced mortality during droughts.
6. Temporary water sources alleviate pressures on vegetation near permanent water by reducing periods of concentration in these regions.

Given the importance that permanent water placement has within an ecosystem, it is now apparent why this is such a vital management tool. Goodman (1982) states that the management strategy adopted for water provision will ultimately influence all other management strategies. Poor water placement may result in a decline in ecosystem stability, resilience and biodiversity (Owen-Smith 1996). In contrast, wise placement of water can control the number and distribution of animals, and switching off artificially provided water will encourage grazing rotation (Clegg, S. 1999).

2.4.2 Veld burning

From the outset, this study does not attempt to determine effects of fire on vegetation. It does attempt to determine the effect fire, or rather burned veld, has on the distribution and apparent habitat utilization of large grazing herbivores. Recommendations are based on species response to burns, and the ecologically sound use of this tool to prevent woody plant encroachment, influence herbaceous species composition and the maintenance of spatial heterogeneity.

Fire is considered to be a major ecological factor in the savanna type biome, with naturally caused fire (in Africa) occurring frequently in the past (Bothma 1989). Generally, fire is known to encourage a vigorous grass sward, where palatable perennials are abundant and woody encroachment halted (Bothma 1989; Tainton 1999).

Trollope (1990) states that the most important factors to consider when implementing a burning programme are: the reasons for burning and the appropriate regime to be applied. Trollope (1990) and Bothma (1989) list the justifiable reasons for using fire in bushveld management:

1. Removal of moribund, and/or unacceptable grass material.
2. Eradication and/or prevention of encroachment of undesirable (includes woody) plants.
3. Inducement of rotational grazing.

Bothma (1989) states that veld burning reduces the height of small trees and shrubs and tends to give the veld an open appearance as it burns away the lower branches and shrubs.

Fire regime refers to the *type* and *intensity* of fire, and the *season* and *frequency* of burn. Fire type refers to either head fires that burn with the wind or back fires that burn against. Head fires are recommended in bushveld as they cause least damage to the grass sward, but maximal damage to woody vegetation, if required (Trollope 1990).

Fire intensity refers to the rate at which heat energy is released per unit length of fire front and is expressed in kilojoules/per second/per metre. Burns that aim to remove moribund/unacceptable grass material should be cool or of low intensity, while burns that intend to control encroaching bush should be high intensity (Bothma 1989; Trollope 1990).

Season of burning, as the name implies, is a burn done during a particular period of the year. Trollope (1990) advises that if the management aim is to remove moribund/unacceptable material, the burn should be applied when the grass is dormant, i.e. after the first spring rains.

Fire frequency will be dictated by the rate of accumulation of moribund/unacceptable material, the rate at which encroachment occurs, and

the rate at which shrubs and trees grow beyond the reach of browsing animals (Bothma 1989).

A *mosaic* pattern of veld burning is usually used on game ranches, such as Malilangwe, to encourage rotational grazing. This is primarily done with the intention of maintaining the species diversity of the vegetation, and also to keep grazing short for grazers (Bothma 1989). Burnt areas need to be large enough to support the grazing pressure of animals that move on to these areas after the burn (Bothma 1989).

2.4.3 Harvesting

Harvesting here refers to control or culling of individuals of a population that has grown to numerous, or which has an unacceptably high growth rate, or simply requires stabilising (Bothma 1989). Harvesting rates are based on estimations of species carrying capacities and appropriate stocking rates.

The relevance of this tool to this study is that some species that apparently compete for habitat with rare or declining populations may require control of some form, whether it be culling, trophy hunting or removal for game auctions (methods not elaborated on here). In fact, starting 2003, and as a result of some herbivore species nearing or exceeding carrying capacity, Malilangwe does intend to implement a species removal programme (Goodman 2002).

Game populations in pre-colonial times were controlled by a combination of factors such as predation, disease, drought, migration and other natural causes (Bothma 1989). These factors are mostly negligible in present enclosed game populations (such as ME) and thus sound management intervention is required in many instances. The important questions relevant to a cropping programme are (after Bothma 1989): Which species? How many individuals of a population? How and when?

An *ideal* cropping system, as suggested by Bothma (1989) should basically satisfy a combination of all practical, economical and scientific conditions. He suggests that such a programme should cause minimal ecological and physiological disruption to the behaviour and reproductive capacity of the animals, must be monitored, and should finally be economically feasible.

Characteristics of harvested populations: the immediate (and desired when used as a tool) consequence of harvesting is to reduce the size of the population, which in turn affects the life expectancy and fecundity of the survivors in a harvested population (Begon *et al.* 1990). Thus, reduction in population density in a resource limited environment tends to increase the fitness of individual survivors.

Harvesting also has an important effect on the rate of regrowth of a population. This is shown by considering a population undergoing density dependent regulation and following a logistic growth curve (Figure 2). If a population is harvested when the growth is most rapid, i.e. mid the growth, then the rate of regrowth will be high.

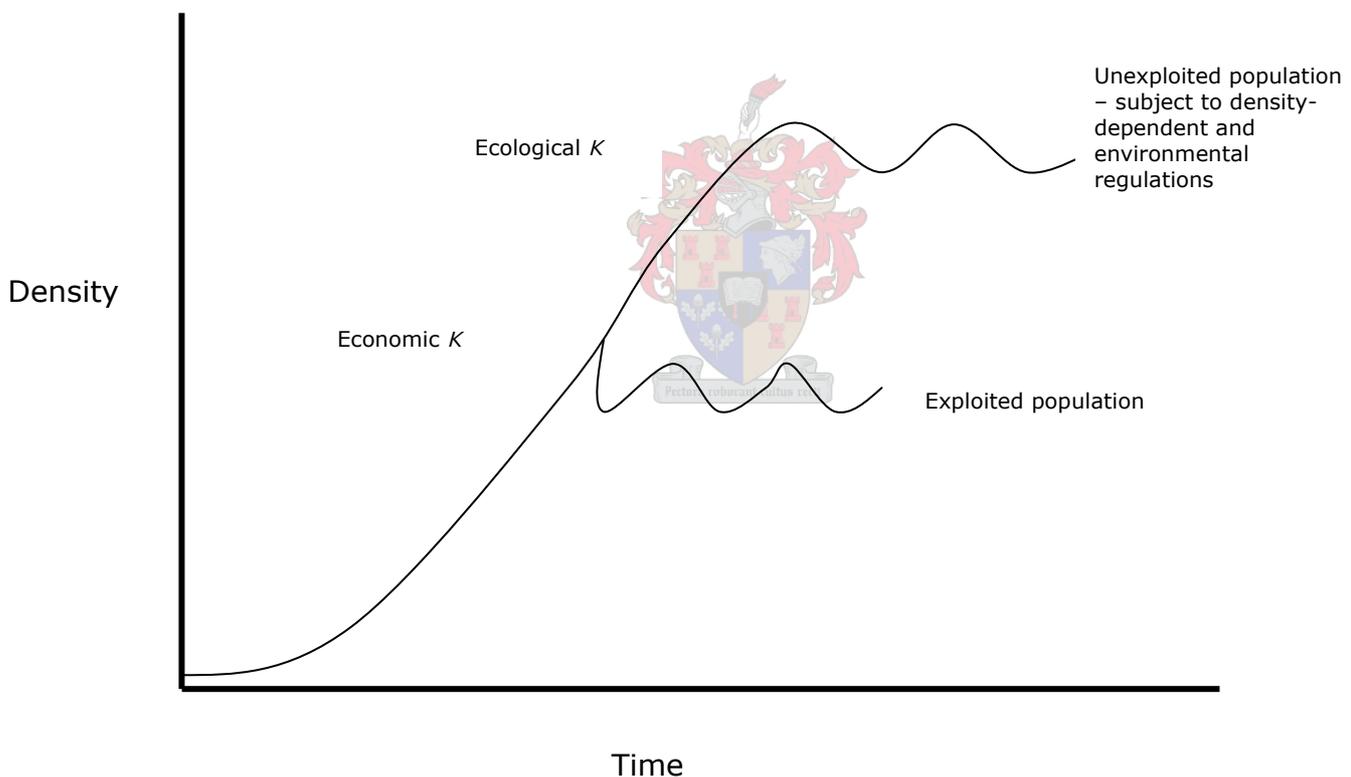


Figure 2: The effects of harvesting at different stages of population growth, with the population growing logistically, after Begon *et al.* (1990) and Bothma (1989).

It is here that an optimal size of the population may be maintained, and which, when subjected to repeated harvesting ensures a *maximum sustainable yield* (Begon *et al.* 1990). This is generally applicable to game populations in wildlife

areas that manage for meat production, and is known as *economic carrying capacity* (Bothma 1989).

However, at Malilangwe, management are more concerned about photographic tourism, and thus require a population at or near carrying capacity, where population numbers are high, but not so high as to be detrimental to the habitat, thus: *ecological carrying capacity*. Management would therefore want to maintain the population at a level just below ecological carrying capacity, assuming predatory off-takes are negligible (Figure 2).

This then begs the question which species, and how many individuals? This is primarily done through the estimation of stocking rates using species carrying capacities.

Carrying capacity and stocking rates: The use of standing crop biomass of animals as an index of carrying capacity has proved useful for natural and managed ecosystems (Tainton 1999). Primary plant production and subsequent animal density are generally positively correlated with mean annual rainfall in savannas (Coe, Cumming & Phillipson 1976). Soil nutrient availability further complicates this relation. Nutrient rich soils within savannas support different types of vegetation and animal types/densities to nutrient poor soils. Herbivore biomass on rich soils can be 20 times as great as herbivore density on nutrient poor soils (Tainton 1999).

A third factor needing to be taken into account is herbivore species richness. Fritz & Duncan (1994, unseen, as quoted in Tainton 1999) suggest that species richness of large ungulates may have a slight effect on the carrying capacity of natural savanna ecosystems. In less productive ecosystems, high species richness may increase carrying capacity by enabling complementary use of various vegetation components (Tainton 1999).

When choosing an appropriate stocking rate managers need to consider a number of points: Carrying capacity is primarily related to land use objectives, as well as the feeding ecology, habitat requirements, competitive interactions and socio-spatial structure of wild herbivore species (Tainton 1999). Habitat suitability for each species is assessed through consideration of food availability (browse and/or grass), soil fertility, aspect, water placement, veld burning programme etc. (Tainton 1999).

At Malilangwe Estate, stocking rate or carrying capacities are based on biomass estimates for each species after Coe *et al.* (1979) and Fritz & Duncan (1994, unseen, as quoted in Tainton 1999). Stocking rates are estimated each year at the end of the hot-dry season. Rates take rainfall and accumulated biomass (herbaceous) into consideration, as well as management objectives. Stocking rates are also re-assessed each year following an aerial survey of the entire reserve (see page 44)

It is not necessary here to elaborate extensively on carrying capacity estimates, as this study does not attempt to calculate stocking rates. What this study does, importantly, attempt is an analysis of habitat suitability for each species at Malilangwe Estate, coupled with an analysis of habitat utilization and potential competitive interactions among species.

2.5 Summary of review

This review of current theory serves as an ecological background to the study. Relevant theories pertaining to habitat selection, ecological separation, competition and facilitation were given mention. The approach was one of succinctness, as nowhere in this study is there an attempt to test any of these theories; rather the research assumptions were based on current paradigms.

Adaptive management and the tools available to wildlife practitioners were also discussed. Again, the intention here was to give a background to the tools available to managers. These tools serve as the basis of the recommendations (Chapter 6).

Efforts are taken (except where necessary) throughout the remaining text to avoid duplication of the abovementioned theories.

Chapter 3: Study Area

3.1 Location

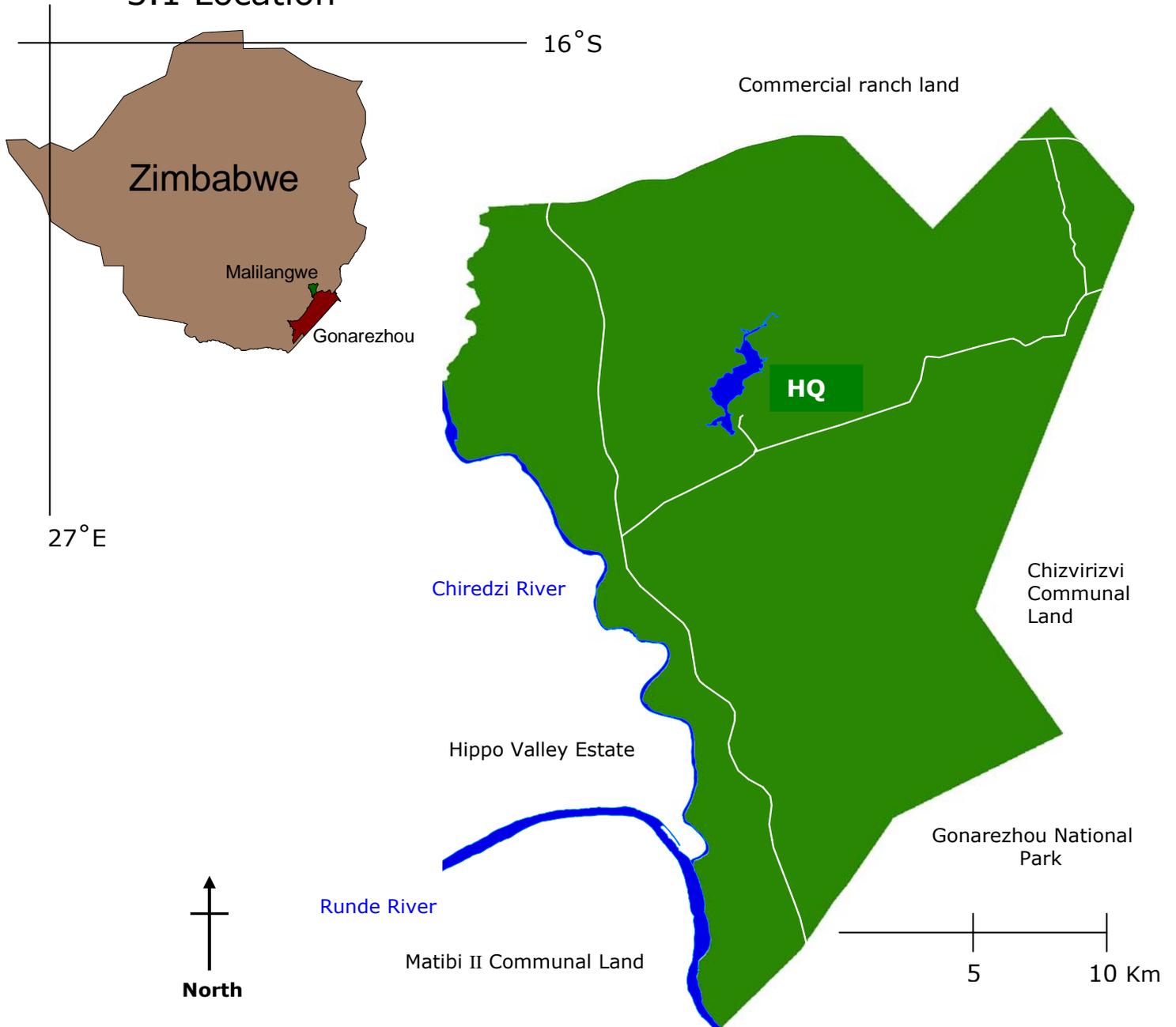


Figure 3: Location of Malilangwe Estate, southeast Zimbabwe.

Malilangwe Estate (ME) lies in the southeast lowveld of Zimbabwe (Figure 3), between the latitudes 20° 58' and 21° 15' S, and longitudes 31° 47' and 32° 01' E (Clegg, S. 1999). The total area of the ranch is approximately 40 000 ha (Clegg, S. 1999).

At the southern boundary of ME is Gonarezhou National Park. The western boundary borders Hippo Valley Estate game section, and is separated by the Chiredzi River. The lower section of the western boundary meets the Runde River with Matibi II Communal Land on the opposite bank. This section is fenced. Along the eastern boundary is Chizvirizvi Communal Land. The entire length of this border is fenced. The northern boundary is marked by the Triangle-Tanganda tar road, and is entirely fenced (Walters 2000).

3.2 History

Prior to the arrival of the British in 1890, the area was partially settled by people of the Changana tribe i.e., the Hlengwe people (Sparrow R.L. pers. comm.). These people were principally settled along the Chiredzi and Runde Rivers. It must also be mentioned that prior to the great Bantu migrations southward *circa*. 2000 BP, the area was inhabited by the San people. They were hunter-gatherers and left a legacy of rock art, many of which remain today.

In 1949, present day ME was allocated to Mr. Ray Sparrow and was named Lone Star Ranche (sic). From 1949 to 1967, cattle were the sole income for Lone Star Ranche. Apart from large predators, a good representation of wildlife was maintained (Sparrow pers. comm.). From 1967 onward, hunting safaris were commenced on the ranch. Mr. Sparrow was a pioneer in the wildlife industry and took serious steps to conserve and utilize wildlife species from the 1960's onwards. In fact in 1972, Mr. Sparrow had to defend in court his decision to keep buffalo, which at that time was against Veterinary Department regulation.

By 1985, the last remaining cattle were sold and trophy hunting and small-scale-agriculture became the main source of income at Lone Star. In 1987 photographic safaris commenced, and the income from this complemented that of trophy hunting (Sparrow pers. comm.).

In 1994, the ranch was sold to the Malilangwe Trust (MT); a Board of Trustees set up to manage external funding, and renamed Malilangwe Estate.

From the outset, the objectives of the Trust were the augmentation and conservation of wildlife resources, with benefits being extended to the local communities (Sparrow pers. comm.). The Trust continues with consumptive and non-consumptive wildlife utilization today, with additional programmes for the re-introduction of locally extinct species and research into the functioning and management of the various ecosystems in the area.

3.3 Climate

ME lies within a semi-arid ecological zone. Mean summer temperatures range from approximately 22 °C to 36 °C (Ferguson 1995). It is not unusual for temperatures to exceed 45 °C (Kelly & Walker 1976). Winters are generally cool, with temperatures ranging from 5 °C to 26 °C (Ferguson 1995).

Rainfall patterns are erratic (Figure 4) and the lowveld is prone to severe drought. Rainfall patterns in the Zimbabwean lowveld appear similar to those experienced in the summer rainfall regions of South Africa (Clegg, S. 1999). Tyson (1986) proposed that rainfall in these regions follows a cyclical pattern. At ME, rainfall cycles apparently follow a sequence of approximately nine years of below average rainfall followed by nine years of above average rainfall (Figure 5). A catastrophic drought occurred in 1991/1992 and management at that time had to take measures to feed wildlife. However, it is thought that the 1992 drought was exceptional (O'Connor 1997) as the amount of rain that fell during that period (72 mm) lies outside the 99 % confidence range as calculated by O'Connor (1997).

Monthly rainfall and temperature fluctuations for the data collection period are given in Appendix 1.

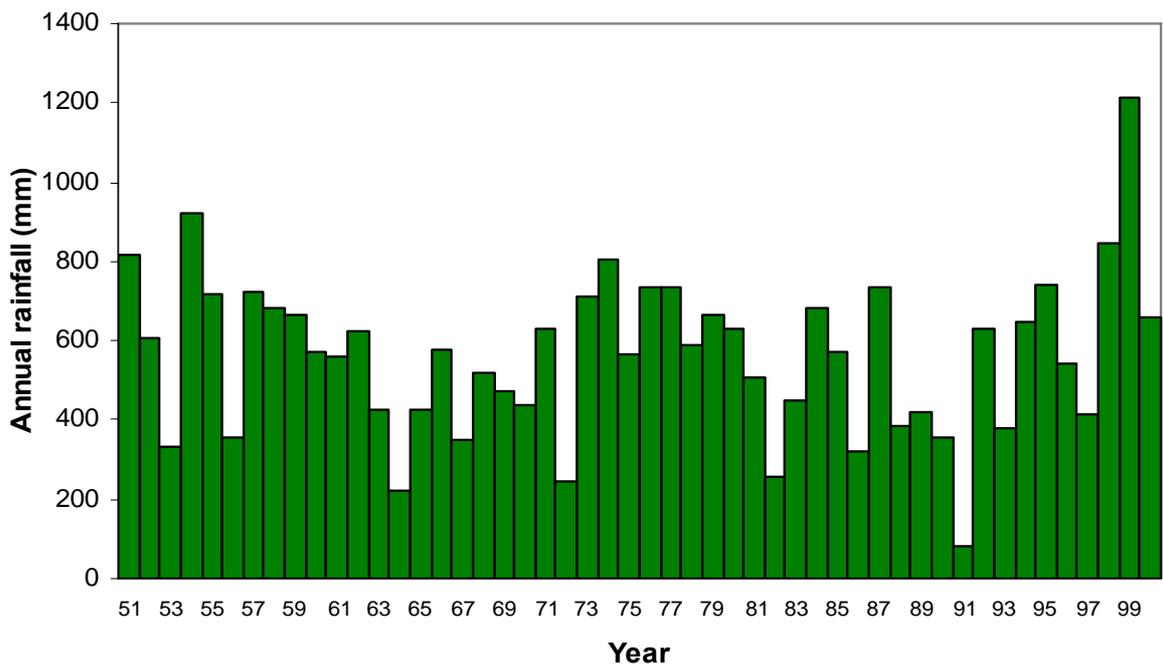


Figure 4: Annual rainfall at Malilangwe headquarters 1951-2000.

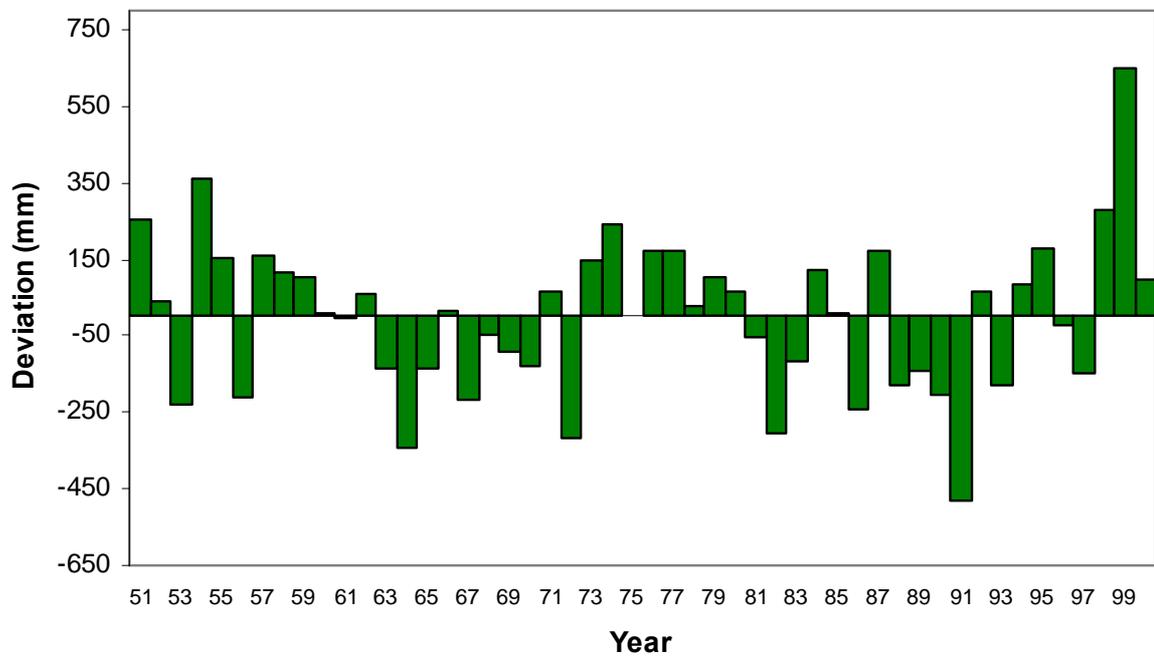


Figure 5: Deviation from the mean annual rainfall (550 mm) at Malilangwe Estate headquarters.

3.4 Geology and soils

The main geological feature of Malilangwe is the prominent sandstone ridge running in a northeast to southwest direction, known as the *hills* or Malilangwe range (Clegg, S. 1999). Topography gently declines in a south-westerly direction towards the two major rivers in the area, the Chiredzi and Runde. The area is described as one of low relief (Booth 1980; Ferguson 1995) with altitudes ranging from approximately 510 m at Hunyugwe hill to approximately 300 m above sea level in the southwest of the property (Figure 6).

There are a variety of soils at ME, derived from alluvium, sandstone, basalt and paragneiss (Chawanji 2000). Paragneiss and sandstone-derived soils dominate the northern part of the reserve, alluvial soils the main river systems and basalt-derived soils dominate the southern section of the reserve.

Paragneiss and sandstone-derived soils are characterized by low mineral and clay content and good drainage (Chawanji 2000).

To the south of the Malilangwe range lies a moderately flat plain underlain by Jurassic basalt of the Umkondo system (Clegg, S. 1999). Soils here are derived from the basalt parent rock and are mostly black, heavy clays (Walters 2000). Clay content is as high as 56 % (Clegg, S. 1999), and soils are prone to shrinking and swelling with changes in soil moisture content. When cracks seal, the soils may become waterlogged.

Basalt-derived soils are fertile but physiologically dry (Chawanji 2000). Water is held well, but is strongly retained against uptake by plant roots, resulting in stunted woody plant growth and a very high percentage of grass cover (Chawanji 2000). In contrast, low run off and good infiltration makes the moisture regime of sandy soils more favourable to woody plant growth (Stalmans 1994).

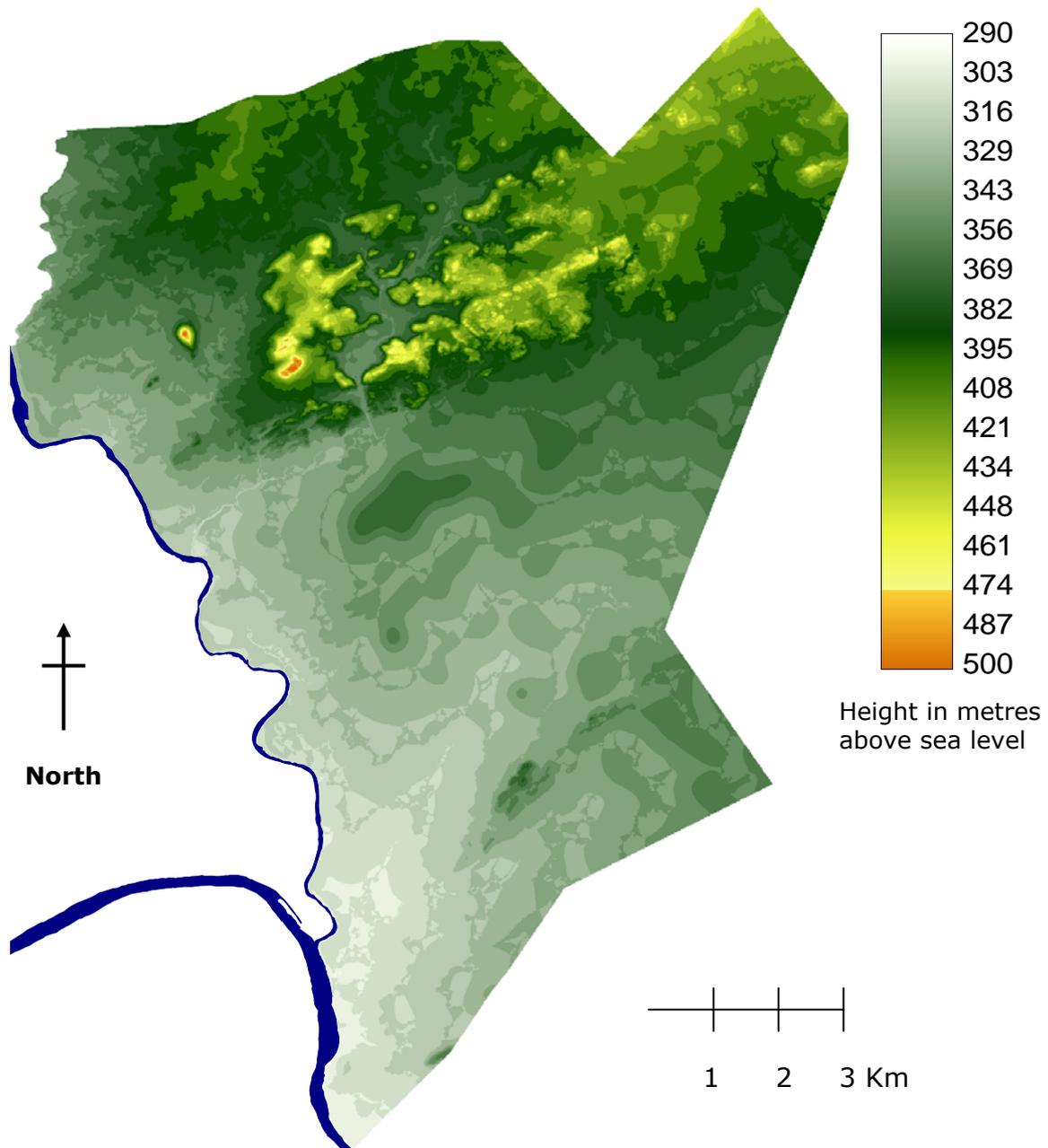


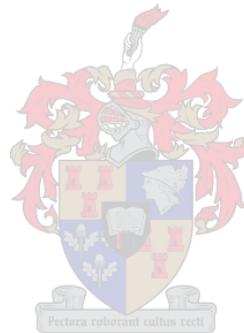
Figure 6: Topography of Malilangwe Estate, showing hills in the northern section and the downward slope of the land to the perennial river systems.

3.5 Vegetation communities

An initial vegetation community map of Malilangwe Estate was composed by Clegg, B. (1999) and is used here. The same author has since composed a more refined map which has been updated recently, and is still under composition. A broader classification of the vegetation communities is suitable here (Figure 7).

This map was developed using LANDSAT imagery and the supervised classification module of *Idrisi* (Clark labs, Clark University 1999). Field knowledge was required in the production of this map, since areas of known species composition were used as training sites to detect areas of similar reflectance.

The map is shown, along with a table of the full vegetation community names. A description of the communities then follows, after Clegg, S. (1999).



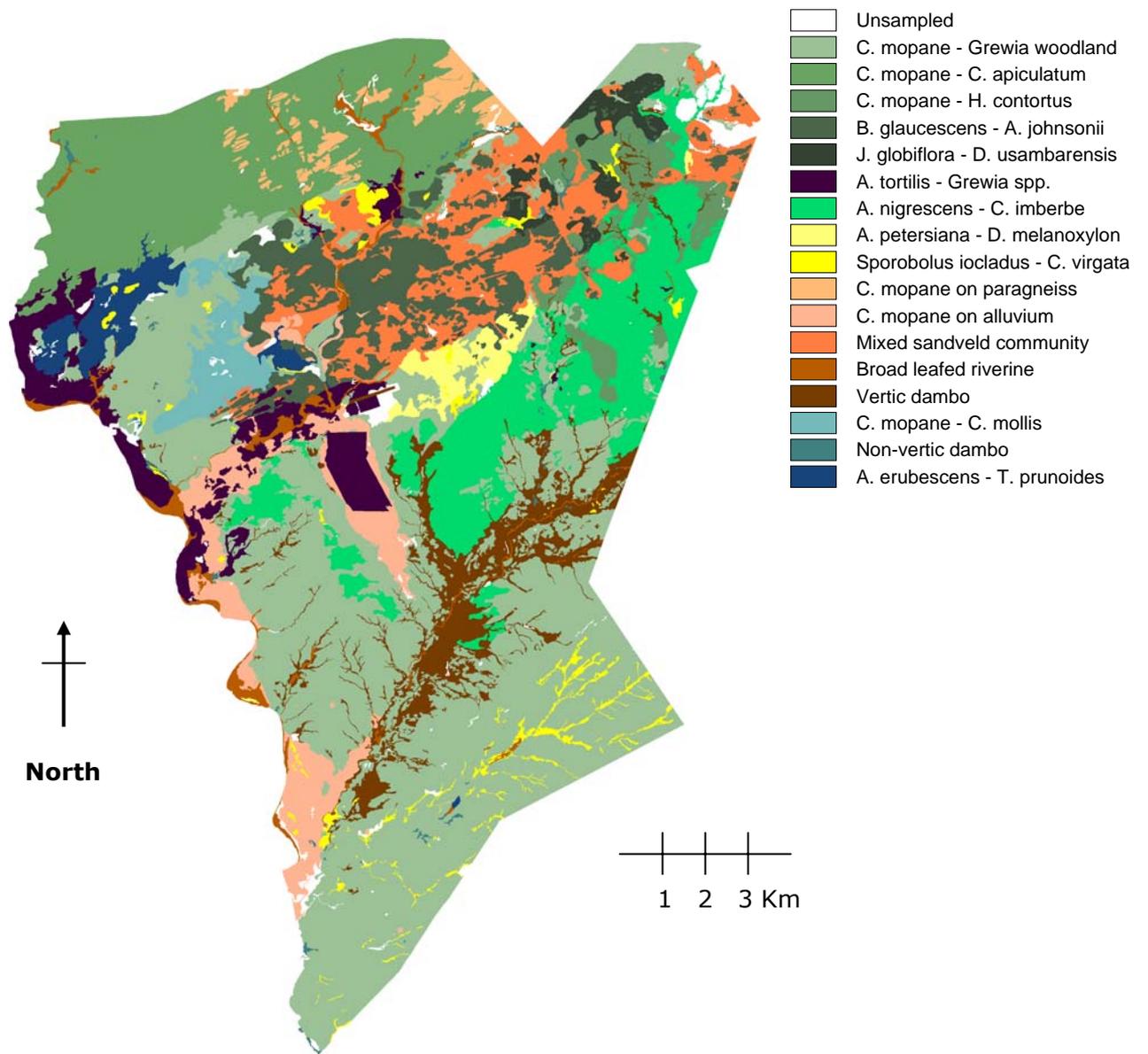


Figure 7: Broad vegetation communities of Malilangwe Estate, after Clegg, B. (1999).

Table 1: Vegetation community classification following Figure 7, also giving percent area coverage.

General communities	Community name	% coverage
<i>Colophospermum mopane</i> communities	<i>Colophospermum mopane</i> – <i>Grewia</i> woodland	36
	<i>C. mopane</i> – <i>Combretum apiculatum</i> woodland	13
	<i>C. mopane</i> – <i>Heteropogon contortus</i>	3
	<i>C. mopane</i> on paragneiss	2
	<i>C. mopane</i> on alluvium	4
	<i>C. mopane</i> – <i>Commiphora mollis</i>	2
<i>Acacia</i> communities	<i>Acacia tortilis</i> – <i>Grewia</i> spp.	4
	<i>Acacia nigrescens</i> – <i>Combretum imberbe</i>	10
	<i>Acacia erubescens</i> – <i>Terminalia prunioides</i>	2
Hill communities (miombo type)	<i>Brachystegia glaucescens</i> – <i>Androstachys johnsonii</i>	7
	<i>Julbernardia globiflora</i> – <i>Diospyros usambarensis</i>	1
	Mixed sandveld community	6
Albizia woodland	<i>Albizia petersiana</i> – <i>Dalbergia melanoxylon</i>	1
Riverine	Broad-leafed riverine	2
Dambo type	Vertic dambo	5
	Non-vertic dambo	1
Sodic patches	<i>Sporobolus iocladius</i> – <i>Chloris virgata</i>	1

Colophospermum mopane communities: Veld dominated by *C. mopane* constitutes the greatest part of ME.

In the southern and some western parts of the estate, short, dense stands of *C. mopane* woodland grow on shallow basalt-derived soils, usually in association with the shrubs *Grewia bicolor* and *Grewia flavescens*. Grasses in this community mostly include *Urochloa mossambicensis*, *Heteropogon contortus*, *Tricholaena monachne*, *Cenchrus ciliaris*, *Aristida adscensionis* and *Enneapogon cenchroides*.

In the northwest section of the estate, *C. mopane* and *Combretum apiculatum* dominate on paragneiss soils. Other woody plants found here are: *Grewia villosa*, *Terminalia prunioides* and *Pterocarpus brenanii*. This community

is mostly rocky and the herbaceous cover is generally poor and dominated by *U. mossambicensis*, *Aristida* spp., *Tricholaena monachne* and *Enneapogon* spp.

The *C. mopane* – *Commiphora mollis* community occurs on rocky slopes and is characterized by a generally dense shrub layer and sparse grass cover.

In the north eastern parts of the estate, slightly more open communities of *C. mopane* occur with *Acacia nigrescens*, *Combretum imberbe* and *Sclerocarya birrea*. The dominant grasses here are *H. contortus* and *Panicum maximum*.

Taller, more open stands of *C. mopane* are found on sandy alluvium along the southern reaches of the Chiredzi River, as well as on sandy soils on the transition of the sands and basalts, in the central part of the estate. *Grewia bicolor* and *Maerua parvifolia* are the dominant shrubs here, forming a sparse under-story. Grass cover, particularly along the sandy alluvium, is sparse.

Acacia communities: These communities also form a large component of the estate. *Acacia tortilis* dominates degraded lands, along with *Dichrostachys cinerea* and *Grewia* spp. In the central part of the estate, this community exclusively dominates old agricultural lands, and along the Chiredzi River *A. tortilis* thrives in lands once cleared in Tsetse operations. *U. mossambicensis* usually dominates the herbaceous layer in this community.

The *A. nigrescens* – *Combretum imberbe* community occurs along the eastern section of the estate, and stretches to the mid-western parts. *Combretum* spp. and *Kirkia acuminata* are also common in this community. Perennial grasses found here include *U. mossambicensis*, *Sorghum versicolor*, *P. maximum*, *Sehima galpinii* and *C. ciliaris*. Commonly found annual grass species include *Brachiaria eruciformis* and *E. cenchroides*.

The small *A. erubescens* – *T. prunoides* community occurs almost exclusively in the north eastern section of the estate. This vegetation is generally thick, with a sparse herbaceous layer. *Adansonia digitata* also occurs here.

Hill communities on sandstone outcrops: This vegetation type is one of the more scenic of the estate and resembles the miombo veld type of the central Mashonaland plateau. The three main communities occurring here are similar and occur in close proximity.

Mosaics of *Brachystegia glaucescens* and *Androstachys johnsonii* dominate where sandstone is exposed and, possibly, where soils are shallow. Among the sandstone outcrops, *Ficus abutilifolia* proliferates, while in the deeper sandy pockets between outcrops, woody species such as *Spirostachys africana*, *Xeroderris stuhlmannii*, *Julbernardia globiflora* and *Terminalia sericea* occur. *Coffea racemosa*, *Monodora junodii* and *Pteleopsis myrtifolia* often constitute a part of the shrub layer in this community. The *J. globiflora* – *D. usambarensis* community forms attractive open parklands between interspersed rocky outcrops. Dominant grasses include *P. maximum*, *D. eriantha*, *Pogonarthria squarrosa* and *Perotis patens*.

Albizia woodland: South of the hills and in flat sandy soils *Albizia petersiana* is dominant, occurring with *Commiphora pyracanthoides*, *Dichrostachys cinerea*, *G. bicolor*, *G. flavescens*, *Hippocratea indica* and *Hippocratea crenata*. Commonly occurring grasses include *U. mossambicensis*, *P. squarrosa*, *D. eriantha* and *P. patens*. *Waltheria indica*, *Hermannia borganiflora*, *Celosia trigyna* and *Pupalia lappacea* also constitute an important part of the herbaceous layer.

Riverine: Riverine vegetation is prevalent along the Chiredzi River, and has a patchy occurrence along the upper reaches of the Mahande and Benji systems. *Xanthocercis zambesiaca* and *Cordyla africana* trees remain as relics of the former forest along the Chiredzi, owing to the decimation that was part of the Tsetse control programme during the late 1950's. Alluvial deposits along the river systems support regenerating woodland, dominated by *A. tortilis*, *C. imberbe* and *L. capassa*.

Dambo: These low lying vleis support a mostly thick herbaceous layer, except where encroached by *C. mopane* due to a changing water regime. Usually interspersed among vertic dambos are sodic patches, supporting a sparse but utilised herbaceous layer.

3.6 Fire regime

A burning programme was only actively pursued at ME after the takeover by the Trust in 1994. The objectives of the burning programme at ME are (Goodman 1997):

1. To ensure an adequate fodder flow for the large mammal populations,
2. retard woody plant growth - where appropriate,
3. maintain or enhance spatial heterogeneity, and
4. Reduce the risk of accidental or arson fires that will threaten the survival of important plant species or destroy the structure/composition of an important vegetation community.

Burns at ME are done in management blocks immediately prior to the first spring rains i.e., mid September. These are predetermined every year, taking into consideration the time-since-last-burn, plant species composition and fuel load (Goodman 1999). Once burnt, blocks are fully mapped and stored in the Malilangwe Geographic Information Systems (GIS) database, the output of which is seen in Figure 8. The burn blocks at Malilangwe prior to the 2001 burn can be seen in Appendix 2.

The veld is monitored and the burning programme is reviewed every year by the Research Dept. and a consultant ecologist. Arson fire is prevented by the use of fire-breaks and an active scout force in constant radio contact with Head Quarters (HQ). Fire-fighting equipment, such as mobile water bowsers and hand-held beaters are on permanent standby at HQ.

Goodman (1997) observed that (since the initiation of the burning programme) there had been a widespread increase in the proportion of palatable perennial grasses in the herbaceous layer. From a production perspective alone, this is encouraging, as perennial grasses tend to even out fluctuations in herbaceous production brought about by rainfall variability (Goodman 1997).

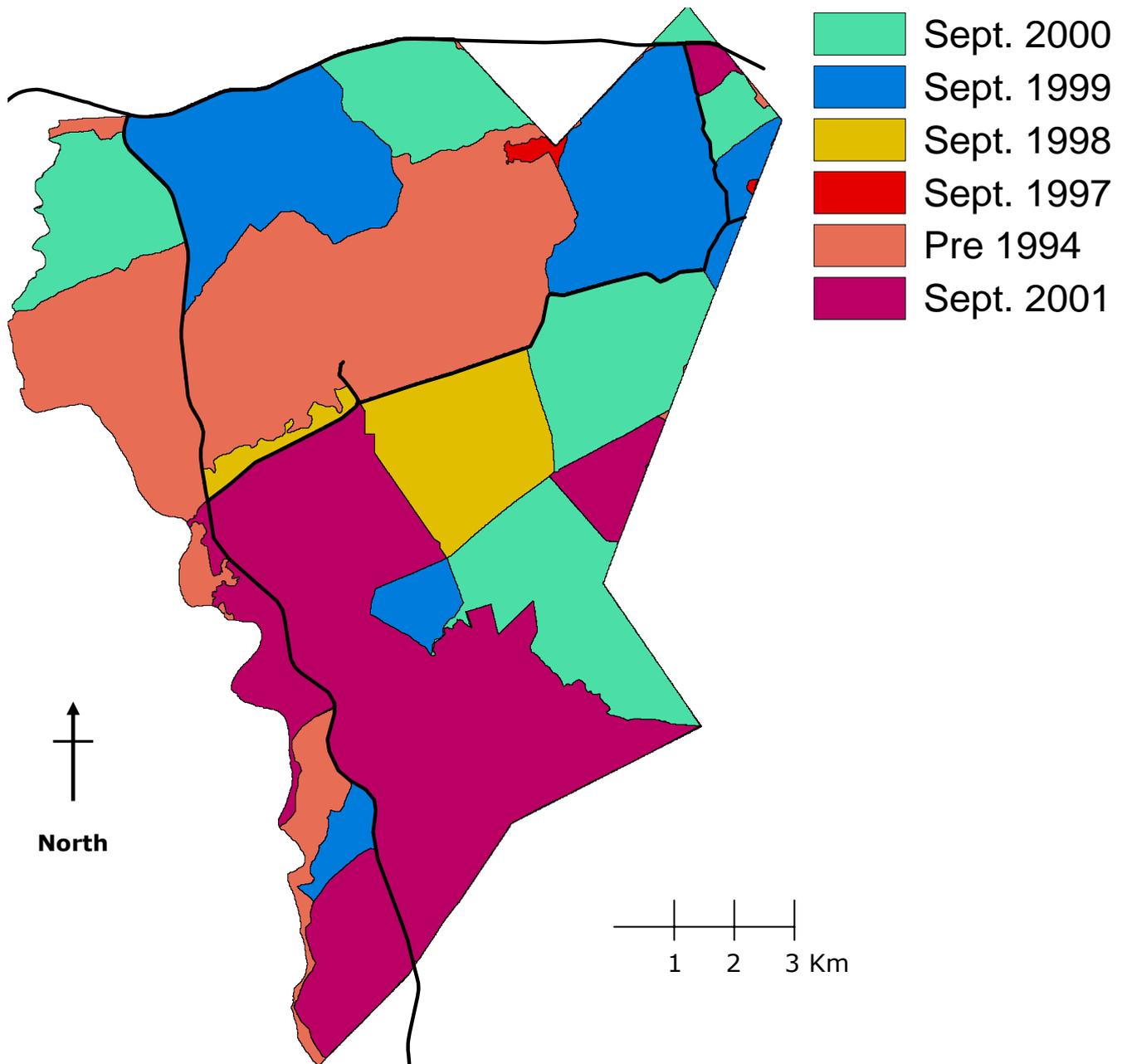


Figure 8: Burn blocks at ME as of October 2001, also showing main access roads.

3.7 Surface water provision

Surface water management is a controversial issue in the wildlife industry, and Malilangwe has been no exception (Goodman 1999). The use and location of artificial watering points has been hotly debated at Malilangwe, and culminated in M.Sc. level research. Clegg, S. (1999) studied the local impacts of water points on the vegetation and distribution of herbivores. She found that:

- Herbaceous and woody species composition changed in response to distance from water with changes best described by asymptotic equations.
- Perennial grass species declined close to water, but *Urochloa mossambicensis* increased close to water in areas outside of the Malilangwe hill range.
- Species diversity of the herbaceous layer declined near water on sandy soils, but was largely unaffected on clay-loam and sandy-clay-loam soils.
- Large herbivore biomass was greatest close to water (< 1 km) during the dry season but not during the wet season. Herbivore species distributions appeared to be influenced by the position of perennial water. However, all range was within easy access of water, and it therefore unlikely that animal distributions were constrained directly by the position of surface water. A more likely explanation is that herbivores were spatially separated on the basis of habitat type.

These findings helped management develop an overall vision for the use and manipulation of water at ME. Supplementary water had to be established in a way that minimized disruption of ecological processes/impact on the biota, minimized maintenance costs and maximized tourist and hunting opportunity.

Management then agreed to a set of objectives and criteria for the establishment and maintenance of surface water. Goodman (1999) lists them:

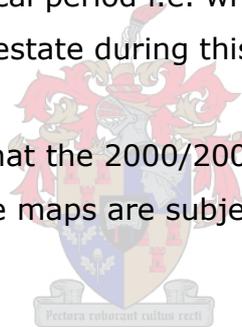
1. Surface water must restore and maintain the biodiversity of the estate's natural systems. Emphasis is on the enhancement and maintenance of species composition within vegetation and animal communities.
2. Surface water must enhance the aesthetic appeal of the estate.
3. The requirements of bow hunting must be met.

4. Water demands should not adversely affect the hydrological resources of the estate.

Surface water availability fluctuates between seasons and years at ME. During 2001, there were approximately 15 perennial water points at Malilangwe, including dams, but excluding rivers and springs. Ten water points were artificially supplied (pers. obs.). Generally, except during droughts, the Chiredzi River is perennial. The Runde River is also perennial, but animals at ME do not have access to this river since it is fenced off. Springs are also perennial, except during drought periods. Perennial water available during the 2001 season is mapped below (Figure 9). Perennial water here includes springs and rivers.

Seasonal water i.e. during the wet season is mapped in Appendix 3. Distance to water during the hot dry season (water plotted end of Sept. 2001) is mapped in Figure 10. This map shows the distance animals have to travel to nearest available water during the critical period i.e. when surface water is scarcest. Note here that no point in the estate during this period was further than 4658 metres from surface water.

It's also important to note that the 2000/2001 rain season recorded above average rainfall, and that these maps are subject to seasonal variability.



