THE EFFECT OF HABITAT ALTERATION BY ELEPHANTS ON INVERTEBRATE DIVERSITY IN TWO SMALL RESERVES IN SOUTH AFRICA

by

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ABSTRACT

Balancing increasing elephant numbers with biodiversity conservation in small reserves has become a concern for many protected area managers. Elephants are considered important agents of disturbance creating heterogeneity and thus contributing to the maintenance of biodiversity. However elephants also damage vegetation through their destructive feeding habits, and this has led to pressure to reduce elephant populations in many reserves. Quantitative data on the impact of elephants on invertebrates, the main component of biodiversity at the species level, are lacking.

The aim of this project was to assess the effect that habitat alteration by elephants has on the diversity of selected ground-dwelling invertebrates (ants, centipedes, millipedes, spiders, scorpions and termites) through the provision of logs and dung as a potential refuge niche for these invertebrate communities, and to determine the effect of spatial (vegetation types) and temporal (season and age of dung) variation on the invertebrates using these refugia. Variation in impacts was considered important because savanna is not homogenous and the impact of the refugia is likely to be dynamic in terms of seasonal trends in invertebrate populations, and in terms of changes in the environmental conditions offered by the refugia.

Elephant impact on vegetation, quantity of refugia (logs and dung) produced and invertebrate diversity associated with refugia were determined for 115 transects within Madikwe Game Reserve in the North Western Province, South Africa. Invertebrate abundance, species richness and diversity were always higher under refugia than in areas without refugia. Vegetation utilisation, frequency of refugia production and invertebrate diversity showed strong temporal variation (seasonal); elephant impact and production of logs were higher in winter than in summer because elephants are more likely to feed on woody vegetation in winter when grass nutrient levels are low. Invertebrate diversity under the logs was higher in summer than in winter, and this probably reflected the higher abundance and diversity of invertebrates that are usually associated with the warmer, wetter summer months.

The effect of adding refugia to three vegetation types on invertebrate diversity was tested experimentally at Makalali Private Game Reserve in the Limpopo Province, South Africa. Logs and elephant dung were set out in five plots each measuring 20m x 20m within mixed bushveld, riverine and mopane woodland. Significant differences were observed in invertebrate abundance, species richness and diversity between the refugia and control plots that lacked refugia and between the three vegetation types sampled. Similarity between invertebrate communities utilising the different refugia types and between the three different vegetation types were tested using the Jaccard similarity coefficient. The three vegetation types shared fewer than 50% of their species, as did the logs, dung and control sites. However the results obtained do illustrate a higher degree of similarity between the refugia substrates (logs and dung) than the control sites and between the more heterogeneous vegetation types (mixed bushveld and riverine) than the mopane veld. This indicated that invertebrate communities associated with refugia were not uniform, but were influenced by vegetation type.

An experimental test of temporal changes in invertebrate community composition illustrated the importance of elephant dung as a microhabitat for different invertebrate groups over different ages of dung (three days, two, four, 12 and 32 weeks old). Colonisation of the dung, by dung beetles was immediate but as the microclimate of the dung changed with time, the new conditions were ideal for other invertebrate taxa. Over a period of eight months, the change of invertebrate communities utilising the dung included dung beetles, followed by millipedes and finally ant and termite communities.

The results of this study illustrated the importance of refugia (logs and dung) produced by elephants for ground-dwelling invertebrate species in the savanna environment. The extent of the influence of the refugia varied both spatially and temporally and this should be considered in future monitoring or in measuring impacts. While further research on a broader range of organisms and at larger scales is necessary, elephants do have a positive impact on at least some components of biodiversity, through the process of facilitation of refugia.

PREFACE

The experimental work described in this dissertation was carried out in the School of Botany and Zoology, University of KwaZulu-Natal, Pietermaritzburg from January 2000 to December 2003, under the supervision of Dr. Michelle Hamer (University of KwaZulu-Natal, Pietermaritzburg) and co-supervision of Prof. Robert Slotow (University of KwaZulu-Natal, Durban).

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

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CHAPTER 1

GENERAL INTRODUCTION

The emphasis placed on the ecotourism industry in South Africa as an economically viable source of revenue has increased tenfold over the past few decades (Department of Environment & Tourism, 1996). In an extremely competitive industry, game reserves and national parks have re-introduced several large mammal species such as lions, elephants, rhino and buffalo in order to elevate their status to a 'Big Five' tourism destination for visitors. However, over a period of time, these large animals, especially elephants, can have an influence on the ecology of the reserve, particularly if fences that delimit the reserves prevent the natural movements of these animals.

Elephants are often described as landscape modifiers: they have the ability to change their habitat, and can therefore either positively or negatively affect the structure and dynamics of the vegetation that surrounds them (Mills, Soule & Doak, 1993, Simberloff, 1998). Rapidly increasing elephant numbers in small reserves where they have been re-introduced are a concern for mangers (Woodd, 1999, Whyte, 2001). Maintaining biodiversity and not just single species preservation, is one of the most important objectives of conservation agencies in South Africa (Joubert, 1986, Poole, Kahumbu, & Whyte, (in press). The effect that elephants have on faunal biodiversity has been briefly investigated (Herrmans, 1995, Cumming, Fenton, Rautenbach, Taylor, Cumming, Cumming, Dunlop, Ford, Hovorka, Jonhston, Kalcounis, Mahlangu, & Portfors, 1997), however, some groups, such as invertebrates, have rarely