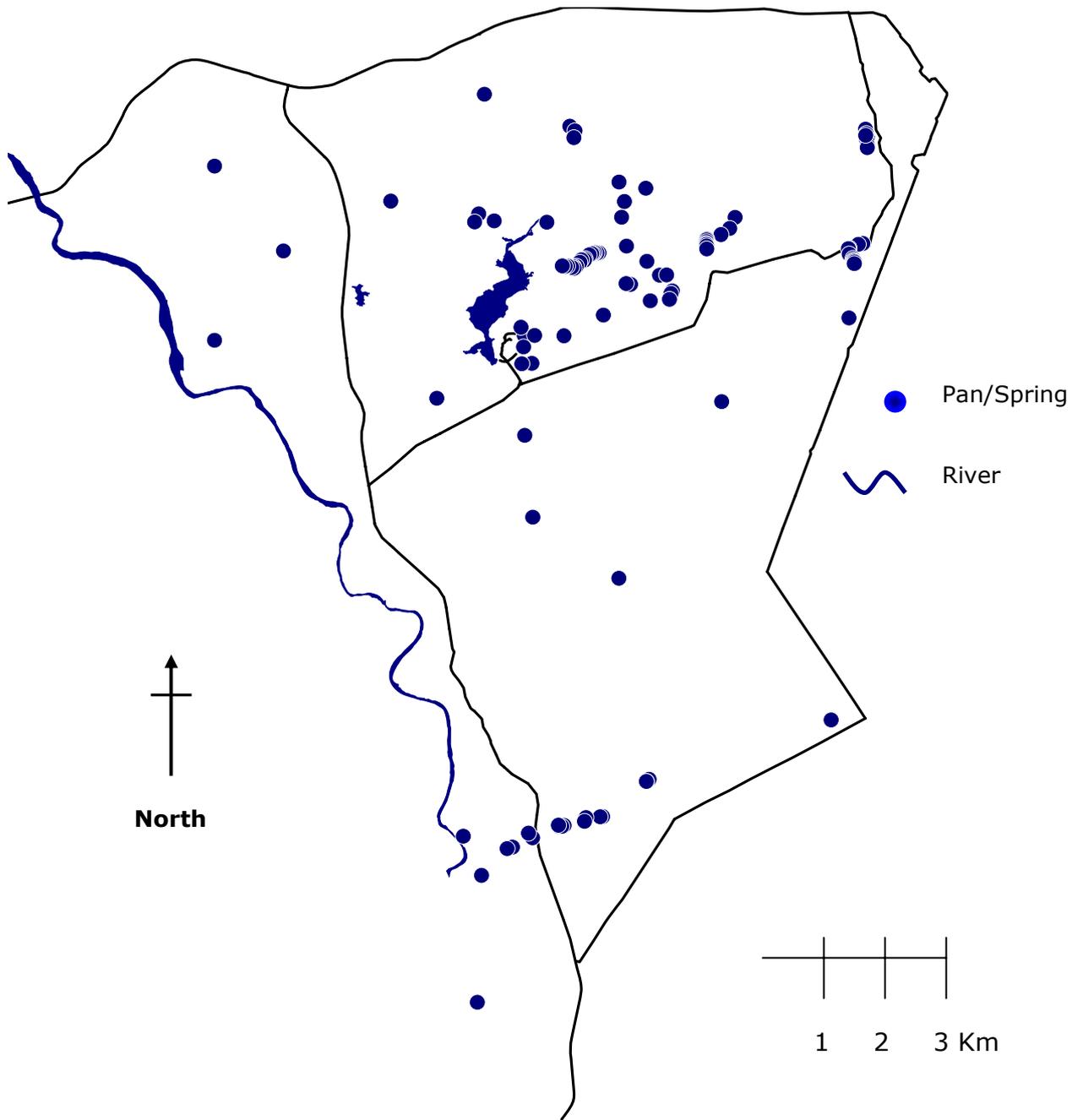


Figure 9: Perennial water at ME during 2001, including springs, pans, dams and rivers.

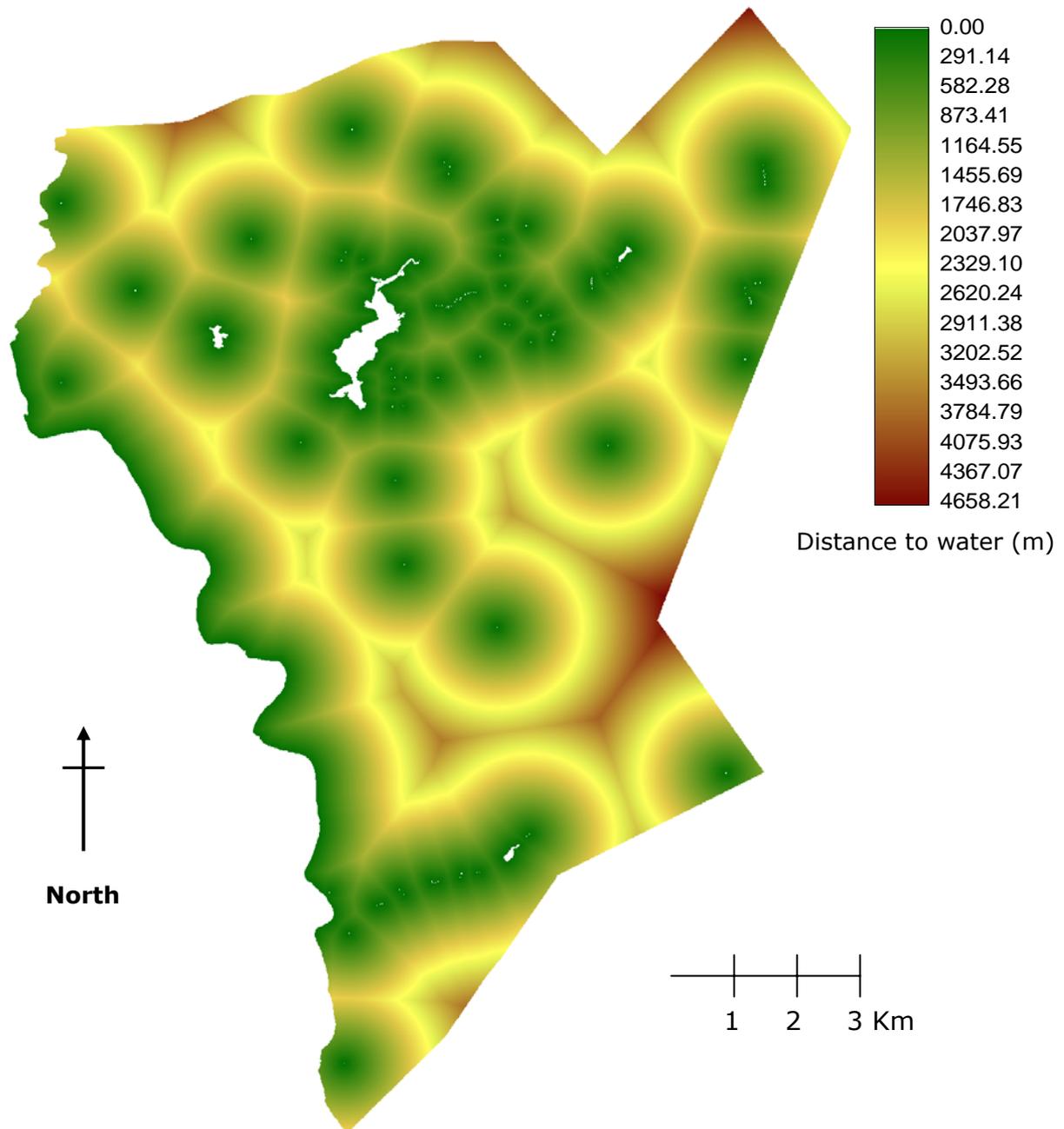


Figure 10: Distance to water in metres during the critical hot dry season (Sept. – Oct.) 2001. Vacant areas represent surface water, including the Malilangwe Dam.

3.8 Herbivore populations

The large herbivore community at ME can be divided into the following categories, after Goodman (2000):

- Grazers: buffalo (*Syncerus caffer*), hartebeest (*Alcelaphus lichtensteinii*), hippopotamus (*Hippopotamus amphibius*), roan antelope (*Hippotragus equinus*), sable antelope (*Hippotragus niger*), waterbuck (*Kobus ellipsiprymnus*), wildebeest (*Connochaetes taurinus*), white rhino (*Ceratotherium simum*) and zebra (*Equus burchelli*).
- Mixed feeders: common duiker (*Sylvicapra grimmia*), eland (*Taurotragus oryx*), elephant (*Loxodonta africana*), impala (*Aepyceros melampus*), klipspringer (*Oreotragus oreotragus*), nyala (*Tragelaphus angasii*) and warthog (*Phacochoerus aethiopicus*).
- Browsers: black rhino (*Diceros bicornis*), bushbuck (*Tragelaphus scriptus*), giraffe (*Giraffa camelopardalis*) and kudu (*Tragelaphus strepsiceros*).

Warthog are here classified as mixed feeders owing to their selection of plant roots and tubers during the dry season. All species are hereafter referred to by their common names, after Instructions to Authors for the *South African Journal of Wildlife Research*.

An annual aerial census is conducted at ME, immediately prior to the onset of the rains *viz.* October. The overall aim of the census is to derive estimates of the most important large herbivore populations on the estate that would be used for:

1. management decisions,
2. determination of spatial distributions of these species, and
3. Provide a record of abundance for future trend analyses (Goodman 2000).

Methods used for annual aerial counts are as follows, after Goodman (2001):

1. A helicopter with four people (pilot, recorder and two observers) was flown on pre-determined, parallel east west orientated transects situated 1 km apart and arranged systematically to cover the whole census area.
2. The helicopter was flown at 300 ft above ground level (90 m) and at an air speed of between 40 and 60 kts. Transects were flown early morning

and afternoon, for a maximum of 3 hrs. The hottest period of the day was avoided.

3. Devices were fitted on either side of the helicopter, which when flying at 90 m demarcated distance classes on each side of the transect line with the following limits: 0 - 30 m, 31 - 90 m, 91 - 200 m, 201 - 350 m and 351 - 500 m.
4. While flying a respective traverse line, observers called the species sighted the distance class that the group was situated in and group size. This was manually saved by the recorder on a notebook PC which was linked to an onboard GPS, allowing each observation to be automatically tagged with its location.
5. Where large groups of buffalo, elephant, hippo, rhino or sable antelope were spotted, the helicopter deviated from the traverse line, a total count of the group was undertaken, the locality captured and the count then re-continued.
6. All data were captured using *Cartalinx* v 1.2 (Clark labs, Clark University 1999), which when connected to the onboard GPS allowed the simultaneous collection of flight path information, animal observations (waypoints) and any set of attributable data desired. Additional information included the species code, distance class and number of animals in the group spotted.
7. Plotting of animal distributions by species was done directly from *Cartalinx* in cases where the number of sightings and their distribution allowed visualisation. Alternatively, where numerous observations were made, these data were exported to *Idrisi* 32 (Clark labs, Clark University 1999), rasterised and plotted as density maps.
8. Where the number of observations allowed, density, and from this population size was estimated using the statistical routines in *Distance* 3.5 release 5 (Thomas *et al.* 1998). Animal observations recorded during the aerial census were edited and exported directly to *Distance* 3.5 from the *Microsoft Access* database developed by *Cartalinx*. Two surveys were done.

Known group counts exist for black and white rhino, hartebeest and roan antelope. All individual rhinos are ear tagged and known to management, while hartebeest and roan antelope occupy separate enclosures on the reserve.

The population estimates of large herbivores at ME during 2001, based on the aerial census and management records, are presented in Table 2. The most recent estimates, i.e. those for 2002, are presented in Appendix 4.

Table 2: Summary of large herbivore population estimates for the study period (Goodman 2001)

Species	Best estimate	Species	Best estimate
Buffalo	453	Nyala	80
Bushbuck	170	Reedbuck	40
Bush pig	100	Rhino – black	36
Common duiker	200	Rhino – white	45
Eland	450	Roan	28
Elephant	111	Sable	108
Giraffe	195	Steenbok	50
Hartebeest	54	Warthog	183
Hippo	19	Waterbuck	91
Impala	4166	Wildebeest	222
Klipspringer	150	Zebra	993
Kudu	554		

Predatory off-take of large herbivores during 2001 is given in Appendix 5. This was recorded by the Research Dept. at ME, and the records come mostly from reports from game scouts in the field, as well as from tourist guides.

Chapter 4: Herbivore/habitat relationships

4.1 Introduction

An understanding of the habitat requirements of a species is pivotal to the effective conservation of that species (Fabricius & Mentis 1990; Putman 1996). Riney (1982) elaborates by stating that *“it is difficult to imagine any management programme or management-orientated study that would not profit from increased understanding of habitat requirements, for they represent one half of the essential core of animal-environment interrelationships. They provide the basis for progressing with the environmental side of management. Populations can of course be managed with information taken from animals alone (other half of the core), but past experience has shown this to be a dangerous numbers game.”*

The habitat requirements of a species, furthermore, need to be understood within a *seasonal context* (Fabricius & Mentis 1990) and within a *competitive context* (Melton 1987). The seasonal context is important as knowledge of the habitat requirements of a species during their *critical season* is essential (Riney 1982). Critical season here refers to the season when food resources are scarce (Sinclair 1975), usually the dry season in southern Africa. By competitive context, the requirements of other species within a competitive guild require consideration, assuming that similar populations utilize resources in a similar way and thus influence one another through competitive interactions (Smith 1996).

Malilangwe Trust had recently invested in a re-stocking programme of major herbivores at the Malilangwe Estate (ME), which included rare species (sable antelope and white rhino) and potentially profitable species i.e. surplus sold at wildlife auctions (buffalo). Management at the estate however did not have an understanding of the utilization of habitat by these species, or the competitive interactions that potentially took place between these species and others of the same guild: basic requirements of an effective conservation programme. This was particularly worrying to the Trust since so much financial input had gone into the herbivore community at ME. Therefore research was invited, and this study commenced with the following objectives:

1. To ascertain the nature and importance of the environmental factors that determine utilization of habitat and ecological separation among the grazing herbivore guild at ME.
2. Quantitatively describe and plot the respective habitat niches of the species comprising this guild, and explore the potential for interspecific competition from these findings.
3. Formulate recommendations, based on the findings of this research, using basic management tools that would ensure the long-term survival of rare and economically viable species, as well as the grazing herbivore community.

The study set out to determine these objectives using a known multivariate technique applied to the grazing herbivore community or guild. A guild is here defined as a group of species, all members of which exploit similar resources in a similar fashion (Allaby 1998; Smith 1996). Thus the study includes mixed feeders, as well as grazers, since mixed feeders select grass for most of the year (Skinner & Smithers 1990).

Furthermore, seasonal differences in habitat utilization among species were considered, and thus the study took place over an entire year. Seasonal difference in species habitat utilization allows insight into possible niche shift among species, and niche separation during the crucial lean period i.e. the hot dry season.

The study does not attempt to test niche theory, or the application of a multivariate technique to the analysis of herbivore/habitat relations. The objective was rather to gain a more thorough understanding of those variables that determine the habitat preferences of large herbivores within an enclosed wildlife area, and the possible competitive interactions that took place between them.

4.2 Methods

The stating of the conservation problem and objectives is the first step of study design (Jongman, ter Braak & van Tongeren 1987). The aims of a study determine the analytical technique to be used, the sampling strategy and analysis and interpretation of results (Gauch 1982; Jongman *et al.* 1987).

The objectives here were in accordance with the needs of management, and have been explained above. These objectives determine the study design explained in this chapter, and the interpretation of results.

This was essentially a *synecological* study. Synecology, or community ecology, is the study of many species simultaneously in relation to their environment (Jongman *et al.* 1987). Studies at this level are mostly descriptive as experimental research is difficult to carry out in complex ecosystems (Fowler & Cohen 1990; Jongman *et al.* 1987). Furthermore, community ecology is inherently complex, involving many species and numerous environmental variables (Gauch 1982).

When relationships between species and their environment are explored, as this study attempts, multivariate statistical techniques are the methods of choice (Anderson & Capen 1981). These authors state that multivariate techniques have three advantages over alternate methodologies when analyzing habitat data among animals, *viz.*

1. Multivariate procedures intrinsically fit ecological problems (and data of this sort),
2. multivariate procedures appear robust in the face of mild deviations from underlying assumptions, and
3. There already exists a hyper-geometric interpretation of the relationship among animals (niche theory) that is essentially based on a multivariate sample space.

Thus, following the formulation of the objectives of this study, it was decided that a descriptive multivariate method was the most appropriate analytical approach. Ideas were then borrowed from the many similar studies already been done on the large African herbivore community leading to an appropriate study design.

Jongman *et al.* (1987) state that once the objectives of a study have been defined, it is necessary to develop a schema that accurately summarizes the procedure to be executed from start to finish. Thus follows the study design, including sampling procedure, duration, study species and environmental parameters to be measured. Field measurements of these parameters are then discussed, followed by a description of the multivariate technique chosen, and the preparation of data. Finally, the data is analysed and results presented.

4.2.1 Study design and data collection

A study design schema is followed here, according to Jongman *et al.* (1987). It follows:

4.2.1.1 Statement of problem

The first step of study design is statement of the problem to be solved, in statistical terms (Jongman *et al.* 1987). This study was specifically interested in defining the physical and biotic variables that define species niches, given that the concept of niche is basic to understanding community organization, and in applied community ecology, for predicting the implications of management alternatives (Gauch 1982).

Hutchinson's (1958) concept of niche was chosen here, as his theory of community niche has been successfully applied to two previous studies with similar objectives *viz.* Fabricius & Mentis (1990), Ferrar & Walker (1974) and Melton (1978). Hutchinson defines the community niche as a parent space within which species niches are located at characteristic distances from one another, with varying degrees of overlap. Green (1971) showed that species locations within a community hyper-volume may be ordered according to the combined influence of several independent environmental variables. An association by herbivore species with one or more habitat variables forms the basis of predictive management.

Therefore, the problem to be solved here, after Jongman *et al.* (1987) was the determination of those environmental and competitive pressures that determine the spacing of species niches within the community niche. Thus, all environmental parameters that could potentially separate species niches needed to be estimated.

4.2.1.2 Random sampling procedure

Gauch (1982) advocates the design of a random procedure for the selection of sampling units in community ecology. Survey routes here could not be completely random, given the size of the study area (40 000 ha) and the complexity of the vegetation structure and composition. A stratified random technique was thus chosen, based on the vegetation communities of the estate shown in Figure 7.

All vegetation communities at ME have been mapped in the Geographic Information Systems (GIS) package *Idrisi32*, version 2 (Clark labs, Clark University 1999) by Clegg, B. (1999). This package allows for an estimation of area and thus percentage coverage of each community (see Table 1). Furthermore, all roads on the estate have been mapped in *Cartalinx* (Clark labs, Clark University 1999), allowing precise distance estimations (metres) of each road. The road network at ME traverses the entire reserve, with fairly good coverage of all vegetation communities (Figure 11), and for this reason roads were used as transects, following Dekker *et al.* (1996).

Since distance covered on each road (represented as arcs in *Cartalinx*, with each join of roads being nodes) could be estimated, and since proportional abundance of each vegetation community was given, a unique sampling strategy was devised whereby all of the reserve would be covered (using all roads, which were well maintained by estate management) and all vegetation communities would be adequately sampled, in proportion to their abundance.

This method was selected in preference to systematic random sampling i.e. permanent transects based in each community, since it ensured sampling of the entire estate. Mwangi & Western (1998) allocated permanent road transects to the Lake Nakuru National Park, Kenya. However, they only recognised five habitat types and sampled these in proportion to abundance. The size of their study area was not specified and their method did not sample the entire reserve. Dekker *et al.* (1996) sampled their study area in proportion to abundance of vegetation communities, and with permanently established routes, however their study area was only 4 605 ha. Ferrar & Walker's (1974) method of dividing their study area into blocks and traversing each block in a zigzag pattern on foot and horseback was rejected owing to the size of ME.

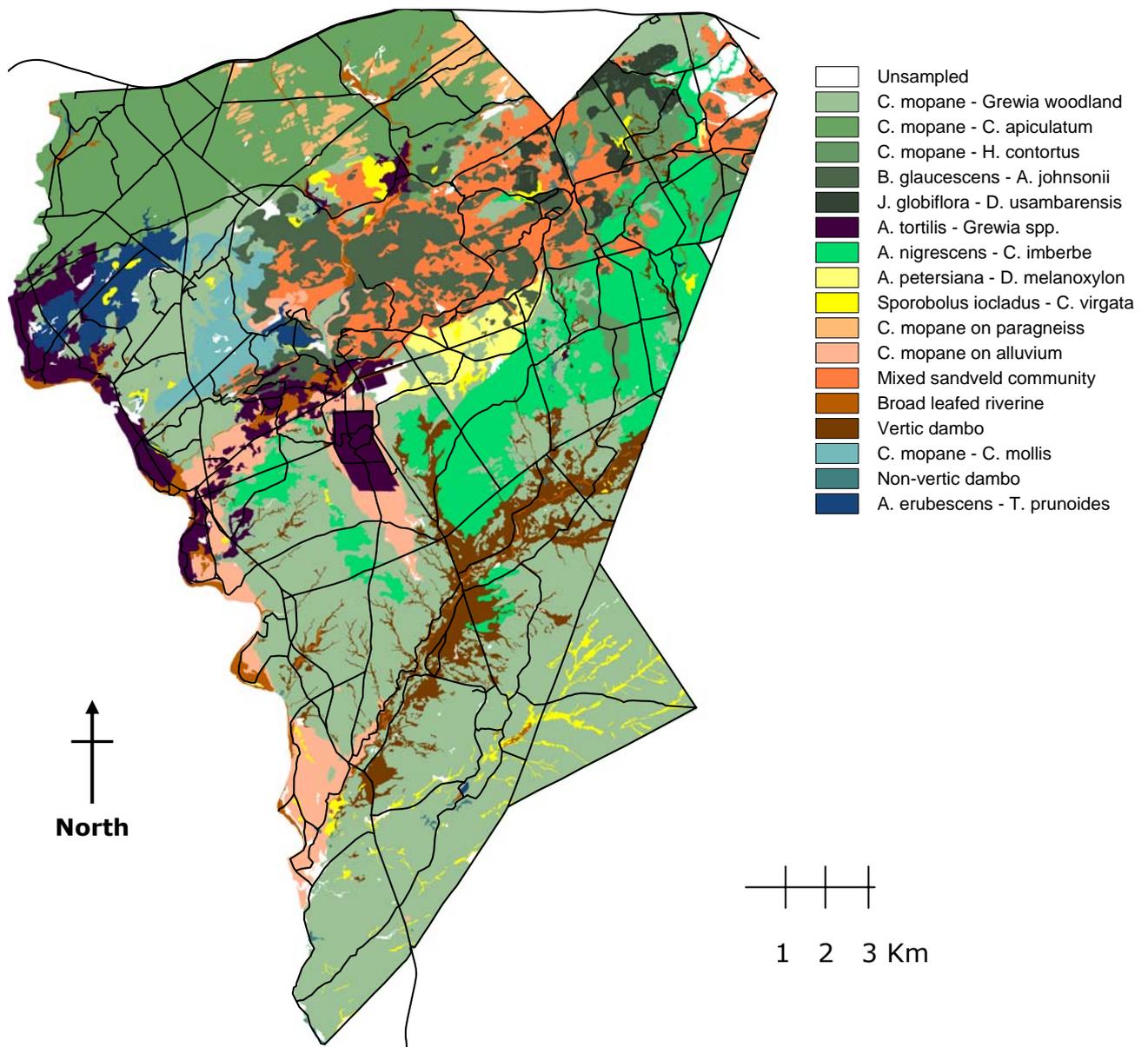


Figure 11: The road network at ME, with the vegetation communities given as a backdrop.

The entire estate was then divided into crude blocks, five in total (Appendix 6), which were each sampled on five consecutive days. This ensured independence of data points. These blocks were merely used as a guide, avoiding over-sampling in one area in preference to another, for example a more attractive part of the estate, as would have possibly happened had the blocks not been used. Block 1 was sampled on Monday mornings and evenings. Block 2 was sampled on Tuesday mornings and evenings, the data for Monday

evenings sampling being collected after Tuesday's data had been collected and so on until Saturday morning. At times, this routine was interrupted due to vehicle or logistical problems. When this occurred, note was taken and usually the missed block was sampled over the weekend. Also, since a large proportion of the estate was dominated by mopane veld, it was sometimes necessary to spend more sampling time in the southern part of the estate, where mopane is dominant. This was noted and care taken not to sample the same route on the same day.

While sampling in each block, a random beginning point was chosen and the block sampled in a random manner, initially, and all routes driven recorded. Routes driven randomly were noted and effort made to ensure that other parts of the reserve were sampled the following week, thus assuring coverage of the entire block.

At the end of each days sampling, the total distance covered in each community was estimated in *Cartalinx* and recorded in a *Microsoft Excel* spreadsheet. Distance covered in each community divided by total distance covered (calculated in *Excel*) gave an indication of percentage distance covered in each of the 17 vegetation communities (Appendix 7). The idea here was to compare percent distance covered in a community to percent abundance of that community, and attempt to equate the two values. Thus, if a vegetation community was seen to be under-sampled (less percent distance travelled in the community in relation to the abundance of that community), note was taken and more time was spent within this community on surveys that followed. Conversely, if a vegetation community was noticed to be over-sampled, care was taken on subsequent drives to avoid that specific community.

Visibility associated with different habitat types was not estimated in accordance with similar multivariate studies i.e. Fabricius & Mentis (1990), Ferrar & Walker (1974) and Melton (1978). Furthermore, a reasonable estimate of visibility would have required at least 15 sightings per vegetation type per species (Goodman pers. comm.) and as this was not feasible, the estimation of visibility was rejected. This also meets the assumptions of the multivariate technique selected and discussed later in the text.

Sampling took place six days a week, between 05:30 – 10:00 and 16:00 – 18:00 local time. Saturdays were usually spent collecting data from the Friday evenings drive, and at times driving in under-sampled communities. Driving

was done in an open vehicle, at an average speed of 25 km/h. A research assistant stood in the back of the vehicle while searching for study animals, and easy communication was possible. Survey routes were used independent of herbivore occupancy and sightings were considered to be random observations, after Dekker *et al.* (1996).

4.2.1.3 Duration

Data collection spanned an entire year, so as to incorporate seasonal differences in habitat utilization. It was decided that data be collected over two months, in the middle of each season, to avoid 'fuzzy' data i.e., the transition in species habitat utilization may not have been clear had data been continuously collected as the changes are likely to be gradual (Goodman pers. comm.).

The year was thus divided into three seasons *viz.* hot-wet (November-March), cool-dry (April-August) and hot-dry (September-October) after Booth (1980). Data collection proceeded from the beginning of December 2000 to February 2001, in June and July and during September and October 2001.

4.2.1.4 Study species and parameters estimated

Since this study was primarily concerned with the utilization of habitat by rare and valuable species, and with their competitive interactions with other species of the same guild, all environmental variables thought to determine the utilization of habitat were considered, and all species comprising the large grazing herbivore community were included.

Study species were therefore all grazing herbivores larger than (and including) warthog. Mixed feeders were included as they may compete with grazers for most of the year. Study animals were: elephant, buffalo, eland, impala, nyala, sable antelope, warthog, waterbuck, wildebeest, white rhino, and zebra. Reedbuck, present on the property, were initially included, but as no sightings were made they were discarded. Hippo were also excluded from the study as they feed at night, and owing to logistical constraints it was not possible to search for them. Hartebeest and roan antelope were kept in enclosures and were thus excluded, as any data obtained from these species within bomas would not reflect their true distribution and habitat preference.

Territories and home ranges of species were not considered, and all individuals of a population were assumed to select habitat best suited to them. Intra-specific competition was assumed to be minimal as population densities

for study animals were below carrying capacity at the commencement of study (see Appendix 14).

Group size and herd composition was not considered in the analysis of data. A species niche was assumed to be both a total of male and female niches. The averaging of data from breeding herds and male groups had the effect of reducing resolution, but it was decided that very little practical implication could come from separating these groups. When data collection was complete and the matrices prepared for analysis, the small sample sizes for most species did not allow for separation according to the socio-spatial structure of each respective species. Thus averaged data was analysed with the intention of describing relations between species, as had also been done by Fabricius & Mentis (1990) and Ferrar & Walker (1974).

Vegetation communities were not included in the multivariate analysis as this study was only concerned with habitat variables and their effect on the utilization of habitat among species. A vegetation community *per se* cannot be manipulated by management and since this was a management oriented study, there was no need to include the communities as variables. Moreover, large herbivores do not select preferable habitat on the basis of vegetation communities that have been classified by human observers. The criteria by which vegetation is classified into communities cannot be compared to the criteria by which animals select habitat and the resources therein. Finally, if management require an understanding of species associations with vegetation communities, this can simply be done using the EXTRACT function in *Idrisi* and the aerial census data.

Lastly, an important assumption made here was that animals have the freedom to select habitat freely, and their choice of habitat is being made on the basis of the characteristics of that habitat. Each sighting reflected this choice, the characteristics being measurable.

All habitat variables thought to determine herbivore distribution are listed in Table 3. The measurement scales of these variables are also given.

Table 3: Summary of the habitat variables used in discriminant function analysis

Number	Mnemonic	Habitat variable
1	ALTI	Altitude of plot taken from GPS (metres A.S.L.)
2	AVAP	Available phosphorus (%)
3	BARE	Percentage of site comprising bare patches
4	CECI	Percentage contribution to biomass – <i>Cenchrus ciliaris</i>
5	CLAY	Percentage clay
6	DCOV	Distance to nearest cover (m)
7	DIER	Percentage contribution to biomass – <i>Digitaria eriantha</i>
8	DOPV	Distance to open vantage point (m)
9	DWAT	Distance to nearest surface water, measured in <i>Idrisi</i> (m)
10	ENCE	Percentage contribution to biomass – <i>Enneapogon cenchroides</i>
11	ENSC	Percentage contribution to biomass – <i>Enneapogon scoparius</i>
12	FORB	Percentage aerial cover of forbs (including saplings) in herb. layer
13	GBAR	Percentage aerial cover of bare ground within herbaceous layer
14	GBRO	Percentage aerial cover of brown (biologically inactive) grass
15	GGRE	Percentage aerial cover of green (biologically active) grass
16	GLIT	Percentage aerial cover of moribund material in the herb. layer
17	HECO	Percentage contribution to biomass – <i>Heteropogon contortus</i>
18	INHT	Mean inflorescence height of grasses (m)
19	NAFT	Nitrogen content (%)
20	PMAX	Percentage contribution to biomass – <i>Panicum maximum</i>
21	PSQU	Percentage contribution to biomass – <i>Pogonarthria squarrosa</i>
22	ROCK	Percentage of site comprising rocks bigger than 5 cm diameter
23	SEDG	Percentage aerial cover of sedges in the herbaceous layer
24	SHVO	Shrub volume (m ³) per ha
25	SINC	Percentage contribution to biomass – <i>Setaria incrassata</i>
26	SLOP	Average slope of the land surface as a percentage of 90° (%)
27	SPAP	Percentage contribution to biomass – <i>Schmidtia pappophoroides</i>
28	SWHT	Mean sward height of grass cover (m)
29	TRVO	Tree volume (m ³) per ha
30	TSBU	Time since last burn (months)
31	UMOS	Percentage contribution to biomass – <i>Urochloa mossambicensis</i>

Field estimation of these variables is now explained:

4.2.2 Field measurements

As mentioned above, sampling strategy involved the use of roads and an open vehicle. While searching for study animals, an observer stood in the back of the vehicle and alerted myself to the presence of an animal, or herd, whereupon its activity was noted. Only if the animal/herd was grazing was the sighting considered a sample. Thus, if animals were obviously moving or resting, they were ignored. An identification peg was placed where the animals were feeding and the drive resumed after recording the date, time, species, number of animals and weather conditions. This method was adopted because time was limited; thus routes were driven for a few hours before it was either too hot, and the animals took to shade, or too dark, if it was an evening drive. Once it was decided that enough pegs had been placed, or it was noted that animals had sought shelter from the sun, the plots were revisited and data collected. Pegs placed in the evening were revisited on the following day.

If the species seen were potentially dangerous i.e. rhino, buffalo or elephant, an identification peg was staked in the ground near the road, as opposed to placing the peg at the exact location of the animals. The spoor was later located.

The precise position of the location (in UTM, see Clarke 1999) was taken via a handheld Global Positioning System (GPS), and was later downloaded into *Cartalinx*. A 20 m x 20 m quadrat was then demarcated, where the position of the centre of the herd served as the centre of the quadrat. If the sighting was of a single animal, a plot of 10 m x 10 m was demarcated. It was assumed that if the animals were feeding, the characteristics of their selected habitats would be adequately recorded within these areas.

The vegetation characteristics of the area were then recorded, dividing vegetation into woody growth and herbaceous cover/composition. All woody growth below 3 m in height was assumed to be a shrub, and all woody growth above 3 m in height was recorded as a tree (Ferrar & Walker 1974). Woody characteristics (variables 24 & 29, Table 3) were estimated using a 3 m pole as a scale. For trees the following estimates were recorded: tree height, canopy height (lowest point of canopy) and canopy width. Tree canopies were assumed to be cylindrical in shape and volume was estimated as such. Shrub volume was estimated by measuring the height and width of the shrub, also assuming that

these were cylindrical in shape. Trees and shrubs bordering the plot were included if more than 2/3 of their canopy was within the plot.

Measurements characterizing the herbaceous layer were made by placing a 1 m² quadrat down twenty times within the plot, in a diagonal line, i.e., ten quadrats placed from one corner of the plot to the other and then repeated from the other corner of the plot. This technique covered most of the plot, enabling most of the herbaceous component to be recorded, and a representative mean to be calculated.

Variables recorded within each quadrat were firstly: mean maximum grass sward height, after Walker (1976), using a 2 m graduated pole, and grass inflorescence height (variables 18 & 28 Table 3). Percentage aerial cover of the herbaceous layer (variables 12 – 16 & 23, Table 3) was visually estimated using an adapted rank-score method (Table 4) from Walker (1976). The quadrat was stood over and rank score values given to each variable.

Table 4: Rank score method used to estimate herbaceous aerial cover, adapted from Walker (1976).

RANK SCORE	RANGE	MIDPOINT OF RANGE (%)
0	0	0
1	1	1
2	2 – 10	6
3	11 – 25	18
4	26 – 50	38
5	51 – 75	63
6	76 – 95	86
7	96 – 100	97

Small-scale topography was estimated by three variables (variables 3, 22 & 26, Table 3). Variable 26 (SLOP) was selected to detect possible association with hilly areas. Slope was visually estimated by deciding on a percent value of 90°. Therefore, if a sample plot lay on a slope of approx. 10° it was given a value of approx. 12%. Variable 22 (ROCK) was selected to show associations with rocky habitat, and was measured by a visual estimation of the entire plot. Rock was assumed to be exposed bedrock, boulders and stones greater than 5 cm in diameter. Variable 3 (BARE) was selected to possibly show association

with middens, stamping grounds etc. A bare area was defined as any natural or induced bare patch over 2 m² and with a maximum herb height of 0.1 m. The percent value of the site thought to comprise bare patches was again visually estimated; usually from either the highest point in the plot, or the centre.

Three soil variables (variables 2, 5 & 19, Table 3) were included in the analysis, all other soil variables being discarded due to collinearity (Appendix 9). Data for soil variables were taken from Chawanji (2000) and assigned to a raster coverage in *Idrisi*, based on Clegg's (2002) vegetation community map (Appendix 13). Once the soil data was in *Idrisi* raster format, a command was used to assign the particular soil characteristics to each sample plot location.

All soil analyses were done by the Zimbabwe Sugar Association (Private Bag 7006, Chiredzi, Zimbabwe). Percent nitrogen after drying was determined using the Sulphuric acid – hydrogen peroxide method. Available phosphorus (P) was calculated by using a modification of the resin extraction method where 15 ml of extract was made up to 25 ml as opposed to the practice of 10 ml extract being made up to 100 ml in the resin extraction method. The modified method provides a more sensitive test. Lastly, the exchangeable cations potassium (K), calcium (Ca), magnesium (Mg), sodium (Na) were determined by Atomic Absorption (A/A), after Clegg, S. (1999).

Distance to nearest water (variable 9, Table 3) was also computed in *Idrisi*. All surface water points were monitored in the middle of each season. This involved driving to all known pans, walking all rivers and recording the surface water locations on a handheld GPS. These data were collected in December 2000, February 2001 (after a very wet period, see Appendix 1), June 2001 and September 2001. The GPS points were then downloaded to *Cartalinx* and vector maps created for water-points in each respective season. These vector maps were then converted to raster maps in *Idrisi* and the Euclidean distance from each water-point in each season was calculated (Figure 10). Species presence raster maps were composed in *Idrisi*, by downloading all GPS points for each respective species plot. Species presence coverages were computed for each species in each season. The distance (m) to the nearest water-point for each species location in each season was then calculated using the EXTRACT function in *Idrisi*.

Time since last burn (variable 30, Table 3) was another important variable estimated in *Idrisi*. Management burns are stored in *Idrisi* vector

format by the research dept. at ME (see Figure 8). These were then converted to raster format and again, using the *Idrisi* function EXTRACT, the precise time since last burn for each plot (in months) was computed. Mowed areas within ME were included as recently burnt (1 month) in the analyses, since freshly mowed areas share similar characteristics with recently burnt areas i.e., a short grass sward where growth is mostly green and vigorous (pers. obs.).

DOPV (variable 8) was visually estimated in metres, an open area being defined as an area without tree, shrub cover > 5 m diameter. DCOV was also visually estimated in metres, cover being vegetation > 2 m in height and width and that afforded cover from predators.

Finally, the most important grass species in the herbaceous layer were ranked according to an approximation of the dry weight technique of 'T Mannelje & Haydock (1963), using the formulae given in Walker (1976). Most of these grass species were discarded because of their infrequent occurrence and low percent contribution to biomass. The remaining species in Table 3 (variables 4, 7, 10, 11, 17, 20, 21, 25, 27, & 31) were used in the multivariate analysis.

An index of predation, or predator presence was not included as it was considered that predatory off-take was negligible (Appendix 5). The objective was to collect data from a minimum of thirty sample plots in each season. In reality this was rarely possible. A species was discarded from the analysis if less than 10 plots were sampled in that season (see Appendix 8).

4.2.3 Analysis of data

The schema followed here is in accordance with that advised by Jongman *et al.* (1987).

4.2.3.1 Multivariate technique chosen

Following consultation of all available literature, a technique was chosen based on studies with similar objectives, study species and habitat *viz.* Fabricius & Mentis (1990), Ferrar & Walker (1974) and Melton (1978). Discriminant Function Analysis (DFA) was chosen as the most suitable multivariate technique.

DFA is an appropriate multivariate technique for the separation of groups according to their characterization by a series of attributes (Ferrar & Walker

1974). It is useful in niche analysis in that it reduces the number of criteria or dimensions used for discrimination, and it does so before the interpretation of species separation is necessary (Legendre & Legendre 1998; Williams 1981).

4.2.3.2 Data inspection and preparation

All data collected were saved in *Microsoft Excel* and were divided into the three respective seasons and saved in subfolders for each of the species. Each sighting of each respective species (sample plot) was saved as a separate *Excel* spreadsheet.

Unfortunately, sample sizes were mostly small. Despite all attempts to secure data, field conditions were often constraining. An essential requirement in the field was that I had to be certain that the animals were feeding, and not merely resting or moving. This was often difficult, particularly given that the vehicle often disturbed the animals. If it was not certain that a group/or single of study animal(s) had selected a site for forage, it was ignored. It was for this reason that sample sizes were small, but accurate indicators of feeding habitat selection.

The data were checked against the original collection sheets which were filed and numbered. Missing values were checked for and all pages were generally needed to correspond with the original hard copies. Also, values calculated in *Idrisi* i.e. distance to water and time since burn, needed to correspond with the sample numbers given to the original data sheets. Once this was done, data were saved in matrices for each season and investigated. Matrices were constructed in an *Excel* spreadsheet and consisted of groups (species) as rows and attributes (environmental variables) as columns.

One of the requirements of DFA is that the data matrix be non-singular (Hope 1968). Singularities occur when a group has both zero mean and variance for any one variable. This was avoided by replacing groups of zeros with a very low value (0.01), where necessary; many grass species were discarded as they proved ineffective (low scores) in initial tests.

The raw data matrices then had to be suitably transformed to allow for valid analysis (Ferrar & Walker 1974; Legendre & Legendre 1998; Williams 1981). DFA is a sensitive form of analysis designed for data containing limited overall variance and an equality of dispersion of group means for each group on each attribute (Hope 1968). However, Williams (1981) adds that data used in

discriminant analysis are rarely completely normal, and thus encourages a "healthy scientific skepticism (sic) in both the interpretation and reporting of the results." Legendre & Legendre (1998) add that the discriminant analysis model is fairly robust to departures from normality, but the statistical tests assume within-group normality of each descriptor.

All data in each season were initially \log^{10} - transformed (all 0 values changed to 0.01 prior to transformation) and checked for normality. Those variables that failed to meet the requirements of normality using \log^{10} , and variables measured as percentage values, were transformed using the square root and then arcsine transformations (Fowler & Cohen 1992; Legendre & Legendre 1998).

The data matrices were then examined for within group correlations. Variables that were strongly correlated, i.e., where value of coefficient $r > 0.7$ (after Fowler & Cohen 1992), were discarded. The lists of discarded variables for each season are given in Appendices 9, 10 and 11. Ecological experience and intuition had to be applied, at times, when deciding on what variables should be left within the matrix.

The grouping variable (species) in each season was also checked, and if there was insufficient data, that species was discarded. Eland were thus discarded from the hot-wet analysis.

4.2.3.3 Application of analytic method

Analysis of each matrix was carried out using discriminant function analysis, in the statistical software package *Statistica* version 6 (StatSoft 2001). There are a number of steps in DFA (Ferrar & Walker 1974; StatSoft 2001):

1. Firstly, the partial *Wilk's lambda* test indicates the statistical significance for the unique contribution of each variable to the discrimination between groups.
2. A series of latent roots and vectors are extracted from the total set of group matrices. These latent roots are known as discriminant functions (DF's) and express the difference between species in terms of a few common gradients which can be identified by the variable weights most strongly associated with each DF. The larger the standardized coefficient, the greater the contribution of the respective variable to discrimination between groups. Only absolute values are relevant here (Melton 1978).

3. For each DF, each individual (site) is given a discriminant score, calculated by summing the products of the variable weights and their respective values for the site concerned. The mean of the discriminant scores for all sites for any one species is the species centroid and can be considered the niche centre.
4. Plotting these species' centroids on each DF separates the species along what are effectively the dimensions of the community habitat niche.

Results of the analyses for each of the three species are now given:

4.3 Results

4.3.1 Hot wet season

The number of variables used to describe species locations was reduced after examination of the data. Discarded variables, and justification, are given in Appendix 9.

4.3.1.1 Discriminating power of habitat variables

The first steps in the analysis procedure are the *Wilk's Lambda* (λ) and *partial Wilk's lambda* determination. F to enter was set at 1.0 and F to remove at 0.

The *Wilk's* λ measures the extent to which groups differ in the positions of their centroids (Legendre & Legendre 1998). A *Wilk's* λ value of 0.0 represents perfect discriminatory power, and a value of 1.0 represents no discriminatory power (Legendre & Legendre 1998).

In *Statistica*, the *partial Wilk's* λ output represents the unique contribution of the respective variable to the discrimination between groups. Thus, the lower the value in the *partial Wilk's* λ column (Table 5), the greater the unique discriminatory power of that variable.

Table 5: Wilk's Lambda values (discriminatory power), and percentage levels of probability for the 28 variables included in the hot-wet season analysis. Variables that significantly contribute to discrimination between groups are indicated by an asterisk. Variables in italics were excluded from the model

Variable	Wilk's Lambda	Partial Wilk's λ	F Remove	p-level
Contribution to sward by <i>Panicum maximum</i>	0.092	0.799	4.500	0.000*
Nitrogen content	0.089	0.828	3.705	0.000*
Distance to cover	0.086	0.857	2.990	0.003*
Grass sward height	0.086	0.864	2.818	0.004*
Contribution to sward by <i>Cenchrus ciliaris</i>	0.085	0.869	2.696	0.006*
Slope	0.085	0.872	2.633	0.007*
Brown (inactive) grass cover	0.084	0.878	2.478	0.011*
Forb cover	0.084	0.882	2.383	0.015*
Contribution to sward by <i>Digitaria eriantha</i>	0.084	0.884	2.349	0.016*
Tree volume	0.083	0.885	2.321	0.018*
Time since last burn	0.083	0.887	2.279	0.020*
Bare patches	0.082	0.899	2.017	0.040*
Distance to water	0.081	0.911	1.749	0.082
Percent clay	0.081	0.913	1.696	0.094
Sedge cover	0.081	0.915	1.658	0.103
Altitude	0.080	0.924	1.466	0.165
Contribution to sward by <i>Urochloa mossambicensis</i>	0.079	0.933	1.293	0.244
Contribution to sward by <i>Pogonarthria squarrosa</i>	0.079	0.933	1.279	0.252
Contribution to sward by <i>Heteropogon contortus</i>	0.079	0.938	1.177	0.313
Contribution made by <i>Schmidtia pappophoroides</i>	0.078	0.947	1.004	0.439
<i>Bare cover in grass sward</i>	0.072	0.974	0.471	0.893
<i>Green (biologically active) grass cover</i>	0.071	0.967	0.611	0.787
<i>Available phosphorus</i>	0.071	0.965	0.645	0.757
<i>Shrub volume</i>	0.071	0.965	0.654	0.750
<i>Contribution made by Enneapogon cenchroides</i>	0.071	0.962	0.706	0.703
<i>Distance to open vantage</i>	0.070	0.952	0.890	0.536
<i>Litter cover</i>	0.070	0.952	0.905	0.522
<i>Rock cover</i>	0.070	0.951	0.922	0.508

The partial *Wilk's* λ in Table 5 (hot-wet season) indicates that contribution to sward by *Panicum maximum* contributes most to overall discrimination, followed by soil nitrogen content, distance to cover and so on. It is noticeable that no single variable contributes greatly to overall discrimination between groups. The p-levels correspond to the *Wilk's* λ value, and represent the significance of each variable.

4.3.1.2 Canonical analysis and dimensionality of the community niche

In order to discern more about the nature of discrimination between groups, a canonical analysis was performed. From here the actual discriminant functions (also know as roots) are computed. The analysis of the hot-wet season data

produced six DF's accounting for 91% of the overall variance between species. The first three DF's accounted for 65 percent of the variance: 31, 20 and 15 percent respectively (Table 6). This is similar to Ferrar & Walker's (1974) finding that the first three DF's accounted for 66 percent of the variance in their data on herbivore/habitat relations at Kyle National Park, Rhodesia. Essentially, the DF's represent the primary dimensions of the community niche (Hope 1968; Ferrar & Walker 1974; Melton 1978).

It is then necessary to know the extent of association between each environmental variable and the DF's, enabling description of the community niche dimensions. Only the first three DF's were used in graphical interpretation of the results to make interpretation simpler, after Ferrar & Walker (1974) and Melton (1978). The remaining variance is due to random or chance variability.

Variable coefficients with a value greater than 0.4 were assumed to be strongly influential in the spacing of species niches, after Ferrar & Walker (1974). Any coefficient of value below 0.4 was excluded, except when the value was greater than 0.3 and given to a habitat variable that could be potentially manipulated by management. For example, if percent soil clay was assigned a value of 0.38, while tree volume a value of 0.36, tree volume was used in the interpretation since woody plant density is an environmental variable that management can monitor and manipulate, while soil type is independent of management applications.

It is important to note here that interpretation of environmental gradients from the DF's is not as easily done as in the study done by Ferrar & Walker (1974). Kyle National Park is a small area with clearly distinguishable habitat types i.e. grassland, woodland and kopjes (pers. obs.). ME on the other hand (although hilly areas are easily distinguished), is a more complex and heterogeneous environment, with 38 known habitat types (Clegg, B. 2002). Thus, interpretation of results will primarily concern species association with one or more particular habitat variable.

Table 6: The standardized coefficients for 20 variables from a DF analysis of 10 species in the hot-wet season. Bold coefficients are those considered strongly influential.

Variables	DF 1	DF 2	DF 3
Explained variance %	31	20	15
Contribution to sward by <i>Panicum maximum</i>	0.573	-0.046	0.046
Grass sward height	0.452	-0.381	0.034
Nitrogen content	-0.425	0.123	-0.401
Distance to cover	0.083	-0.391	-0.218
Forb cover	-0.029	0.342	-0.382
Slope	0.304	0.248	0.280
Bare patches	-0.158	-0.028	0.466
Distance to water	-0.083	-0.345	-0.027
Time since burn	0.078	0.484	0.221
Contribution to sward by <i>Cenchrus ciliaris</i>	0.389	0.264	-0.173
Contribution to sward by <i>Digitaria eriantha</i>	0.279	-0.258	0.365
Tree volume	-0.139	0.081	-0.242
Contribution to sward by <i>Urochloa mossambicensis</i>	-0.033	0.111	0.225
Brown grass cover	0.118	-0.348	-0.313
Altitude	-0.196	0.348	-0.053
Clay	-0.094	-0.642	0.220
Sedge cover	0.032	-0.440	0.067
Contribution to sward by <i>Pogonarthria squarrosa</i>	0.104	-0.236	-0.390
Contribution to sward by <i>Heteropogon contortus</i>	0.222	0.228	-0.226
Contribution to sward by <i>Schmidtia pappophoroides</i>	0.067	0.049	-0.166
<i>Eigen value</i>	<i>1.014</i>	<i>0.655</i>	<i>0.445</i>
<i>Cum.Prop</i>	<i>0.310</i>	<i>0.511</i>	<i>0.647</i>

The first DF shows a gradient from tall grass where *Panicum maximum* is abundant to a shorter grass sward on nitrogen rich soils. *P. maximum* is a grass typically associated with tall tree canopies (pers. obs.) and thus the presence of this grass is indicative of an open woody habitat, usually riverine.

The second DF shows a gradient from clay type soils relatively further from water, on which sedges occur and woody growth is open to areas where soil clay content is low, woody growth more dense and fire less common.

The third primarily DF concerns soil nitrogen content and bare patches, thus a gradient from un-patchy swards on fertile soils to patchy grass growth on less fertile soils. The first three DF's account for 65% of explained variance.

The actual separation of species along these community niche gradients is now given:

4.3.1.3 Species separation within the community niche

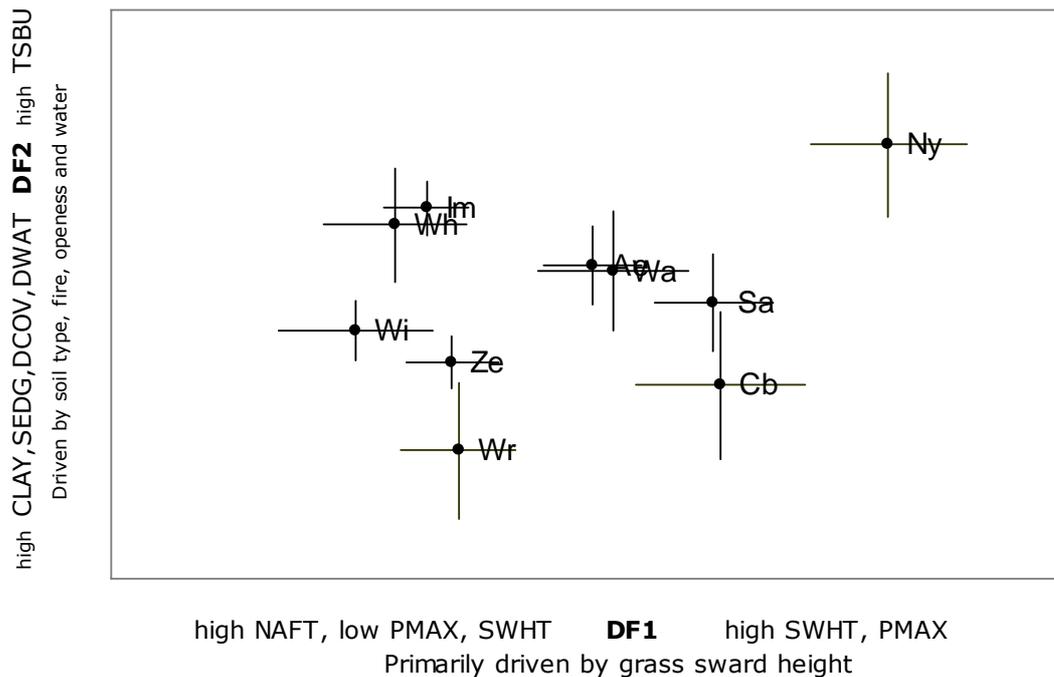


Figure 12: Location of species niches within the community niche for the hot wet season. Their location is determined by the habitat factors represented along the first two environmental gradients.

Species centroids: Ae = elephant, Cb = buffalo, Im = impala, Ny = nyala, Sa = sable, Wa = waterbuck, Wh = warthog, Wi = wildebeest, Wr = white rhino and Ze = zebra.

Variable mnemonics: CLAY = soil clay content, DCOV = distance to cover, DWAT = distance to water, NAFTA = soil nitrogen, PMAX = *Panicum maximum*, SEDG = sedge cover, SWHT = grass sward height, TSBU = time since burn.

The distributions of the species centroids for the hot wet season are illustrated in Figures 12, 13 and 14. Two standard errors on either side of the mean represent the niche breadth for each species. In all cases the axes are scaled in proportion to the variance extracted by each DF. The extent of species separation is represented by the distances between, and location of, the species centroids in relation to the three main DF's. Ferrar & Walker (1974) add that

the specific location of the species centroids is not hugely important, but rather their relative position or pattern. The *community niche* is considered as the parent space within which species niches are located at characteristic distances from one another, with varying degrees of overlap (Ferrar & Walker 1974).

Following Figure 12, nyala are ecologically separate from all other species, selecting habitat characterized by a tall grass sward close to water on alluvial soils, dominated by *P. maximum*, not recently burnt and in a woody habitat. This is typical of the riverine habitats at ME where nyala are generally abundant (pers. obs.). Sable and buffalo also select habitat where a tall grass sward is dominant and where fire has been more recent. White rhino, wildebeest, warthog, zebra and impala apparently select a relatively shorter grass sward during this season, where *P. maximum* does not thrive, and thus in more open habitat. White rhino prefer more recently burnt and open habitat on clay soils, while warthog and impala appear to prefer more sandy or alluvial soils in areas that haven't been recently burnt. Waterbuck and elephant are intermediate in their choice of habitat along these environmental gradients.

Following Figure 13, nyala, sable antelope and buffalo select a taller grass sward, while wildebeest, warthog, impala, zebra and white rhino appear to prefer short grass areas on nutrient rich soils. Warthog and rhino are not averse to patchy soils where grass growth is sparse, while wildebeest prefer an apparently lush, but short grass sward.

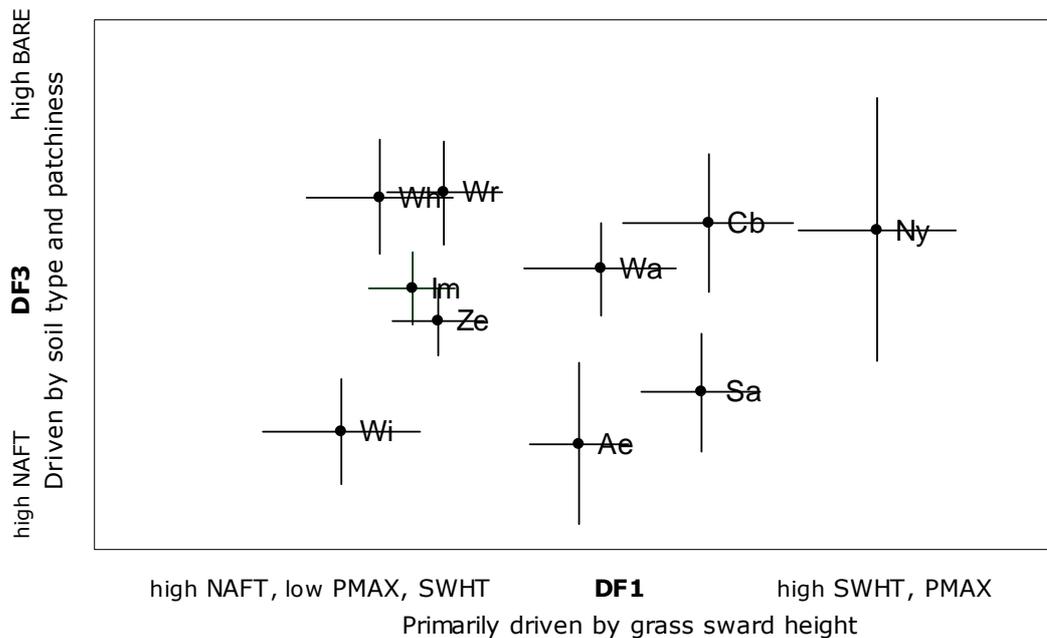


Figure 13: Location of species niches within the community niche for the hot wet season. Their location is determined by the habitat factors represented along the first and third environmental gradients.

Species centroids: Ae = elephant, Cb = buffalo, Im = impala, Ny = nyala, Sa = sable, Wa = waterbuck, Wh = warthog, Wi = wildebeest, Wr = white rhino and Ze = zebra
Variable mnemonics: BARE = bare patches, NAFT = nitrogen content, PMAX = contribution of *Panicum maximum*, SWHT = grass sward height.



Following Figure 14, nyala again show a preference for habitat in close proximity to water, where plant growth is dense and fire uncommon. White rhino conversely prefer open habitat further from water and recently burnt. Rhino, buffalo, warthog and nyala all appear to select areas where grass growth is patchy, while wildebeest, sable and elephant prefer a dense sward.

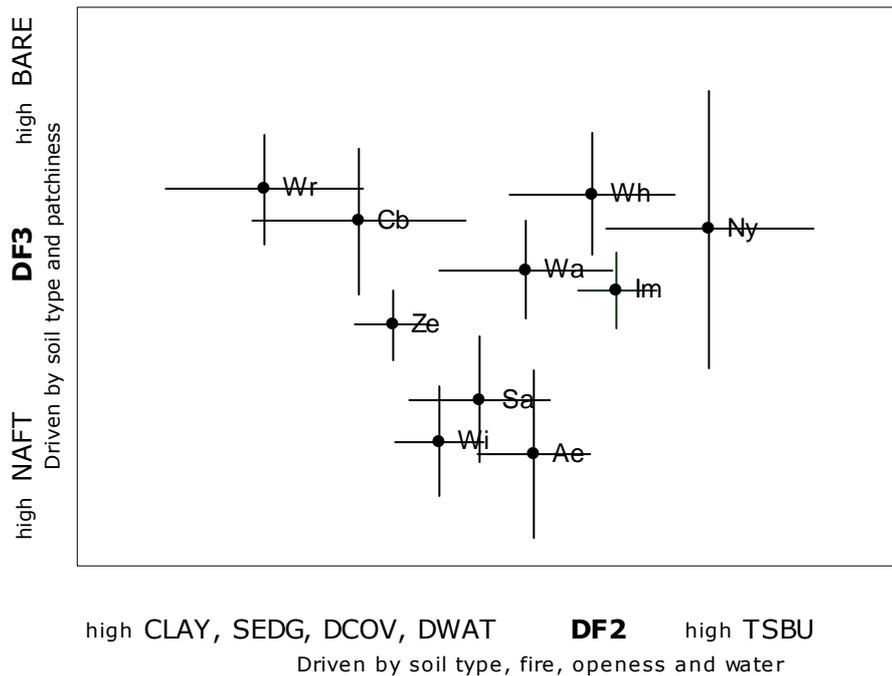


Figure 14: Location of species niches within the community niche for the hot wet season. Their location is determined by the habitat factors represented along the second and third environmental gradients.

Species centroids: Ae = elephant, Cb = buffalo, Im = impala, Ny = nyala, Sa = sable, Wa = waterbuck, Wh = warthog, Wi = wildebeest, Wr = white rhino and Ze = zebra
Variable mnemonics: BARE = bare patches, CLAY = soil clay content, DCOV = distance to cover, DWAT = distance to water, NAFT = soil nitrogen content, SEDG = sedge cover, TSBU = time since burn.

To summarize, grass sward height, the presence of *P. maximum* (and the habitat with which this grass species associates with i.e. closed woody canopies), time since last burn, distance to water, soil type and patchiness of the grass sward are all important determinants of large herbivore utilization during the wet season.

Nyala are distinctly separate from all other herbivores during this season, selecting a dense vegetation type on alluvial soils and near water. Buffalo, waterbuck and sable antelope also select a taller grass sward, with only waterbuck staying close to water sources. White rhino, warthog and wildebeest select relatively short grass areas during this season, as do impala and zebra. Buffalo, wildebeest, white rhino, sable antelope and zebra apparently prefer

more recently burnt veld during this season, possibly drawn to the fresh growth.

Competitive niche overlap is high among species during this season, but since resources were particularly plentiful when data was collected (pers. obs.) it is improbable that real competition exists between species. Competition at the feeding level is unknown.

4.3.2 Cool dry season

The same analytical procedures used in the hot-wet season were used here. Data collection for the cool-dry season took place from the beginning of June to the end of July 2001. By this stage the data collection techniques and herbivore habits were more familiar and a relatively substantial amount of data were collected.

The first procedure in analysis was the normalization of the data followed by a check for correlation between variables (Appendix 10).

4.3.2.1 Discriminating power of habitat variables

The partial *Wilk's lambda* statistic indicates the unique contribution of the respective variable to the discrimination between groups.

The overall Wilk's λ measures the extent to which groups differ in their centroids (Legendre & Legendre 1998). Again, as in the hot-wet season, no one variable contributes greatly to discrimination between groups (Table 7). This is likely due to fact that no grazing species selects a habitat type that is markedly unique in vegetation structure and composition.

Table 7: Wilk's Lambda values (discriminatory power), and percentage levels of probability for the variables included in the cool-dry season analysis. Variables in italics were excluded from the model. Variables indicated by an asterisk are those that significantly contribute to discrimination between groups.

Variable	Wilk's Lambda	Partial Wilk's λ	F Remove	p-level
Distance to cover	0.118	0.842	3.687	0.000*
Clay content	0.117	0.850	3.466	0.000*
Contribution to sward by <i>Heteropogon contortus</i>	0.114	0.869	2.965	0.002*
Grass sward height	0.114	0.871	2.922	0.002*
Contribution to sward by <i>Digitaria eriantha</i>	0.114	0.874	2.852	0.002*
Percent contribution of <i>Urochloa mossambicensis</i>	0.113	0.881	2.654	0.005*
Nitrogen content	0.110	0.906	2.049	0.030*
Percent slope	0.109	0.907	2.030	0.032*
Time since burn	0.109	0.907	2.013	0.034*
Distance to water	0.109	0.911	1.932	0.043*
Bare patches	0.108	0.916	1.807	0.062
Contribution to sward by <i>Panicum maximum</i>	0.108	0.921	1.700	0.083
Distance to open vantage	0.107	0.926	1.574	0.117
Tree volume	0.107	0.930	1.491	0.145
Contribution to sward by <i>Setaria incrassata</i>	0.107	0.931	1.465	0.155
Contribution to sward by <i>Cenchrus ciliaris</i>	0.106	0.934	1.403	0.181
Brown (inactive) grass cover	0.106	0.934	1.399	0.183
Shrub volume	0.106	0.936	1.346	0.208
Altitude	0.105	0.941	1.245	0.265
Rock cover	0.105	0.942	1.210	0.286
<i>Sedge cover</i>	0.096	0.972	0.565	0.841
<i>Litter cover</i>	0.096	0.970	0.601	0.812
<i>Contribution made by Enneapogon scoparius</i>	0.096	0.967	0.662	0.758
<i>Bare cover in grass sward</i>	0.096	0.964	0.732	0.694
<i>Available phosphorus</i>	0.095	0.959	0.845	0.586
<i>Forb cover</i>	0.095	0.958	0.863	0.569
<i>Green (biologically active) grass cover</i>	0.095	0.955	0.925	0.512
<i>Contribution made by Pogonarthria squarrosa</i>	0.095	0.954	0.953	0.486

Distance to nearest cover contributes most to the overall discrimination between species, followed by soil clay content, percent contribution to biomass of *H. contortus*, grass sward height and contribution to biomass by *D. eriantha* and *U. mossambicensis*. Time since last burn and distance to water are also important determinants of habitat utilization by herbivores during this season.

Distance to nearest cover is more indicative of vegetation structure than actual predator avoidance (which was the rationale for its estimation) suggesting that herbivore habitat preferences are largely influenced by vegetation structure during the winter period.

The same may be said for soil clay content. The animals do not select habitat based on the soil type *per se*, rather their preference or avoidance of clay soils is influenced by the vegetation type and structure associated with these soils. Herbaceous growth on clay soils tends to be more dense and vigorous than on sandy soils (pers. obs.)

It is worth noting that distance to water, not important during the wet season, is now an important determinant of the herbivore community niche. As the year has progressed, so surface water has become a determining factor.

4.3.2.2 Canonical analysis and dimensionality of the community niche

Grass sward height proves to be the most important variable of the first discriminant function (following Table 8), defining a gradient from one of tall grass where *D. eriantha* is abundant to a shorter sward.

The second discriminant function is one of high presence of the palatable perennials *U. mossambicensis* and *P. maximum* vs. areas further from water where the sward is patchy and dominated by other grass species.

The third function defines a gradient ranging simply from areas of closed vegetation where *H. contortus* and (to a lesser extent) *P. maximum* are abundant to more open areas where other grass species are more abundant. These three DF's account for 63% of the explained variance extracted.



Table 8: The standardized coefficients for 20 variables from a DF analysis of 11 species in the cool dry season. Bold coefficients are those considered strongly influential.

Variables	DF 1	DF 2	DF 3
Explained variance %	28	20	15
Grass sward height	-0.542	0.334	0.045
Contribution to sward by <i>Urochloa mossambicensis</i>	0.094	-0.666	0.186
Distance to cover	-0.034	0.215	0.551
Clay content	-0.376	0.366	0.237
Contribution to sward by <i>Digitaria eriantha</i>	-0.461	-0.381	0.002
Time since burn	-0.082	-0.001	0.100
Contribution to sward by <i>Heteropogon contortus</i>	-0.266	0.004	-0.450
Distance to water	-0.205	0.424	0.049
Slope	-0.098	0.080	-0.137
Tree volume	-0.227	-0.186	0.188
Nitrogen content	-0.223	-0.136	0.299
Bare patches	0.243	0.355	-0.248
Brown grass cover	-0.246	-0.228	0.055
Rock cover	0.209	0.056	-0.086
Distance to open vantage	-0.174	-0.155	-0.290
Contribution to sward by <i>Panicum maximum</i>	-0.165	-0.413	-0.307
Shrub volume	-0.055	-0.222	0.243
Contribution to sward by <i>Setaria incrassata</i>	-0.165	-0.182	0.214
Contribution to sward by <i>Cenchrus ciliaris</i>	-0.193	-0.191	-0.142
Altitude	0.113	-0.268	-0.286
<i>Eigen value</i>	<i>0.768</i>	<i>0.559</i>	<i>0.437</i>
<i>Cum.Prop</i>	<i>0.275</i>	<i>0.476</i>	<i><u>0.633</u></i>

4.3.2.3 Species separation within the community niche

Following Figure 15, the species niche centroids are plotted along the first two DF's. Again, the axes are scaled in proportion to the variance extracted by each DF (Table 8).

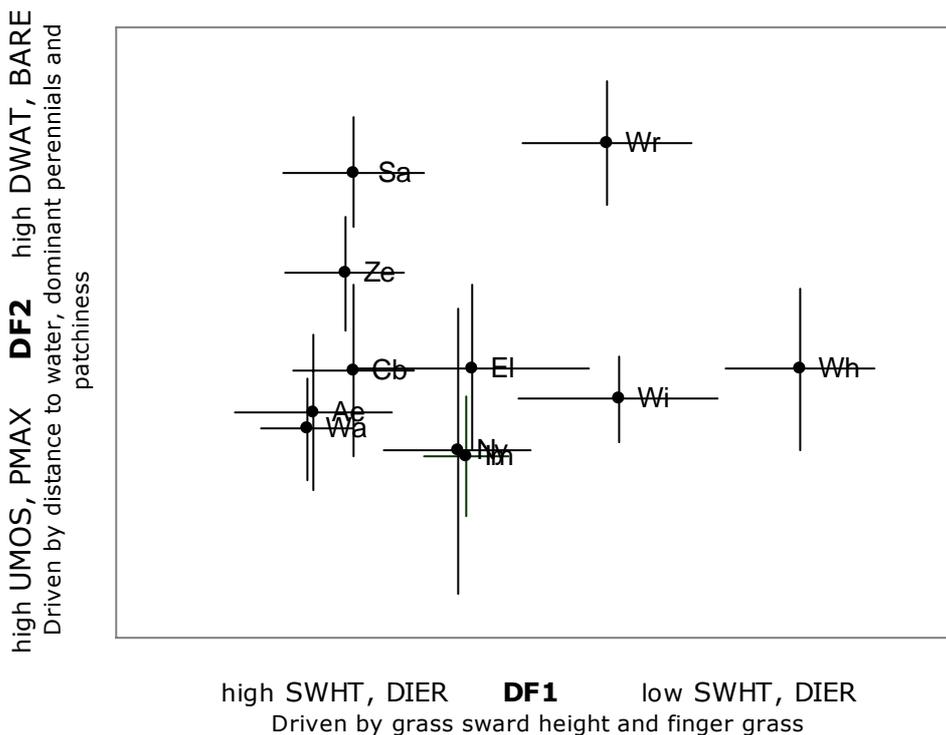


Figure 15: Location of species niches within the community niche for the cool dry season. Their location is determined by the factors represented along the first and second environmental gradients.

Species centroids: Ae = elephant, Cb = buffalo, El = eland, Im = impala, Ny = nyala, Sa = sable, Wa = waterbuck, Wh = warthog, Wi = wildebeest, Wr = white rhino and Ze = zebra.

Variable mnemonics: BARE = Bare patches, DIER = *Digitaria eriantha*, DWAT = distance to water, PMAX = *Panicum maximum*, SWHT = grass sward height, UMOS = *Urochloa mossambicensis*.

Along the first environmental gradient, warthog are apparently ecologically separate from other species during this season, selecting areas where the grass sward is low and where *D. eriantha* is less abundant. Wildebeest and white rhino also select a relatively short grass sward during this season, while most other species, particularly elephant, waterbuck, zebra and sable antelope prefer areas where the grass sward is relatively taller.

White rhino and sable are ecologically separate from the other species by selecting areas further from water. Zebra also show a preference for these areas. All other herbivore species apparently stay near water, particularly nyala, and select a relatively thicker grass sward where the species *P. maximum* and/or *U. mossambicensis* are more abundant.

There is apparent niche overlap among many of the species, although this does not imply competition (Putman 1996), particularly given that resources were still plentiful during this period (pers. obs.). There appears to be only a slight niche overlap between sable antelope and zebra, while white rhino do not experience niche overlap with any species.

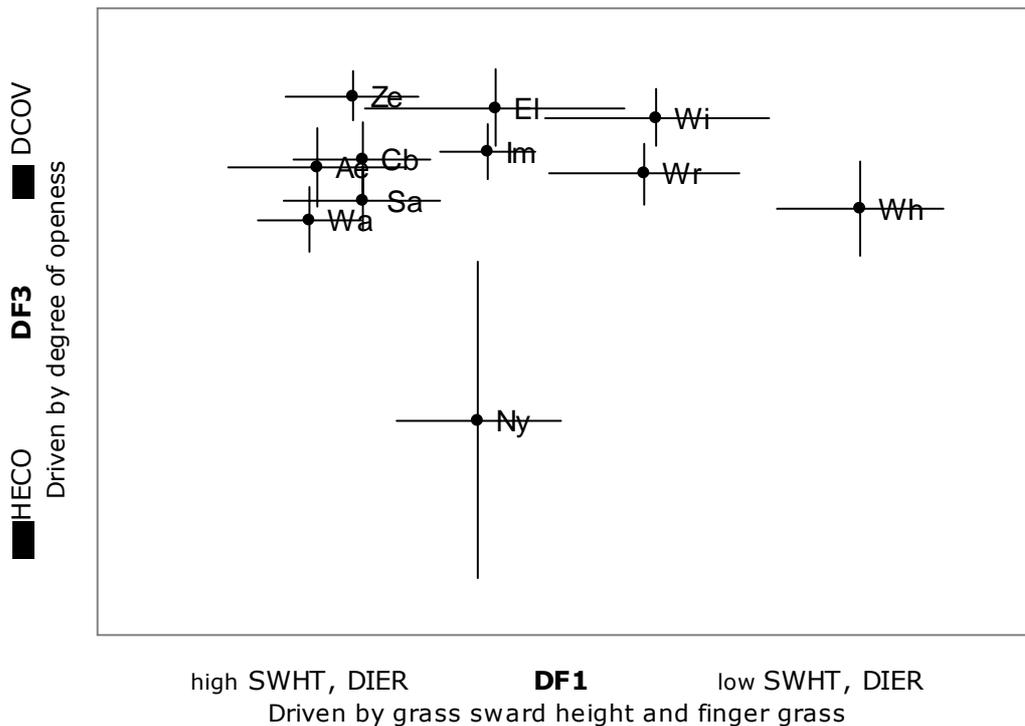


Figure 16: Location of species niches within the community niche for the cool dry season. Their location is determined by the factors represented along the first and third environmental gradients.

Species centroids: Ae = elephant, Cb = buffalo, El = eland, Im = impala, Ny = nyala, Sa = sable, Wa = waterbuck, Wh = warthog, Wi = wildebeest, Wr = white rhino and Ze = zebra.

Variable mnemonics: DCOV = Distance to cover, DIER = *Digitaria eriantha*, HECO = *Heteropogon contortus*, SWHT = grass sward height.

Following Figure 16, distance to cover separates nyala from all other species. Distance to cover was estimated with predator avoidance in mind, but may be interpreted as a measure of openness, i.e. areas where distance to suitable cover from predators is small represents dense vegetation while open veld is represented by high distance to cover. Nyala thus prefer dense vegetation where grass sward height is high, presumably as a predator avoidance strategy. Zebra, eland and wildebeest apparently prefer open areas. Sable antelope and

waterbuck appear to select less open areas, probably near watercourses, but their niches do not overlap with nyala.

Sable antelope here experience niche overlap with waterbuck, elephant and buffalo, while the white rhino population do not experience obvious niche overlap.

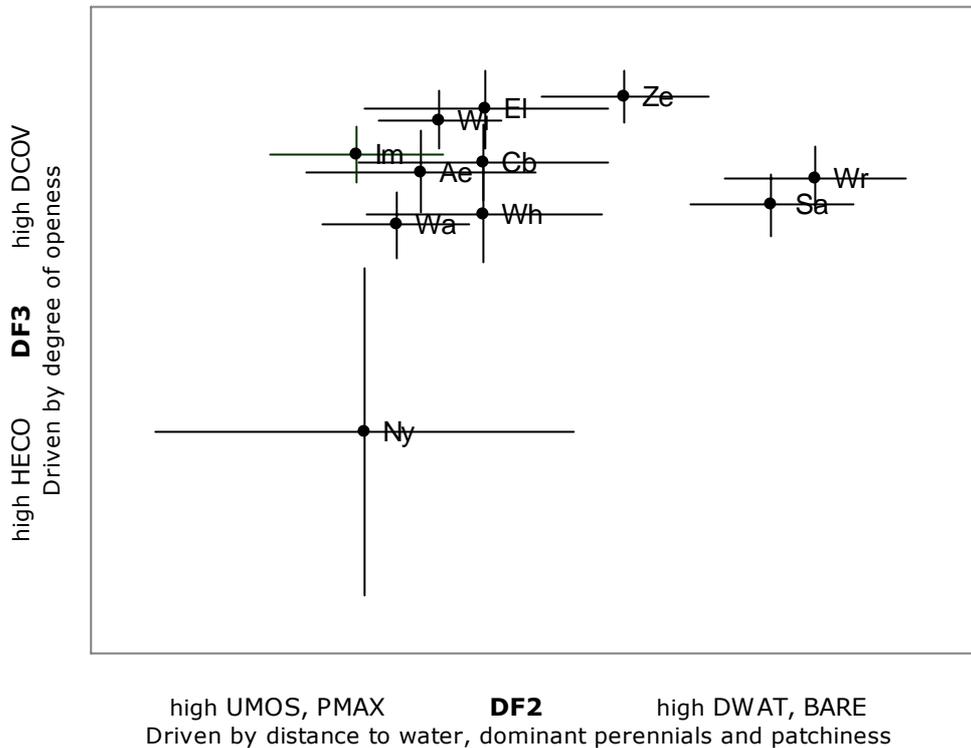


Figure 17: Location of species niches within the community niche for the cool dry season. Their location is determined by the factors represented along the second and third environmental gradients.

Species centroids: Ae = elephant, Cb = buffalo, Ei = eland, Im = impala, Ny = nyala, Sa = sable, Wa = waterbuck, Wh = warthog, Wi = wildebeest, Wr = white rhino and Ze = zebra.

Variable mnemonics: BARE = Bare patches, DCOV = Distance to cover, DWAT = distance to water, HECO = *Heteropogon contortus*, PMAX = *Panicum maximum*, UMOS = *Urochloa mossambicensis*

Following Figure 17, nyala once more are ecologically distinct, utilizing a dense vegetation type close to water and in a grass sward where *P. maximum* and *U. mossambicensis* are abundant. White rhino and sable antelope are also ecologically distinct by selecting more open and patchy veld relatively further from water. There is a large degree of niche overlap among other species along

these two environmental gradients, with all remaining herbivores selecting a relatively open veld near water, and usually in areas where *U. mossambicensis* and *P. maximum* are abundant.

To summarize: grass sward height, patchiness of the sward, distance to water, degree of openness and contribution to the grass sward by the perennials *D. eriantha*, *H. contortus* and *U. mossambicensis* largely define herbivore distribution during the cool dry winter season.

Warthog, wildebeest and white rhino show a preference for short grass areas over this period, while waterbuck, buffalo, sable antelope and zebra apparently prefer a relatively tall grass sward. Sable antelope and white rhino show no apparent association with the grasses *U. mossambicensis* and *P. maximum* and appear to prefer a more patchy grass sward. These two species, along with zebra, appear to forage further from water than all other herbivores. This trend becomes apparent as the seasons progressively dry. Nyala, impala, elephant, waterbuck and wildebeest all appear to select habitat relatively close to surface water.

4.3.3 Hot dry season

Data was collected in the hot-dry season during September and October 2001. During this season, literature (Eltringham 1979; Leuthold 1977; Owen-Smith 1992) supports the view that mixed feeders select browse in preference to grasses. Thus, the mixed feeders avoid direct competition with the predominantly grazing species during this crucial period, when resources are low. For this reason, two analyses were done: one involving DFA of all species, and another of 'pure' grazing species. This enabled a more complete insight into relations between the grazing species during the critical hot-dry season.

As with the other seasons, data was initially normalized and any variables that were correlated were subsequently discarded. The results are presented in Appendix 11.

4.3.3.1 Discriminating power of habitat variables

Following Table 9, distance to water is the most important habitat variable in discriminating between species utilization. Water is a limiting factor during the hot-dry season. This does not necessarily imply that all animals are dependent on water, or at least found within close proximity to water. It does suggest that,

at this time of year, some species tend to stay close to water sources and the associated habitat types, while other species venture further in order to forage.

Distance to open vantage, percent contribution of *P. maximum* and sedge cover are also important variables that significantly contribute to discrimination between species. Distance to open vantage is more indicative of woody plant density than actual distance to a safe vantage point, and thus predator avoidance. This can also be said for percent contribution of *P. maximum* to herbaceous biomass, although this is a palatable grass species (pers. obs.).

Table 9: Wilk's Lambda values (discriminatory power), and percentage levels of probability for the variables included in the hot dry season analysis. Variables in italics were excluded from the model. Variables indicated by an asterisk are those that significantly contribute to discrimination between groups.

Variable	Wilks' Lambda	Partial Wilk's λ	F Remove	p-level
Distance to water	0.134	0.773	5.465	0.000*
Contribution to sward by <i>Panicum maximum</i>	0.121	0.853	3.194	0.001*
Distance to open vantage	0.121	0.855	3.165	0.001*
Sedge cover	0.117	0.882	2.483	0.008*
Forb cover	0.117	0.887	2.374	0.011*
Time since burn	0.116	0.892	2.253	0.017*
Grass sward height	0.116	0.895	2.182	0.021*
Brown grass cover	0.116	0.895	2.180	0.021*
Litter cover	0.115	0.903	1.988	0.037*
Nitrogen content	0.115	0.904	1.969	0.039*
Contribution to sward by <i>Heteropogon contortus</i>	0.114	0.906	1.919	0.045*
Contribution to sward by <i>Urochloa mossambicensis</i>	0.114	0.909	1.873	0.051
Distance to cover	0.114	0.909	1.857	0.054
Altitude	0.114	0.911	1.821	0.060
Shrub volume	0.112	0.926	1.482	0.149
Bare patches	0.112	0.928	1.432	0.169
Slope	0.111	0.934	1.311	0.227
Tree volume	0.110	0.943	1.118	0.351
<i>Clay content of soil</i>	<i>0.101</i>	<i>0.972</i>	<i>0.542</i>	<i>0.859</i>
<i>Green grass cover</i>	<i>0.099</i>	<i>0.956</i>	<i>0.845</i>	<i>0.586</i>
<i>Available phosphorus</i>	<i>0.099</i>	<i>0.953</i>	<i>0.918</i>	<i>0.517</i>
<i>Contribution to sward by Digitaria eriantha</i>	<i>0.099</i>	<i>0.953</i>	<i>0.921</i>	<i>0.515</i>
<i>Contribution to sward by Pogonarthria squarrosa</i>	<i>0.099</i>	<i>0.951</i>	<i>0.945</i>	<i>0.493</i>
<i>Rock cover</i>	<i>0.098</i>	<i>0.950</i>	<i>0.975</i>	<i>0.467</i>

4.3.3.2 Canonical analysis and dimensionality of the community niche

Following Table 10, DF 1 is overwhelmingly defined by distance to water followed by contribution of *P. maximum* to the grass sward and distance to open vantage. Thus the gradient is one of areas close to water where

vegetation is dense (high distance to open vantage) and usually woody (pers. obs.) and *P. maximum* abundant vs. relatively open areas further from water where the grass sward is typically dominated by species other than *P. maximum*.

DF 2 is characterized by brown grass cover, percent contribution of *U. mossambicensis* to biomass patchiness of the sward. The gradient is one of a dense grass sward that is mostly senescent vs. a more open, shorter patchy sward that holds less senescent leaf and stalk cover and where *U. mossambicensis* is generally abundant.

DF 3 concerns a gradient of tall grass under a relatively dense tree canopy that has not been burnt recently and where shrubs are common vs. short grass areas that are relatively recently burnt and where brown grass cover is high and generally composed of *P. maximum*.

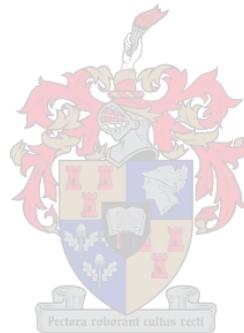


Table 10: The standardized coefficients for 18 variables from a DF analysis of 11 species in the hot dry season. Bold coefficients are those considered strongly influential.

Variables	DF 1	DF 2	DF 3
Explained variance %	32	27	13
Distance to water	-0.712	-0.277	-0.064
Grass sward height	-0.190	0.298	0.538
Distance to open vantage	0.477	0.061	-0.384
Contribution to sward by <i>Urochloa mossambicensis</i>	0.207	-0.415	0.096
Sedge cover	-0.178	0.383	0.218
Contribution to sward by <i>Panicum maximum</i>	0.509	0.280	-0.444
Altitude	0.094	0.232	0.285
Tree volume	0.125	-0.212	0.373
Nitrogen content	0.262	-0.290	-0.040
Forb cover	-0.342	0.029	-0.030
Brown grass cover	0.053	0.498	-0.568
Distance to cover	-0.225	-0.125	0.317
Litter cover	-0.227	-0.028	0.028
Time since burn	0.212	-0.051	0.393
Contribution to sward by <i>Heteropogon contortus</i>	0.114	0.148	-0.179
Shrub volume	0.071	-0.244	0.384
Bare patches	0.087	-0.321	0.230
Slope	0.099	0.187	0.336
<i>Eigen value</i>	<i>0.906</i>	<i>0.780</i>	<i>0.345</i>
<i>Cum.Prop</i>	<i>0.319</i>	<i>0.594</i>	<i>0.715</i>

4.3.3.3 Species separation within the community niche

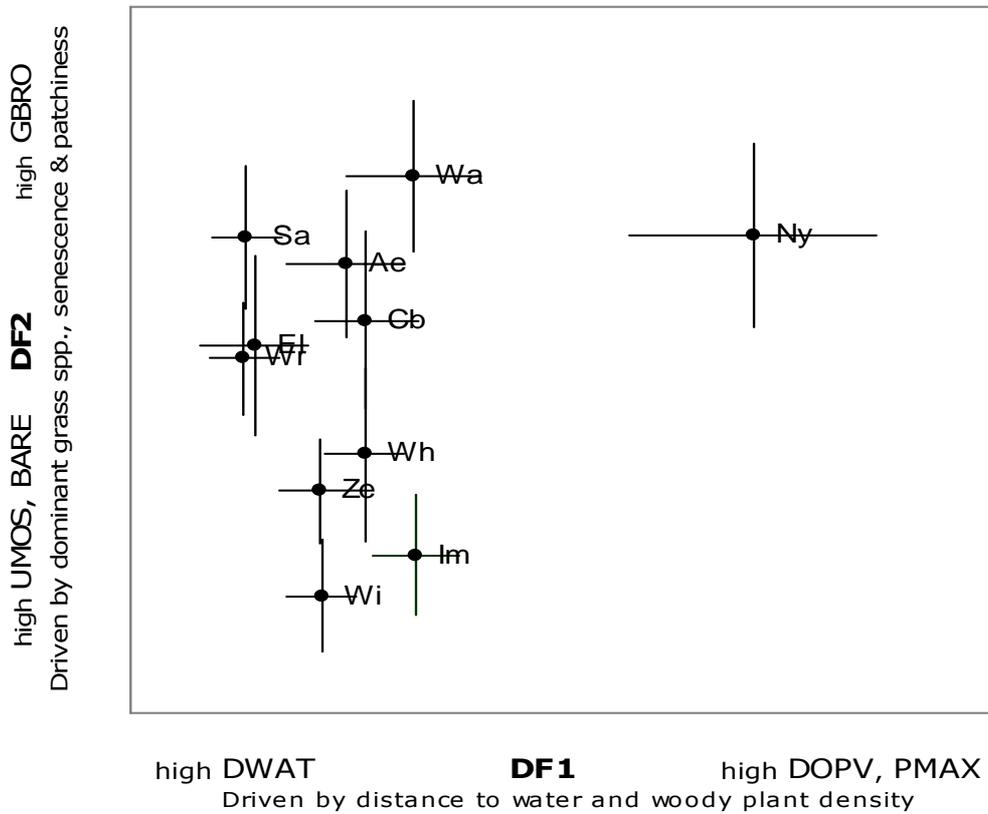


Figure 18: Location of species niches within the community niche for the hot dry season. Their location is determined by the factors represented along the first and second environmental gradients.

Species centroids: Ae = elephant, Cb = buffalo, El = eland, Im = impala, Ny = nyala, Sa = sable, Wa = waterbuck, Wh = warthog, Wi = wildebeest, Wr = white rhino and Ze = zebra.

Variable mnemonics: BARE = bare patches, DOPV = distance to open vantage, DWAT = distance to water, GBRO = brown grass cover, PMAX = *Panicum maximum*, UMOS = *Urochloa mossambicensis*.

Following Figure 18, nyala are once more ecologically separated from other species along an environmental gradient concerning distance to surface water and woody plant density (high distance to vantage is here taken to be indicative of dense vegetation, usually comprising shrubs and tree saplings). Nyala prefer a dense vegetation type close to water sources and where *P. maximum* is the abundant grass species. All other species appear to prefer habitat relatively further from water, particularly sable antelope, eland and white rhino. Wildebeest, impala, zebra and to a lesser extent warthog prefer relatively short grass that is patchy in appearance and dominated by *U. mossambicensis*.

Waterbuck and sable antelope appear to prefer a more dense grass sward that is mostly senescent (although this does not imply that the animals are feeding on senescent leaves and stems) and dominated by grasses other than *U. mossambicensis*. Waterbuck appear to prefer habitat that is relatively closer to surface water. The remaining species appear intermediate in preference, although all avoid the preferred riverine habitat of nyala.

Competitive niche overlap is high, although feeding level selection is not explored and there is unlikely to be intense competition here given that mixed feeders select browse during this period.

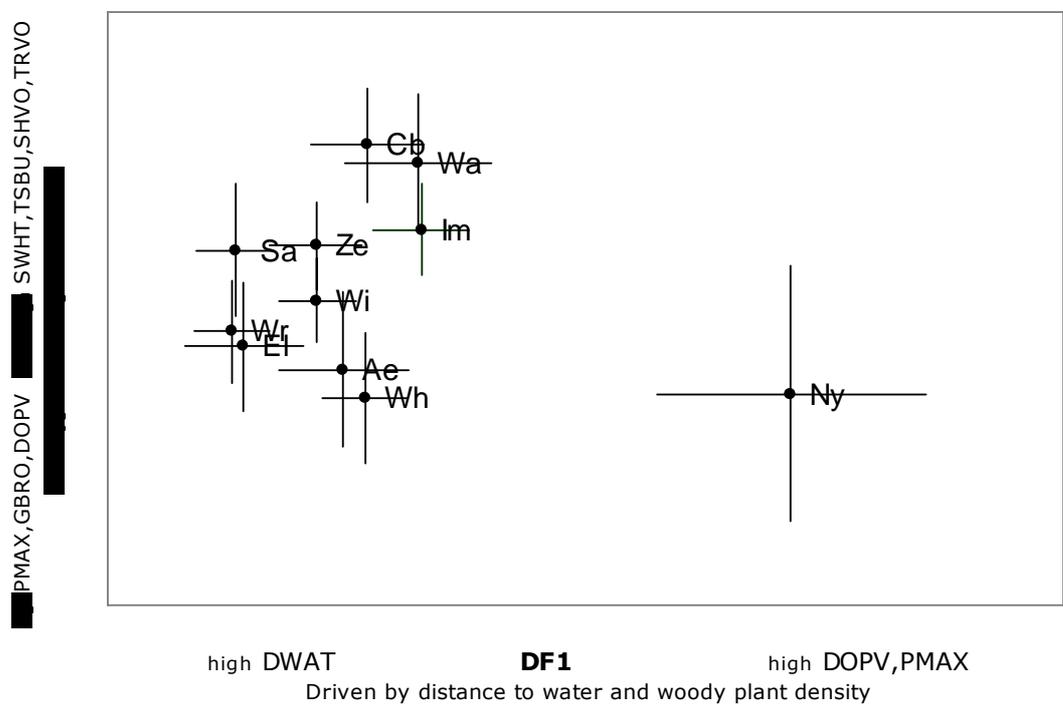


Figure 19: Location of species niches within the community niche for the hot dry season. Their location is determined by the factors represented along the first and third environmental gradients.

Species centroids: Ae = elephant, Cb = buffalo, El = eland, Im = impala, Ny = nyala, Sa = sable, Wa = waterbuck, Wh = warthog, Wi = wildebeest, Wr = white rhino and Ze = zebra.

Variable mnemonics: DOPV = distance to open vantage, DWAT = distance to water, GBRO = brown grass cover, PMAX = *Panicum maximum*, SHVO = shrub volume, SWHT = grass sward height, TRVO = tree volume, TSBU = time since last burn.

Following Figure 19, nyala are ecologically separate from other species selecting a dense grass sward in vegetation that is generally dense but not necessarily dense in woody density. Nyala are likely to select riverine type vegetation under

tree canopies where *P. maximum* thrives, but where the actual density of the trees is relatively low. Waterbuck and buffalo conversely select areas where the grass sward is relatively greener and under a more woody cover. These species generally take to the hills during this period (pers. obs.) also explaining the preference for areas not recently burnt, as the hills have not been exposed to fire in recent times (Clegg, S. pers. comm.). The remaining species appear to prefer intermediate habitat that is relatively further from water and experiencing a high degree of niche overlap along these gradients.

Following Figure 20, the animals appear spread out over these two environmental gradients. Waterbuck, nyala and sable antelope apparently prefer a denser grass sward that tends to be more senescent and where presence of *U. mossambicensis* is low, however, waterbuck and sable antelope prefer a taller grass sward where tree volume and shrub volume is relatively high. Nyala apparently prefer an open tree canopy where the grass sward is dense, as do warthog. Impala, wildebeest and zebra appear similar in their habitat preferences choosing a patchy grass sward in intermediate areas of tree and shrub volume. Niche overlap is high with sable antelope sharing habitat with nyala and waterbuck and white rhino with eland.



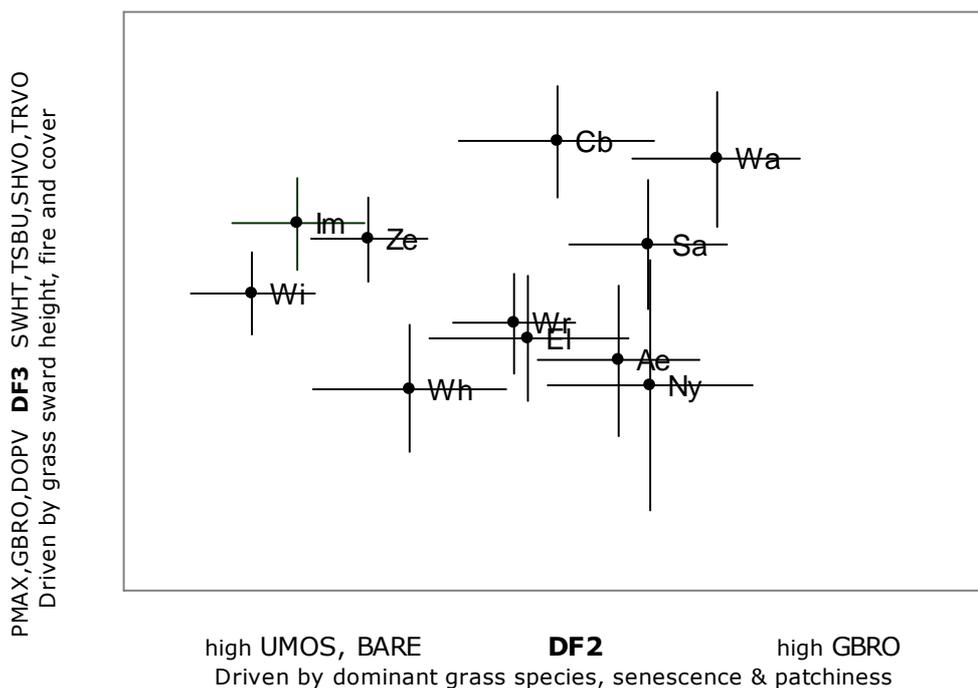


Figure 20: Location of species niches within the community niche for the hot dry season. Their location is determined by the factors represented along the second and third environmental gradients.

Species centroids: Ae = elephant, Cb = buffalo, El = eland, Im = impala, Ny = nyala, Sa = sable, Wa = waterbuck, Wh = warthog, Wi = wildebeest, Wr = white rhino and Ze = zebra.

Variable mnemonics: BARE = bare patches, DOPV = distance to open vantage, GBRO = brown grass cover, PMAX = *Panicum maximum*, SHVO = shrub volume, SWHT = grass sward height, TRVO = tree volume, TSBV = time since last burn, UMOS = *Urochloa mossambicensis*.

To summarize: among all study species during the hot dry season, water is the main determinant of distribution, with nyala never venturing far from water sources (or the associated habitat) and sable antelope, eland and white rhino venturing furthest. Cover also determines herbivore distribution here with sable eland and white rhino preferring open areas and nyala dense vegetation types, that are usually woody (pers. obs.). Height, degree of senescence and patchiness of the grass sward are important determinants here, with sable antelope, buffalo, waterbuck and nyala preferring a relatively denser and tall sward that happens to comprise of mostly senescent leaves and stems. Wildebeest, zebra and warthog apparently prefer shorter grass areas where the sward is patchy and dominated by *U. mossambicensis*.

Competitive niche overlap for habitat appears high during this season, with many species having similar habitat preferences along these broad environmental gradients. Competition at the feeding level is not explored.

4.3.3.4 Discriminating power of habitat variables for grazers

It is necessary at this time of year to view centroid locations of 'pure' grazer's as it must be remembered that mixed feeders shift their feeding strategy to mostly browse at this time of year (Skinner & Smithers 1990). Grazers are here defined as species that predominantly graze throughout the year. Herbivores excluded from this analysis, i.e. mixed feeders are defined as those species that select more plant foliage, roots etc. during the dry period than grass. Thus eland, elephant, impala, nyala and warthog were excluded here.

From the management perspective, this is an important analysis. Management here are primarily concerned about sable antelope and white rhino, both 'pure' grazers. Furthermore, it is during the critical dry season when interspecific competition is assumed to be most intense (Sinclair 1975; Schoener 1982) and where species are assumed to adopt their essential niches (Putman 1996). Thus, insight into the utilization of habitat among grazers and their spatial distribution (along those environmental gradients shown to be important) is vital and will enable management to make more educated decisions concerning the conservation of their rare and valuable species.

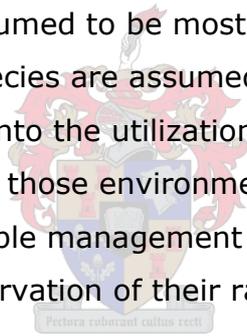


Table 11: Wilk's Lambda values (discriminatory power), and percentage levels of probability for the variables included in the hot dry season analysis of grazers only. Variables indicated by an asterisk are those that significantly contribute to discrimination between groups. Variables in italics were excluded from the model.

Variable	Wilks' Lambda	Partial Wilk's Λ	F Remove	p-level
Distance to water	0.215	0.842	3.977	0.002*
Altitude	0.211	0.859	3.481	0.006*
Sedge cover	0.211	0.859	3.475	0.006*
Contribution to sward by <i>Heteropogon contortus</i>	0.210	0.861	3.420	0.007*
Nitrogen content	0.204	0.886	2.741	0.023*
Shrub volume	0.201	0.898	2.397	0.042*
Slope	0.201	0.901	2.322	0.048*
Grass sward height	0.201	0.902	2.307	0.049*
Forb cover	0.200	0.906	2.188	0.061
Rock cover	0.199	0.910	2.098	0.071
Distance to cover	0.198	0.916	1.944	0.093
Contribution to sward by <i>Urochloa mossambicensis</i>	0.195	0.928	1.653	0.152
Tree volume	0.194	0.933	1.519	0.190
Brown grass cover	0.192	0.942	1.294	0.272
<i>Contribution to sward by Pogonarthria squarrosa</i>	0.178	0.986	0.292	0.916
<i>Green grass cover</i>	0.176	0.975	0.544	0.743
<i>Contribution to sward by Digitaria eriantha</i>	0.176	0.974	0.566	0.726
<i>Available phosphorus</i>	0.175	0.969	0.662	0.653
<i>Bare patches</i>	0.175	0.969	0.674	0.644
<i>Clay content</i>	0.175	0.966	0.734	0.600
<i>Contribution to sward by Panicum maximum</i>	0.175	0.965	0.755	0.584
<i>Time since burn</i>	0.173	0.957	0.952	0.451
<i>Litter cover</i>	0.173	0.955	0.965	0.461

Following Table 11, distance to water again appears to be an important determinant of grazing herbivore distribution. Altitude is a variable that separates species preferring the hills during this season from those preferring the low-lying areas. The same may be said for sedge cover. Sedge *per se* is unlikely to be an important determinant of herbivore distribution but rather the habitat with which sedges are associated i.e. valleys within the hills (pers. obs). Grass sward height is once more an important determinant of distribution, as is forb cover and presence of the palatable perennial *H. contortus*.

4.3.3.5 Canonical analysis and dimensionality of the community niche

Table 12 shows the first three DF's accounting for 91% of the explained variance. The first DF is defined by a gradient of a tall and largely senescent grass sward where *H. contortus* is abundant and where sedges may occur vs. a shorter sward that is in open veld and where *H. contortus* is unlikely to be

found. Distance to cover here also considers grass, and so habitat characterized by low distance to cover does not necessarily imply high woody density.

DF 2 is defined by a gradient of areas further from water where *H. contortus* is abundant vs. higher altitude areas closer to water, where tree and shrub volume is higher.

DF 3 follows a gradient of high altitude areas vs. areas where rock and forb cover are high as well as sedge cover.

Table 12: The standardized coefficients for 14 variables from a DF analysis of 6 species in the hot-dry season. Bold coefficients are those considered to be strongly associated with each DF.

Variables	DF 1	DF 2	DF 3
Explained variance %	52	27	12
Distance to water	0.144	0.603	-0.202
Altitude	0.096	-0.386	-0.695
Contribution to sward by <i>Heteropogon contortus</i>	0.386	0.378	0.338
Contribution to sward by <i>Urochloa mossambicensis</i>	-0.278	0.237	0.207
Grass sward height	0.478	-0.169	0.048
Shrub volume	-0.236	-0.325	-0.224
Sedge cover	0.535	0.010	0.415
Nitrogen content	-0.399	-0.067	0.348
Rock cover	0.267	0.246	0.456
Forb cover	0.271	0.134	0.517
Slope	0.383	-0.359	0.179
Distance to cover	-0.430	-0.039	-0.106
Tree volume	-0.228	-0.343	0.156
Brown grass cover	0.429	-0.012	-0.006
<i>Eigen value</i>	<i>1.189</i>	<i>0.625</i>	<i>0.284</i>
<i>Cum.Prop</i>	<i>0.517</i>	<i>0.789</i>	<i>0.912</i>

4.3.3.6 Species separation within the community niche (grazers only)

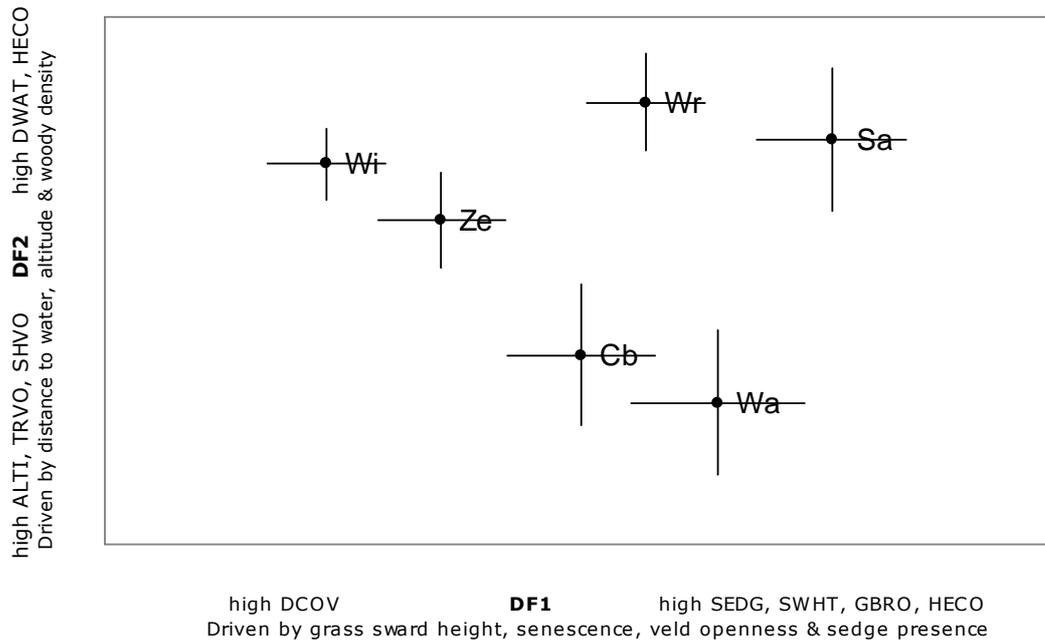


Figure 21: Location of grazing species niches within the community niche for the hot dry season. Their location is determined by the factors represented along the first and second environmental gradients.

Species centroids: Cb = buffalo, Sa = sable, Wa = waterbuck, Wi = wildebeest, Wr = white rhino and Ze = zebra.

Variable mnemonics: ALTI = altitude, DCOV = distance to cover, DWAT = distance to water, GBRO = brown grass cover, HECO = *Heteropogon contortus*, SEDG = sedge cover, SHVO = shrub volume, SWHT = grass sward height, TRVO = tree volume.

Following Figure 21, the grazing herbivores are ecologically well separated during the hot-dry period, suggesting exclusive niche use by each species as a means of avoiding competition, after Schoener (1982). Sable antelope and white rhino apparently associate with low altitude and open habitat further from water and in relatively tall grass. Both species apparently select a grass sward that is mostly senescent and thus not recently burnt. Buffalo and waterbuck are ecologically similar along these two environmental gradients and experience slight niche overlap. Both associate with water, usually in high altitude areas, characterized by a relatively dense tree and shrub cover and medium to tall grass sward where sedges may be present. Wildebeest and zebra are also ecologically similar in their habitat preferences, both species apparently preferring areas where the grass sward is low, the leaf and stalk cover relatively green and within low altitude, open habitat.

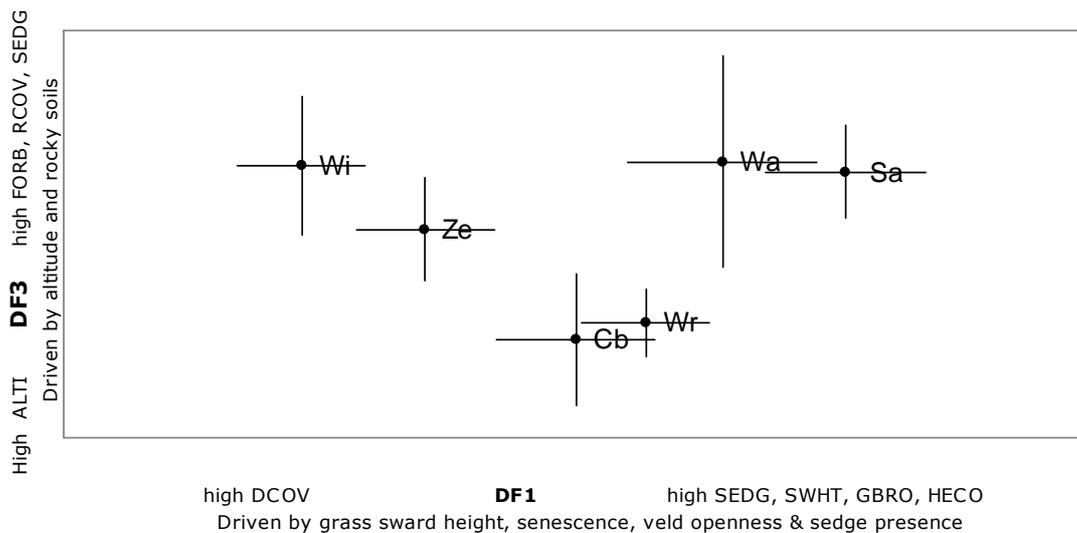


Figure 22: Location of grazing species niches within the community niche for the hot dry season. Their location is determined by the factors represented along the first and third environmental gradients.

Species centroids: Cb = buffalo, Sa = sable, Wa = waterbuck, Wi = wildebeest, Wr = white rhino and Ze = zebra.

Variable mnemonics: ALTI = altitude, DCOV = distance to cover, FORB = forb cover, GBRO = brown grass cover, HECO = *Heteropogon contortus*, RCOV = rock cover, SEDG = sedge cover, SWHT = grass sward height.

Following Figure 22, sable antelope and waterbuck apparently select similar habitat along the second and third environmental gradients, both preferring relatively tall grass on mostly rocky soils where forbs are present. Buffalo and white rhino also appear ecologically similar along these gradients both apparently selecting relatively higher altitude habitat where forb and rock cover is low. Zebra and wildebeest are again similar, preferring low altitude habitat where the forb and rock cover is relatively high and grass height low.

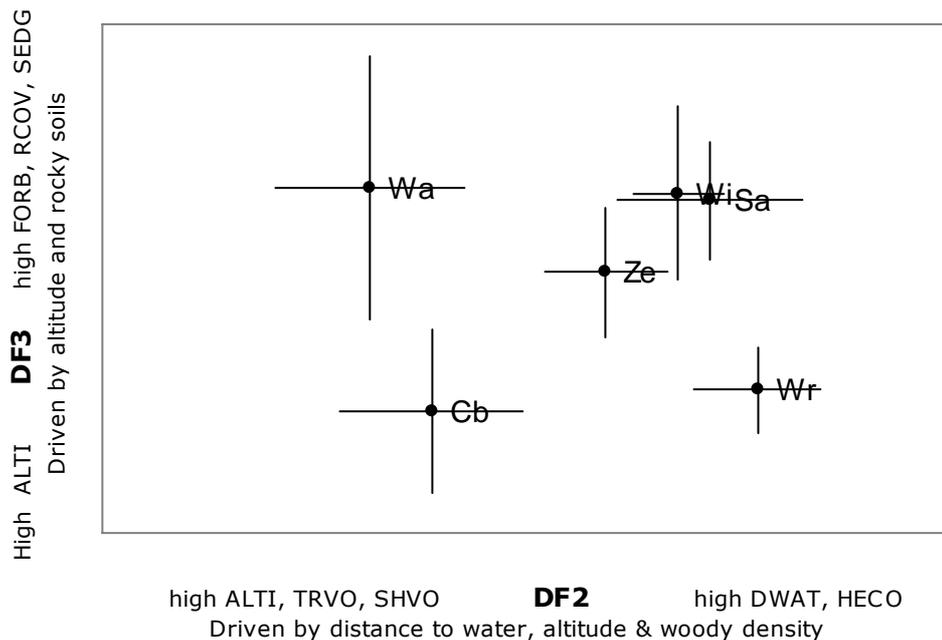


Figure 23: Location of grazing species niches within the community niche for the hot dry season. Their location is determined by the factors represented along the second and third environmental gradients.

Species centroids: Cb = buffalo, Sa = sable, Wa = waterbuck, Wi = wildebeest, Wr = white rhino and Ze = zebra.

Variable mnemonics: ALTI = altitude, DWAT = distance to water, FORB = forb cover, HECO = *Heteropogon contortus*, RCOV = rock cover, SEDG = sedge cover, SHVO = shrub volume, TRVO = tree volume.

Following Figure 23, sable antelope and wildebeest are ecologically similar both preferring low-lying and open habitat further from water and where rocky soils and forb cover are relatively high. There is quite considerable niche overlap between these species along these gradients. The remaining species are ecologically separate, with white rhino and buffalo preferring non-rocky type soils in higher altitude areas, while waterbuck show a wide niche breadth along the gradients of altitude, soil rockiness, sedge cover and woody density.

To summarize: distance to water, tree and shrub volume, grass sward height, altitude, sedge and forb cover and contribution to biomass by the grass *Heteropogon contortus* all contribute to the determination of grazing herbivore distribution during the critical hot dry season.

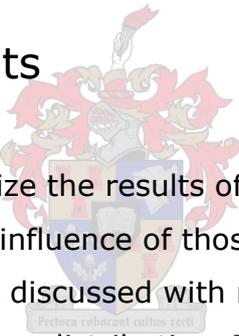
Sable antelope and white rhino appear to utilize a relatively tall and mostly senescent grass sward in a relatively open veld further from water. The

utilization of a mostly senescent grass sward does not imply that these species are taking dead plant parts. Personal observation revealed that small patches of green grass, among a mostly senescent sward, were taken. The method of measurement relied on a mean value for greenness/brownness of sward and thus the resolution was not sufficiently adequate to account for small green patches.

Wildebeest and zebra also apparently select areas relatively further from water and in open veld, but prefer a shorter grass sward. Buffalo and waterbuck apparently prefer a medium to tall grass sward that is relatively close to surface water, at a higher altitude and where tree and shrub volume is relatively high.

Very little competitive niche overlap is apparent, suggesting that grazing species adopt their essential niches during the critical period when resources are scarce (Putman 1996), thus avoiding direct interspecific competition (Schoener 1982).

4.4 Summary of results



It is necessary here to summarize the results of the DFA with management implications in mind. Thus, the influence of those habitat variables that may be manipulated by management is discussed with reference to seasonal differences and apparent effects on herbivore distribution. These results are not discussed at length here so as to avoid duplication of the final discussion in Chapter 6, where results are integrated and discussed with the implications to management in mind.

4.4.1 The distribution of large grazing herbivores along essential habitat gradients and potential for competition among them

The influence that surface water, fire, woody density, herbaceous structure and composition and extent of veld openness, have on herbivore distribution is summarized here.

Since this study essentially centres on the rare species (sable antelope and white rhino) and economically valuable species (sable antelope and buffalo), this discussion mostly considers these species. White rhino are economically valuable in the sense that they attract photographic tourists.

Owing to their protected status, these species are the property of the State and cannot be sold by Malilangwe at auction.

4.4.1.1 The influence of surface water

The presence and spacing of surface water is a vital management tool, and ecologically has a profound effect on the distribution of large herbivore species, particularly in a semi-arid environment such as ME.

The rainfall for the study duration was above average, as had been the preceding years and therefore most springs and certainly the major river systems were perennial (pers. obs.). No point in ME during the critical dry period during the study was further than 4.7 km from surface water (Figure 10), and therefore this 'window in time' was a relatively wet one. Nevertheless, distance to surface water was shown in the analyses to have a very important effect on herbivore distribution, particularly as the year became progressively drier, becoming the most important determining variable during the hot dry season. Moreover, an apparent separation of species was shown, some species preferring to stay near water all year, and others preferring to venture relatively further from water as the veld progressively dried.

Buffalo, impala, nyala, waterbuck and warthog stayed relatively close to water sources during the entire year. Eland, elephant, sable antelope, wildebeest, white rhino and zebra were shown to utilize habitat relatively further from water.

Impala, nyala, waterbuck and warthog are all classified by Goodman (1982) as non-mobile water dependent species that stay near water sources, thus helping to explain the distribution of these species at ME and the influence that water has on them. A likely explanation for the fact that buffalo were shown to be associated with water during the entire year is that the species probably prefer the habitat associated with surface water i.e. the hills and riverine type vegetation.

Eland, elephant, sable antelope, wildebeest, white rhino and zebra are classified as mobile water dependent species, with the exception of eland which are considered water independent (Goodman 1982), capable of travelling up to 10 km from surface water. All of these animals were shown to travel relatively further from water than other animals during the dry period.

No animal at ME during the study period needed travel further than 5 km from water, nonetheless, it is important to note that the analysis revealed a spatial separation among the large herbivores, with the non-mobile dependent species shown to always stay relatively close to water, and the mobile dependent species (with the exception of buffalo) shown to utilize habitat relatively far from surface water. Sable antelope and white rhino particularly travel further from surface water than all other species, even eland, in search of forage.

4.4.1.2 The influence of fire

A veld burning programme is pursued at ME with the objectives of maintaining plant species diversity, removing moribund and/or unacceptable grass material and preventing the encroachment of undesirable plants.

What is of interest here is how large grazing herbivores responded to burnt veld during the study period, i.e. was there an obvious movement of some species onto freshly burnt or recently burnt areas, implying that these areas held attractions such as a fresh, palatable and open grass sward. This was measured by recording the time since last burn for every sample plot.

Time since last burn is an important determinant of herbivore distribution during the wet and hot dry seasons. It appears to have little effect on the spatial distribution of 'pure' grazers during the hot dry season, possibly since other habitat factors were found to be more influential on grazing species distribution, and also possibly due to the freshness of the burns when data was collected, i.e. the grass sward had not had much time to re-grow, and in fact grass growth was only available to short grass grazers such as wildebeest during this period (pers. obs.).

During the wet season, freshly and recently burnt areas were characterized by a relatively short and vigorous grass sward, with little or no moribund (pers. obs.). Buffalo, sable antelope, wildebeest, white rhino and zebra showed positive associations with recently burnt areas during this period. Warthog were not shown to associate with freshly burnt areas over this period although the occasional personal sighting was made of warthog in freshly burnt areas. Impala, nyala and waterbuck showed no apparent preference for freshly burnt veld during this season. This may be due to the fact that nyala and

waterbuck particularly associated with riverine type vegetation that had not been recently burnt during the study period.

During the cool dry season, time since burn does not appear to have an important effect on herbivore distribution, other factors coming into play, namely distance to water, the height of the grass sward and the openness of the veld.

Bothma (1989) states that fire encourages the growth of perennial grasses in the herbaceous layer. This was not explored in this study, but the analyses did reveal strong associations among species with the perennial and mostly palatable (van Oudtshoorn 1992) grasses *P. maximum*, *U. mossambicensis* and *H. contortus*.

To conclude, there is apparent association with burnt veld by grazing species, particularly short grass grazers, and particularly during the wet season when the above average rainfall had allowed for vigorous growth.

4.4.1.3 The influence of woody plant density

Actual tree and shrub volume was shown to have relatively little effect on the distribution of grazing herbivores at ME, not being important during the wet and cool dry seasons. During the hot dry season, woody density was shown to be important in the ecological separation of all species with buffalo, waterbuck, impala, zebra and sable antelope showing positive associations with veld where tree and shrub volume was relatively high. Sable antelope and zebra were also shown to be associated with open veld (veld where the distance to open vantage was low) suggesting that these species prefer open woodland.

The analysis of 'pure' grazing species only showed that waterbuck, buffalo and to a lesser extent zebra preferred a more-woody habitat. Zebra apparently preferred open woodland, taking distance to cover into consideration. Wildebeest apparently preferred a less woody and open veld (openness here indicated by distance to cover) while sable antelope apparently preferred a less woody veld but actively selected habitat where cover from predators (in the form of dense vegetation, whether this be woody or not) was nearby.

Taking distance to cover and distance to open vantage to be indicative of veld openness (a high distance to cover value indicates relatively open veld, from the animals perspective, as would a low distance to open vantage value),

nyala are shown to associate with a relatively closed veld during the entire year, as are waterbuck, and to a much lesser extent warthog. Wildebeest, white rhino and zebra on the other hand associate with a relatively open veld for the entire year. Sable antelope apparently preferred an intermediate veld type during the year, where cover was available if needed. Elephant were shown to be associated with a more closed habitat, but it is likely that these animals are catholic in their choice of open vs. closed veld (pers. obs.).

4.4.1.4 The influence of herbaceous structure and composition

Herbaceous structure and composition is here defined by grass sward height, degree of patchiness and the contributions made by dominant grass species. Grass height is shown to be an important determining habitat variable, with some herbivores preferring a short sward and others a long sward. Species composition is also important. Associations by large grazing herbivores with a particular sward type is of particular interest to management as this variable may be manipulated through various means, namely fire, mowing and surface water placement. This will be explored further in Chapter 6.

Buffalo, sable antelope and waterbuck associated with a relatively tall grass sward for the entire year. Conversely, wildebeest and warthog associated with a short grass sward all year.

Impala apparently preferred a relatively short grass sward during the wet season (possibly as a predator avoidance strategy since this is when their young are dropped and visibility is important) and then shifted their preference to a relatively tall sward for the remainder of the year. Nyala were shown to prefer a tall grass sward during the wet and cool seasons, and then apparently shifted their preference to a medium to short sward, although their niche breadth along this gradient was wide. White rhino selected a relatively short grass sward during the wet and cool seasons (bearing in mind that the mean grass sward during these seasons was tall given the above average rainfall) and then apparently shifted their preference to a medium to tall grass sward during the hot dry season. Personal observation however, revealed that individual rhino mostly selected short grass species (particularly *Enneapogon scoparius*) within a tall grass sward. Finally, zebra were associated with a relatively short sward during the wet season, then shifted their preference to a taller sward

over the cool period, and then once more shifted their preference to a relatively short sward during the hot dry period.

The grass species *P. maximum*, *D. eriantha*, *H. contortus* and *U. mossambicensis* proved to be important determinants of herbivore distribution, although an animals association with a grass sward where one or more of the above-mentioned grass species occurred did not necessarily imply that the plant was being fed on. Nonetheless, all of these grass species have high grazing value (Stalmans 1994; van Oudtshoorn 1992), and are classified as perennials (although *U. mossambicensis* is generally considered biennial (van Oudtshoorn 1992)) therefore making them desirable grass species from management's perspective.

Nyala strongly associate with *P. maximum* during the hot wet season, although it is likely that the associated high canopy volume that this grass thrives under also contributes to this relation (pers. obs.)

Elephant, waterbuck, nyala and impala all associated with *U. mossambicensis*, *P. maximum* and *D. eriantha* during the cool season, while sable antelope and zebra associated with *D. eriantha* but not *U. mossambicensis* and *P. maximum*. White rhino did not utilize a grass sward where any of these grass species were abundant.

Among grazers during the hot dry season, sable antelope and waterbuck associated with a grass sward where *H. contortus* was usually present. Wildebeest and zebra avoided a grass sward where this species was present, although this doesn't imply that these animals deliberately avoided this species, but rather their habitat preference i.e. a short grass sward in open areas, was a habitat type where *H. contortus* was typically uncommon.

4.4.1.5 Potential for interspecific competition

Since this study is primarily concerned about three grazing herbivores, and since interspecific competition is assumed to shape the herbivore community during critical periods, after (Schoener 1982), and lastly since the hot dry season during the study period was the only season where resources could be considered limiting (Sinclair 1975), interspecific interactions among grazers during the critical season is specifically of interest here.

The potential for interspecific competition among grazers and mixed feeders may be inferred from the Figures in this Chapter. Interspecific

competition among grazers and mixed feeders during the critical dry season is unlikely as this is when mixed feeders turn to browse as their primary food intake (Eltringham 1979; Skinner & Smithers 1990). As the cool dry season during the study period was not likely to be a critical one due to the presence of large swards of biologically active (green) grass (pers. obs.), the interspecific interactions among species were not likely to have been serious enough to produce niche shifts, indicative of potential competition.

So, can interspecific competition among grazing species be inferred from the findings of this study? Are there any apparent niche shifts? Moreover, what are the implications?

Competition is notoriously difficult to prove, especially here. Putman (1996) comments on these difficulties by stating: "*the interpretation of measures of niche overlap in terms of the implications for competitive interaction is extremely problematical. A degree of overlap in resource use may be an essential pre-requisite for competition: but observation of high levels of overlap or separation in the field is itself ambiguous. High observed overlap may imply competition, but only if resources are limited; observation of high overlap might equally well be considered indicative of a lack of competition - on the basis that if severe competition were being experienced some niche-shift would have been expected, resulting in reduction of overlap.*

By that same token, observation of low levels of overlap in the field may not imply lack of competition - but may in fact reflect the end result of changes in the ecology of some or all species as a direct result of competition for shared resources.

Only where we find evidence of a clear shift in resource use of a species may we suspect a competitive interaction - or better still, where clear overlap in resource use is accompanied by an inverse relationship in population sizes of a given species pair."

These comments raise some very interesting points, especially; can a possible shift in utilization by a species or clear overlap among species be accompanied by an inverse relationship in population sizes of a species pair? Malilangwe's Research Dept. have on file graphical representations of species population trends (Appendix 12) after Goodman (2002), but these data have unfortunately only been collected over the past five years and trends are vague.

However, future trends, along with these results will help management and this is discussed further in Chapter 6.

The DF analysis for grazers during the hot dry period noticeably produces an ecological separate community, along habitat gradients of grass height, veld openness, distance to water and herbaceous layer characteristics. Along the first two, and most important environmental gradients (Figure 21), a pattern emerges whereby the six species appear paired with similar habitat preferences *viz.* sable antelope and white rhino, waterbuck and buffalo, and lastly wildebeest and zebra. There is slight niche overlap between buffalo and waterbuck. Along the third (and least important) environmental gradient there is apparent niche overlap between sable antelope and waterbuck, and buffalo and white rhino. These similarities and slight overlaps cannot be inferred as competition, or even the lack of it, after Putman (1996).

An important consideration, however, is the relationships between Type I, II and III (after Collinson & Goodman 1982) species. According to these authors, white rhino, buffalo and zebra are classified as Type I species i.e. bulk grazing species capable of causing an initial and drastic change in the climax vegetation and in the physical environment. This impacts negatively on sensitive and selective Type II species (sable antelope and waterbuck) which, and as a result, will decline in abundance. Other species, i.e. wildebeest are likely to benefit and increase in abundance as a result of the effects of Type I species, and are termed Type III species. Type III species have the ability to further modify and perpetuate the new environment state created by Type I species.

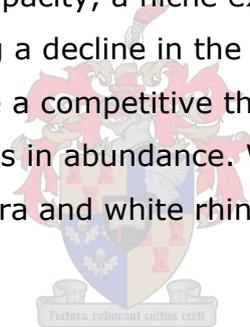
Therefore, the sable antelope population could experience a decline in abundance as a result of increasing bulk grazing populations (here white rhino). Wildebeest on the other hand could possibly possibly benefit from the effects of bulk grazing species, owing to a process of facilitation.

The only apparent niche shifts from the cool season to the hot season that could imply interspecific competition, or the results of that competition, after Putman (1996), are along the distance to surface water gradient. It becomes apparent during the cool dry season that some species, particularly sable antelope and white rhino, are foraging relatively further from water sources. During the dry season, and despite surface water been readily available over this period, sable antelope, wildebeest, white rhino and zebra all

utilize habitat relatively further from water. Sable antelope and white rhino in particular show a preference for longer grass further from water. This is discussed further in Chapter 6.

To conclude; possibly the most serious potential competitive threat offered to sable antelope during the critical period is from white rhino. Both of these species utilize a medium to tall grass sward further from water and in typically open woodland. White rhino however utilize a less rocky habitat and thus sable antelope are separating themselves from their most serious potential competitor along this gradient. Moreover, the potential for competition at the feeding level is not explored here, and the species may indeed be utilizing different grass species.

Zebra may also potentially pose a threat (to sable antelope) owing to their bulk grazing Type I status. However zebra do show a preference for more open veld during this season and a relatively shorter grass sward. If the zebra population exceeds carrying capacity, a niche expansion will possibly occur (Smith 1996), possibly causing a decline in the abundance of sable antelope at ME. Waterbuck potentially face a competitive threat from buffalo, particularly if the buffalo population increases in abundance. Wildebeest are likely to benefit from the grazing effects of zebra and white rhino.



4.5 Conclusion

This study set out with three primary objectives, these being: the establishment of the nature and importance of the environmental factors that determine utilization of habitat by grazing species at ME, the description of respective species niches within the community hyper-volume and the potential for competition among them, and lastly, the formulation of recommendations based on basic management tools that would ensure the long-term survival of rare and economically valuable species.

The determination of the nature and importance of the environmental variables that separate species ecologically has apparently been achieved here. Certain environmental variables were shown to be influential on herbivore distribution, these being distance to water, grass sward height, extent of veld openness, and the composition and density of the grass sward height, including contribution made by dominant perennials.

During the critical dry season, when resources were assumed to be limiting, a clear ecological separation of species was shown and this can be inferred as an ecological mechanism that allows for co-existence between species (Smith 1996).

However, if resources decline, or become more limiting, the sable antelope (Type II) population is likely to decline in abundance and condition as a result of the effects of competitive interaction with the white rhino population (Type I) and possibly buffalo and zebra populations (also Type I species). The waterbuck population (Type II) are also likely to decline in condition and abundance as a result of competition with successful Type I species populations, and wildebeest (Type III) will likely benefit from the effects of buffalo and zebra, assuming that the species are not out-grazed.

All of these inferences assume that grazing species populations occur at levels immediately below their carrying capacities. Should populations exceed carrying capacity, or should there be a prolonged period of resource scarcity (drought), niche expansion may occur among some species, coupled with a decline in available resources. The ecologically sensitive species, particularly sable antelope and waterbuck, will possibly experience niche compression and a resultant decline in condition, recruitment and abundance.

The most important management objective in the long run should be the maintenance of Type I herbivore populations below carrying capacity, and close monitoring of the sensitive species, particularly sable antelope.

Chapter 5: The application of a GIS-based habitat suitability model

5.1 Introduction

Based on current knowledge pertaining to habitat selection and ecological separation, is the premise that *habitat quality* is perceived through the needs of a particular species, and is largely defined by structure and diversity of vegetation cover (Jarman & Sinclair 1979; Smith 1996; Tainton 1999). Since knowledge of habitat suitability is important, much research has been done in ecology into the modelling of habitat suitability for a species (Dettmers & Bart 1999; Lenton, Fa & Del Val 2000; Neu, Byers & Peek 1974).

Most of the literature on habitat suitability (HS) models has cited the use of habitat suitability indices. The habitat suitability index (HSI) is depicted as a score ranging from 0.00 to 1.00, representing *poor* to *good* habitat or unsuitable to suitable habitat (Bender, Roloff & Haufler 1996). Implicit in the use of these models is the assumption that different habitat ratings reflect differences in habitat quality, based on the premise that HS can be linked to habitat attributes by some functional relationship (Bender *et al.* 1996).

A further assumption of most models, including the one used here, is that study species are spaced according to the *ideal free distribution*. This theory states that each individual will go to the habitat of highest suitability and that such choices ultimately determine a distribution: the ideal free distribution (Fretwell & Lucas 1970).

HSI models test the ability of a given habitat to provide life requisites for a species through the determination of a numerical index of appropriateness and assignment of that value to a given vegetation type at a given point in time (Lenton *et al.* 2000). Given that there exists a vast array of environmental variables that determine habitat quality, and that these variables are spatially explicit (Hirzel 2001), recent models of HS for a given species, have been based on Geographic Information Systems (GIS) (Hirzel 2001; Lenton *et al.* 2000). GIS were designed to store and maintain spatially explicit data, display and analyze this data, and communicate the results to the relevant decision-makers (Hirzel 2001), making GIS ideal for HS models.

Because predictive HS models have broad relevance to wildlife management (Dettmers & Bart 1999), and that MT have a considerable GIS database, the research department encouraged the application of a predictive habitat suitability model. A recent GIS-based software package, *Biomapper*, developed by Hirzel, Hausser & Perrin (2001), was therefore used in the computation of HS maps for the species comprising the grazing herbivore community at Malilangwe Estate (ME).

The motivations behind the use of predictive HS maps are essentially management based. The research department at ME estimate carrying capacities (and stocking rates) for each of their herbivore species, based on annual aerial game surveys and ongoing monitoring of the vegetation (Goodman 2001). Current carrying capacity estimates assume utilization (by a species) of the entire estate. This is inaccurate, given that species generally only utilize their preferred habitat types (Smith 1996). Often, the actual habitat utilization of a species, especially during dry months, is a small proportion of the estate. This has been verified by the plotting of species utilization determined only by scout sightings (Clegg, S. pers. comm.). MT however required a more thorough understanding of the suitability of habitat for each species before sound carrying capacity estimates could be made.

Furthermore, habitat suitability maps that could be used and analysed in the research departments GIS database had other benefits. The creation of *Idrisi*-based HS maps could potentially be used to predict areas of competitive resource overlap among species and could be used in further analytical procedures such as the determination of future road placement, camp placement and other environmental impact type studies.

It was for these reasons that *Biomapper* was chosen as a suitable GIS technique, along with its robustness and ability to use presence data only (Hirzel, Hausser, Chessel & Perrin 2002). Species data collected for the discriminant analysis were used as presence data here. Logistical and financial constraints restricted this study to presence data only, and absence data was not considered (making *Biomapper* suitable). Furthermore, absence data is often difficult to obtain accurately (Hirzel *et al.* 2002).

To conclude, the primary objectives of this study were to:

1. Develop habitat suitability maps for each respective grazing species during the hot dry season, based on presence data. These HS maps (in *Idrisi* raster format) would then be available for the research department at ME to use in the decision making process, specifically in the estimation of species carrying capacities, and determination of areas suitable for species expansion. Surface area can be computed in *Idrisi*. Furthermore, HS maps produced in the hot-dry season indicate the most likely habitat that will be used by a species during a drought period, seen as the critical habitat.
2. The production of HS maps that can be used to predict areas of competitive overlap between species. This will help management in the decision-making process by indicating where ecologically sensitive species could potentially lose habitat to more competitive species, and where monitoring should particularly be focused.
3. The development of suitability maps that will be used as a basis for culling operations. This is based on the assumption that members of a species found in areas determined to be unsuitable, are utilizing those areas due to the pressures of intraspecific competition (Owen-Smith 1983). Thus if culling is to be carried out, it is preferable to cull members of the species that have expanded their range into unsuitable habitat.
4. Produce predictive HS maps that will be used by the research department at ME in future management assessments. For example, the estate is currently considering the re-routing of existing roads. The present road network was established during when cattle were the prime source of income. These roads are to be re-routed taking various impacts into consideration such as ecologically sensitive veld, based on soil type and vegetation type. The new road networks will also be sensitive to the needs of the tourist, and so will consider areas where the likelihood of seeing photographically desirable species, such as sable antelope, white rhino, buffalo and waterbuck, is high. This will be deducted from the HS maps.

Moreover, the future placement of camps, bomas and quarries will consider the sensitivity of these areas according to the HS maps. For example, it would be unwise for management to establish a holding

boma (for bulk grazing species) in any area that is prime habitat for sable antelope, given that this is an ecologically sensitive and highly valuable species.

5. Produce and print habitat suitability maps for each grazing species that can then be utilized by the guiding department, helping guides locate photographic species such as white rhino, buffalo and sable. This is based on the assumption that the probability of finding species in suitable habitat (indicated by HS index) is high.
6. Gain more insight into the fundamental niches of the study species. The ENFA produces scores representing the habitat variables associated with the distribution of each species. These scores, together with those of DFA (Chapter 4) will give a better understanding of the environmental variables that influence the distribution of grazing herbivore species at ME.

Presence data in this analysis was taken from the data collected for the discriminant analysis, due to financial and logistical constraints. All individuals were assumed to select the most suitable habitat (assuming *ideal free distribution* after Fretwell & Lucas (1970)), and individual presence data was averaged and assumed to represent desirable habitat for the species. Logistical constraints restricted data collection and small data samples only allowed for a general analysis of species, i.e. sex and age differences were not considered. The use of GIS collars is advised in future research at ME, allowing for adequate species presence data to be collected, and HS maps composed for both breeding herds and male herds. This will be particularly pertinent to future culling operations.

The resolution (pixel size) of all eco-graphical maps was 20 m x 20 m on the ground. This resolution was deemed accurate enough to take spatial heterogeneity of habitat variables on the ground into account.

Finally, only data from the dry season was analysed here. This was because the only independent species presence data available for validation of the maps was the aerial census data collected mid-hot dry season. Only grazing species were considered, as mixed feeders turn to dicotyledonous food sources during this season (Eltringham 1979; Skinner & Smithers 1990). Study species

were thus buffalo, sable antelope, waterbuck, white rhino, wildebeest and zebra.

5.2 Methods

Conservation ecology increasingly relies on multivariate, spatially-explicit models to attempt some level of ecological realism for research (Hirzel 2001; Hirzel *et al.* 2002). Areas of ecological research where spatially explicit models are used include population viability analysis, biodiversity-loss risk assessment, landscape management for endangered species and ecosystem restoration (Araujo & Williams 2000; Mladenoff & Sickley 1998).

Spatially-explicit ecological research studies often combine GIS with multivariate statistical tools to determine the link between a species and its environment, or more specifically, to quantify the parameters of habitat suitability models. *Biomapper*, a GIS-compatible software package developed by Hirzel *et al.* (2001), was used here to primarily compute HS maps for each of the respective grazing herbivore. *Biomapper* additionally provides output information about the niche of a focal species, through the ENFA. This analysis is based on the concept of ecological niche after Hutchinson (1957), and provides information on the marginality and specialization of the species.

A crucial advantage of the ENFA and indeed, *Biomapper* is that only presence data is required, i.e., species absence data is not needed. This is important because many data bases either lack absence data, or the absence data is unreliable (Hirzel 2001; Hirzel *et al.* 2002).

Biomapper is used here as absence data was not reliably available, and moreover, *Biomapper* is a robust technique that tied in well with the GIS database at ME. *Biomapper* was used specifically to determine predicted spatial distribution and overlap, and at the time of data collection, no other technique was known to do this with the same rigour (Goodman pers. comm.).

The input data used in *Biomapper*, apart from species presence data, are quantitative maps of the habitat variables thought to be important in species habitat utilization. These maps were composed in *Idrisi 32* (Clark Labs 1999), hereafter *Idrisi*, and used as layers in *Biomapper*. The ENFA and input data used in this study are discussed further:

5.2.1 Biomapper

The software package *Biomapper* is linked to GIS. A *Biomapper* module imports data from a GIS package (in this case *Idrisi*), prepares that data, and is responsible for the ENFA and HS map computation. HS maps may then be displayed and further analyzed in *Idrisi*. *Idrisi* is used as the framework for the *Biomapper* software because it is widely used by ecologists, its development environment is open and easy to use and it is relatively affordable (Hirzel 2001).

The study area is modelled as a *raster* map composed of n adjacent isometric cells (pixels). Raster data is the data structure for maps based on grid cells (Clarke 1999). The dependent variable used is *presence data* of the focal species in a set of sampled locations. Species presence is saved as *Boolean* (binary) data i.e., 1 indicates presence of a species and absence is indicated by 0 on a raster map. Presence-only data is a new approach and makes *Biomapper* unique. Absence data is often difficult to obtain accurately. A location in the study area may be classified in the absence set because:

1. The species was not detected even though it was present (McArdle 1990, unseen, as cited in Hirzel 2001),
2. the species is absent for historical reasons although the habitat is suitable,
3. The habitat is truly unsuitable (Hirzel 2001).

Only the last cause is relevant to predictions, and occurrence of false absences may cause considerable bias (Hirzel 2001; Hirzel *et al.* 2002). Thus presence-only data is more preferable, and justifies the use of this method, especially given the data collection constraints during the study period.

The independent data comprises individual maps that quantitatively describe habitat variables, termed eco-graphical variables (EGV). Each EGV is stored in an individual raster map composed of isometric (square used here) cells. These maps represent topographical features (e.g. altitude, slope) and ecological data (e.g. vegetation type and cover, grass species abundance, distance to water), and this quantitative information is attached to each cell. This data structure is perfectly suited to represent landscape processes and moreover, is a mode capable of being subjected to a wide range of spatial analyses and operations (Hirzel 2001).

EGV are stored in 'information layers', allowing them to be overlaid and analyzed. Using the species presence data as input, the ENFA computes suitability functions by comparing the species distribution in the EGV space with that of the whole set of cells. The actual algorithm used here can be seen in Hirzel (2001).

It is useful to elaborate further on the ENFA used in *Biomapper*. The mathematics behind this analysis is given in Hirzel (2001). Presence data and the EGVs used in this study are also elaborated on.

5.2.1.1 Marginality, specialization and the ecological niche

Following Hirzel (2001) and Hirzel *et al.* (2002), species are expected to be non-randomly distributed regarding eco-graphical variables. A species with a particular environmental optimum (e.g. grass sward height) is expected to occur preferentially in those cells representing its optimum range. This can be quantified by comparing the grass sward height in which the species was observed with that of the whole set of cells. These distributions may differ with respect to their means and variances. The study species may exhibit a degree of *marginality* i.e.; species mean differs from the global mean, and *specialization* i.e., species variance is lower than the global variance. Formally, Hirzel (2001) defines marginality as the absolute difference between global mean and species mean, divided by $1.96*$ standard deviation of the global distribution (* = 95% confidence limit). Note: the principle of the method is explained here, the multivariate extension of this principle is provided in Hirzel (2001). Specialization is defined as the ratio of the standard deviation of the global distribution to that of the focal species.

These statistics are extended to a larger set of variables according to the concept of niche as an n dimensional hyper-volume (Hutchinson 1957). Thus, the ecological niche in *Biomapper* is the subset of cells in the eco-graphical space where the study species can be expected to occur. This multivariate niche can be quantified on any of its axes by an index of marginality and specialization.

A factor analysis extracts the combinations of original variables on which the study species shows most of its marginality and specialization, assuming that a species may specialize on a combination of optimum variables. Thus, in

ENFA, the first axis is chosen so as to account for all of the marginality of the species and the following axes so as to maximize specialization.

5.2.1.2 Factor extraction and interpretation

Raster maps are used in the analysis, each of these being composed of n isometric cells covering the whole study area. Following Hirzel (2001), each cell is associated to a vector whose components are the values of the EGV in the underlying area and can be represented by a point in the multidimensional space of the EGVs.

If distributions are multi-normal, the scatter plot will have the shape of a hyper-ellipsoid (see example in Hirzel 2001). The cells representing species presence constitute a subset of the global distribution and are plotted as a smaller hyper-ellipsoid within the global ellipsoid. The first factor, i.e., marginality factor is represented by a straight line passing through the centroids of the two ellipsoids and is represented by the standardized distance between these centroids.

The species centroid is then transformed into a sphere, the variance of which equals unity in all directions. This is done to obtain the specialization factor. The first specialization factor is the one that maximizes the variance of the global distribution, while being orthogonal to the marginality factor. The specialization factors are then extracted in turn, each step removing one from the space. The amount of specialization accounted for by a factor is necessarily lower than that extracted accounted for by the previous one.

5.2.1.3 Interpretation of factors

The coefficients of the *Marginality Factor* (MF) express the marginality of the focal species on each EGV. The higher the absolute value of a coefficient, the further the species departs from the mean available habitat regarding the corresponding variable. Negative coefficient values indicate that the study species prefers values that are lower than average with respect to that EGV, while positive coefficients indicate preference for higher than average values. The coefficients of the next factors (*Specialization Factors*) are interpreted differently; the higher the value, the more restricted is the range of the study species on the corresponding variable.

5.2.1.4 Habitat suitability map

Biomapper computes the suitability for the study species of any cell in the study area. Following Hirzel (2001) and Hirzel *et al.* (2002), the suitability of any cell from the global distribution is calculated from its situation relative to the species distribution on all selected niche factors. Specifically, the suitability of any cell equals the sum of all cells from the species distribution that lay further from the *median* (most robust), divided by the total number of cells from the species distribution. The count is normalized in a way that the suitability index ranges from 0 to 1.

An overall suitability index of the focal cell is then computed from a combination of its scores on each factor. Repeating this procedure for each cell allows the production of a habitat suitability map, where suitability values range from 0 to 1.

5.2.2 Species presence data

Species presence data was collected while studying the habitat utilization of grazing herbivores (see Chapter 4). All plots recorded for discriminant analyses were also given a location with a handheld GPS. These GPS locations, measured in the Universal Transverse Mercator (UTM) coordinate system (Clarke 1999), were then separated by specie. The data points were downloaded into *Cartalinx* (Clark Labs 1999) and then imported into *Idrisi* as vector maps. These vector maps were transformed to raster maps in *Idrisi* using the raster to vector command POINTRAS. Species points were represented as 1 and all other cells were represented by the value 0.

Logistical restrictions unfortunately meant that this was the only presence data available. Ideally, GPS collars should be placed on a chosen number of individuals from each study species, and the locations set to be recorded during times of day when the individuals are most likely to be feeding, and thus selecting suitable habitat. GPS collars were beyond the budget of this study and were not used. The time given to collecting data for the discriminant analysis took priority here, and so it was decided that the locations given to each plot for the discriminant analysis could be used as presence data. The sampling strategy for discriminant analysis is discussed in Chapter 4, and basically consisted of a stratified random technique using the road network as transects.

Group size was not considered when collecting presence data. Pixel size of 20 m x 20 m was taken as adequate resolution and groups assumed to fall within this range, particularly since this was the size of plot used for DFA.

5.2.3 Environmental variables

Ecographical variable maps were composed in *Idrisi*. The variables used, as well as the discard criteria are given in Table 13. All EGV maps and species presence maps had to meet the requirements of *Biomapper* i.e.; they had to be overlayable. This was ensured through the use of a template map, upon which layers were composed. Overlayability merely implies identical minimum and maximum coordinates for each map.

Maps that quantified soil and vegetation characteristics for the hot dry season were created using Clegg's (2002) vegetation community map (see Appendix 13) as a template. This vegetation map is still in preparation and so is not discussed in detail. The vegetation communities determined by Clegg, B. (2002) are not important here and the map was simply used as a template for the characteristics of the vegetation i.e. herbaceous composition and height, tree canopy volume. The map was used here since it defined variables at a finer resolution than the vegetation community map composed by Clegg, B. (1999) and shown in Figure 7.

Soil data collected by Chawanji (2000) was assigned to the respective plant community database in which they occurred using the *Idrisi* command ASSIGN. Tree canopy volume was measured and assigned by Clegg, B. (2002), and his data were used. Tree canopy volume was here used as a measure of tree/shrub density and so included all woody vegetation > 1 m in height. Canopy volume was measured in m³/ha.

Characteristics of the herbaceous component, i.e., grass sward height, green grass cover, forb and sedge cover and the percent contribution to herbaceous biomass of *Digitaria eriantha*, *Panicum maximum* and *Urochloa mossambicensis*, were taken from the data collected for the discriminant analysis. Only these grass species were selected as they were shown to be important in discriminant analysis. Every data plot was downloaded and saved as a vector presence point in *Cartalinx*, the mapping module associated with *Idrisi*. These points were then converted to a raster image in *Idrisi*, with every plot represented by a corresponding number. Using *Idrisi*, each data point was

assigned to the respective vegetation community in which it occurred. From here, the mean grass height, greenness of cover etc. for those plots falling in a particular vegetation community were then assigned to that respective community.

The remaining EGV maps comprised of topographical and physical features such as elevation, percent rockiness, distance to nearest surface water and time since last burn for the hot dry season. Distance to water and time since burn were created as raster maps, where each pixel represented that cells distance to closest surface water or time since last burn (months).

The EGV maps and species presence maps were then imported into *Biomapper*, and were saved as a *project*. Once all maps were imported, they were tested for normality of the distribution. *Biomapper* uses the *Kolmogorov-Smirnov* test for normality. Maps that were not normally distributed were transformed using the *Box-Cox* method (Legendre & Legendre 1998) within the package. Hirzel (2001) advises that if maps that are not normally distributed after transformation, it is best to then use the raw untransformed data, as the ENFA is fairly robust. The Box-Cox transformation method proved to be ineffective here and thus untransformed data was used in analysis.

ENFA was carried out on the project. The initial result of this analysis is a variable correlation matrix. All variables that were strongly correlated i.e., where coefficient value of $r > 0.7$ (after Fowler & Cohen 1992) were discarded; only leaving nine EGVs for further analysis (see Table 13). Following this, an ENFA was carried out for each respective species presence map and the results represented as a factor table and HS map and given below.

5.3 Results

Results are presented as HS maps and a scores output from the ENFA, for each grazing species. Within the scores output, the Marginality Factor (MF) is the first score given for the respective variables, followed by specialization factors of declining contribution to extracted variance. EGVs that have high values in the MF column indicate species preference for that variable if the value is positive and avoidance of that variable if the value is negative (see Table 14).

HS maps are presented as Figures 24 - 29. The keys on all HS maps represent the Habitat Suitability indices and are scaled from 0 - 100; 100

indicating suitable habitat for the species based on presence data, and 0 indicating unsuitable habitat.

HS maps were composed for the hot dry season only here, since no independent data was available for the other seasons and thus maps could not be validated. HS maps were composed for all species during the wet and cool seasons and given to management in *Idrisi* raster format for reference.

As mixed feeders (eland, elephant, impala, nyala and warthog) turn to browse in this season (Barrett & Spitz 1991; Lewis 1986; Munro 1980), analysis was not carried out because of insufficient environmental data and particularly since mixed feeders are unlikely to respond to the composition of the herbaceous layer. Warthog are classed as mixed feeders here, due to their active selection of roots and bulbs during the dry season (Barrett & Spitz 1991).

Noteworthy correlations in Table 13 are those between GGRE and the soil minerals nitrogen, potassium and magnesium. This implies that biologically active grass growth is dependent on these soil nutrients. Also notable, and as in preceding seasons, greenness of grass is correlated with sward height, implying that taller, vigorous grass growth is usually biologically active (green).

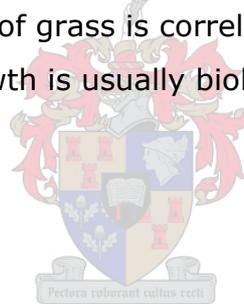
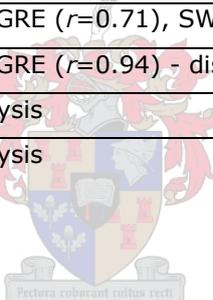


Table 13: Variables used in the ENFA, hot dry season

Ecographical variable	Discard criteria
Available phosphorus (%)	Correlated with FORB ($r=0.77$) - discarded
Canopy volume (m^3/ha)	Used in analysis
Clay (%)	Corr. with SWHT ($r=0.89$) - discarded
<i>Digitaria eriantha</i> (%)	Used in analysis
Distance to water (m)	Used in analysis
Elevation (m. A. S. L.)	Corr. with GGRE ($r=0.87$), DWAT ($r=0.74$) - discarded
Forb cover (%)	Used in analysis
Greenness of grass (%)	Used in analysis
Magnesium (%)	Corr. with GGRE ($r=0.85$) - discarded
Nitrogen content (%)	Corr. with GGRE ($r=0.87$), SWHT ($r=0.86$), FORB ($r=0.79$) - discarded
<i>Panicum maximum</i> (%)	Used in analysis
Potassium (%)	Corr. with GGRE ($r=0.71$), SWHT ($r=0.79$) - discarded
Rock cover (%)	Used in analysis
Sand (%)	Corr. with ROCK ($r=0.7$) - discarded
Sedge (%)	Corr. with DIER ($r=0.9$) - discarded
Silt (%)	Corr. with GGRE ($r=0.71$), SWHT ($r=0.73$) - discarded
Sward height (cm)	Corr. with GGRE ($r=0.94$) - discarded
Time since burn (months)	Used in analysis
<i>Urochloa mossambicensis</i> (%)	Used in analysis



5.3.1 Buffalo

At this crucial time of year, buffalo (Table 14) exhibit a preference for habitat characterized by a biologically active grass sward where the palatable perennials *Panicum maximum* and *Digitaria eriantha* are abundant.

D. eriantha in particular is found in the hill region of ME, and this further explains buffalo's close association with the hills from the discriminant analysis. The low coefficient value given to DWAT value implies that buffalo prefer areas where water is more readily available. The relatively high variance extracted by the MF indicates that buffalo are sensitive to shifts from this axis.

The high positive association with canopy cover on the second axis suggests that buffalo prefer woodland type habitat during the critical dry season. The HS map for buffalo shows that the most suitable habitat is within the hills and near the perennial river system i.e. the Chiredzi River.

Table 14: The extracted scores from the ENFA for buffalo during the hot dry season, 2001.

Scores	MF	Spec 1	Spec 2	Spec 3	Spec 4
Canopy Volume	0.09	0.89	0.23	-0.43	-0.09
<i>Digitaria eriantha</i>	0.63	0.05	-0.14	0.02	-0.27
Distance to water	0.04	0.38	-0.80	0.26	0.14
Greenness of grass	0.43	-0.19	0.12	-0.39	0.53
Time since burn	0.47	-0.06	0.03	0.23	0.30
Forb	0.16	-0.13	0.51	0.72	-0.31
<i>Panicum maximum</i>	0.35	0.01	-0.10	0.01	-0.21
Rock cover	0.22	0.01	-0.04	-0.17	-0.08
<i>Urochloa mossambicensis</i>	0.09	0.03	-0.08	-0.03	-0.62
% variance	48	23	13	5	4

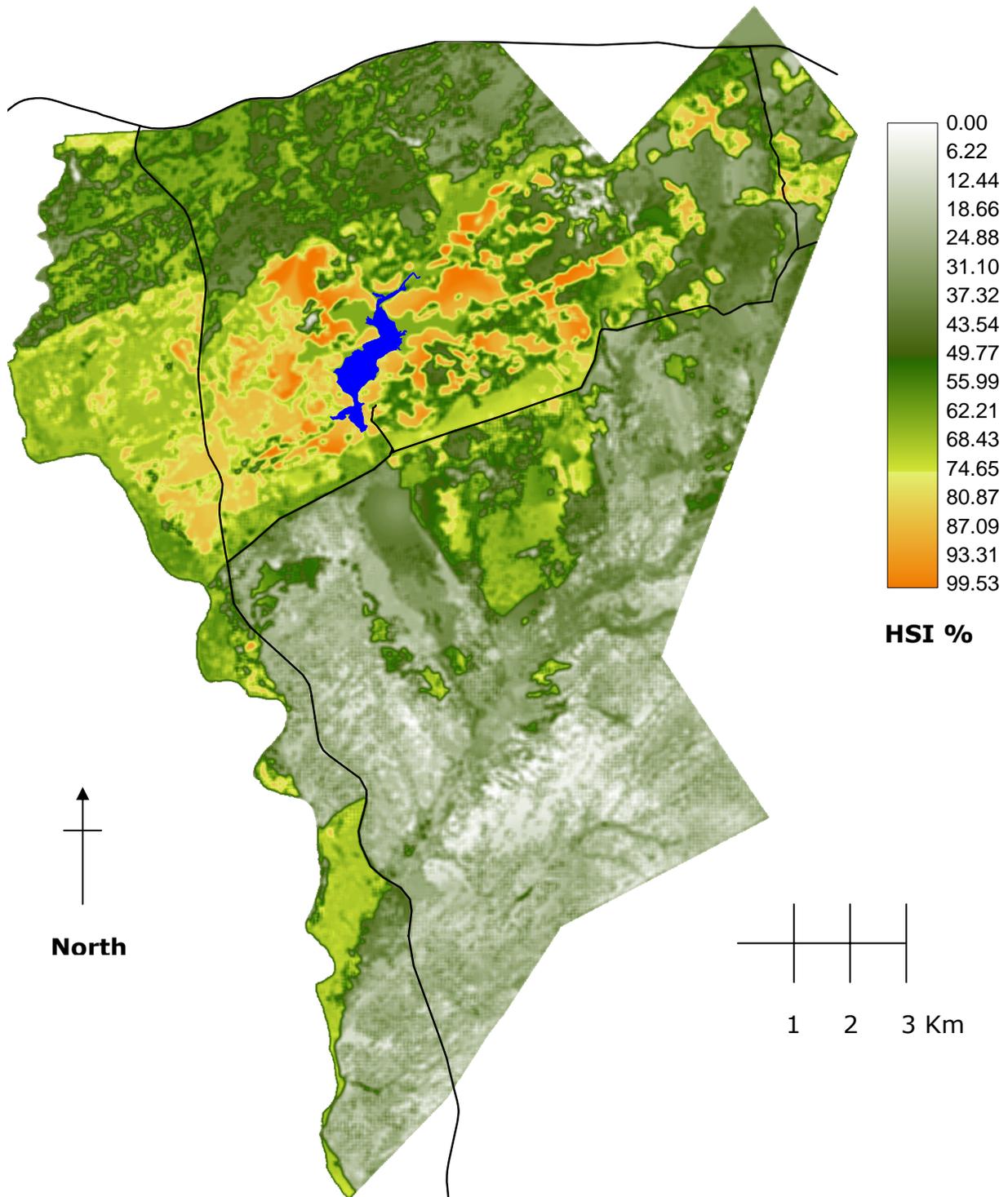


Figure 24: Habitat suitability map for buffalo during the hot dry season, 2001. Also represented are the main access roads and the Malilangwe Dam.

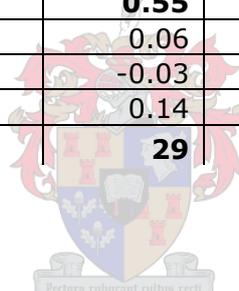
5.3.2 Sable antelope

Sable antelope at ME (Table 15) show a marked preference for a greener grass sward (also taller grass - as the two variables are positively correlated) where forbs are relatively abundant. This finding is similar to that of the discriminant analysis where sable antelope are strongly associated with a taller grass sward.

The animals appear insensitive to shifts in habitat on the first axis as it only accounts for 29% of the extracted variance. The species show a strong aversion to a grass sward where *P. maximum* is abundant.

Table 15: The extracted scores from the ENFA for sable antelope during the hot dry season, 2001.

Scores	MF	Spec 1	Spec 2	Spec 3	Spec 4
Canopy Volume	0.21	-0.13	-0.19	0.02	0.73
<i>Digitaria eriantha</i>	0.33	0.06	-0.02	0.01	0.23
Distance to water	0.37	-0.10	0.05	-0.03	-0.10
Greenness of grass	0.60	0.37	-0.40	0.24	-0.41
Time since burn	0.16	-0.09	0.80	-0.45	-0.08
Forb	0.55	-0.18	0.32	-0.16	0.03
<i>Panicum maximum</i>	0.06	-0.89	-0.18	0.01	-0.18
Rock cover	-0.03	-0.03	0.04	0.81	-0.06
<i>Urochloa mossambicensis</i>	0.14	-0.04	-0.14	0.26	0.43
% variance	29	40	8	6	6



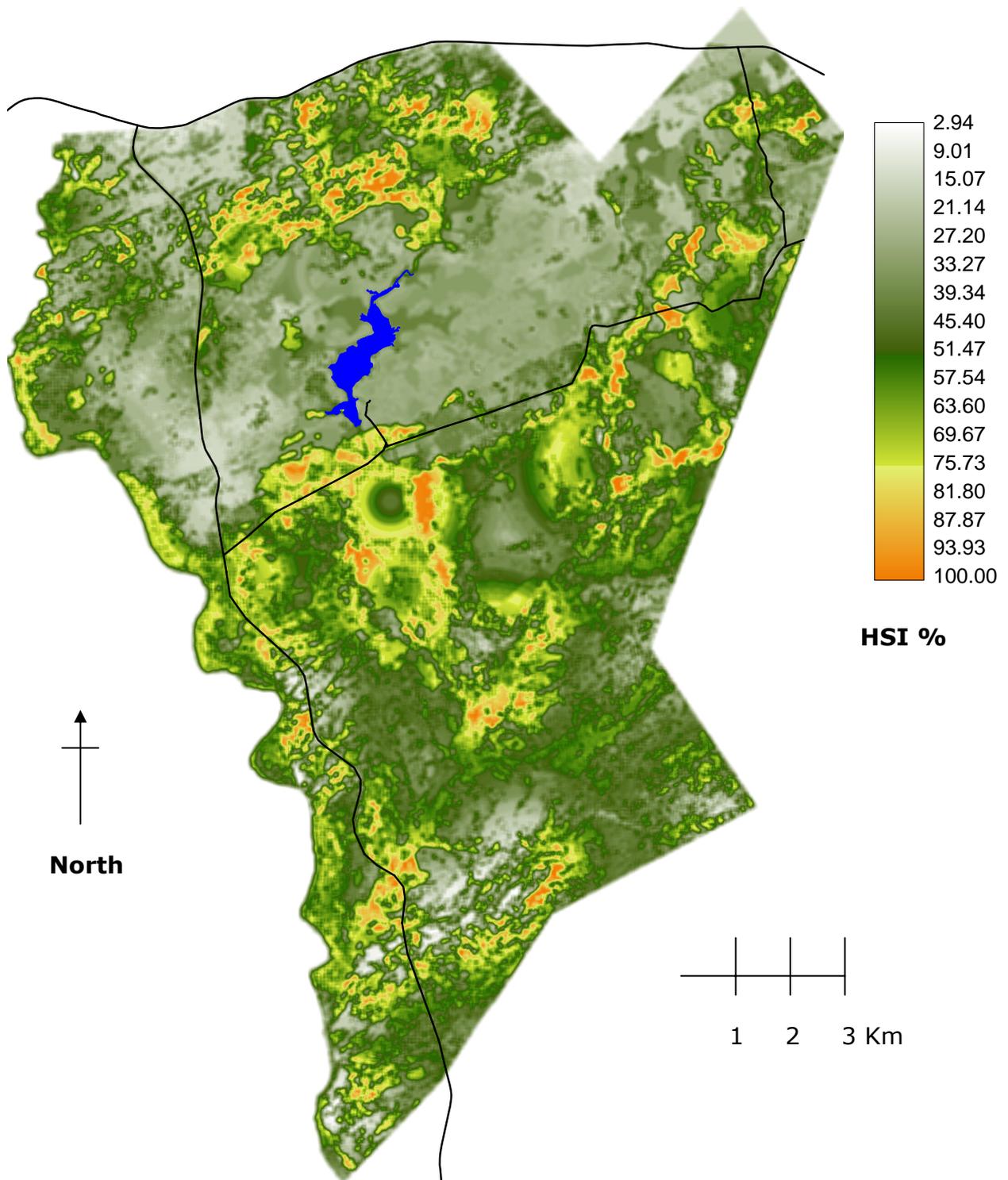


Figure 25: Habitat suitability map for sable antelope during the hot dry season, 2001. Also represented are the main access roads and the Malilangwe Dam.

5.3.3 Waterbuck

Waterbuck (Table 16) show a marked preference for greener grass that is dominated by *D. eriantha* and a lesser preference for *P. maximum*. It is possible that waterbuck utilize these grass species, although this is unconfirmed.

The coefficient value for distance to water is strongly negative implying that the species prefer values lower in this range, i.e. distances close to water, similar to the findings of discriminant analysis. Waterbuck appear very sensitive to shifts from the optimum habitat represented by the MF, as the percentage variance extracted by this factor is high.

Table 16: The extracted scores from the ENFA for waterbuck during the hot dry season, 2001.

Scores	MF	Spec 1	Spec 2	Spec 3	Spec 4
Canopy Volume	0.15	0.22	0.64	0.34	0.15
<i>Digitaria eriantha</i>	0.80	-0.01	-0.13	0.28	-0.16
Distance to water	-0.04	-0.80	0.04	-0.06	-0.58
Greenness of grass	0.42	0.19	0.43	-0.61	0.12
Time since burn	0.27	-0.20	-0.14	-0.39	0.14
Forb	0.12	-0.46	-0.53	0.37	0.64
<i>Panicum maximum</i>	0.25	-0.13	-0.26	0.04	-0.22
Rock cover	0.04	0.00	0.06	-0.03	0.07
<i>Urochloa mossambicensis</i>	0.09	0.03	-0.09	0.36	-0.33
% variance	53	23	9	6	4



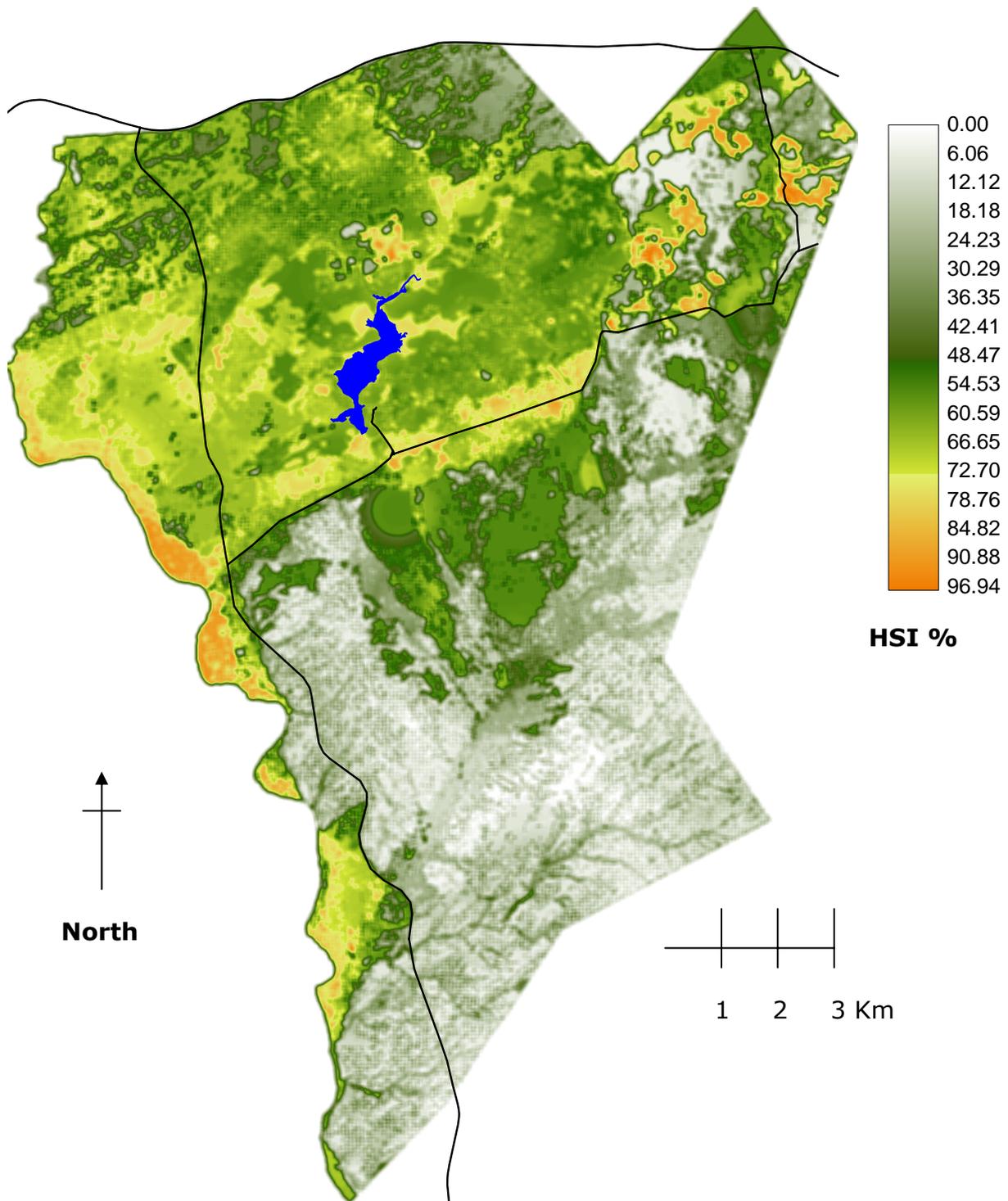


Figure 26: Habitat suitability map for waterbuck during the hot dry season, 2001. Also represented are the main access roads and the Malilangwe Dam.

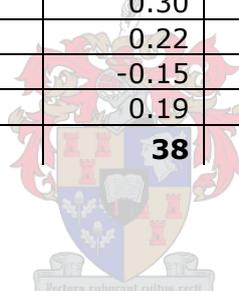
5.3.4 White rhino

White rhino (Table 17) show a marked preference for habitat where the percentage green grass is high. The coefficient value for the variable *distance to water* is also relatively high, indicating that the species prefer habitat further from water during the critical season.

The findings of the discriminant analysis also showed that prefer to utilize habitat further from water, and in fact, it appears that this variable separates them ecologically from other species.

Table 17: The extracted scores from the ENFA for white rhino during the hot dry season, 2001.

Scores	MF	Spec 1	Spec 2	Spec 3	Spec 4
Canopy Volume	0.13	-0.08	0.56	-0.11	-0.40
<i>Digitaria eriantha</i>	0.11	0.01	0.02	0.30	0.42
Distance to water	0.56	-0.04	0.10	0.02	0.11
Greenness of grass	0.66	-0.04	-0.55	0.19	-0.51
Time since burn	0.16	-0.08	0.12	-0.28	0.24
Forb	0.30	-0.13	0.20	-0.10	0.22
<i>Panicum maximum</i>	0.22	-0.03	0.02	-0.71	0.33
Rock cover	-0.15	-0.97	-0.33	0.13	-0.14
<i>Urochloa mossambicensis</i>	0.19	-0.15	0.46	0.50	0.39
% variance	38	44	7	4	2



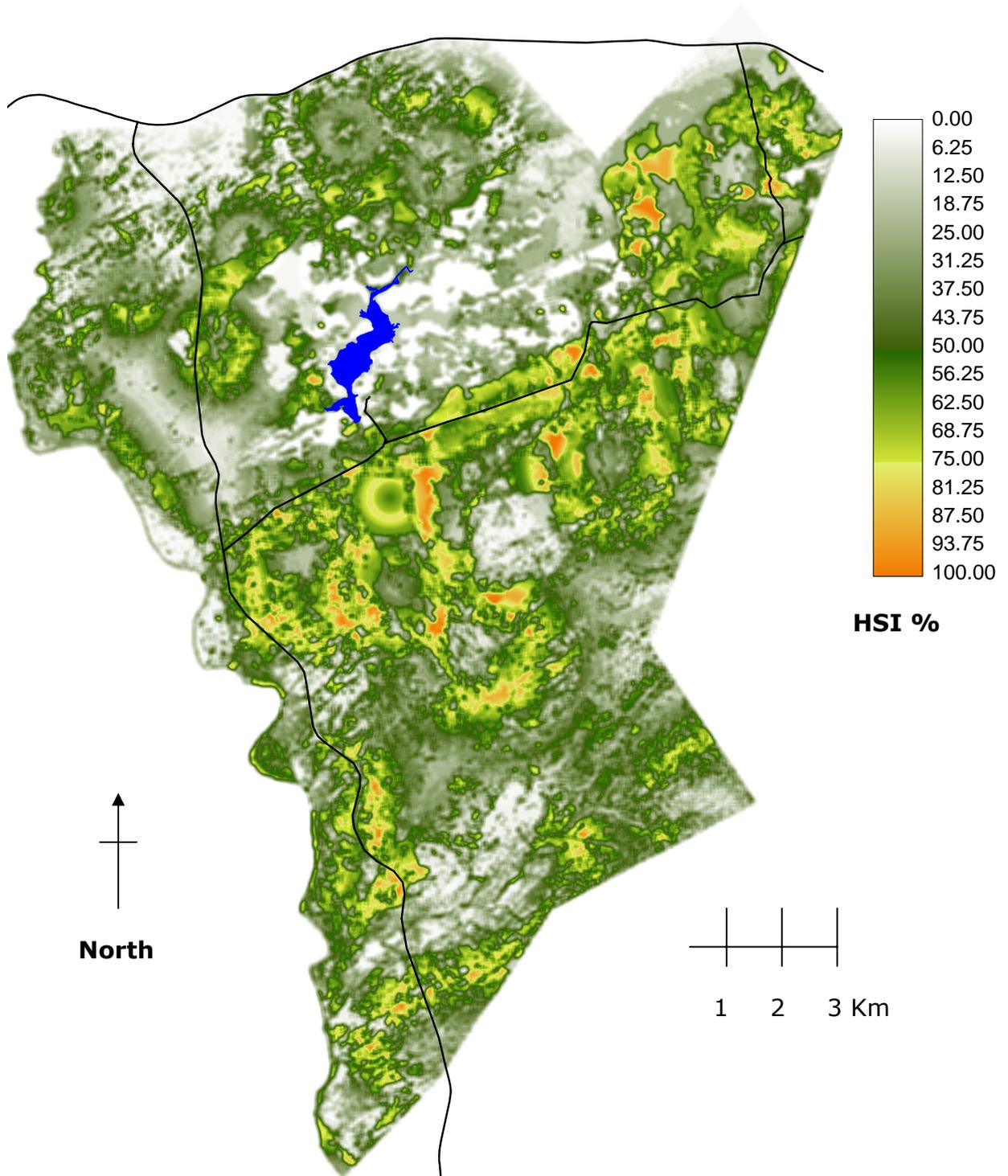


Figure 27: Habitat suitability map for white rhino during the hot dry season, 2001. Also represented are the main access roads and the Malilangwe Dam.

5.3.5 Wildebeest

Wildebeest (Table 18) show a distinct preference for a relatively green sward where *U. mossambicensis* is abundant during the hot dry period. The species also show a marked avoidance of rocky areas, instead selecting flat terrain, devoid of rocky outcrops. The coefficient value for *D. eriantha* is low suggesting an avoidance of this grass sward, and possibly the habitat in which it thrives, i.e. woody areas near rocky outcrops. An apparent anomaly here is that a green grass sward suggests a relatively tall grass sward. It is possible that the resolution used here (taking mean values for each vegetation type) does not account for finer level selection, revealed by the DFA.

Another coefficient value worth mentioning is that given to the variable *time since burn*. A small value indicates negative association, and thus from these findings wildebeest partially associate with areas where time since burn is minimal, i.e., recently burnt.

Table 18: The extracted scores from the ENFA for wildebeest during the hot dry season, 2001.

Scores	MF	Spec 1	Spec 2	Spec 3	Spec 4
Canopy Volume	0.20	0.08	0.14	-0.73	-0.06
<i>Digitaria eriantha</i>	0.01	-0.13	-0.91	-0.06	-0.21
Distance to water	0.17	0.16	0.24	-0.03	-0.81
Greenness of grass	0.47	-0.09	0.15	-0.20	0.32
Time since burn	0.02	-0.17	0.05	-0.11	-0.05
Forb	0.27	-0.10	-0.12	0.46	0.22
<i>Panicum maximum</i>	0.09	0.03	-0.02	0.42	-0.38
Rock cover	-0.05	-0.95	0.19	0.09	0.02
<i>Urochloa mossambicensis</i>	0.79	-0.03	-0.11	0.12	-0.03
% variance	51	25	9	4	3

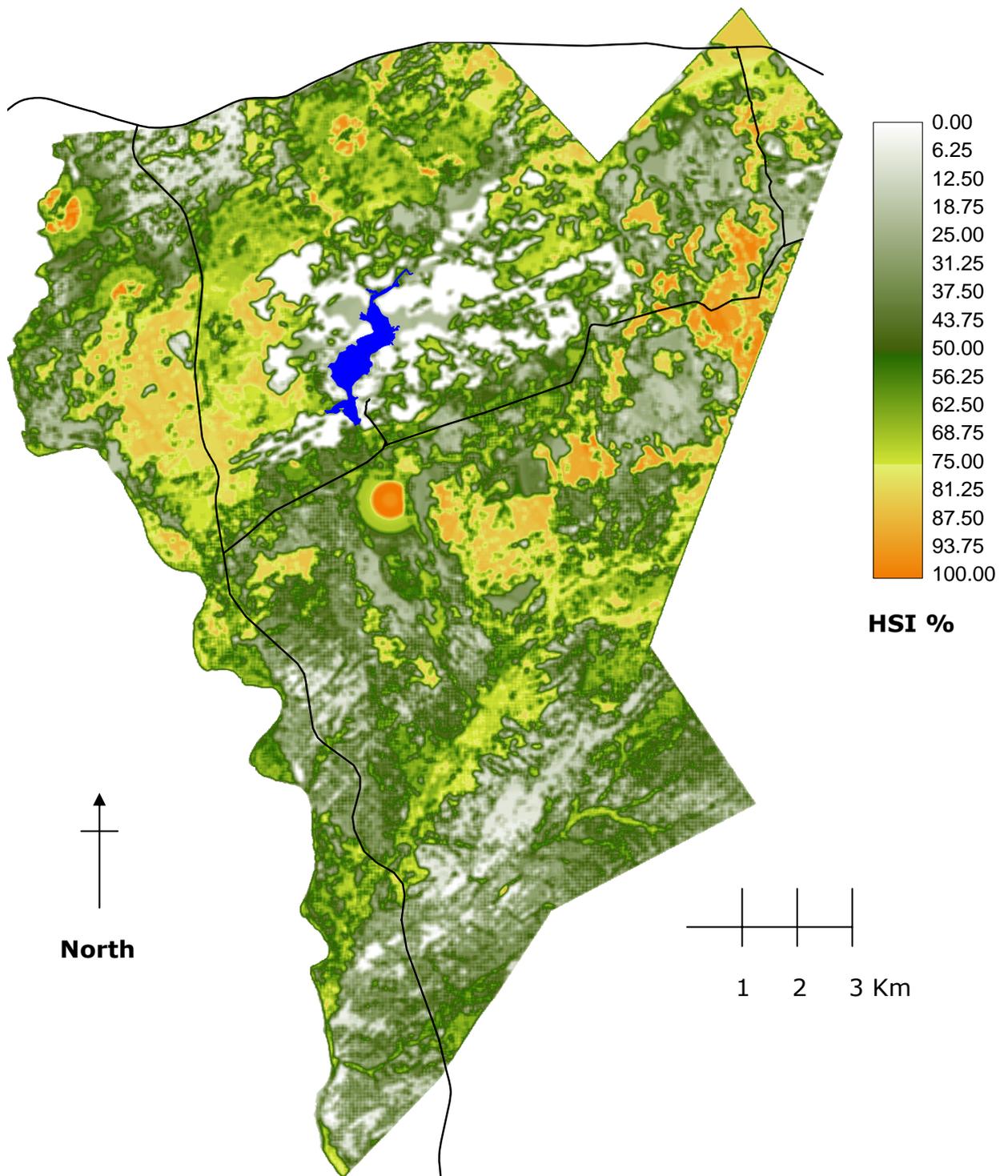


Figure 28: Habitat suitability map for wildebeest during the hot dry season, 2001. Also represented are the main access roads and the Malilangwe Dam.

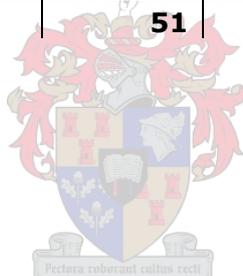
5.3.6 Zebra

Zebra (Table 19) show a discernible preference for habitat where the grass layer is mostly green and where forbs and *U. mossambicensis* are abundant.

A negative coefficient score is given to the variable rock cover suggesting that the species avoid rocky areas. The high coefficient value given to the first axis suggests that the species may be sensitive to shifts from this preference.

Table 19: The extracted scores from the ENFA for zebra during the hot dry season, 2001.

Scores	MF	Spec 1	Spec 2	Spec 3	Spec 4
Canopy Volume	0.35	0.00	0.05	-0.25	-0.74
<i>Digitaria eriantha</i>	0.04	-0.85	0.48	0.18	-0.01
Distance to water	0.29	0.32	0.08	0.75	-0.18
Greenness of grass	0.53	-0.02	-0.03	-0.45	0.04
Time since burn	0.21	0.11	-0.19	0.33	-0.25
Forb	0.41	-0.02	0.07	0.15	0.52
<i>Panicum maximum</i>	0.25	-0.05	0.03	-0.07	0.24
Rock cover	0.03	-0.40	-0.85	-0.09	0.09
<i>Urochloa mossambicensis</i>	0.48	-0.09	-0.03	-0.02	0.15
% variance	51	13	10	6	6



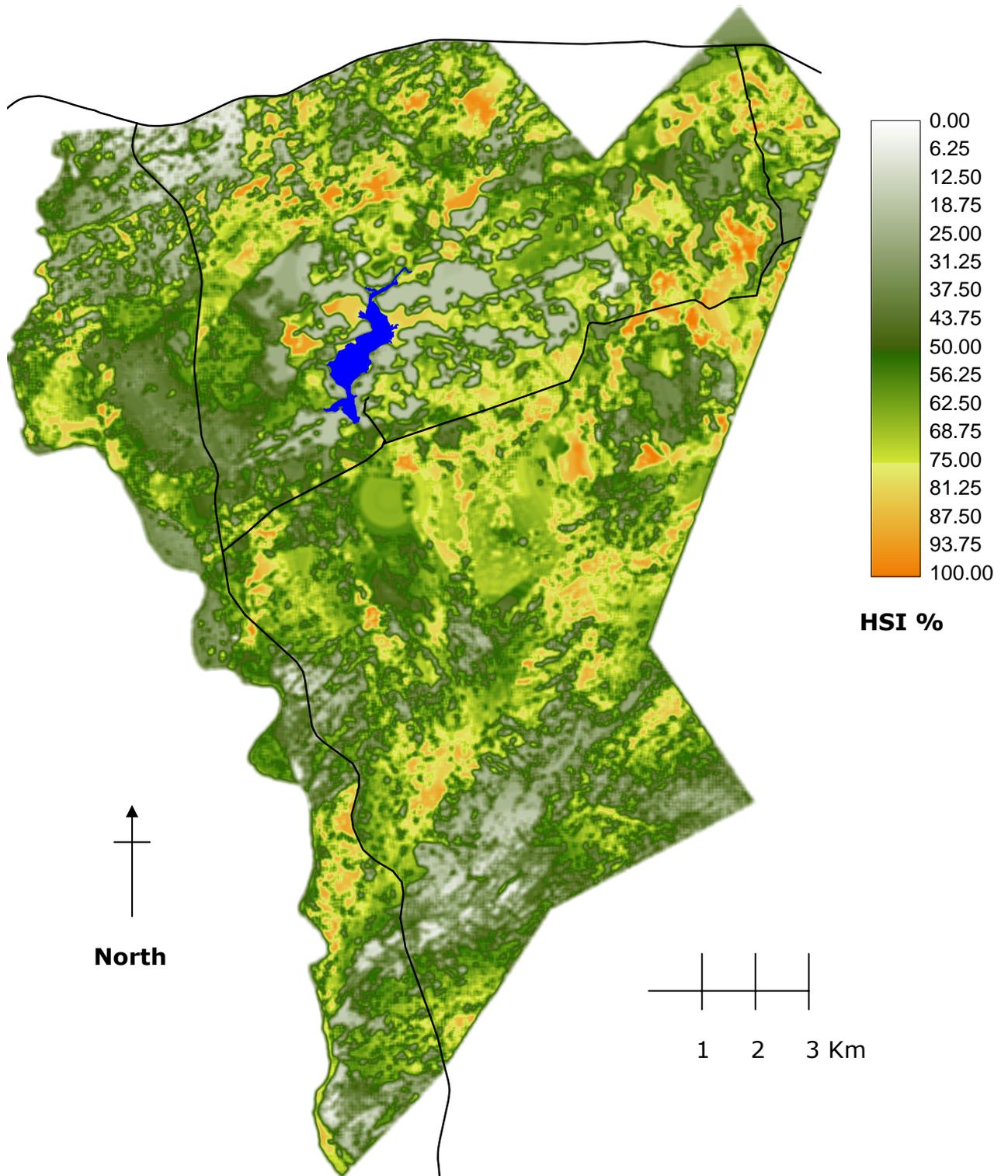


Figure 29: Habitat suitability map for zebra during the hot dry season, 2001. Also represented are the main access roads and the Malilangwe Dam.

5.4 Validation

HS maps were validated here using the VALIDATE function in *Biomapper*. Separate HS maps were composed for each of the grazing herbivore species using the presence data collected during the 2001 aerial census (late September). This data was independently collected (Goodman 2001) and thus was suitable for a validation analysis. All species presence data from the aerial census were analysed in *Biomapper* using the same habitat variables used in the above ENFA. Maps were then saved and tested (and provided to the Research Dept. for reference). The VALIDATE function in *Biomapper* uses the Pearson's correlation coefficient to assess the accuracy of each result map against each truth (predictive) map (Hirzel 2001). Explained variance (R^2) and standard deviation values were computed. The higher the explained variance value, the greater the similarity between maps. Thus:

Table 20: Results of the validation analysis of HS maps composed for grazing species, by comparing composed maps against predictive maps using independently collected species presence data. The greater the R^2 value, the higher the predictive power of the result map.

Species	Pearson's R^2	SD
Buffalo	0.923	0.018
Sable antelope	0.741	0.152
Waterbuck	0.781	0.078
White rhino	0.862	0.072
Wildebeest	0.944	0.038
Zebra	0.988	0.005

Results show that all composed HS maps correlate strongly with test maps, and thus species presence data appears to have been suitably indicative of respective species range given that aerial census data is independently collected, and covers the entire reserve. Most accurate maps here appear to be buffalo, wildebeest and zebra. This may be because buffalo and wildebeest tend to congregate in particular areas of the reserve during the dry season, while zebra are widespread, avoiding only certain areas.

5.5 Further analysis

It is necessary here to analyse the species HS maps further, making them more suitable to management. A primary objective behind the composition of HS maps was to map overlap in habitat use between competing species, thus assisting management with decisions pertaining to species off-take. The results of the DFA during the hot dry season (Figure 21) assisted here i.e., species shown to experience overlap in habitat use, or those species that appear ecologically 'similar' were compared. Therefore, overlap between sable antelope and white rhino was mapped, as was overlap between sable antelope and zebra. Overlap between buffalo and waterbuck was considered, as these two species tend to use the hills and riverine areas. Finally overlap between zebra and wildebeest was mapped since both of these species tend to utilize a short grass sward in relatively open veld during this period. Apparent overlap is mostly considered along the first two environmental gradients, although species did separate themselves ecologically along the third and least important gradient (Figures 22 and 23).

To compare maps, some alterations were necessary. Firstly, all HS indices for each map were altered, with any value below 0.5 (50%) assumed to be unsuitable habitat, and any value above 0.5 for each map assumed to be suitable. These values were re-assigned with a new 0 value being given to unsuitable habitat and a value of 1 being given to suitable habitat for each species. These transformations resulted in raster maps represented by 0 or 1 values. This enabled the maps to be overlaid, using the OVERLAY function in *Idrisi*. Two respective maps were overlaid, for example white rhino and sable antelope, by multiplying the values in each respective map. By using only 0 and 1 values, any overlap between species is represented as a 1 value while areas of no overlap are represented as 0 values, simply by virtue of the fact that 1 multiplied by 0 equates to zero, and 1 multiplied by 1 equates to 1.

This technique appears simple, but it functions well, and makes only one assumption: that any value between 0.5 and 1 on the HS index equates to suitable habitat, and any value below 0.5 equates to unsuitable habitat for each species. Moreover, the maps have been provided to the Research Dept. in *Idrisi* raster format should that Dept. want to analyse the maps further.

The results are now given, with 1 representing overlap between species, and 0 representing areas of no overlap. As mentioned earlier, it is assumed that mapped areas of habitat overlap between species represent habitat on the ground where the species potentially compete. Therefore, should management be concerned about the effects of competition between species, it is within these areas where this competition is likely to take place, and in the case of bulk grazing species, where the grass sward is likely to be altered to the detriment of more sensitive species.

5.5.1 White rhino and sable antelope

Figure 30 indicates fairly extensive overlap in suitable habitat between these two species, particularly along the eastern section of the estate. Importantly, it is within this habitat that management needs to closely monitor the effects that white rhino have on the vegetation over time.

If management elect to crop individuals from the white rhino population because their numbers are increasing (see Appendix 12), individuals should be cropped from unsuitable habitat. This seems illogical, but if a few individual white rhino were removed from suitable habitat that overlapped with habitat suitable to sable antelope (Figure 30), these home ranges/territories would quickly be filled, and possibly by less fit individuals. Thus, individuals should be removed from habitat deemed unsuitable to white rhino but suitable to sable antelope as these are likely to be less fit individuals, and moreover, will alleviate pressure on the territory holders in suitable habitat, who are likely to be in prime condition, after Owen-Smith (1983). Given this, Figure 31 indicates overlap between unsuitable habitat for white rhino, and suitable habitat for sable antelope. It is from these areas where individuals of the white rhino population should be removed.

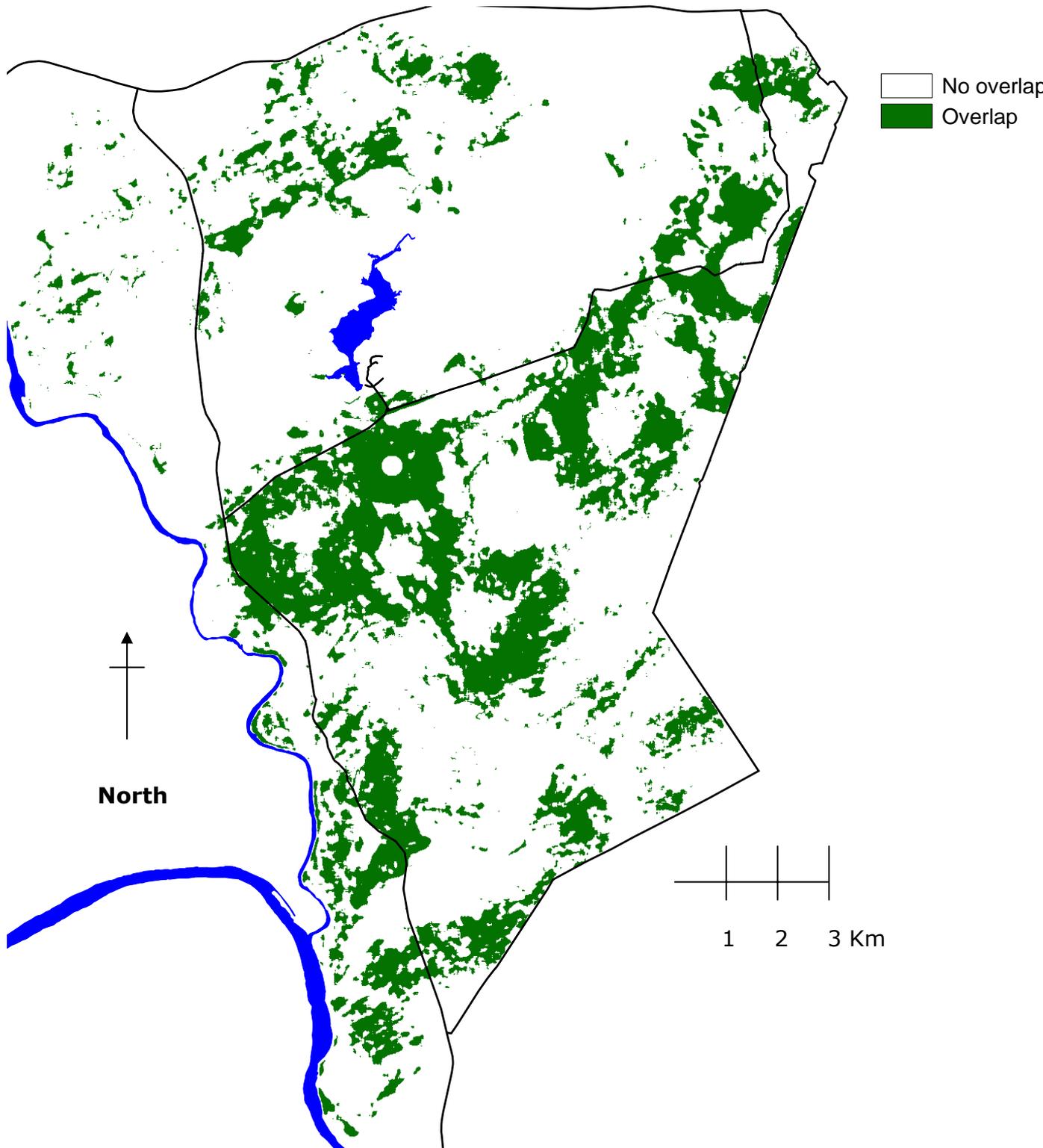


Figure 30: Overlap in suitable habitat (represented by green) between sable antelope and white rhino during the hot dry season, 2001. Main roads, perennial river systems and Malilangwe Dam indicated for reference.

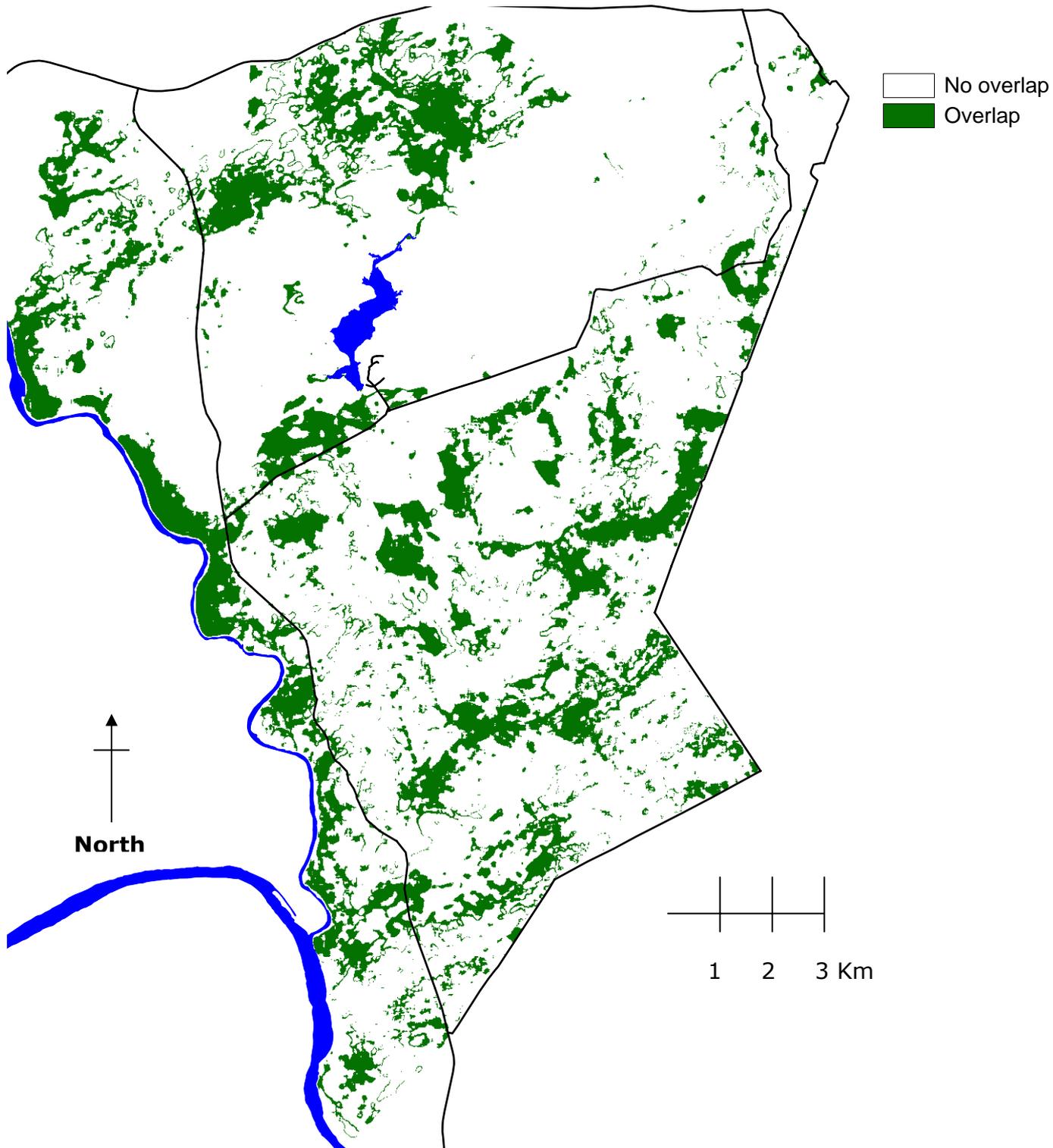


Figure 31: Overlap in suitable habitat (represented by green) for sable antelope and unsuitable habitat for white rhino, during the hot dry season, 2001. Main roads, perennial river systems and Malilangwe Dam indicated for reference.

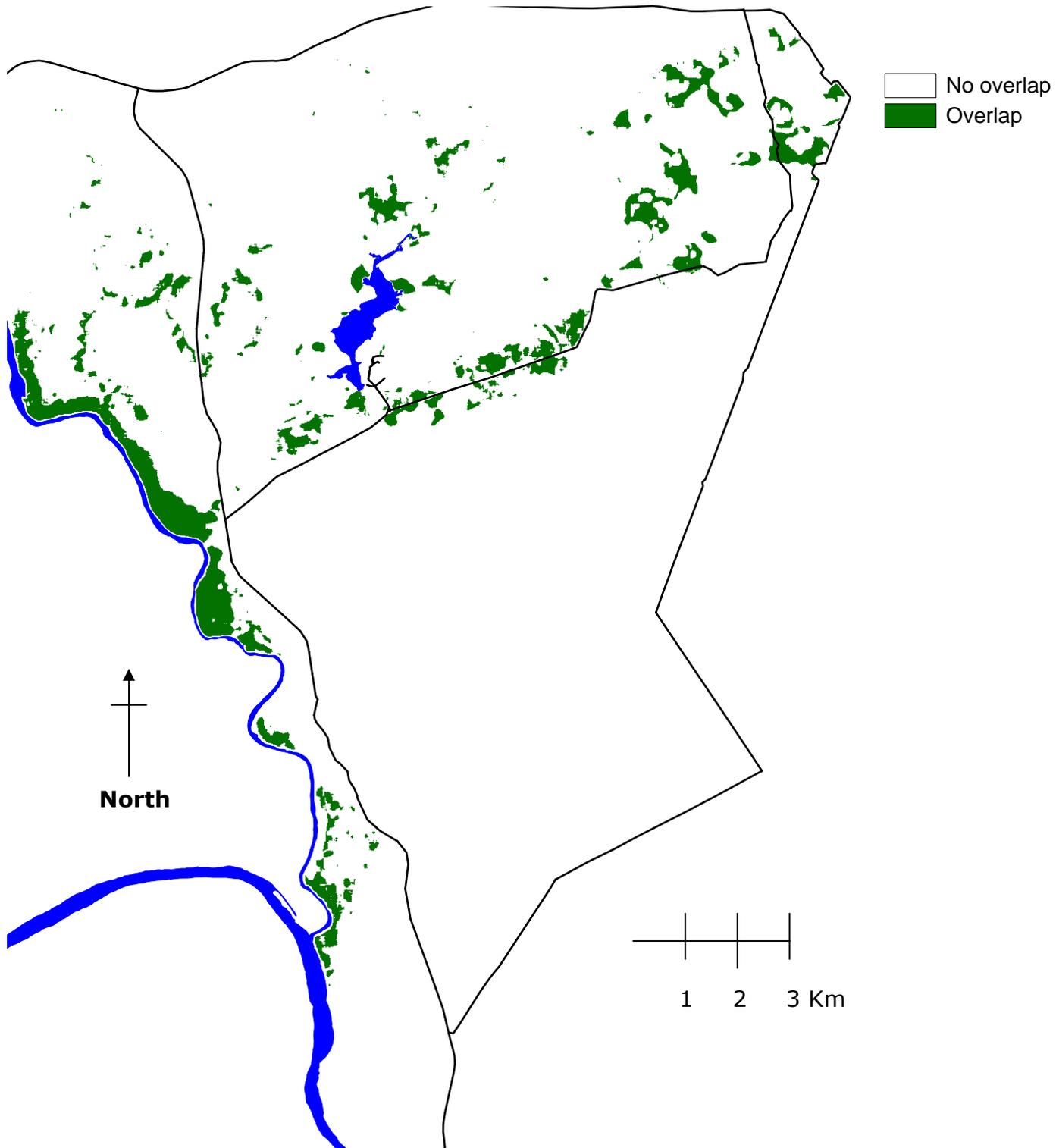


Figure 32: Overlap in suitable habitat (represented by green) between buffalo and waterbuck during the hot dry season, 2001. Main roads, perennial river systems and Malilangwe Dam indicated for reference.

5.5.2 Buffalo and waterbuck

Following Figure 32, it is apparent that both of these species utilize habitat in the hills and along the Chiredzi River. Waterbuck appear to be dependent on this habitat since they particularly choose to stay near water at ME, and buffalo appear to select riverine type vegetation as an *ecological refuge* (Sinclair 1974). Management need to be particularly cautious with their buffalo population, not allowing it to exceed carrying capacity (especially during dry periods) as the effects that this will have on the grass structure and composition is likely to negatively impact waterbuck. Thus, the effects that buffalo have on the vegetation within areas of habitat overlap needs to be monitored.

5.5.3 Zebra and wildebeest

These two species experience extensive overlap in suitable habitat (Figure 33). Competition for suitable habitat is an unknown between these two species, since wildebeest are classified as Type III species, benefiting from the effects that Type I species (here zebra) have on the veld, i.e. shortening of grass sward (Collinson & Goodman 1982). I speculate though that these two species potentially compete for forage, particularly green grass parts during this season. Again, the (Type I) bulk grazing species (here zebra) needs to be closely monitored by management, with their population not being allowed to exceed carrying capacity, especially, in fact, critically, during chronic dry periods.

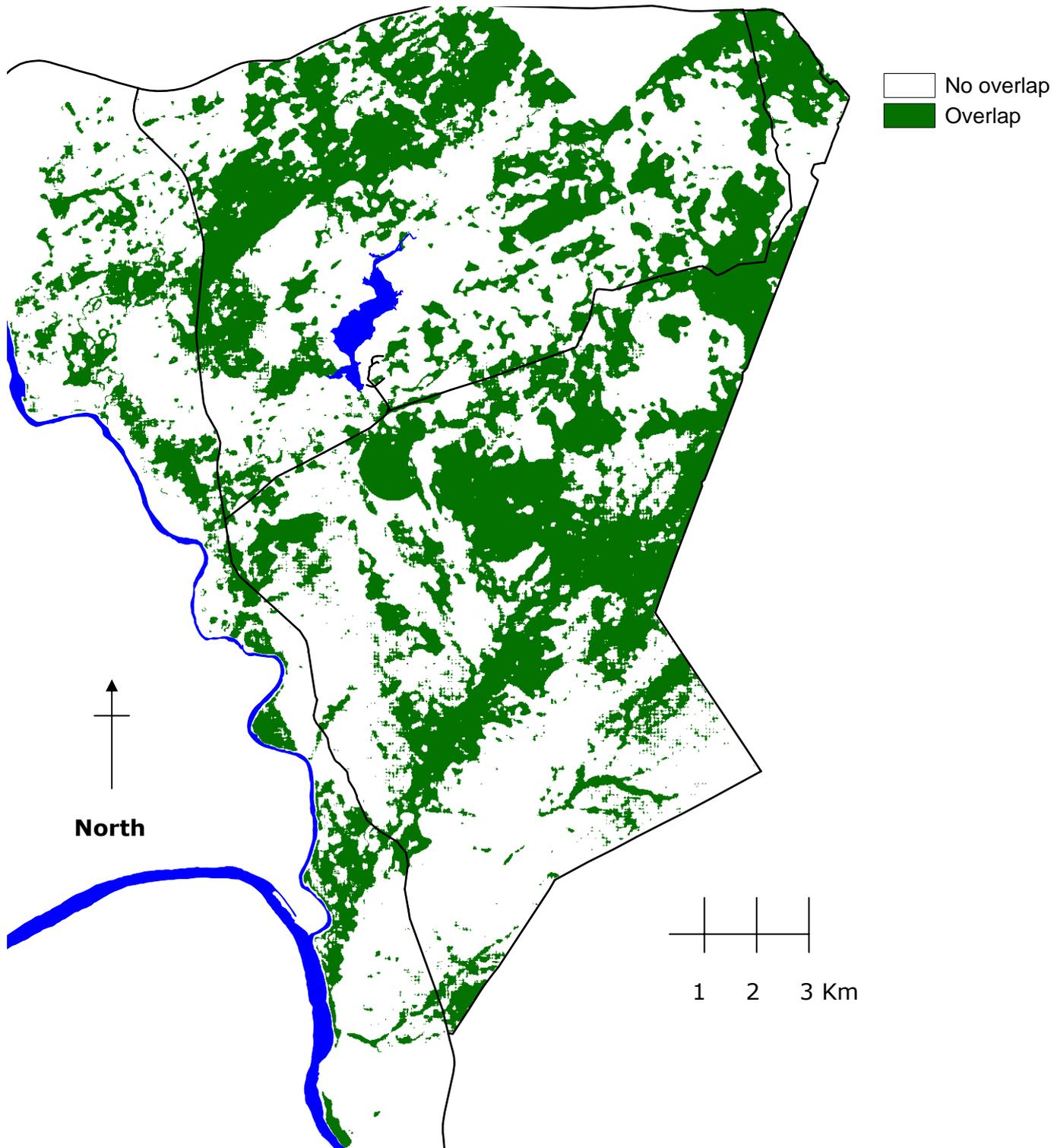
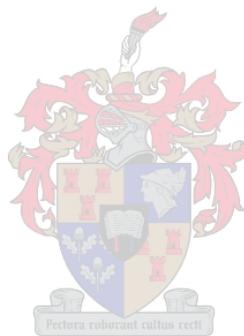


Figure 33: Overlap in suitable habitat (represented by green) between zebra and wildebeest during the hot dry season, 2001. Main roads, perennial river systems and Malilangwe Dam indicated for reference.

5.5.4 Zebra and sable antelope

Overlap between these two species is important to note. As mentioned earlier, the animals do appear to ecologically separate themselves along several gradients, specifically grass sward height during the dry season. However, since zebra are bulk grazers, they have the ability as a species, especially if carrying capacity is exceeded, to alter the grass sward. A likely outcome of the effects that overgrazing by these species has will be a transition of the grass sward to a shorter and less palatable state, much to the detriment of the selective grazer sable antelope (Hirst 1975). Again, the zebra population at ME needs to be closely monitored, particularly since the overlap in suitable habitat appears extensive (Figure 34).



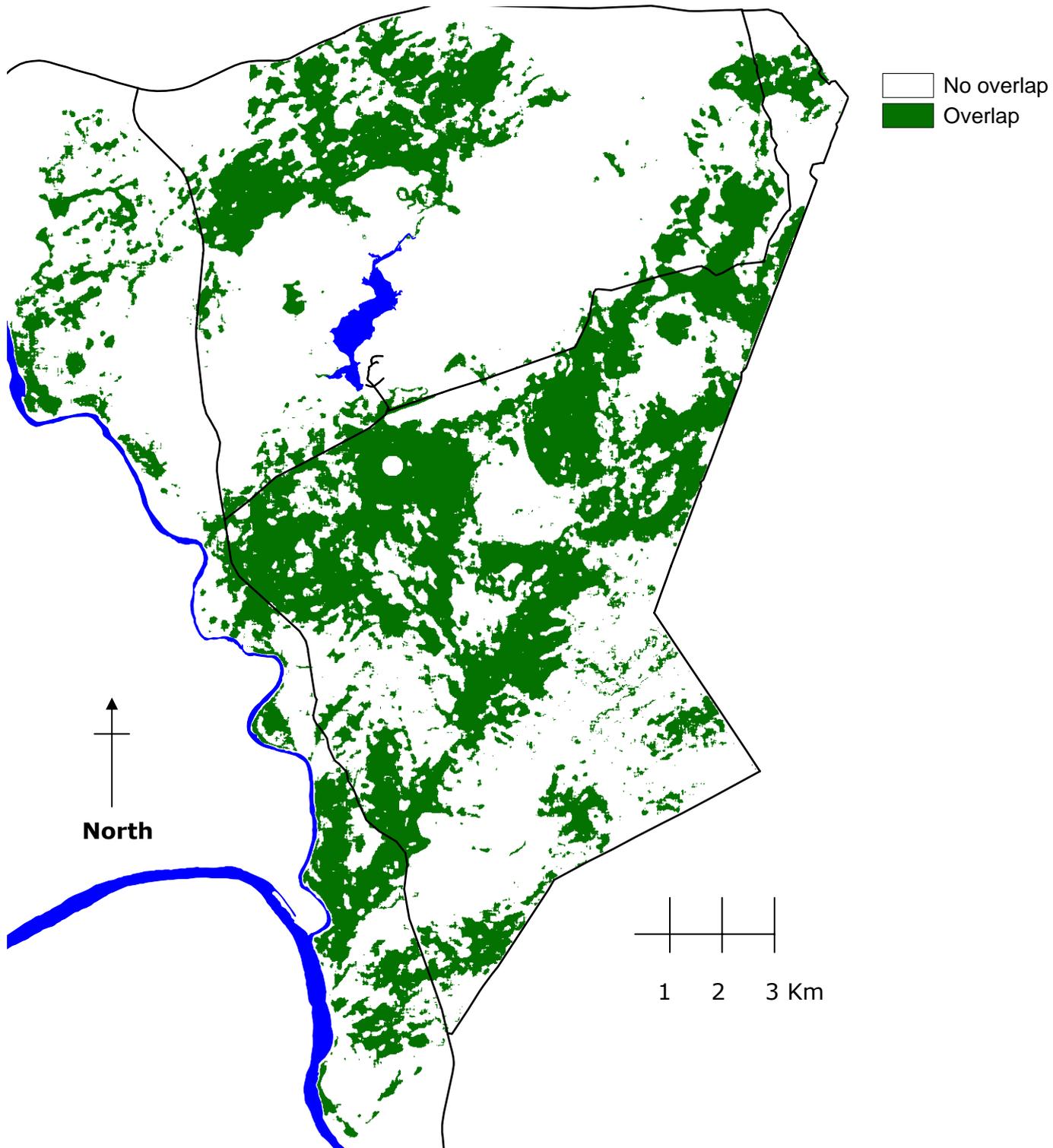


Figure 34: Overlap in suitable habitat (represented by green) between zebra and sable antelope during the hot dry season, 2001. Main roads, perennial river systems and Malilangwe Dam indicated for reference.

5.6 Discussion

The ENFA has provided some valuable information pertaining to habitat selection among the grazing herbivore species at ME during the critical dry season.

Firstly, greenness of grass is seen to be highly valued by all species. During the dry season, non-growing (senescent) grass essentially is no longer food for herbivores (Sinclair 1975). Proteins and carbohydrates are transported to the roots of grasses, leaving a highly lignified and indigestible remnant sward with low nutrient content. Although bulk grazers are better able to deal with this (Tainton 1999), all grazing animals will select a relatively greener sward where possible, and this is shown here. It must be remembered that greenness of grass here is relative to a senescent sward. A relatively greener grass sward during the study period was available in the hills, and along most river systems and vleis (pers. obs.), and it appears that the animals more or less focus their attention along these areas.

From the results of the ENFA, distance to surface water again appears to ecologically separate species with sable antelope and white rhino apparently utilizing habitat further from perennial surface water. It is possible that these animals are avoiding the trampled sward near water, as well as possible the increased levels of grazing competition and predator associations. Sable antelope are particularly sensitive to overgrazing, or the effects of, and will avoid a utilized sward where possible. White rhino are possibly selecting a greener and less utilized grass sward away from perennial water (green grass still apparently occurs along low-lying lands and vleis, although the water is sub-surface).

Canopy volume does not appear to be an important habitat variable to grazing species, although sable antelope, wildebeest and zebra appear to associate with an open canopy. The results of DFA showed wildebeest and zebra to associate positively with an open veld, far from available cover. It seems that this is most likely due to predator avoidance. Sable antelope thus apparently prefer a relatively closed veld, with a taller grass sward.

Zebra and wildebeest apparently associate with a grass sward where *U. mossambicensis* is abundant. It is not known whether this is due to an actual preference for this palatable grass, but nonetheless, it is encouraging since this

grass species appears abundant at ME and moreover is capable of withstanding heavy grazing pressure (Stalmans 1994).

The implications of overlap of suitable habitat between species have been discussed above. The maps produced here are simple but appear useful. It is up to management at ME to monitor habitat use of species, particularly bulk grazing species, and their effects on the veld. Moreover, if sable antelope appear to shift their veld use, this could be indicative of the fact that suitable range has been lost.

Management should consider removing excess individuals of a chosen population from without suitable habitat. It is likely that populations nearing or exceeding carrying capacity will expand their resource use to avoid density-dependent regulatory mechanisms. Thus, individuals (particularly within bachelor herds) may range out of suitable habitat. If these individuals are removed, pressure will be alleviated, to the benefit of the population within suitable habitat.

Should management elect to remove individuals from a population because their number appears to have a detrimental effect on a more sensitive population, it may not be appropriate to remove individuals from areas of habitat overlap since this is *suitable* habitat to both species, and the vacuum will quickly be filled, and possibly by less fit individuals. Thus, individuals from a chosen population should be cropped from areas that are deemed unsuitable, and especially if this overlaps with suitable habitat of a more sensitive species. It is up to management to determine home ranges or territories of individuals of a population chosen for cropping, and discover where home ranges lie in unsuitable habitat.

Chapter 6: Integrated discussion of results and recommendations

6.1 Introduction

This chapter serves primarily as a final synthesis of the results of the two analyses, i.e. DFA (all seasons) and ENFA (hot dry season only) and also considers the options available to management if they are to sustain their large grazing herbivore community.

Firstly, the basic habitat preferences of each species are given. This merely serves as a reference for management, since the habitat preferences of grazing species at ME may differ from the preferences of the same species in different study areas and cited by relevant literature. Species distributions are also discussed here and the data taken from the *Idrisi* vector coverages for each species in each season. This data is available to the Research Dept. at Malilangwe. Place names are sometimes used when explaining species distributions and these are again relevant to management since they are familiar with all the names.

This is followed by a more pertinent discussion of the results in the context of those habitat variables that may be manipulated by management i.e. tools. This discussion mostly involves the hot dry season as this is the critical season for the grazing species (Schoener 1982).

Finally, recommendations are made with long term objectives in mind, and mention is also given to the likely reactions of the grazing species during a drought and the options available to management in this situation. Recommendations focus on the rare and/or valuable species i.e. buffalo, sable antelope and white rhino.

6.2 Incorporation of results

6.2.1 Basic habitat preferences by species

As mentioned above, the apparent habitat preferences of each of the study species is given mention here. The rationale being that this serves as a basic reference for management.

6.2.1.1 Buffalo

Sinclair & Gwynne (1972) observed that buffalo are almost exclusively grazers, and apparently require a plentiful supply of grass, shade and water (Leuthold 1977; Mloszewski 1983). During the hot wet season at ME, buffalo selected relatively open areas of intermediate to tall grass sward height, on clay to loam soils and that hadn't been recently burnt. Point data in *Idrisi* showed the species to be generally scattered along the base of the hills, among the heavy clay soil areas south of Malilangwe Dam, in the Chimiza area and down to the Hartebeest paddock. The animals may be attracted to the grass species prevalent in these areas.

During the cool-dry season buffalo selected areas where the grass sward height was relatively tall and where the perennials *D. eriantha*, *P. maximum* and *U. mossambicensis* were abundant. They generally stayed closer to water than species such as sable and white rhino and avoided bare areas. Buffalo tended to be distributed along the base of the hills, as far south as Makeche, and east as Manyoka during this season. Some individuals, generally solitary bulls, were sighted along the Chiredzi River.

During the summer months, the buffalo population apparently focused its activity to the hills or major river systems, seeking the perennial water and associated grasslands where *D. eriantha* and *P. maximum* thrived. Mloszewski (1983) found that during dry periods, buffalo search for green remnants near water or in depressions, or make do with low nutrient grass, in anticipation of the rains. Furthermore, Sinclair (1974) describes riverine vegetation as the *ecological refuge* of buffalo during dry months, given the potential for interspecific competition in open grassland habitat. It is not known here if buffalo do in fact select the hills and rivers during this season to avoid competition (most likely with the other bulk grazers white rhino and zebra), but

it does seem probable that the animals are selecting these areas for the relatively greener grass sward.

To conclude, buffalo appear to shift their selection of habitat during the year from open and relatively recently burnt areas on clay soils during the wetter periods to possible ecological refuges during the drier months, i.e. the hills and rivers. The animals stay relatively close to water sources for during the year and prefer a relatively medium to tall grass sward. Jarman & Sinclair (1979) note that buffalo in east Africa showed high selectivity for habitat only in the dry season, associating randomly with vegetation communities in the wet season.

6.2.1.2 Eland

Eland are described as intermediate feeders that prefer shrubs, forbs and tree foliage (Buys 1990; Fabricius & Mentis 1990). They are highly versatile in their habitat requirements and are not dependent on water (Skinner & Smithers 1990). Eland were not included in the discriminant analysis of the hot wet season due to insufficient data.

During the cool dry season, the species showed a preference for areas of intermediate grass sward height, where *U. mossambicensis* and *D. eriantha* were more common. They tended to stay closer to water than some other species, but it is not likely that this was an important factor in their distribution, given that Grossman *et al.* (1999) classified the species as water independent.

During the hot dry season, eland moved relatively far from water sources and appeared to prefer more open habitat of intermediate grass height. Hilly and rocky areas were avoided as were dense riverine habitat, probably as a predator avoidance mechanism.

Conclusively, the species are generally intermediate in their habitat choice at ME, selecting areas further from water as the year progressed and mostly avoiding rocky habitat and dense vegetation.

6.2.1.3 Elephant

The essential habitat requirements of elephant include access to surface water, preferably fresh, and shade (Western & Lindsay 1984). Leuthold (1977) classified elephants as intermediate feeders, preferring grasses, but also selecting the bark, leaves, shoots, and fruits of dicotyledons.

The habitat utilization of elephant at ME is wide ranging. Results show that during the hot wet season, elephant preferred areas where the grass sward height was tall to medium, and generally dominated by *P. maximum*, under an open tree canopy. Elephant avoided riverine areas during the rain season where *P. maximum* can reach > 2 m in height (pers. obs.). Furthermore, the species avoided more rocky areas and tend to move in the low-lying flatlands where the soil clay content is high. The 'sticky' nature of these soils at this time of year did not seem to be a deterrent.

The animals appeared to be intermediate in their avoidance of heavily wooded areas, suggesting that access to grasses is more influential during this season, in approximation with the findings of Guy (1976) and Western & Lindsay (1984). Grasses during the wet season have relatively high digestible protein content (relative to browse), and thus grass is more likely to be selected (Guy 1976; Sinclair 1985).

During the cool dry season, elephant shifted their selection strategy to areas of relatively higher grass sward height, closer to water and with a higher percent contribution of the grasses *D. eriantha* and *U. mossambicensis*. This suggests that the species were staying closer to clean sources of water and selecting the more palatable grass species i.e., *D. eriantha*, as well as shifting their feeding strategy to include browse, in accordance with the findings of Lewis (1986).

Over the hot dry season, the animals apparently turned to browse in preference to graze, although bulls were occasionally seen taking tufts of grass (*Cenchrus ciliaris* and *Ischaemum afrum*) while moving. Lewis (1986) found that the proportion of food intake by elephant in the Luangwa valley, during the hot dry season, was 75% browse and 21% graze respectively. The habitat preferences of elephant over this period appears to be defined primarily by distance to water, although personal observation showed that the species select certain habitat based on the available browse, with a particular preference for the *Albizia petersiana* – *Dalbergia melanoxylon* woodland.

Conclusively, elephant appear to select habitat during the wet season based on the height and proportion of green grass, then shifting their criteria for selection of habitat as the veld progressively dries to areas closer to water, and in particular to favoured vegetation communities that apparently provide preferable browse.

6.2.1.4 Impala

Impala are associated with woodlands throughout their range in southern Africa, preferring open structure where cover and surface water is available (Pettifer & Stumpf 1981; Skinner & Smithers 1990). Leuthold (1977) classified impala as intermediate (mixed) feeders preferring fresh grass when available.

During the wet season at ME, impala apparently preferred areas where grass sward height was relatively low, and selected habitat that was neither too rocky nor too high in clay content. A possible explanation for the avoidance of tall grass by this species during this period may be as a predator avoidance strategy, particularly since the young are dropped during the rain season (Skinner & Smithers 1990). The population appeared intermediate with regard selection of woody habitat.

Thus impala preferred lightly wooded areas that were neither rocky nor high in clay content and where grass was generally short. A review of species distribution showed that they avoided the central part of the hills during the rains as well as the black clay areas. There appeared to be a high occurrence of impala in the Nyari Pan area, possibly attracted to the fresh growth of grass, and relatively open veld in that area (pers. obs.).

Over the cool-dry season, impala apparently shifted their feeding strategy. They showed a preference for areas of medium to tall grass sward height, closer to water, fairly open and usually abundant in *P. maximum* and *U. mossambicensis*. Munro (1980) found that impala diet changed from predominately grass in the wet season to mostly dicotyledons in the dry season. He added that impala appear to select succulent food with high levels of crude protein but preferred grazing to browsing when palatable grass was available. Dunham (1980) studied impala dietary intake in the Sengwa area, Zimbabwe, and discovered that during the wet season impala actively selected grass. In the late wet and early dry seasons forbs were the principal food, and intake of woody dicotyledons was highest in the mid-dry season, when diet quality was at a minimum. Attwell & Bhika (1985) made similar observations on Starvation Island, Kariba.

Impala at ME during the dry season appeared to select intermediate habitat relatively close to water. The animals were widespread through the reserve but notably moved to the hills and rivers during the dry season (pers. obs.).

6.2.1.5 Nyala

Nyala are mixed grazers/browsers, taking the leaves, twigs, flowers and fruits of a wide variety of plants. During the wet season, their diet comprises almost entirely grass (Anderson 1975, unseen, as cited in Skinner & Smithers 1990), and they then apparently shift their food preference to browse during the dry season.

During the wet season at ME, nyala showed a distinct preference for areas that were characterized by high grass sward height and abundance of *P. maximum*. They also showed an association with more rocky areas. Nyala were almost entirely found in riverine habitat (pers. obs.) and these findings confirm this. Interestingly, they appear to have no competitive niche overlap, suggesting a highly specialized niche.

Over the cool dry season nyala showed a strong association with *P. maximum* and other tall grass, as well as woody habitat. The species actively selected dense woody vegetation where *P. maximum* was abundant (this grass species thrives under tree canopies).

During the hot dry season, nyala were separated once more from the remaining species by distance to water, woody vegetation density and abundance of *P. maximum*. Nyala are classified as non-mobile water dependent species (Goodman 1982), but I would speculate that their association with riverine habitat at ME was also due to their preference for a thick dense vegetation type. Importantly, nyala do not appear to seasonally change their habitat selection strategy at ME, and appear to always be associated with the Chiredzi, Nyamsaan and Nyamasikana Rivers (pers. obs.).

6.2.1.6 Sable antelope

Sable antelope generally avoid open grassland habitats, and rather favour low-lying areas with good quality graze (Magome 1992). They are classified as fresh grass grazers (Leuthold 1977) and are water dependent but are able to range fairly far from water sources (Goodman 1982; Grossman *et. al.* 1999). The antelope are highly species selective and crop grass at 40 to 140 mm above the ground (Grobler 1981).

At ME, during the wet season, sable antelope were distributed entirely along the eastern section of the estate and apparently selected habitat characterized by an intermediate to tall and relatively dense grass sward on less rocky soils, with a tendency toward clay soils. They were also associated with

more open woodland and did not show any apparent preference for freshly burnt veld. Their association with the eastern section of the estate can be attributed to the generally open woodland typical of this area, the dense grass sward associated with the clay type soils and most likely the grass species that grow here.

Their association with tall grass appears to contradict Grobler's (1981) finding that the species select grass below 14 cm. Skinner & Smithers (1990) further asserted that the species feed below 30 cm. Although personal observations of their feeding habits were minimal, I suggest that the sable antelope at ME feed between the levels of 10 cm to 100 cm. During the wet season, leaf growth was lush and tall, and there is no apparent reason why the antelope would not feed at breast height.

During the cool dry season, sable antelope again occurred in the eastern section of the reserve, also seen in the hills, but most sightings occurred in the Makeche and Mahande areas. From the results of the DFA, the antelope moved to areas where grass sward height was relatively tall. Sable antelope foraged at a greater distance from water sources than did other species during this time, except for white rhino. It is possible that this was employed as a strategy to avoid competitors.

Again, during the hot dry season, sable notably foraged further from water sources than the other grazers, excluding white rhino. They were associated with a taller grass sward that tended to be dry and have a high percent contribution of *H. contortus*. Interestingly, Wilson (1975) showed that the first food choice of sable antelope was *H. contortus*. The species were assumed here to avoid competition to a large extent by selecting plant species generally avoided by other ungulates, after Magome (1992) and Wilson (1975). Additionally, the antelope appear to select green parts of a generally dry grass sward in accordance with the findings of Grobler (1981). The finding that sable antelope at ME select habitat relatively far from water sources apparently contradicts the findings of Du Toit (1992) who stated that sable antelope associate with woodland adjacent to vleis and water. This contradiction is most likely due to the differences in habitat of the study areas and the competitive milieu of ME.

It must also be noted that it is possible here that the water itself moves away from the preferred habitat type of sable antelope i.e., it dries as the

surface water 'retreats' to the hills and perennial rivers. The animals don't need to 'follow' the water since the distances remain negligible.

Conclusively, sable antelope at ME appear to base their selection of habitat on grass height, grass species composition, distance from surface water and openness of the veld, including woody cover. The sable antelope population at ME spend a large part of the year in the eastern section, and tend to scatter to the central and south western parts of the reserve during the dry period, most likely as a response to select only suitable habitat during this period.

6.2.1.7 Warthog

Warthog actively selected areas characterized by low grass sward height in all seasons at ME, in accordance with Skinner & Smithers (1990), who state that warthog are invariably associated with short grass. Within a short grass sward, warthogs characteristically kneel on their forelegs, and use the upper end of their hard snouts as a digging tool to get at hard-to-reach roots and tubers (Barrett & Spitz 1991).

Over the wet period at ME, warthog preferred a more barren rocky soil type, where grass growth was patchy and stayed near water. Their distribution during this season appeared to be influenced by the openness of the veld and grass height, with the species utilizing the sodic areas near the Mahande river system and the open rocky veld near Nhorro Dam.

During the cool dry season, warthog selected habitat distinguished by short grass in medium wooded areas, where *D. eriantha* was abundant. Warthog also stayed relatively near water sources, in accordance with the findings of Barrett & Spitz (1991), who stated that water is a limiting factor for warthog and furthermore is a major determinant of the species' home range.

Over the dry period, warthog were found relatively close to water, in more recently burnt veld characterised by low tree and shrub volume. The warthog population at ME appeared to avoid the southern parts of the reserve where grass cover was patchy and usually dominated by unpalatable species (pers. obs.) and also possibly where root and tuber occurrence was relatively low. Grass height, distance to water and available cover appear to be the main determinants of habitat utilized by warthog.

6.2.1.8 Waterbuck

Waterbuck are associated with water throughout their range at ME, in accordance with the findings of Herbert (1972) and Melton (1983). Melton (1978) believed that waterbuck selected habitat primarily on the basis of water availability, but a considerable amount of weight can be accorded to good quality of grass. They have been known to settle in habitat purely on the basis that artificial water was provided and moved if that source was depleted (Melton 1978). Waterbuck are classified as fresh grass grazers dependent on surface water (Hanks *et al.* 1969; Leuthold 1977).

The distribution of the Malilangwe population appears to be entirely situated in the hills, particularly near Induna dam, and along the Chiredzi River. During the wet season, waterbuck showed a preference for areas of intermediate grass sward height, in intermediate cover. Personal observation revealed that the species are mostly associated with the grasses *D. eriantha* and *P. maximum*. Melton (1978) stated that waterbuck are associated with long grass during this period, particularly *P. maximum*. Hirst (1975) made similar observations, stating that the habitat requirements of waterbuck are a dense woody component, tall grass and local water sources. Although tall grass does not appear to be a habitat requirement of waterbuck at ME, this may be due to the fact that the mean grass sward at ME may be higher than that at the Timbavati Nature Reserve, the study area of Hirst (1975).

During the cool dry season, waterbuck appeared to shift their selection strategy to areas of taller grass, closer to water and with a high percent contribution of *D. eriantha*, *P. maximum* and *U. mossambicensis*. This is more in line with the findings of Hirst (1975) and Hanks *et al.* (1969).

During the hot dry season, waterbuck exhibited a preference for more hilly areas that had a high proportion of sedge and woody cover and were close to water sources. Results also showed that the animals actively selected a relatively tall and green grass sward at this time of year, and particularly favoured a grass sward where *D. eriantha* was abundant. Van Outdshoorn (1992) classed *D. eriantha* as a highly palatable grass species, and I speculate here that waterbuck actively selected this grass as a food source.

6.2.1.9 White rhino

Player & Feely (1960) listed four factors as habitat determinants of white rhino i.e., quality graze, water, cover and topography. The same authors also stated that grass quality is the most important determinant of habitat selection.

At ME, during the wet period, white rhino appeared to select a low to medium height grass sward on low-lying clay soils, particularly along the Mahande River system. The animals appear to select habitat further from water than any of the other species during this season, and also showed a preference for freshly burnt veld.

Over the cool period, white rhino appeared to select a patchy grass sward of low to intermediate height, and that was noticeably further from water i.e., > 1 km. Grossman *et al.* (1999) state that white rhino are dependent on regular access to surface water, but are capable of moving up to 10 km from a water source.

During the hot dry season, white rhino selected relatively open habitat at lower altitudes and relatively far from water sources. Moreover their apparent choice of a short-to-medium height grass sward was in accordance with previous findings (Pienaar 1994). The species appear to select greener grass among a generally dry sward. Pienaar, Bothma & Theron (1993) and Pienaar (1994) found that white rhino select 'sweet', shade loving grasses such as those species belonging to the genera *Urochloa*, *Panicum* and *Digitaria*, and although this study did not explore the utilization of food plants, it is likely that these grass species were selected, along with *Enneapogon scoparius* which the animals were often seen to be feeding on.

Of further interest are the findings of Grobler & Jones (1980) and Owen-Smith (1981) who stated that white rhino increase the favourability of their habitat by promoting an increase in short grasses that are relatively protein-rich. This is done by cropping the grass close to the ground. Obviously, this is to the detriment of some of their competitors, notably sable antelope, after Goodman (1982).

White rhino at ME almost exclusively utilize the eastern section of the reserve, which incidentally is more or less the same habitat utilized by sable antelope.

6.2.1.10 Wildebeest

At ME, wildebeest actively selected areas characterized by low grass sward height, low tree volume and high percent contribution of *U. mossambicensis* in all seasons. Melton (1978) also showed that wildebeest have a specific preference for short grass areas, and Owen-Smith (1985) put this down to their broad muzzles. Hence, the species are physiologically adapted to short grass, and in fact, Skinner & Smithers (1990), went as far as saying that a short grass sward was the single most important habitat characteristic affecting wildebeest distribution.

Over the wet period, wildebeest were distinctly associated with short grass in relatively open areas. Personal observation revealed that the species are mostly found in the old fields, near Nyari pan and in the areas near James Dam during the wet season.

During the cool months, wildebeest again selected a short grass sward where *U. mossambicensis* was abundant and in an open veld relatively close to water.

Over the dry period, wildebeest were closely associated with a relatively (very) short and green grass sward dominated by *U. mossambicensis*. The species also appeared to venture relatively far from water sources and generally occurred in low lying and sometimes rocky veld. Literature supports the view that wildebeest are attracted to freshly burnt areas, particularly when the first rains arrive (Skinner & Smithers 1990) and personal observations showed that the species were at times found in burnt veld and mowed areas, selecting the fresh growth.

Wildebeest appeared to completely avoid the hills at ME, as well as riverine type vegetation, with grass sward height possibly being a limiting factor.

6.2.1.11 Zebra

Zebra are similar to wildebeest and white rhino at ME in their general selection of habitat. They were associated with short grass during the wet season, but move toward longer grass areas during the cool-dry season and then short grass during the dry months, more or less in keeping with Smuts' (1974) observations that the species preferred short grass but will also feed in long grass. Zebra also selected more open areas where *U. mossambicensis* was dominant (pers. obs.). The animals appear widespread throughout the year,

generally only avoiding the sandstone outcrops and the dense vegetation growth immediately east of Matsanga pan.

During the wet season, zebra tended to select recently burnt veld and stayed relatively further from water. The species may be attracted to the relatively vigorous grass growth of recently burnt veld during this season.

Over the cool period, zebra appear attracted to a relatively short grass sward where *D. eriantha* was usually present. The species also appear to select areas relatively far from water, possibly avoiding the habitat associated with surface water.

During the critical dry period, zebra again, and importantly, selected a more open habitat relatively far from surface water and appear attracted to a relatively short grass sward that is relatively green. The presence of forbs and the grass *U. mossambicensis* appear to be important determinants of habitat utilization. Smuts (1974) mentions that although zebra are predominantly grazers, they will occasionally take forbs, sedges and even browse during the dry period. Zebra appear to avoid rocky habitat during this season as well as veld where *D. eriantha* thrives, usually in the hills. The reasons for this are unknown.

6.2.2 The distribution of large grazing herbivores along essential habitat gradients, the potential for competition among them and the implications for management.

This discussion importantly focuses on the habitat variables that may be manipulated by management and the influence that these variables have on the large herbivore community at ME. Effort is taken not to duplicate the discussion given in Chapter 4, but there may be instances when this occurs. Habitat variables that may not be manipulated by management (such as altitude) are not given particular mention, since this study is primarily concerned with the management of the large herbivore community at ME. Also, the discussion primarily focuses on the 'pure' grazers during the dry season, as it is among this community that the rare and economically valuable species exist, and during the critical hot dry season when resources are assumed to be limiting (Sinclair 1975) and essential niches occupied (Putman 1996).

It must be remembered here that the results of the analyses pertain to mean values, and so the finding that sable antelope prefer a tall grass sward for

example, implies that most of the individuals of this population are found to select a relatively tall grass sward, but there may be instances in reality when individuals select a relatively short grass sward. The same can be said for distance to water: findings show that white rhino utilize habitat further from water, but there will be occasions when individuals of the Malilangwe population are found in habitat close to water.

6.2.2.1 The influence of surface water

Given that the study period was relatively wet (674 mm for 2001, mean annual rainfall is 559 mm) surface water still came out as the most important determinant of large herbivore distribution at ME, particularly during the dry period. This is in keeping with Owen-Smith's (1996) statement that surface water availability forms the primary limitation on the distribution of large herbivore populations. Notably, no point in ME during the dry period was further than 4.7 km from surface water (Figure 10) and so surface water *per se* cannot be a limiting factor as most animals, even non-mobile water dependent species, are capable of travelling up to 6 km away from water in search of food (Goodman 1982). The critical finding of this study therefore is that surface water ecologically separates species, with non-mobile water-dependent species (except buffalo) preferring to stay near water sources as the year progressively dried and mobile water-dependent and water-independent species selecting habitat further from water sources. The ecological separation of grazing species during the critical dry season showed that waterbuck and buffalo utilize habitat near surface water while zebra, wildebeest, sable antelope and most notably, white rhino utilize surface water that is relatively distant from surface water.

So, what are the most probable causes of this apparent ecological separation along this gradient, and importantly, what are the implications?

A starting point here is research done by Clegg, S. (1999) on the effect that perennial water at ME had on vegetation and herbivore distribution. She found that grazer biomass at ME was highest closest to water (0-1 km), and that it was within this zone that grazing intensity was the highest. Perennial grass cover was shown to decrease close to water points, with the exception of *U. mossambicensis* (an increaser species according to Stalmans (1994)), and *P. maximum*. However, she also discovered that herbaceous biomass was not

adversely affected close to water, nor were there any apparent signs of bush encroachment.

These results suggest a number of possibilities. Firstly, since there appears to be increased herbivore activity close to water points, and although this does not appear to have affected herbaceous biomass, trampling possibly occurs (pers. obs.) and the grass sward near water points would be characteristically short (Tainton 1999). It is probable that the more sensitive sable antelope avoid habitat close to water due to the increased activity of other herbivores, browsers included. Sable require a relatively tall grass sward (Wilson 1975) that is in good enough condition for the animals to be able to select palatable parts of the plant, and quite possibly the grass sward near water points is in poor shape due to trampling, and more suited to bulk grazers. The trampling effect could also be undesirable to other mobile water dependent species (white rhino, wildebeest and zebra) and since the animals don't really have to travel beyond 4.7 km further from water to locate more desirable food plants, it may be in their interest to travel relatively further than non-mobile water dependent species to attain desirable plant cover.

Secondly, Clegg, S. (1999) states that it is within the zone close to water (0-1 km) that grazing intensity is highest. Therefore, some of the grazing animals could be moving out from water sources to graze so as to avoid direct competition and select preferred grass species that may be over-utilized close to water points. This seems likely for sable antelope, a sensitive grazing species that apparently utilizes grasses that are generally not heavily utilized by other species (Du Toit 1992; Wilson 1975). Zebra and white rhino are bulk grazers and an increased grazing intensity near water may not necessarily be a deterrent, but since these animals don't have to travel very far to reach veld where grazing intensity is lower, they may elect to do so.

Thirdly, although *U. mossambicensis* and *P. maximum* appear unaffected by the increased herbivore activity near water points, other palatable perennials are, according to Clegg, S. (1999). Thus, it is likely that sable antelope in particular utilize habitat further from water as an effort to locate palatable grass plants, again given that these animals are highly species selective. Since white rhino and zebra are bulk grazers (Tainton 1999), this factor does not seem like a plausible explanation for their utilization of habitat further from water. However, these animals may be selecting other palatable grass species that are

not commonly found near water. Wildebeest appear to prefer areas where the grass is short and dominated by *U. mossambicensis*, and so their apparent utilization of habitat further from water may here be influenced by other factors such as time since burn.

Fourthly, it is possible that predatory off-take is higher near surface water because of the increased prey activity. This is not known, and indeed, research is currently being undertaken at ME to explore this. Nonetheless, I speculate that some animals, particularly sable antelope, wildebeest and zebra avoid habitat close to water as a predator avoidance strategy. Appendix 5 shows that lion prey on all of these species, particularly zebra. It is also known that zebra associate with wildebeest as a predator avoidance strategy (Ben-Shahar 1995; Sinclair 1985).

Finally, it is possible that some herbivores utilize habitat further from water simply because their preferred habitat happens to occur further from water at ME. All of those grazing species shown to utilize habitat further from water (sable antelope, white rhino, wildebeest and zebra) also show a preference for a more open habitat type. Most perennial surface water at ME occurs either in the hills or along perennial rivers. The vegetation type in the hills is generally dense and woody, and rocky habitat is generally avoided by these species. Riverine vegetation is mostly very dense.

This all said, what are the implications?

From a management perspective, the fact that sable antelope are competing with white rhino and possibly zebra for habitat further from water, (and that these animals are likely to be out-competed by bulk grazers in the long run (Collinson & Goodman 1982)), suggests that the bulk grazing species populations at ME will need to be closely monitored. The same must be said for buffalo, which appear to directly compete with waterbuck for habitat close to water, and again, are likely to out-compete waterbuck, a Type II species after Collinson & Goodman (1982).

Management at ME have implemented a surface water strategy based on Clegg's findings, and most of the artificial water points in the habitat preferred by the more sensitive species have been 'dried'. This decision appears to be ecologically sound, remembering that most artificial water points at ME were created when cattle were the primary income source, and so were located in a systematic manner without consideration of the local ecology (as per the

common practice of that time). The drying of certain water points in habitat that is preferred by rare species such as sable antelope assists these species by drawing away other herbivores and the associated effects of trampling and grazing. Owen-Smith (1996) states that abundant water points favour common ungulates at the expense of rare species, and thus with species diversity being a Trust objective (Malilangwe Trust 2000), the reduction of artificially placed water is commendable.

It is essential here that those habitat types suitable to sable antelope in particular be maintained, and the manipulation of surface water is a good way of achieving this. Furthermore, by maintaining veld that is further from surface water and relatively underutilised, management will maintain a grass sward that is in good condition which acts as a back-up for drought periods (Owen-Smith 1996).

6.2.2.2 The influence of fire

This study importantly showed that burnt veld is attractive to many species only after the rains have commenced. Prior to the rains, grass growth is only really available to short grass grazers such as zebra and wildebeest (pers. obs.). During the wet season, freshly burnt veld was generally characterized by a fresh, vigorous and relatively short grass sward (pers. obs.). Buffalo, sable antelope, white rhino, wildebeest and zebra all associated with burnt veld during this period. It is possible that the 2000 management burns were done in areas where sable antelope and white rhino prefer, i.e. along the eastern section of the estate, but it is also likely that these species selected the fresh grass growth in the recently burnt veld.

Fire importantly is shown to encourage palatable perennial grass growth (Bothma 1989; Norton-Griffiths 1979; Tainton 1999) and this is obviously beneficial to grazing species, particularly selective feeders such as sable antelope. It must be noted that buffalo shifted their distribution during the wet season from the hills to the flat basalts where the veld had been burnt, suggesting that the animals were attracted to fresh grass growth.

Norton-Griffiths (1979) and Wilson & Hirst (1977) state that fire is mostly beneficial to populations of grazing ungulates by helping to maintain grasslands in a more palatable and productive, sub-mature phase of growth. Furthermore,

fire halts the spread of woody growth, thus maintaining a more open grassland vegetation type, which benefits most grazing animals (Norton-Griffiths 1979).

Malilangwe appears to have a sound burning programme, especially since palatable grass species have been shown to have increased in abundance (Goodman 2000) and moreover, bush encroachment has been discouraged, much to the advantage of the more rare species such as sable antelope and white rhino. The burning programme at ME also ensures that burn blocks are of adequate size to sustain the increased grazing pressure immediately post burn (Goodman 2000).

6.2.2.3 The influence of woody plant density

Woody density appears to influence the distribution of herbivore species primarily through the cover that it provides, or in other words the influence of woody structure has on lateral vegetation density and visibility. Waterbuck, buffalo and to a lesser extent zebra were shown to prefer a more-woody habitat while sable antelope, white rhino and wildebeest appear to select a less woody habitat. Thus, cover or openness of the veld ecologically separates species. The implications of this are that an encroached veld would be detrimental to sable antelope and possible white rhino. By the same token, a management policy that sought to open the veld could be detrimental to waterbuck and buffalo, and also to sable antelope during the calving season when cover is selected to hide the young (Wilson 1975).

The environmental variables distance to cover and distance to open vantage were shown in this study to be important determinants of herbivore distribution. These variables were measured as indicators of predator avoidance, and although this still holds, distance to cover is also an indicator of the degree of openness of the veld. Here, wildebeest and zebra in particular were shown to select open veld during the hot dry season while waterbuck and sable antelope chose a relatively more closed veld, within reach of cover. Personal observation at ME revealed that wildebeest and zebra prefer to associate with a relatively open habitat (sometimes where canopy volume was high, but the veld open) with short grass. The animals could be selecting this habitat type during the dry season because of their preference for a short grass sward, but also as a predator avoidance strategy. Sable antelope and waterbuck were observed in woodlands, where grass growth was generally tall, thus

providing cover from perceived danger if necessary. Since sable antelope in particular appear to depend on this habitat type, it is advisable to implement strategies that conserve this.

Management at ME have in the past cleared encroached vlei areas through mechanical clearance, and at present employ a burning programme designed to halt woody encroachment, and this seems advisable. Long-term monitoring of the veld, based on techniques given by Wilson and Hirst (1977) is advised. If the veld is shown to have become more-woody over time, species apparently reliant on open veld could decline in abundance.

6.2.2.4 The influence of herbaceous structure and composition

Grass sward height was shown here to a major determinant of herbivore distribution at all times of year, and importantly during the dry season. Mean grass sward heights (taken from raw data for all species) were 39 cm during the wet season, 36 cm for the cool dry and 35 cm during the hot dry season. Sable antelope and waterbuck were shown to select a relatively tall grass sward during the critical dry season, although the actual feeding level of these species is not known. Buffalo and white rhino apparently preferred a medium to tall grass sward, while zebra and particularly wildebeest selected a relatively short grass sward.

Greenness of grass was shown to be important to all species from the ENFA, particularly to sable antelope and white rhino. The DFA did not show greenness of grass to be an important determinant of herbivore distribution, and this apparent anomaly is most likely due to the fact that all species are selecting a green grass sward in different habitats, since DFA is concerned with differences in species locations along environmental gradients. Most literature (Grobler 1981; Hirst 1975; Jarman & Sinclair 1979) points to the fact that grazing species will actively select green parts of grass plants during the critical dry season, among a relatively dry grass sward. Personal observation showed that sable antelope selected green parts of tall grass plants, white rhino generally selected short and relatively green grass species in a taller and more-brown sward, buffalo generally chose green growth in the hills, particularly near springs as did waterbuck while zebra and wildebeest generally congregated on freshly burnt/mowed and other open veld.

Although this study did take species composition of the sward into account, and showed some species to associate with grasses such as *H. contortus* and *U. mossambicensis*, in reality this does not indicate food preferences of each of the grazing species. In fact little can be inferred from these results regarding contributions to the grass sward and further study is advised. Ferrar & Walker (1974) stipulate that it is at the feeding level where the most critical partitioning of resources occurs.

The implications of these results are that this study has shown grass sward height in particular to be a main determinant of herbivore distribution. Since buffalo and white rhino are bulk grazers, more or less dependent on a relatively short grass sward, the condition of the veld at ME seems to be adequate from personal observation. However, sable antelope are an ecologically sensitive species, particularly at the feeding level where they are known to be species specific (Du Toit 1992). Moreover, the antelope are dependent on a tall grass sward to hide their young from predators and the adults take refuge in cover when danger threatens (Wilson & Hirst 1975). Therefore, these antelope are likely to be susceptible to changes in their habitat, specifically a shortening of the grass sward, and shift from palatable grass species to unpalatable grasses. A general shortening of the sward may be brought about by overgrazing, particularly by bulk grazers. Also, if artificial water points were placed in habitat suitable to sable antelope, a correspondent increase in herbivore utilization will be to the detriment of the population at ME.

Another species worth mentioning here is wildebeest, since this species is almost entirely dependent on a short grass sward (Skinner & Smithers 1990). Thus if the veld at ME were to be underutilised, or not burnt, the grass sward is likely to become longer, but given that bulk grazers exist at ME, and that their effects on the sward (shortening) is generally beneficial to wildebeest (Collinson & Goodman 1982), the population at ME is likely to succeed. This also assumes that density-dependent effects are minimal and that predatory off-take is negligible.

6.2.2.5 The potential for interspecific competition

Putman (1996, after research done by Wiens 1989) suggests a range of types of evidence (implying competition) which may be sought at different levels of

cogency. Thus, although competition can rarely be proven without doubt, ever-increasing strength of supposition may be drawn from:

Weak:

1. Observed patterns (of population trend or shifts in resource use between sympatry and allopatry) are consistent with predictions from competition.
2. Species overlap in resource use.
3. Intraspecific competition occurs.

Suggestive:

4. Resource use by one species reduces availability of resources for another species.
5. One or more species is negatively affected.

Convincing:

6. Alternate process hypotheses are not consistent with observed patterns.

Thus, one can see (from above) that interspecific competition among grazing species at ME is difficult to prove, if not impossible. However, given this situation, an alternative logic is proposed by de Boer & Prins (1990, unseen as cited by Putman 1996) who argue by converse i.e., seeking not to prove competition, but rather establishing "*hurdles of disproof.*" While studying similar species to those in this study (buffalo, elephant, wildebeest and zebra), and the competitive interactions between them, they argue that interspecific competition between any two species is only possible where three separate conditions are met:

1. There must be habitat overlap.
2. There must be overlap in forage consumed by the two species within those shared.
3. The shared dietary resources must be limiting.

This approach allows for inference of where *potential* for competition exists among the grazing community at ME. This study has satisfied the first condition of de Boer & Prins (1990) i.e. habitat overlap, or lack of, has been shown between species. Overlap in forage consumed between the study species is not

known, and in fact neither is it known whether any of the available food resources are limiting (although it was assumed), especially given the above average rainfall that ME has experienced prior to, and during the study period.

Therefore, further study is necessary into the feeding ecology of the grazing herbivores at ME. Since it is known here that during the hot dry season (and considering the first two environmental gradients extracted by DFA), there is little apparent overlap in resources, except between buffalo and waterbuck, study into ecological separation at the feeding level would help clarify these findings.

Putman (1996) further states that "*only where clear overlap in resource use is accompanied by an inverse relationship in population sizes of a given species pair ... may we suspect a competitive interaction.*" Since ME have kept records of species population trends over the past five years (Appendix 12), long-term comparison may be made between trends. Thus far, all species populations appear stable, but management at Malilangwe would be advised to monitor these trends, and where a grazing species population is shown to decline, the findings of this study could help understand why. Importantly here, the white rhino population appears to be increasing, and this will have to be curbed if Malilangwe want to avoid a situation whereby sable antelope potentially lose habitat to the more competitive Type I species, after Collinson & Goodman (1982). It is worth noting that the sable antelope population, although stable, declined in abundance from an estimated 150 in 1997 to 108 in 2001 (Appendix 12). During the same period the white rhino population almost doubled in number.

Since the potential for competition at the feeding level is unknown at ME, a review of available literature into feeding preferences can indicate where competition is most likely to occur, assuming that those species that apparently select 'similar' habitat will possibly also experience competition at the feeding level. Therefore, the results of the DFA indicating species niches along the first two environmental gradients is assumed to be the best evidence of habitat overlap among species during the critical season (Figure 21), and ecologically 'similar' species at ME compared, i.e. sable antelope and white rhino, buffalo and waterbuck, and zebra and wildebeest:

Sable antelope are known as selective feeders, usually taking grass leaf between the heights of 4 to 30 cm (Grobler 1981; Skinner & Smithers 1990).

Preferred grass species appear to be *H. contortus*, *Digitaria* spp., *P. maximum*, *U. mossambicensis*, *Eragrostis* spp., *Setaria* spp., *Brachiaria* spp., *Aristida congesta* and *Tricholaena monachne* (Grobler 1974; Grobler 1981; Magome 1992; Wilson 1975; Wilson & Hirst 1975). White rhino are generally accepted to be non-selective bulk grazers, preferring a short grass sward at about 10 cm (Monks 1995; Perrin & Brereton-Stiles 1999), although they have been recorded to shift their preference to a taller grass sward during the dry season (Owen-Smith 1992). Favoured grass species are *U. mossambicensis*, *Digitaria* spp., *P. maximum*, *Eragrostis* spp., *Cenchrus ciliaris* and *Dactyloctenium aegyptium* (Lamprey 1963; Monks 1995; Owen-Smith 1992; Pienaar *et al.* 1993; Pienaar 1994; Player & Feely 1960; Skinner & Smithers 1990). Therefore literature points to the fact that sable antelope and white rhino generally select similar palatable species, although at different feeding levels. The most likely outcome of competitive interactions between these two species at ME is that white rhino will cause a shift in the grass sward height keeping it at a generally low level, which will impact negatively on the more sensitive and selective sable antelope. However, it is also known that sable antelope avoid this situation by selecting grass plants unselected by other species (Du Toit 1992), possibly *H. contortus* at ME, and this requires further study. Also note here that these two species separate themselves along the gradient of soil rockiness; sable antelope associating with a more rocky soil type.

Buffalo and waterbuck appear to have similar habitat preferences for the entire seasonal year, and so what is the potential for competition at the feeding level between these two species? Firstly, buffalo, like white rhino are classified as Type I species that are capable of causing an initial and drastic change in the climax vegetation, impacting negatively on Type II species such as waterbuck and sable antelope (Collinson & Goodman 1982). It is possibly because of buffalo that sable antelope avoid habitat near water. Both waterbuck and buffalo are associated with tall grass swards (Melton 1978; Sinclair 1974; Sinclair 1977), and tend to favour the palatable perennial species *H. contortus*, *D. eriantha*, *P. maximum* and *U. mossambicensis* (Hanks *et al.* 1969; Herbert 1972; Lamprey 1963; Melton 1978; Mloszewski 1983; Skinner & Smithers 1990). Therefore, competition at the feeding level is likely to occur between these two species at ME, and given that waterbuck are more sensitive to this;

are likely to be negatively impacted. The buffalo population at ME needs to be monitored and preferably kept at or below carrying capacity.

Finally, zebra and wildebeest appear to have similar habitat preferences for most of the year, particularly during the dry period. Both species are short grass grazers, with wildebeest not grazing higher than 15 cm above ground and zebra not grazing below 10 cm (Sinclair 1974; Skinner & Smithers 1990). Both species also show a preference for the following grasses: *D. eriantha*, *P. maximum*, *U. mossambicensis*, *C. ciliaris*, *Chloris virgata* and *Eragrostis superba* (Lamprey 1963; Melton 1978; Skinner & Smithers 1990). Thus, given the available literature, it is possible that these animals compete at the feeding level at ME, but it is not known here what the possible outcome may be since wildebeest are classified as Type III species, likely to benefit from the effects that Type I species (here zebra) have on the vegetation, after Collinson & Goodman (1982).

Most of the grazing herbivores at ME appear to pose a potential competitive threat to the sable antelope population. Firstly, white rhino appear ecologically similar (along two environmental gradients only) during the critical dry season. Both species utilize habitat further from water, and select a medium to tall grass sward. Owen-Smith (1981) suggests that sable antelope may be negatively impacted by bulk grazing species such as white rhino.

Other bulk grazers similarly pose a potential threat to sable antelope. Buffalo utilize habitat closer to water during the critical dry season, and I speculate here that it is for this reason that sable antelope choose to venture further from water. Although buffalo don't appear to pose a direct threat to sable antelope, if the buffalo population at ME increases beyond carrying capacity, niche expansion will likely occur (Smith 1996) and buffalo could utilize habitat that the sable population are reliant upon; to their detriment. Zebra and possibly wildebeest could also negatively impact the sable antelope population. Zebra and sable antelope appear to separate themselves ecologically by utilizing grass swards of differing heights, but if the zebra population exceed carrying capacity, or if drought occurs, niche expansion is likely to include utilization of a taller grass sward (Smuts 1974). Given that zebra are a Type I species, an increase in their use of available forage will be to the detriment of sable antelope. Wildebeest are unlikely to directly compete with sable antelope but are capable of maintaining an altered vegetation type to their advantage

i.e. a short grass sward, and thus can possibly reduce the range available to sable antelope. Waterbuck also apparently compete, experiencing slight overlap. The effects of this are unknown, but both populations need to be monitored. Importantly, it appears that sable antelope at ME avoid direct competition by avoiding open habitat and selecting underutilized grass species, after Magome (1992).

To conclude, the findings of this study indicated resource overlap between species and even mapped areas of overlap in suitable habitat. The research conducted here did not however explore potential for overlap in forage consumed by ecologically similar species, nor was it known here whether dietary resources were limiting; prerequisites for the inference of competition between species (Putman 1996). By showing resource overlap between species, this study has given management at ME a better idea of the competitive interactions among their grazing guild, and particularly indicated what competitive threats are posed to the sable antelope population. The most important implication here is that bulk grazer populations need to be kept at, or below ecological carrying capacity.

6.2.2.6 Broader implications of this research

It is doubtful whether in fact these findings can be fully applied to other conservation areas within southern Africa given that the utilization of habitat among species is mostly unique to the specific conservation area. This study did not attempt to test current theory or even contribute to knowledge, but rather was management oriented and focused on rare and valuable species.

It is here that the study is most beneficial to other conservation areas. A known and tested multivariate technique was applied to a grazing herbivore guild here with the primary objective of providing a thorough understanding of the utilization of habitat among species and specifically the competitive interactions between them, with explicit interest given to rare and economically valuable species. This has been achieved and has provided management at the study area with a better understanding of their large herbivore community. Recommendations have importantly been made that can be implemented and monitored over time, and this is where ecological research in southern Africa is pivotal, given the current economic and political constraints.

Also, and no less importantly, a new and robust habitat suitability analysis based on presence data has been applied to a large grazing herbivore community with relative success. Management have been supplied with habitat suitability maps, indicating suitable habitat for each of their grazing herbivore species during the critical dry season and moreover, these maps have helped management understand where overlap in habitat use occurs between species, forming the basis of future decisions. It is here where the suitability model has been successful, and particularly its use is advised in similar situations.

6.3 Management recommendations

Management recommendations here specifically focus on the three species that management at ME are concerned about i.e. sable antelope (rare, ecologically sensitive and economically valuable), white rhino (rare and economically valuable through tourist attraction) and buffalo (economically valuable at wildlife auctions). Recommendations also focus primarily on the results of the hot dry season, given that this is the critical season when resources are assumed to be limiting (Sinclair 1975). Finally the recommendations given here pertain to those habitat variables that can be manipulated by management.

6.3.1 Surface water management

As mentioned earlier in the text, the provision of surface water is a pivotal management tool that can be greatly beneficial to the veld and wildlife species if applied correctly (Owen-Smith 1996). Since research specifically into the provision of surface water at ME has been done (Clegg, S. 1999) and recommendations implemented, it is difficult here to elaborate, except to advise the maintenance of present surface water. Thus:

1. It is important to allow those areas utilized by sable antelope and white rhino further from water to remain so (further from water). The fact that these species in particular separate themselves ecologically by utilizing habitat further from water implies the importance of this habitat. Thus it is advised to keep the eastern section of the estate dry. The Goto pan should be dried, if not already done so. Also, if Nyamsaan pan is no longer used for bow-hunting, it is advisable to allow it to dry, given that

pools hold water in the Nyamsaan River approx. 1 km north west of the pan for most of the year.

2. The present surface water strategy also (and wisely) helps to maintain a taller grass sward in the habitat suitable to sable antelope, and this is essential for the survival of the species. Buffalo appear dependent on water and associated habitat in the hills and along perennial rivers and this seems suitable, especially since it restricts the range of buffalo and thus their effects on the veld which will be to the detriment of sable antelope.

6.3.2 The application of fire

3. The present burning programme at ME appears suitable. Sable antelope, buffalo and white rhino are attracted to recently burnt veld immediately post rainfall, and zebra and wildebeest select freshly burnt veld during the dry season. The new and vigorous growth is beneficial to all species, and so long as burnt areas are large enough to sustain grazing pressure, the current programme is commendable. Furthermore, the ENFA showed all grazing species to be reliant on a green grass sward during the dry season and burning is shown to encourage a perennial grass sward (Trollope 1990) that is more likely to hold green growth, for longer (Bothma 1989). Note must be taken here that zebra and wildebeest apparently associate with *U. mossambicensis*, and thus this grass should be valued given that it is not only palatable, but capable of withstanding heavy grazing pressure (Stalmans 1994). R. L. Sparrow, stockman, states that *U. mossambicensis* is the backbone of the lowveld.
4. Management however need to consider more frequent burns in habitat favoured by sable antelope, after Wilson & Hirst (1977), who state that "*burning enhances the protein content of available forage and pushes the succession back to sub-climax stages,*" thus providing the rarer species with nutritionally improved forage in their preferred areas. Burn blocks in the eastern section every two years could be considered, but closely monitored as this could attract increased buffalo and zebra activity, to the detriment of the sable antelope population. Sinclair (1975) however cautions frequent burning in sensitive veld and thus the monitoring of veld condition is required if this recommendation is followed.

6.3.3 Harvesting

ME is an enclosed conservation area and so natural migrations cannot occur. Competitive interactions can assume unnatural proportions because of this, much to the detriment of selective feeders (Wilson & Hirst 1977). Moreover, many of the mega-herbivores present on the estate can overshoot their ecological carrying capacity and deplete resources before density-dependent mechanisms check their growth (Owen-Smith 1983), and thus it is vital for management to maintain these populations at or immediately below ecological carrying capacity.

Huston (1979) states that intense interspecific competition will eventually result in low diversity among competing species, while high species diversity is maintained where competition is low. It is in this state that management at ME needs to attain. Given that sable antelope (and waterbuck) is the sensitive Type II species here, harvesting mostly applies to bulk grazers.

5. The white rhino population very importantly needs to be maintained at, or below ecological carrying capacity. Off-take (for re-introduction elsewhere) is advised since current population estimates put their number just above carrying capacity (Appendix 4). White rhino offer the most serious competitive threat to sable antelope and need to be checked.
6. Zebra need to be kept at ecological carrying capacity. An increase in their number, or a drought would see these species expand their resource use to the detriment of sable antelope.
7. Buffalo need to be maintained at ecological carrying capacity. The species already pose a serious competitive threat to waterbuck, and given their influence as a Type I species, buffalo can potentially alter the vegetation in their favoured habitat, to the detriment of waterbuck and possibly smaller species dependent on cover.
8. The effect that elephant and other large mixed feeders have on ecologically sensitive species is unknown here, although elephant could possibly open the veld to the detriment of waterbuck and possibly sable antelope. Again, this is largely an unknown, and elephant don't appear to offer serious competition at the feeding level during the wet season,

however, it is advisable to keep their population at ecological carrying capacity.

9. Hippo are unknown here and need to be researched. The Research Dept. are advised to research the habitat utilization of hippo during the critical dry period. It is possible that hippo utilize habitat similar to buffalo and waterbuck, and given their bulk grazer status (Skinner & Smithers 1990) are likely to maintain a shortly cropped grass sward. These species could potentially be competing for food resources with waterbuck at ME.
10. Management is advised to use *vacuum zones* when harvesting species, after Owen-Smith (1983). He advocated creating *dispersal sinks* through the removal of individuals of a particular species settling within designated regions. This emulates the dispersal process of species that formerly would have operated (prior to the creation of boundaries in wildlife areas), and is particularly relevant to mega-herbivores, whose populations react slowly to over-utilization of resources.

Therefore, all individuals of a species that colonize an 'unsuitable' region are culled at irregular intervals, allowing enough time for re-colonization to take place. This concept is applicable to ME given that habitat suitability maps now exist, as well as an understanding of potential interspecific competition for habitat. If management elect to cull, it is better to approach the exercise with this knowledge than in a 'haphazard' manner. Also, it is better to cull from male only herds here. These associations are usually found in marginal land, and the individuals of these herds are reproductively not important.

Conclusively, ME has a multipurpose role to play in conservation, and maintenance of the whole spectrum of herbivores is important.

6.3.4 Drought

Droughts appear inevitable in the southeast lowveld of Zimbabwe (following past rainfall records). Another drought will occur in time and management needs to be prepared. An advisable way of looking at drought is to simply view it as an extended period of depleted resources. If one considers this, it will become apparent that species will likely exceed carrying capacity (given that resources are minimal) and niche expansion will possibly occur. The likely

scenario here is that competitive interactions would substantially increase, the veld could become heavily overgrazed, and palatable perennial grass species could be depleted. Moreover the influence that Type I animal species have on the veld will be exemplified, much to the detriment of Type II species (sable antelope and waterbuck). Given this:

11. Supplementary feeding is advised during a drought period. Overgrazing and severe drought are likely to eliminate palatable grasses from the sward (O'Connor 1995) and management need to recognize that a reduction in grazing pressure during and after a severe drought event is required if it is desired that a shift in grass sward composition be avoided. Supplementary feeding here seems more desirable than culling large sections of species populations, although this is a viable alternative.

6.3.5 Monitoring

Monitoring is an essential element of management. Fortunately, the Research Dept. has done very well with the setting up of a resource base and the continued monitoring of herbivore populations. Recommendations here pertain mostly to monitoring of population trends, recruitment and mortality, as well as vegetation monitoring. Thus:



12. It is essential that grazing species population trends be monitored over time. At present an effective method has been developed (Appendix 12) following annual aerial census. This is effective since the technique used is consistent. Trends need to be monitored in the long-term, and any apparent declines need to be closely monitored. For example, if the sable antelope population is seen to decline, the results of this study can help management and the Research Dept. ascertain the cause of this, given that essential habitat requirements have been listed and potential competitors identified. Moreover, carrying capacities for each species are reviewed each year, allowing for identification of those species exceeding carrying capacity.
13. Species mortality and recruitment needs to be monitored as best that can be achieved. A drop in species recruitment may be indicative of

density dependent effects that may be brought about due to loss of suitable habitat, particularly among more sensitive species.

14. Body condition of grazing herbivores needs to be monitored, and suitable methods such as kidney fat index (Bothma 1989; Wilson & Hirst 1977) are advised. Since individuals of populations are culled at ME, it would be wise for management to set up a database recording kidney fat indices, or even bone marrow indices (Bothma 1989), that would enable that department to monitor body condition of species over time. A drop in body condition could indicate that a respective species population has exceeded carrying capacity, possibly due to loss of suitable habitat or this could even indicate a diseased population that requires veterinary attention. Such decisions rest with management and the Research Dept., but a database (and the data itself) would ultimately be beneficial to the estate and possibly conservation as a whole.
15. It is essential that a veld monitoring strategy be implemented whereby mean grass height, herbaceous cover and composition, lateral visibility and canopy cover (see Wilson & Hirst 1977, page 92) be estimated and monitored in each vegetation community. These habitat variables have been shown to be major determinants of species distribution at ME and are essential to the survival of selective and sensitive grazing species such as sable antelope.
16. Finally, further research into feeding level selection and ecological separation among the grazing herbivore community is advised, particularly since competition between species is difficult to infer without this knowledge.

To close, this study set out with the primary objective of gaining a better understanding of those habitat variables that influenced the distribution and habitat use by the grazing herbivore community, and the potential for interspecific competition among them. This objective appears to have been met. Distance to water, grass sward height and herbaceous composition, openness of the veld, time since burn and woody plant density all appear to influence herbivore distribution at ME. Potential for interspecific competition among the 'pure' grazing species has been explored, with species apparently separating themselves ecologically during the critical hot dry season, possibly

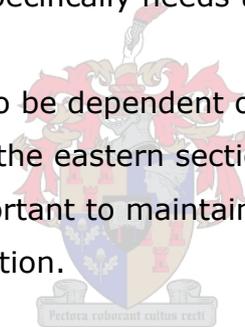
as a mechanism to avoid direct competition for resources. Although potential for competition has been inferred, it is far from being proved.

HS maps have also been composed and validated for the 'pure' grazers during the critical dry period. These maps have helped to understand species distribution and assist with predictive assessments such as habitat overlap between species.

Recommendations have been made within the context of the tools available to management *viz.* surface water, fire and harvesting.

Concerns about the rare and economically valuable species have been addressed. Buffalo appear confined to ecological refuges during the critical dry season. It is in management's interest to maintain these refuges by keeping the buffalo population below ecological carrying capacity. White rhino appear to be dependent on a medium-to-tall grass sward in open habitat further from water, and also appear to be thriving (given that the population is increasing). The white rhino population specifically needs to be kept at or below ecological carrying capacity.

Sable antelope appear to be dependent on a relatively tall and dense grass sward in habitat along the eastern section of the reserve and notably further from water. It is important to maintain a tall and vigorous grass sward for the sable antelope population.



It is hoped that these findings will be used for the greater benefit of the grazing herbivore community at Malilangwe Estate.

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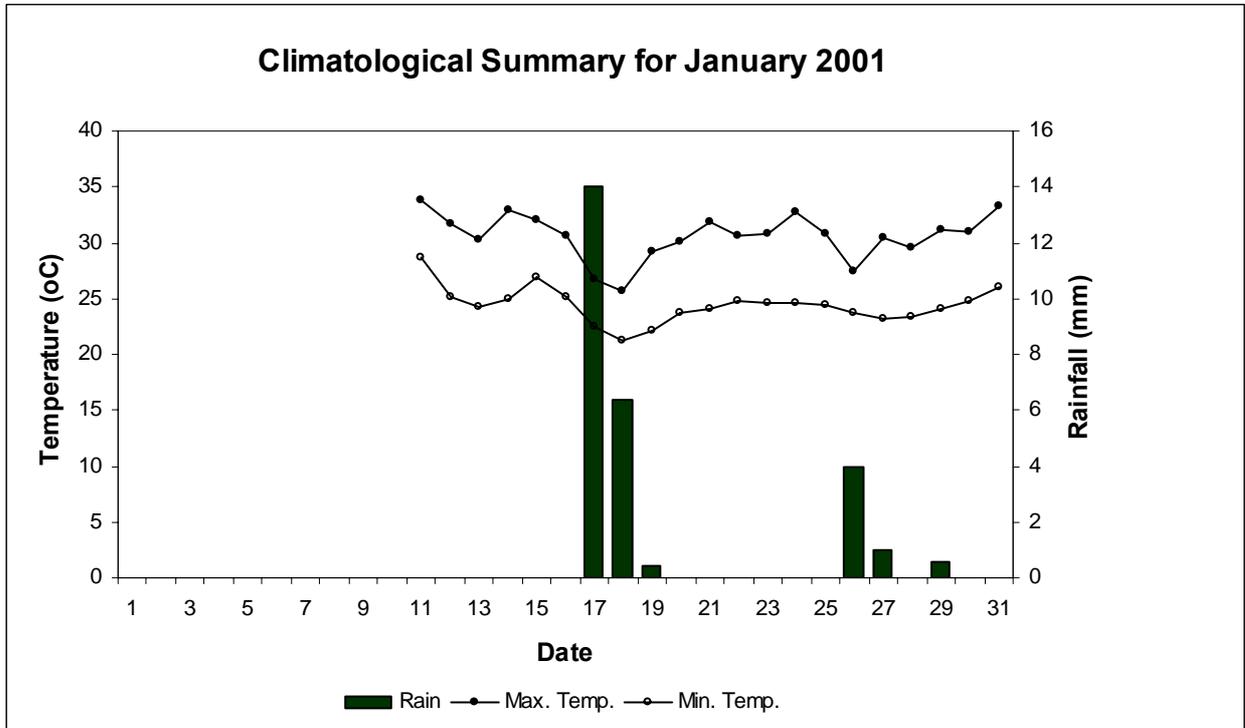
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Note: Instructions to authors for the *South African Journal of Wildlife Research* used throughout this document.

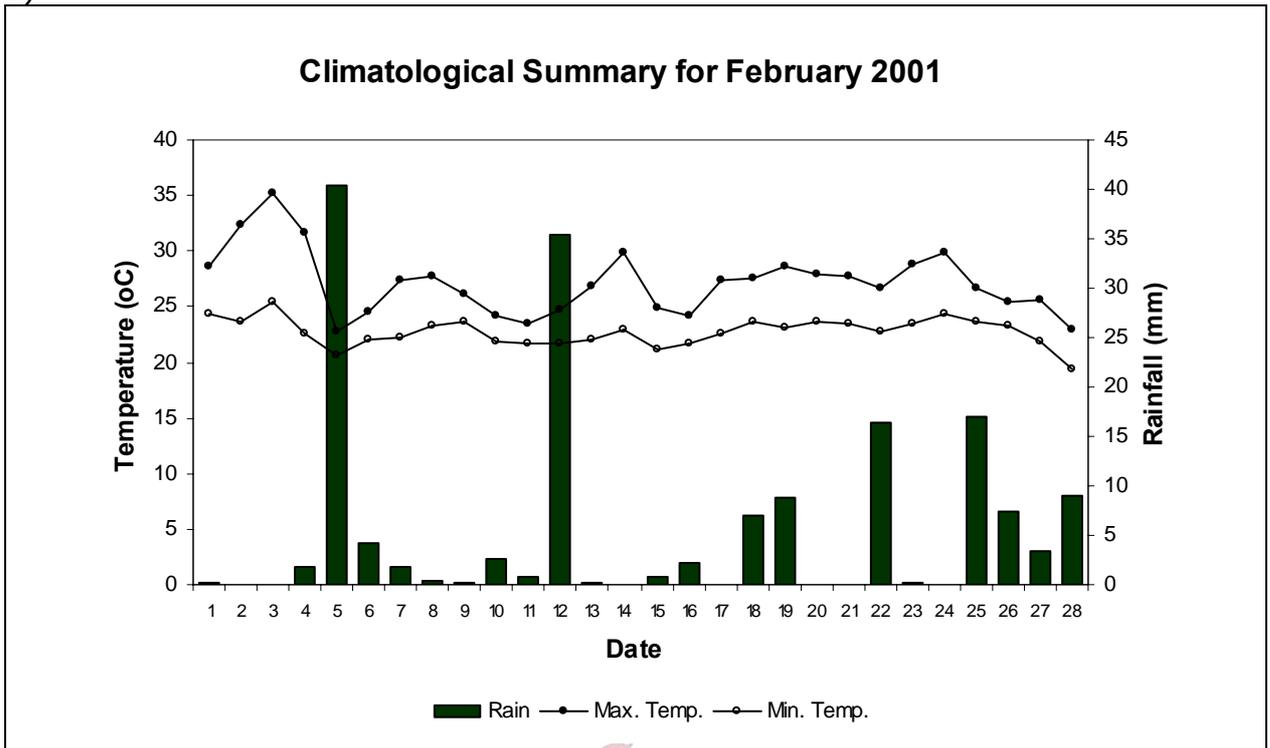
Appendices

Appendix 1: Monthly climatological summaries (January 2001 – October 2001). Gaps in data caused by faults in database system at HQ.

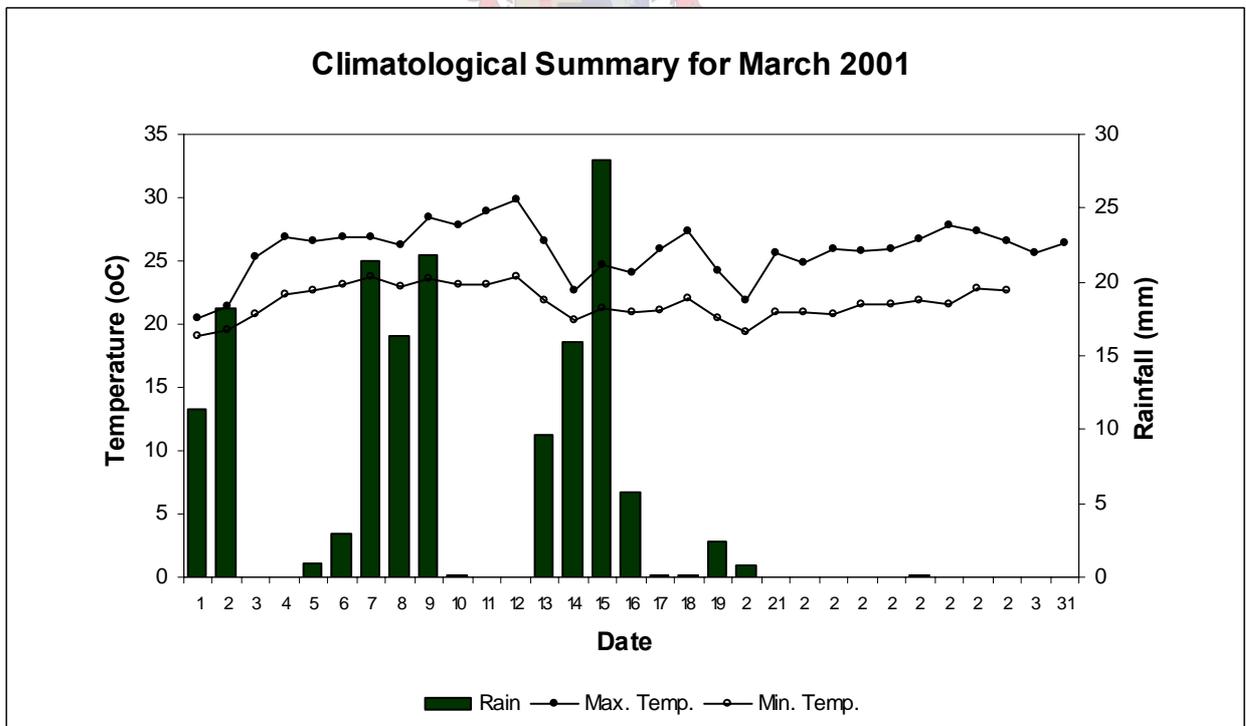
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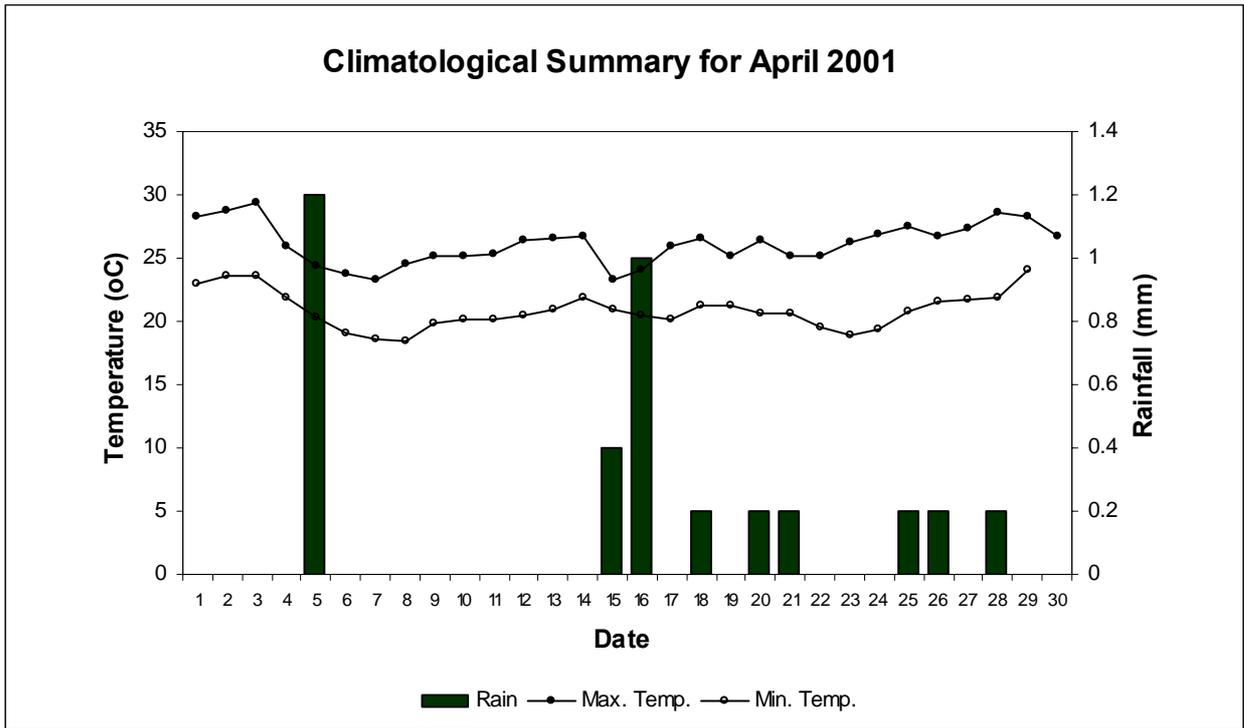
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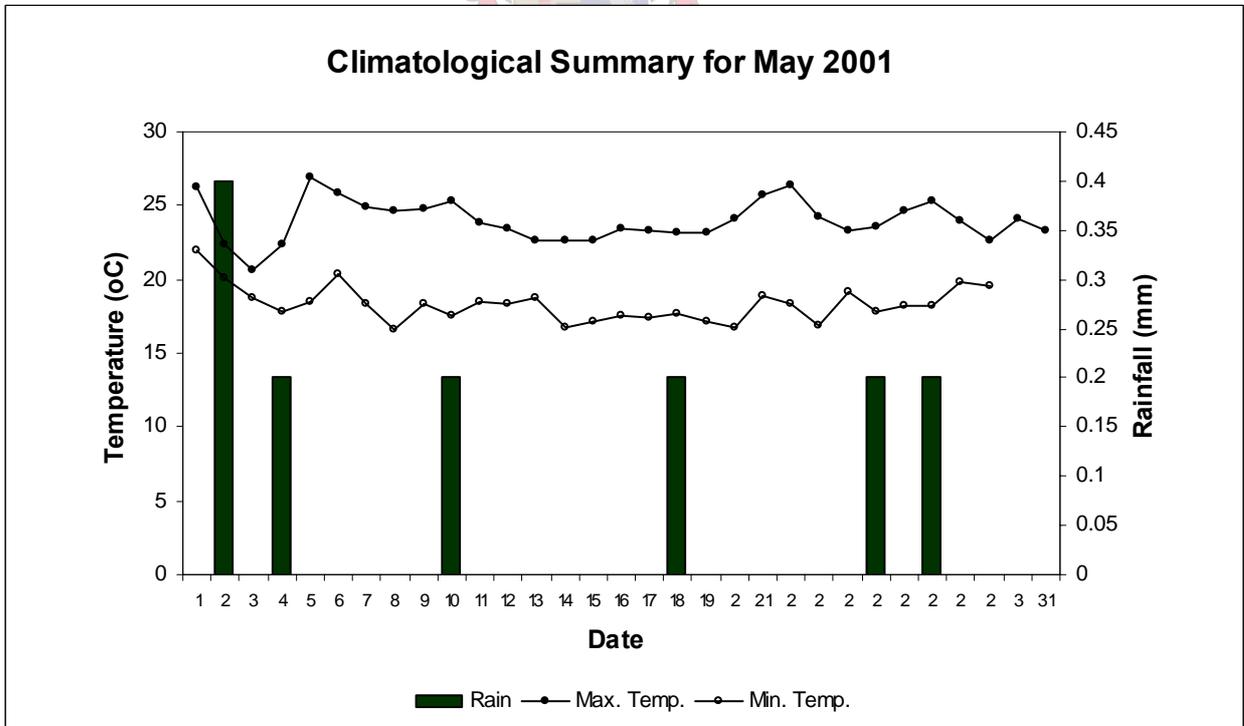
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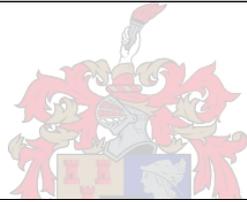
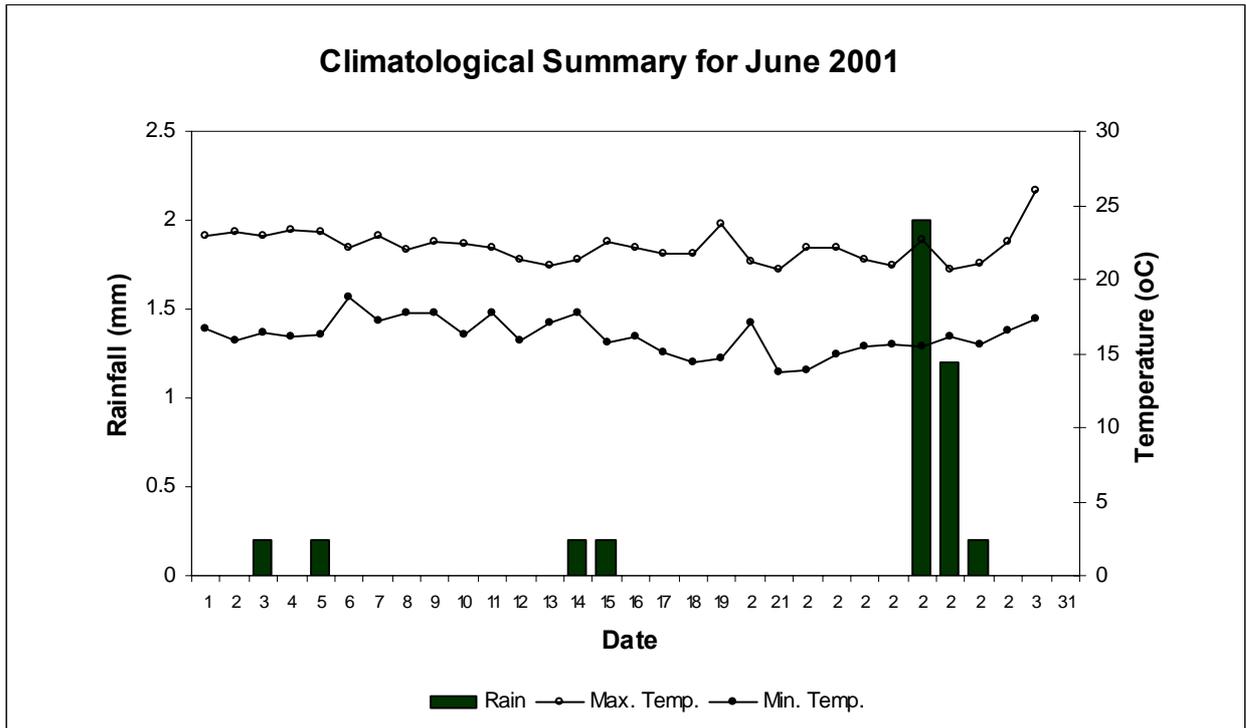
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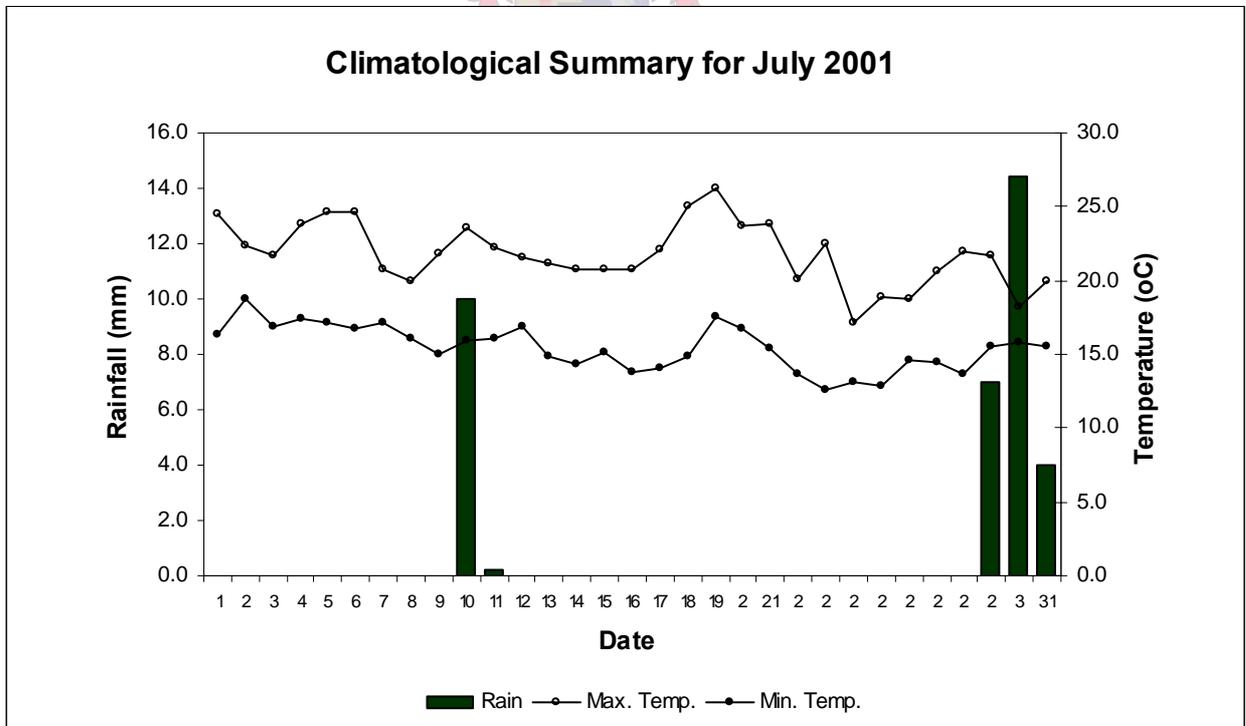
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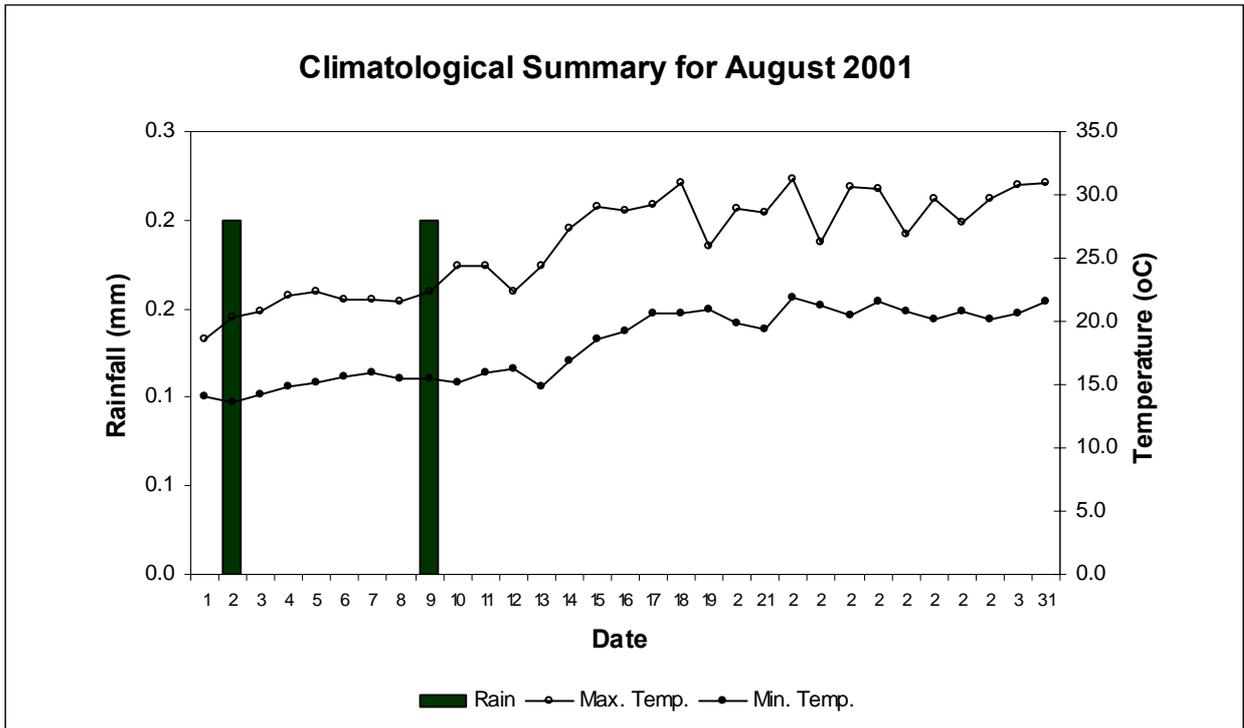
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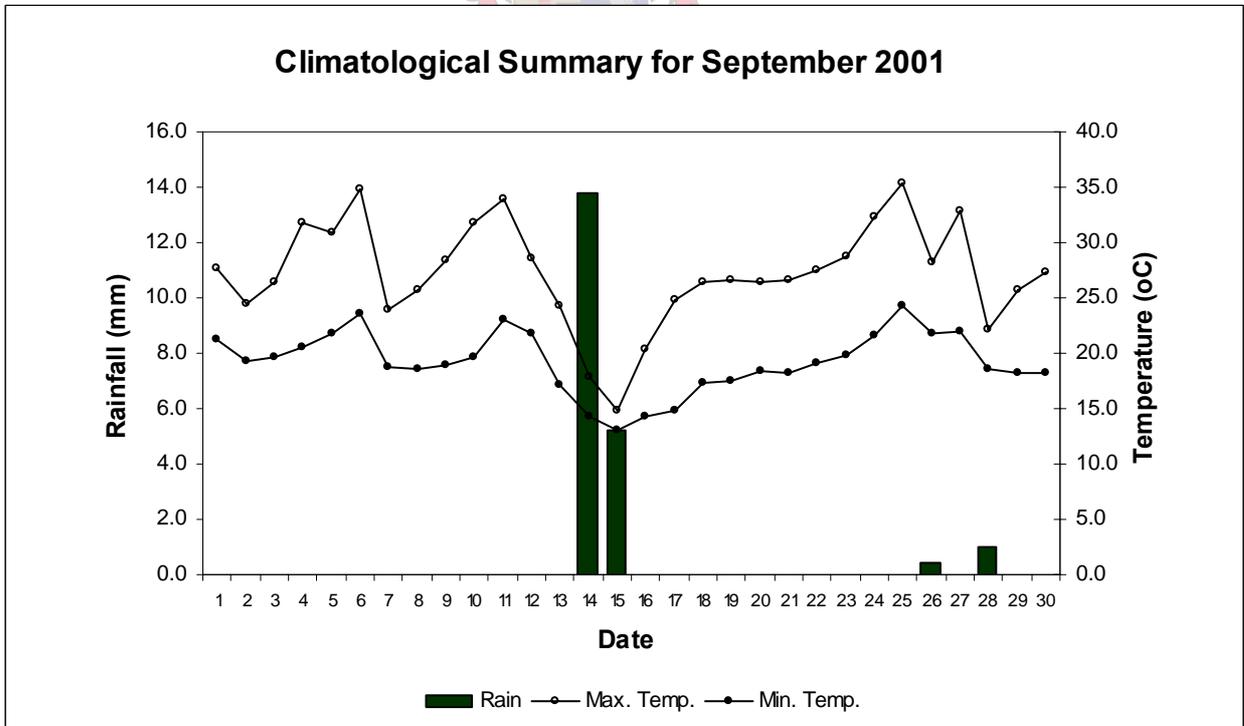
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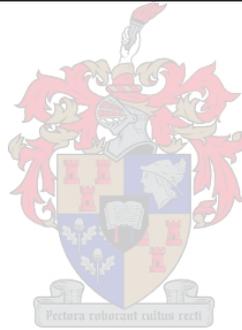
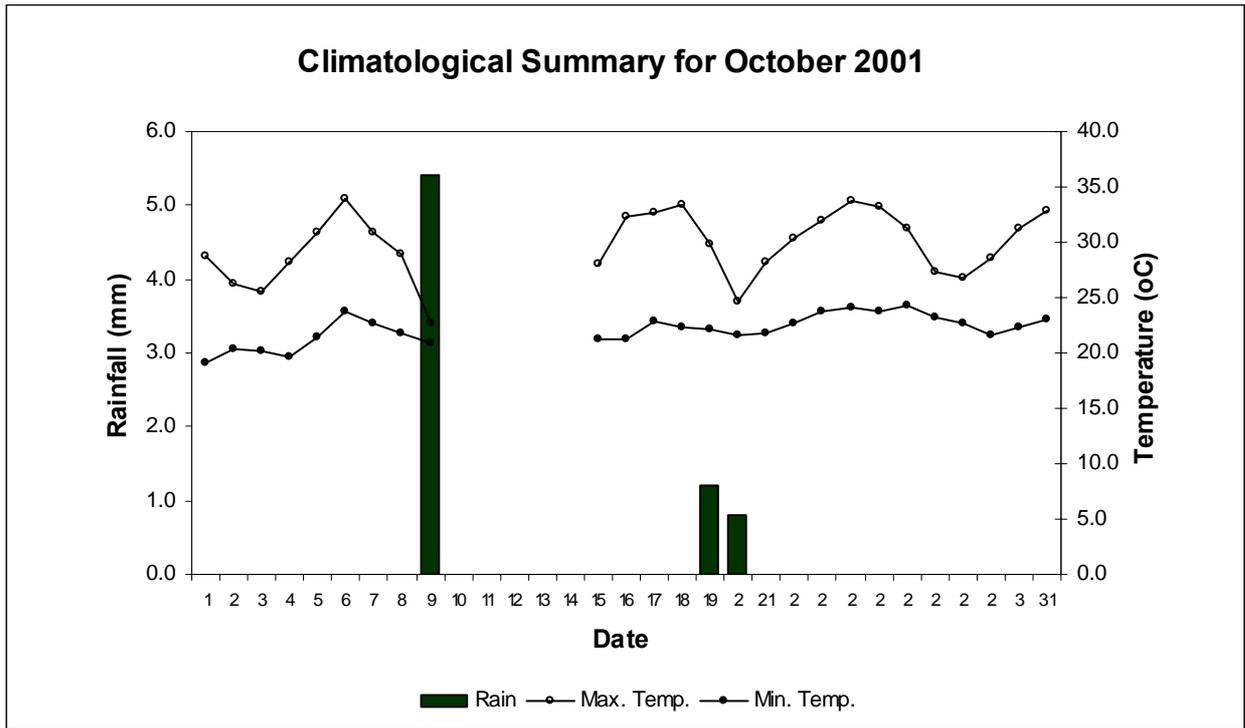
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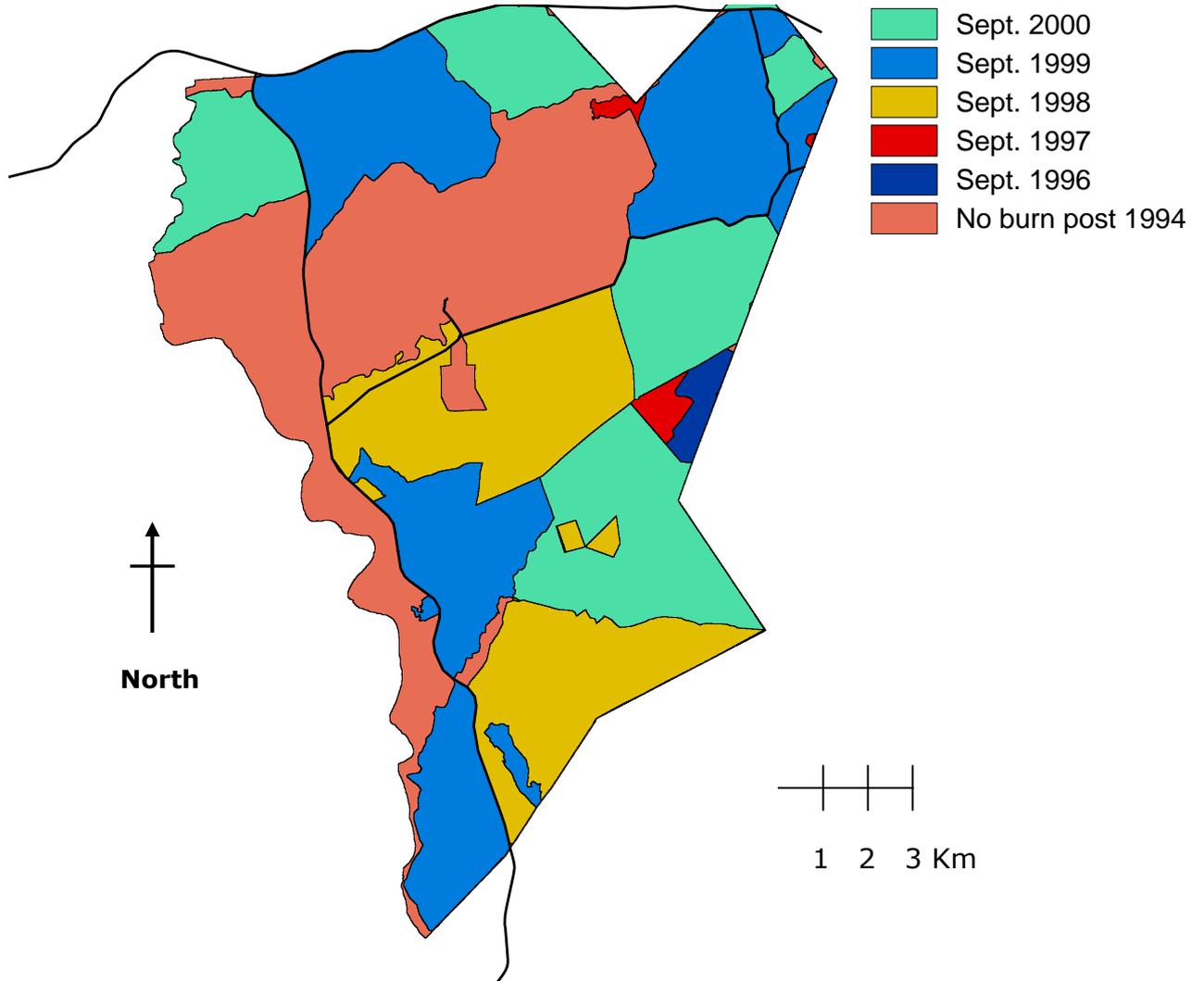
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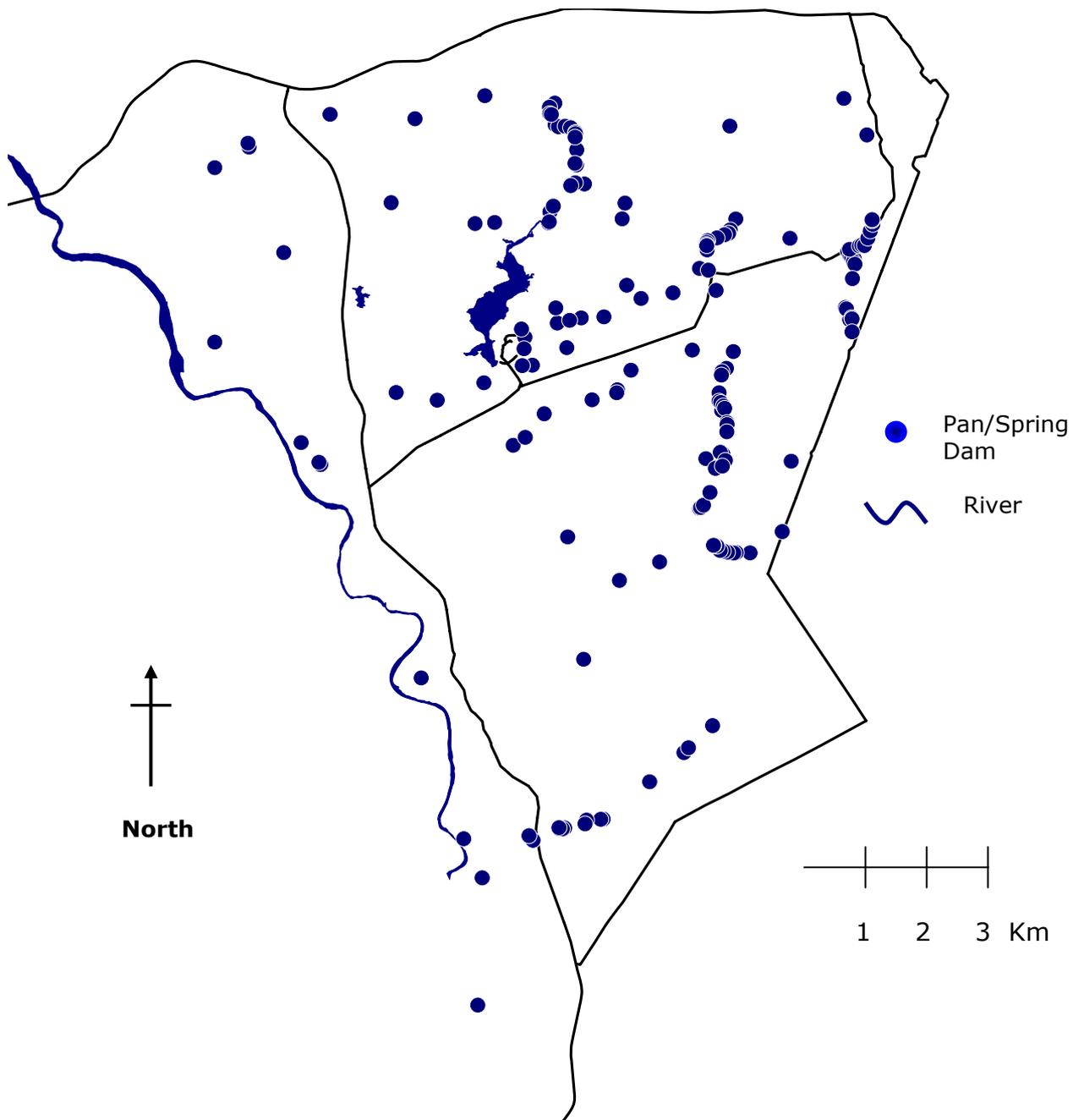
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Appendix 2: Pre-2001 management burn blocks at ME, with main roads indicated.



Appendix 3: Seasonal water (late wet season) during 2001 at ME.

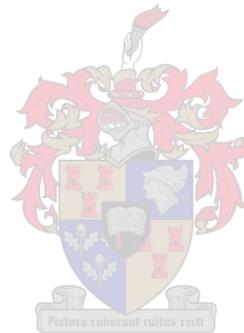


Appendix 4: Herbivore population estimates and carrying capacities for 2002, taken from Goodman (2002). Note that immigrations have taken place since 2000 due to poaching on neighbouring land.

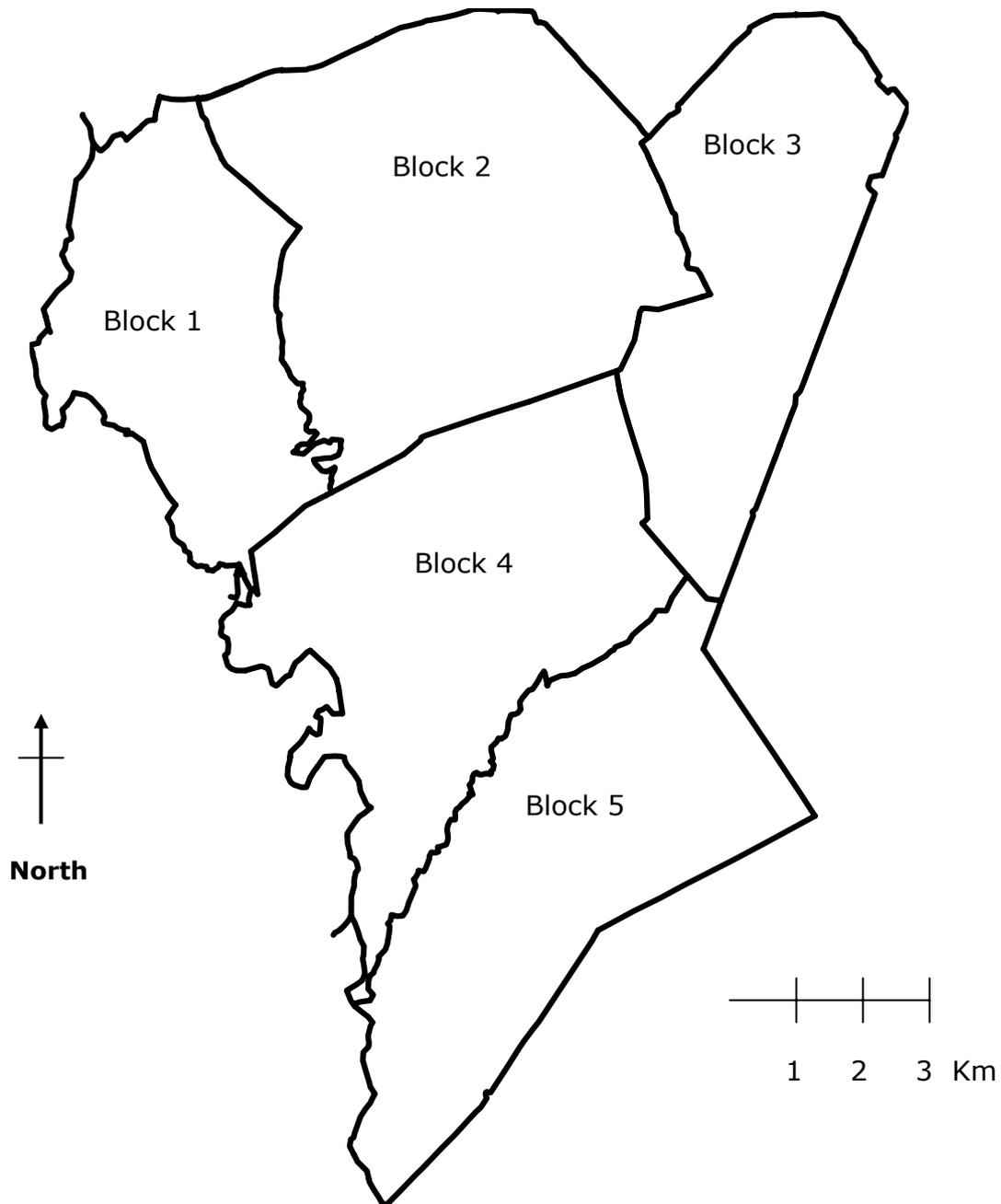
Species	Mean Mass (kg)	Biomass (kg ha⁻¹)	Carrying Capacity Estimate	Current Population Estimate
Bulk grazers				
Rhino/White	1500	1.98	55	57
Hippo	1000	1.06	45	41
Buffalo	450	11.88	1050	1093
Roan	220	0.17	32	34
Zebra	200	4.22	845	843
Sable	185	0.63	140	124
Waterbuck	160	0.51	130	112
Concentrate grazers				
Wildebeest	165	1.31	320	296
Hartebeest	125	0.20	65	77
Reedbuck	48	0.13	110	40
Warthog	45	0.24	210	102
Mixed feeders				
Elephant	1725	5.46	120	132
Eland	340	2.24	265	228
Nyala	75	0.20	110	50
Impala	40	4.12	4120	3962
Browsers				
Rhino/Black	816	1.08	55	37
Giraffe	750	2.97	160	145
Kudu	136	1.80	530	513
Bushbuck	30	0.12	160	115

Appendix 5: Known annual predatory off-take, 2001 (Source: Research Dept., ME).

Predator/prey	Lion	Leopard	Cheetah	Hyaena	Wild dog
Buffalo	9				
Eland	14	1	1		
Impala	5	27	2	2	46
Nyala					
Sable antelope	1				
Warthog	2				
Waterbuck	4	1			
Wildebeest	13	1			
White rhino					
Zebra	21	2		4	



Appendix 4: Sample blocks used during field sampling, 2001.



Appendix 7: Sampling distance (m) covered in each vegetation community over three seasons, 2001.

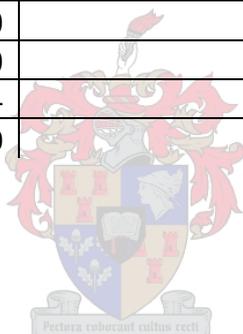
a) Hot wet season

Vegetation community number	Total distance covered in metres	Proportional distance covered (%)	Proportional area of community (%)	Total vegetation comm. area (km²)
1	431218	35	36	136.0
2	122798	10	13	51.0
3	33906	3	3	11.0
4	21522	2	7	25.0
5	10188	1	1	5.0
6	145296	12	4	17.0
7	108728	9	10	38.0
8	66728	5	1	5.0
9	5452	0	1	2.0
10	14676	1	2	6.0
11	70596	6	4	16.0
12	102872	8	7	25.0
13	17596	1	2	6.0
14	55278	4	5	20.0
15	5734	0	2	7.0
16	1310	0	1	3.0
17	14892	1	2	7.0
	1228,790			



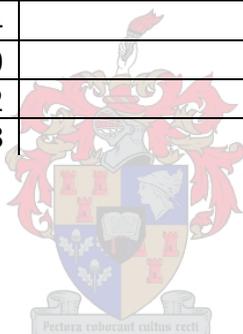
b) Cool dry season

Vegetation community number	Total distance covered in metres	Proportional distance covered (%)	Proportional area of community (%)	Total vegetation comm. area (km²)
1	298954	32	36	136.0
2	56738	6	14	51.0
3	20610	2	3	11.0
4	17176	2	7	25.0
5	23520	2	1	5.0
6	68588	7	5	17.0
7	120726	13	10	38.0
8	36568	4	1	5.0
9	1470	0	1	2.0
10	1474	0	2	6.0
11	63618	7	4	16.0
12	107172	11	7	25.0
13	6876	1	2	6.0
14	98726	10	5	20.0
15	0	0	2	7.0
16	5580	1	1	3.0
17	15344	2	2	7.0
	943,140			



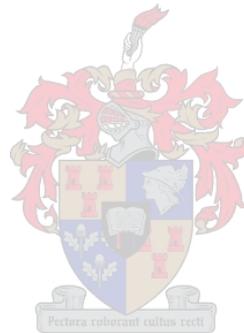
c) Hot dry season

Vegetation community number	Total distance covered in metres	Proportional distance covered (%)	Proportional area of community (%)	Total vegetation comm. area (km ²)
1	266194	28	36	136.0
2	98962	10	13	51.0
3	33932	4	3	11.0
4	26276	3	7	25.0
5	16104	2	1	5.0
6	64542	7	4	17.0
7	101160	11	10	38.0
8	28722	3	1	5.0
9	2246	0	1	2.0
10	12068	1	2	6.0
11	44840	5	4	16.0
12	111420	12	7	25.0
13	20780	2	2	6.0
14	76586	8	5	20.0
15	16344	2	2	7.0
16	5580	1	1	3.0
17	18012	2	2	7.0
	943,768			



Appendix 8: Number of sightings (plots) per species in each of the three seasons.

Species	Hot wet season sightings	Cool dry season sightings	Hot dry season sightings
African elephant	23	21	18
Cape buffalo	27	29	23
Eland	7	18	15
Impala	43	38	34
Nyala	12	14	9
Sable antelope	25	23	26
Waterbuck	19	22	28
Warthog	17	19	14
Wildebeest	28	29	31
White rhino	19	22	21
Zebra	41	38	37



Appendix 9: Transformation techniques used and discard criteria of habitat variables in the hot wet season.

Variable	Transformation technique and discard criteria
TRVO	1 added as constant – Log ¹⁰ used as transform technique
SHVO	1 added as constant – Log ¹⁰
SWHT	Arcsine used as transformation technique
INHT	Correlated with SWHT ($r = 0.7$), discarded
GBRO	Arcsine
GGRE	Arcsine
GBAR	Arcsine
GLIT	Arcsine
FORB	Arcsine
SEDG	Log ¹⁰
ALTI	Log ¹⁰
DWAT	Log ¹⁰ (after Melton 1978)
DOPV	0 values equated to 1 & Log ¹⁰
DCOV	Log ¹⁰
TSBU	Log ¹⁰
SLOP	0 values equated to 1 & log ¹⁰ transform
RCOV	Arcsine
BARE	Arcsine
CLAY	Arcsine
NAFT	Arcsine
AVAP	Arcsine
SAND	Correlated with CLAY ($r = 0.98$) & NAFT ($r = -0.76$) - discarded
SILT	Correlated with SAND ($r = -0.92$)- discarded
CALC (calcium)	Correlated with SAND ($r = 0.91$) & CLAY ($r = 0.7$) - discarded
KELE (potassium)	Correlated with SAND ($r = -0.71$) & NAFT ($r = 0.8$) - discarded
MAGN (magnesium)	Correlated with SAND ($r = -0.91$) & CALC ($r = 0.91$) - discarded
SODM (sodium)	Correlated with WCON ($r = 0.84$) & AVAP ($r = 0.8$) - discarded
PHSC (soil pH)	Correlated with CLAY ($r = 0.9$) & SAND ($r = -0.91$) - discarded
WCON (soil water conductivity)	Correlated with pH ($r = 0.87$)- discarded
CECI	Arcsine
DIER	Arcsine
ENCE	Arcsine
HECO	Arcsine
PMAX	Arcsine
PSQU	Arcsine
SPAP	Arcsine
UMOS	Arcsine
All other grass species.	Discarded – zero scores frequent.

Appendix 10: Transformation techniques used and discard criteria of habitat variables in the cool-dry season.

Variable	Transform technique and discard criteria
TRVO	1 added as constant – Log ¹⁰ transform
SHVO	1 added as constant – Log ¹⁰ transform
SWHT	Arcsine transform
INHT	No data – discarded
GBRO	Arcsine
GGRE	Arcsine
GBAR	Arcsine
GLIT	Arcsine
FORB	Arcsine
SEDG	Arcsine
ALTI	Log ¹⁰ transform
DWAT	Log ¹⁰ transformation used, following Melton (1978)
DOPV	0 values equated to 1 & Log ¹⁰ transform
DCOV	Log ¹⁰ transform (following Melton 1978)
TSBU	Log ¹⁰
SLOP	0 values equated to 1 & log ¹⁰ transform
RCOV	Arcsine
BARE	Arcsine
CLAY	Arcsine
All other soil variables	As in Appendix 9
CECI	Arcsine
DIER	Arcsine
ENSC	Arcsine
HECO	Arcsine
PMAX	Arcsine
PSQU	Arcsine
SINC	Arcsine
UMOS	Arcsine
All other grass species	Discarded – zero scores frequent.

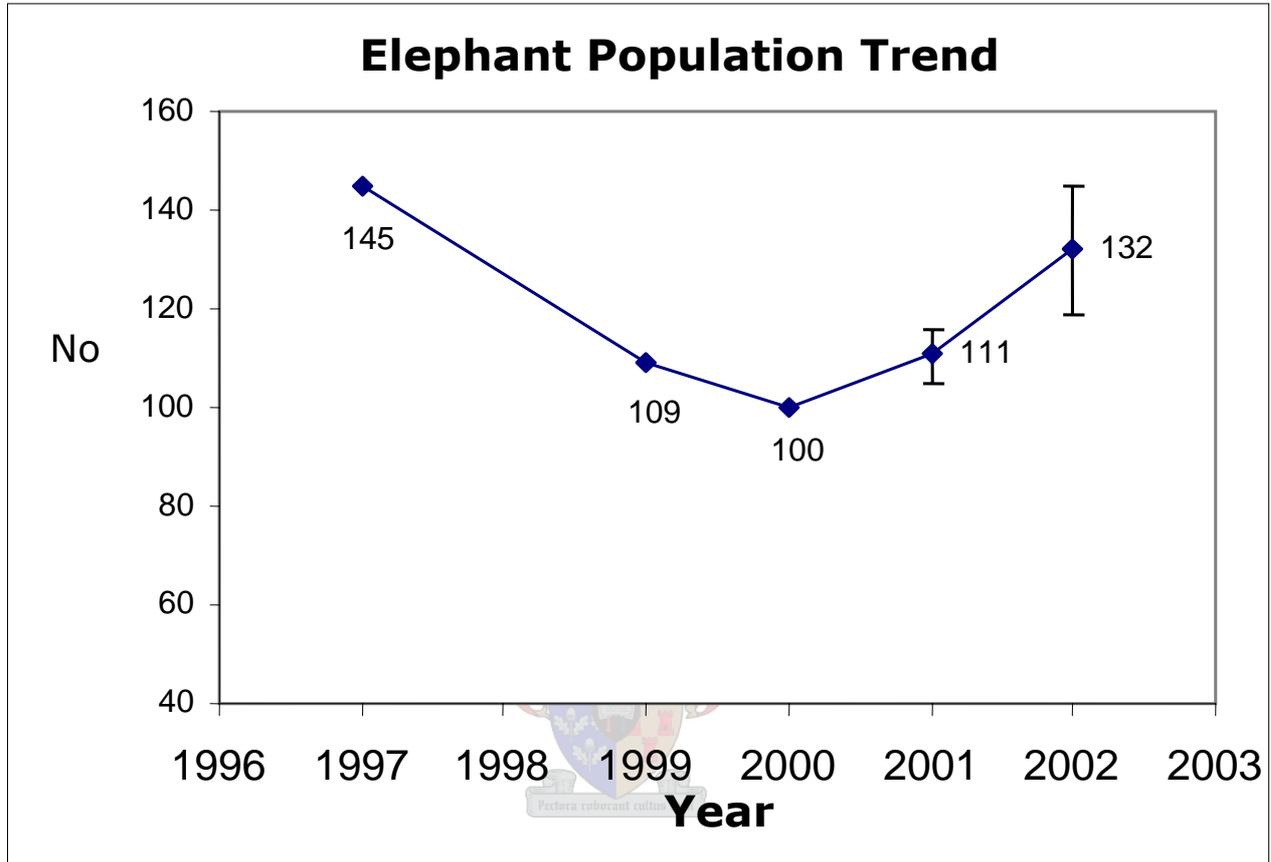
Appendix 11: Transformation techniques used and discard criteria of habitat variables in the hot-dry season.

Variables	Transformation technique and discard criteria
TRVO	1 added as constant – Log ¹⁰ transform
SHVO	1 added as constant – Log ¹⁰
SWHT	1 added as constant – Log ¹⁰
INHT	No data collected - discarded
GBRO	Arcsine transform
GGRE	Arcsine
GBAR	Correlated with GLIT ($r = - 0.74$) - discarded
GLIT	Arcsine
FORB	Arcsine
SEDG	Arcsine
ALTI	Log ¹⁰
DWAT	Log ¹⁰
DOPV	0 values equated to 1 & Log ¹⁰
DCOV	Log ¹⁰
TSBU	Log ¹⁰
SLOP	Arcsine
RCOV	Arcsine
BARE	Arcsine
CLAY	Arcsine
AVAP	Arcsine
NAFT	Arcsine
All other soil variables	As with hot-wet season
DIER	Arcsine
HECO	Arcsine
PMAX	Arcsine
PSQU	Arcsine
UMOS	Arcsine
All other grass species	Discarded – zero scores frequent.

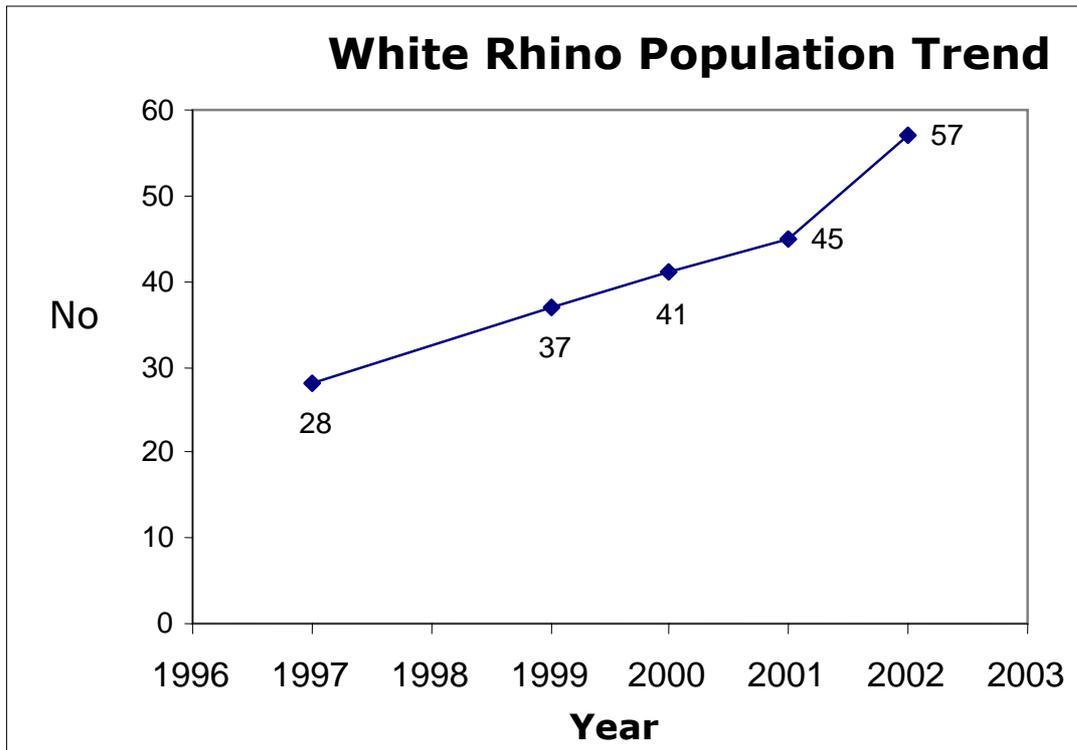
Appendix 12: Short term trends in the population sizes of some large herbivore species on Malilangwe Estate, taken from Goodman (2002).

Increasing Populations

a) Elephant

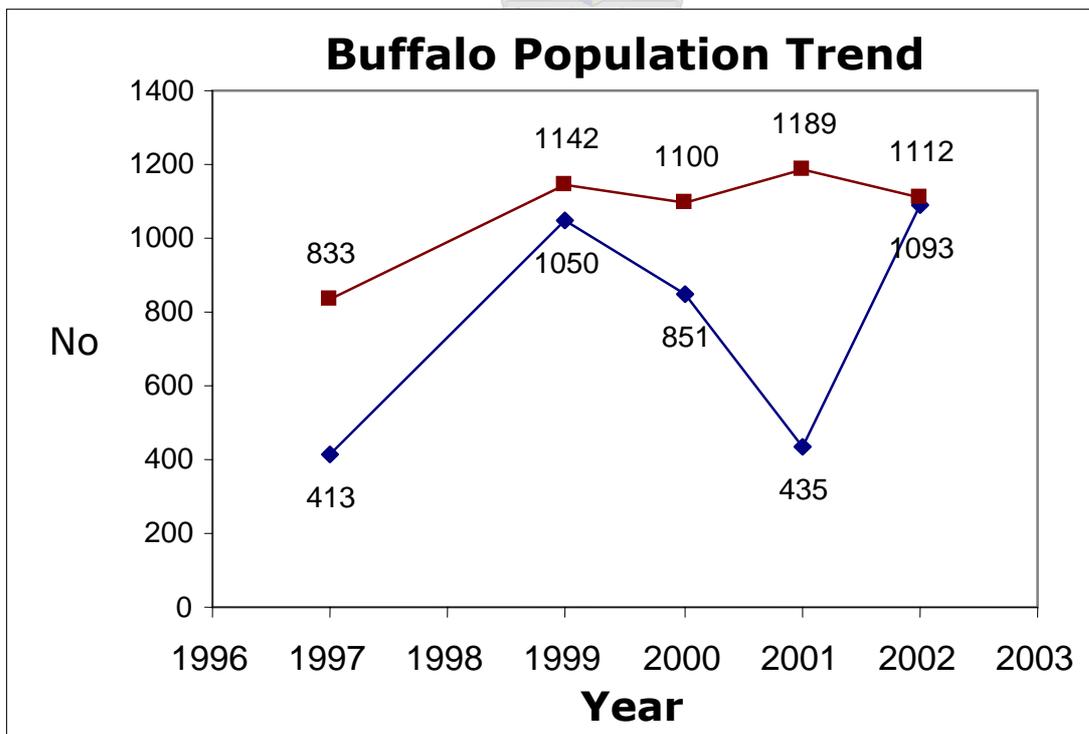


b) White rhino

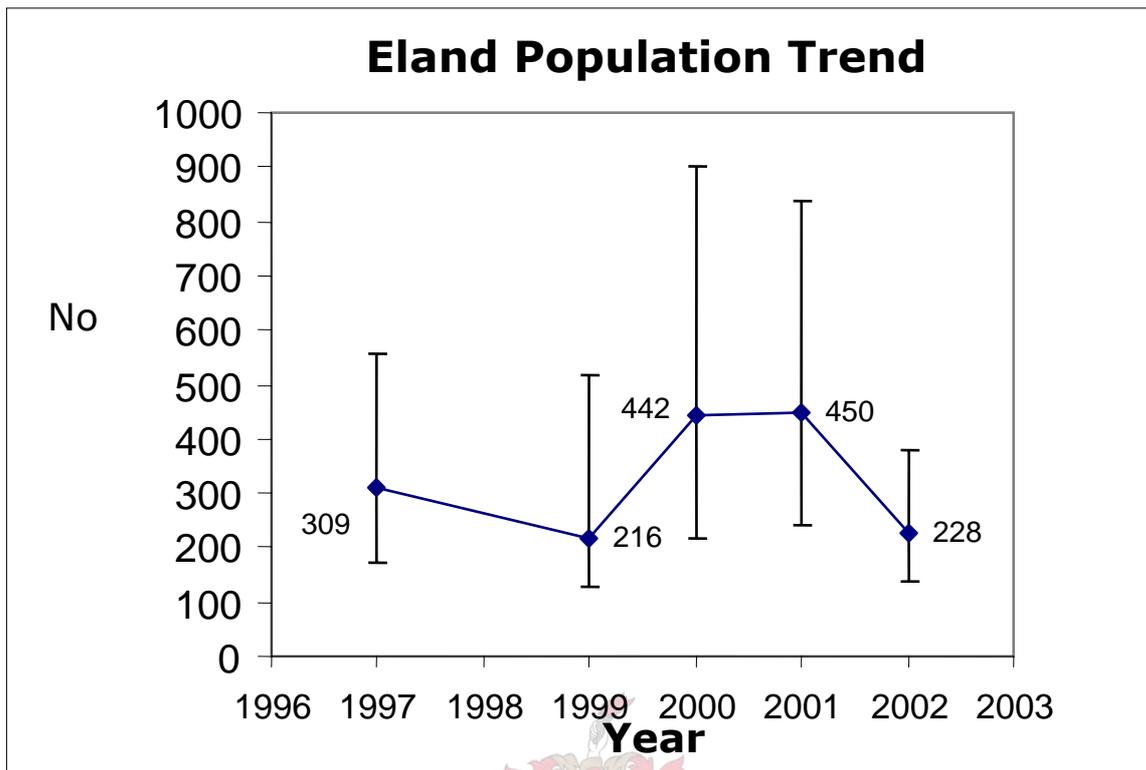


Stable populations

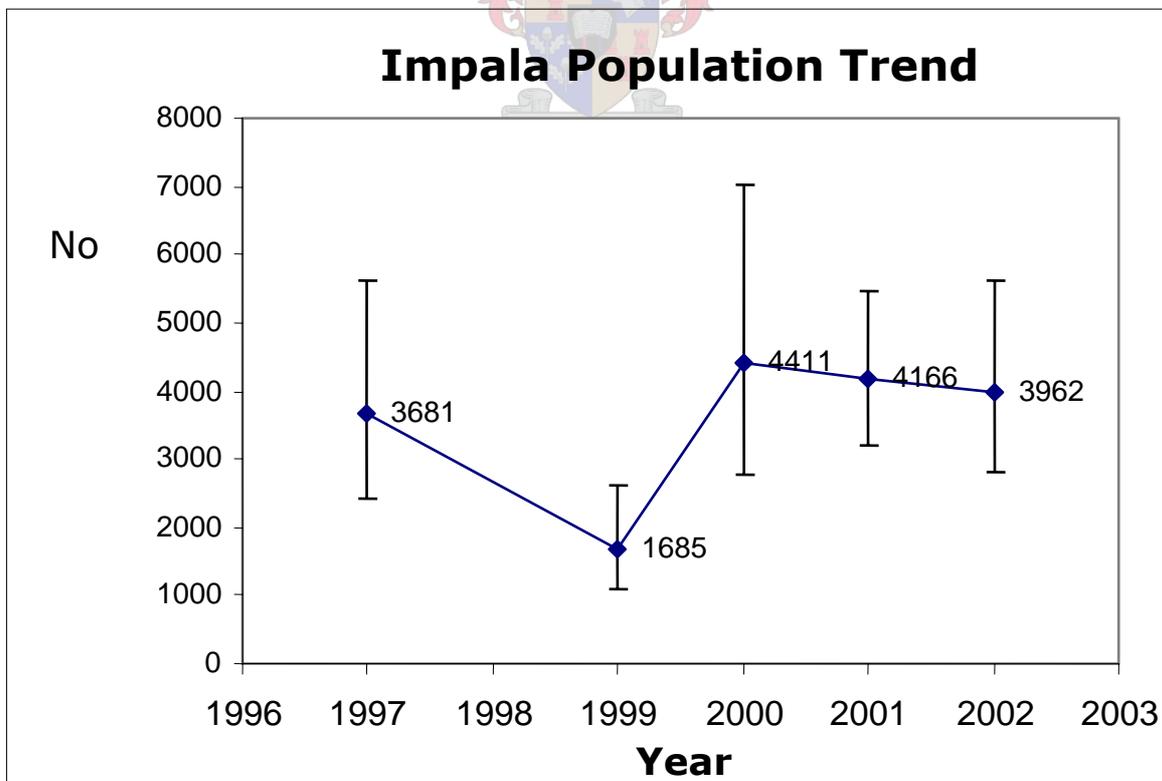
c) Buffalo (purple trend indicates Hippo Valley population)



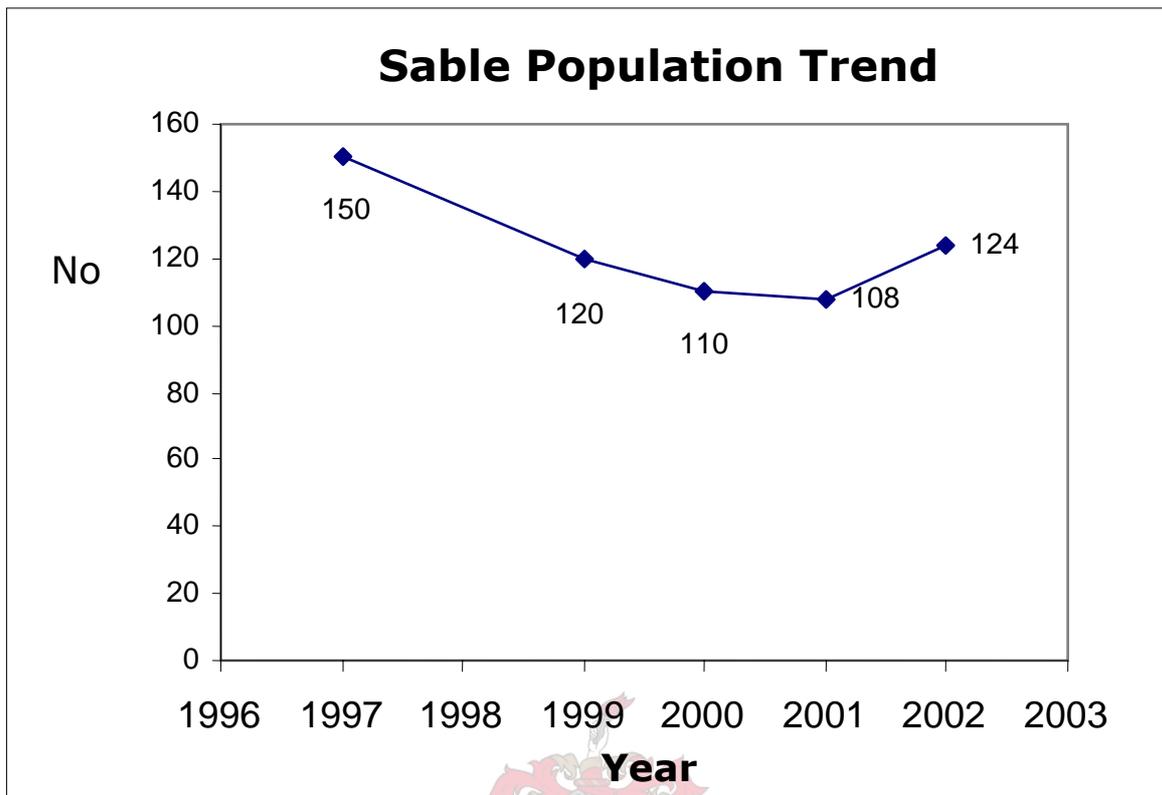
d) Eland



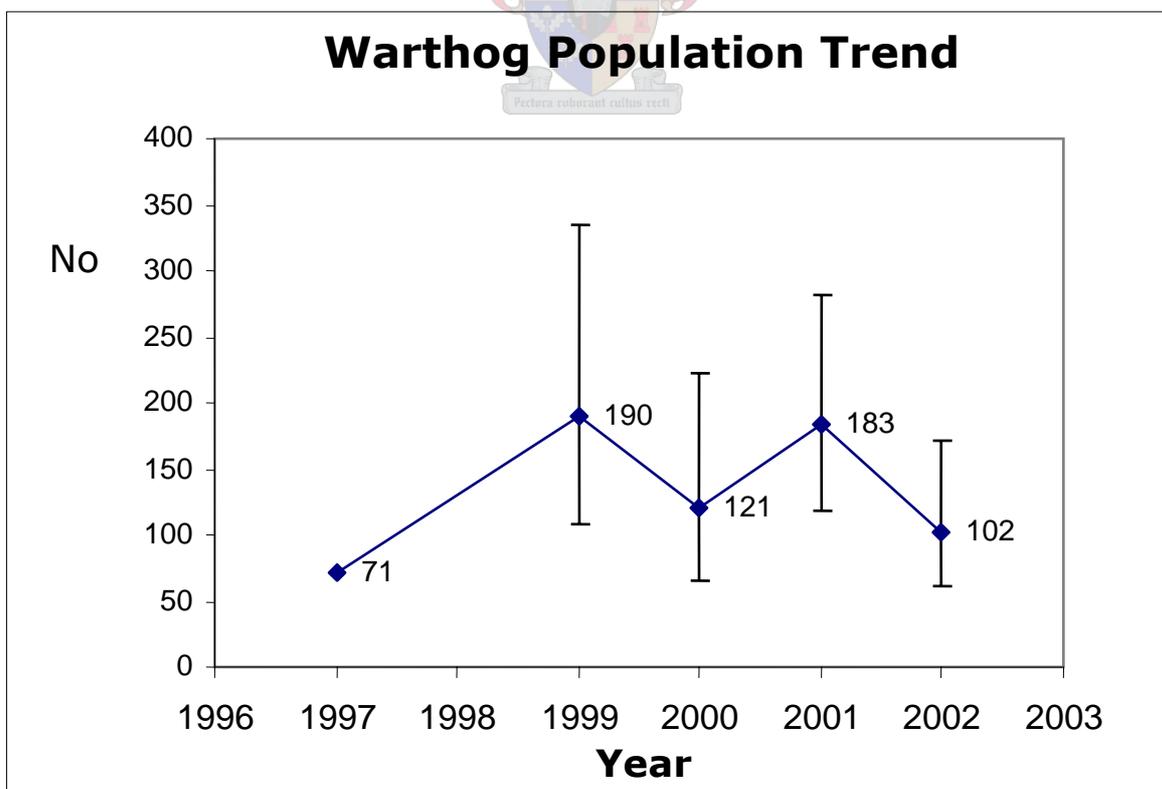
e) Impala



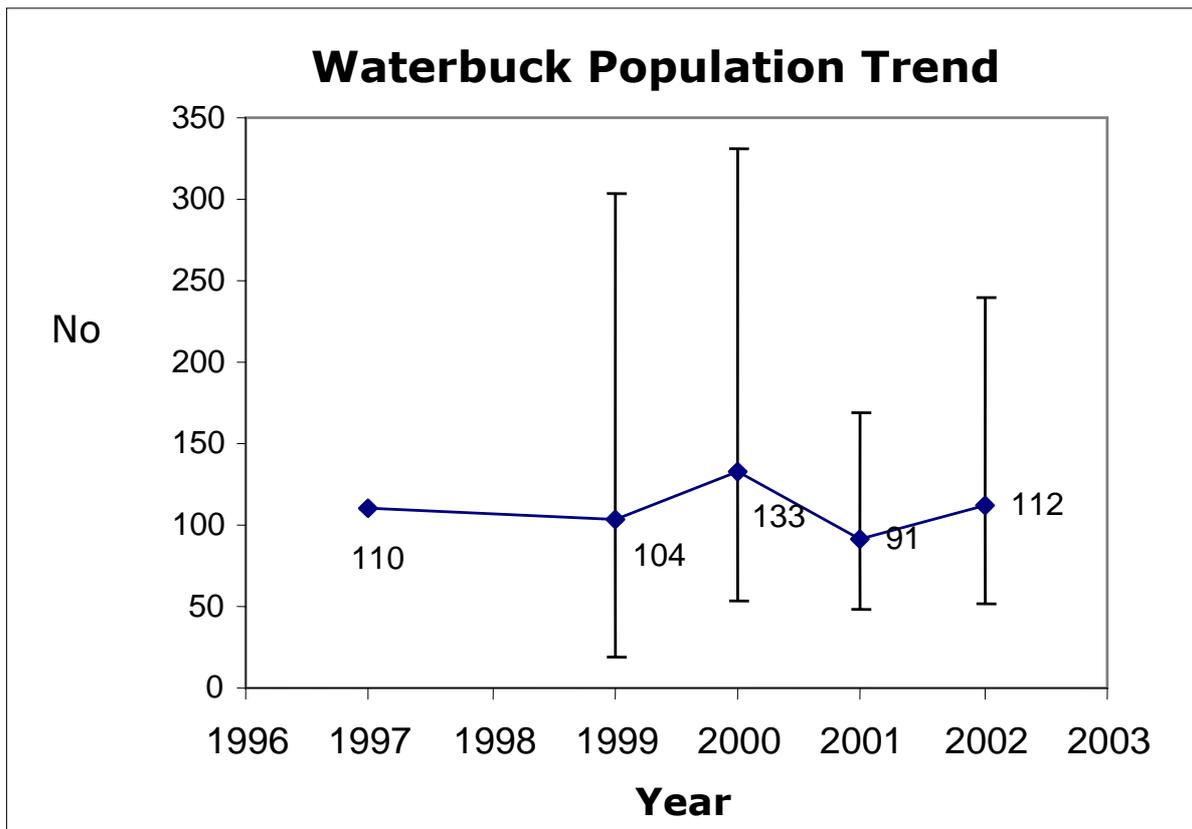
f) Sable antelope



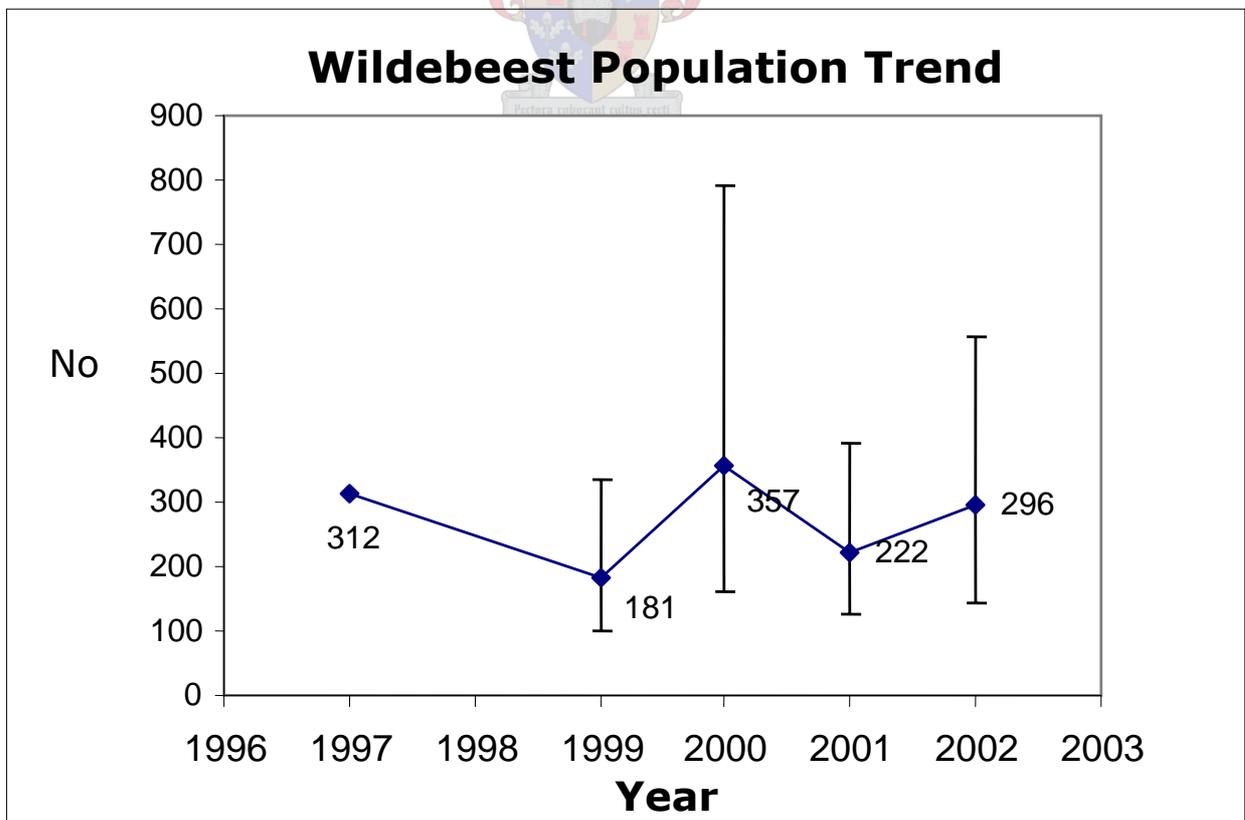
g) Warthog



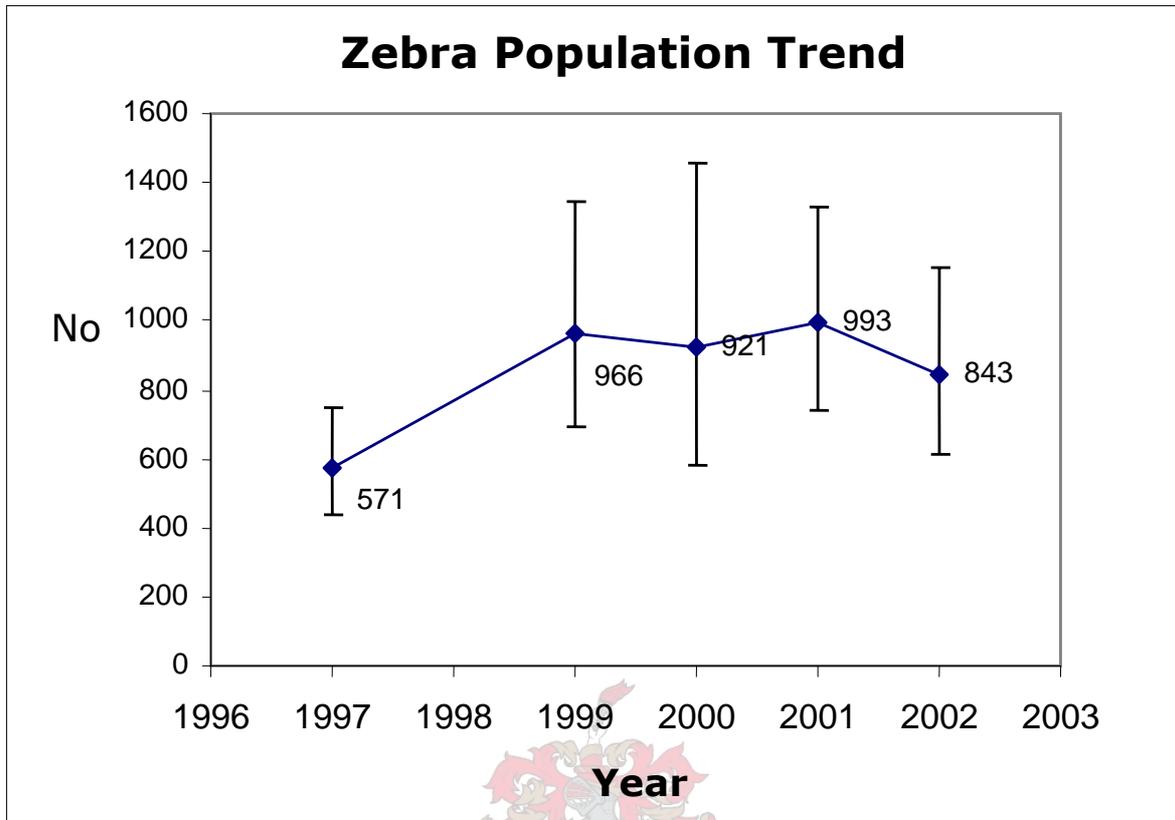
h) Waterbuck



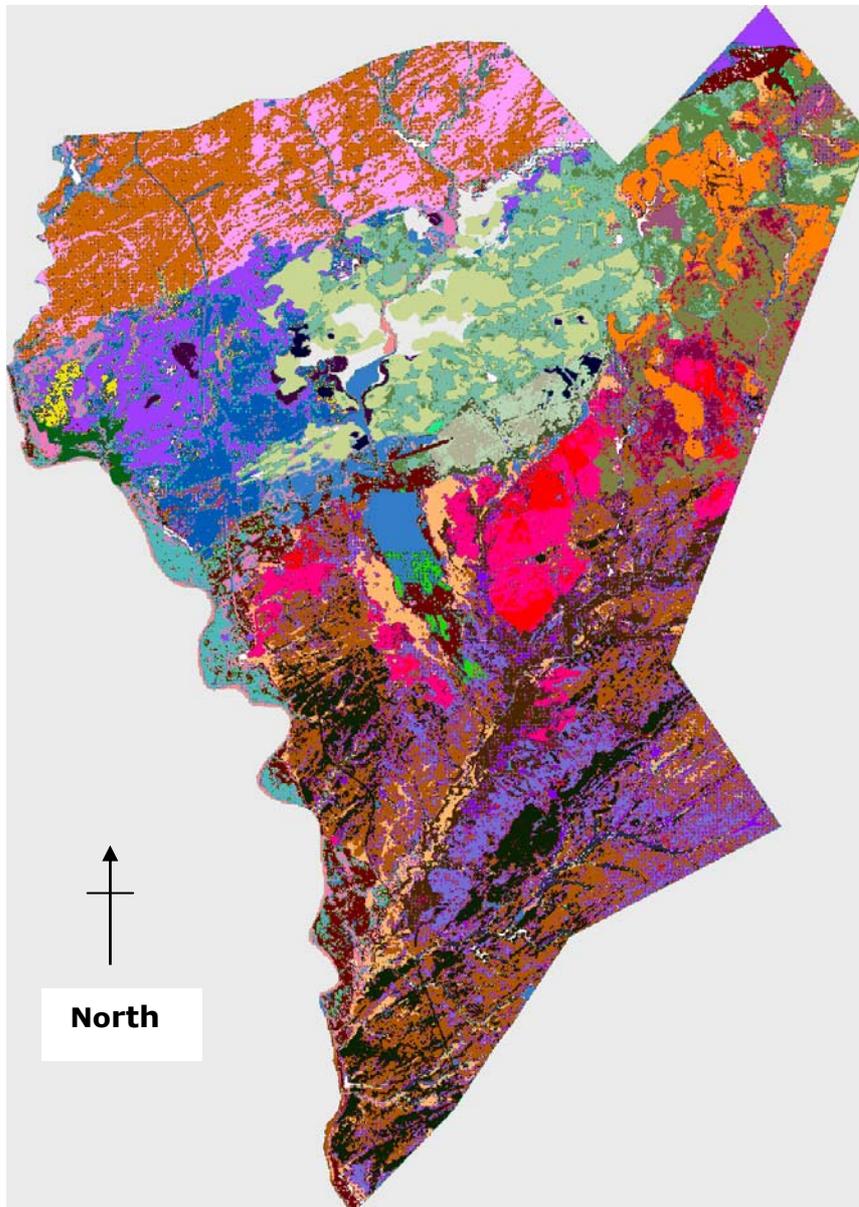
i) Wildebeest



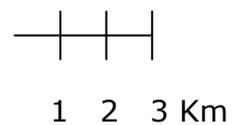
j) Zebra



Appendix 13: Vegetation communities at ME, used as a template for the ENFA. Coverage composed by Clegg, B. (2002).



- S. africana* - *N. hildebrandtii*
- B. glaucescens* - *A. johnsonii*
- J. globiflora* - *D. usambarensis*
- L. stuhlmannii* - *P. myrtifolia*
- L. stuhlmannii* - *D. melanoxylon*
- C. mopane* - *A. petersiana*
- A. petersiana* - *S. potatozum*
- A. galpinii* - *C. megalobotrys*
- A. tortilis* - *D. cinerea*
- A. tortilis* - *L. capassa*
- A. tortilis* - *C. sepiaria*
- S. consimilis* - *S. iocladius*
- A. burkei* - *S. persica*
- C. mopane* - *G. bicolor*
- A. erubescens* - *M. sericea*
- C. mopane* - *T. prunoides*
- C. mopane* - *A. anthelmintica*
- C. mopane* - *E. rigidior*
- C. mopane* - *C. mollis*
- C. mopane* - *C. apiculatum*
- C. mopane* - *H. contortus*
- C. mopane* - *E. scoparius*
- C. mopane* thicket
- L. capassa* - *H. coriacea*
- A. nigrescens* - *C. apiculatum*
- A. nigrescens* - *C. adenogonium*
- A. robusta* - *U. mossambicensis*
- S. incrassata* - *I. afrum*
- B. glaucescens* - *M. junodii*
- A. nigrescens* - *U. mossambicensis*
- A. nigrescens* - *S. galpinii*
- D. melanoxylon* - *A. borleae*
- A. digitata* - *G. americanus*
- C. mopane* - *S. galpinii*
- A. nigrescens* - *S. incrassata*
- C. mopane* - *A. adcensionis*
- Unsampled



Appendix 14: Large herbivore (study species) population estimates at commencement of study (Goodman 2000) and recent ecological carrying capacities estimated by Goodman (2002)

Species	Best population estimate as of 2000	Most recent carrying capacity estimate
Buffalo	453	1050
Eland	450	265
Elephant	111	120
Impala	4166	4120
Nyala	80	110
Sable antelope	108	140
Waterbuck	91	130
Warthog	183	210
White rhino	45	55
Wildebeest	222	320
Zebra	993	845

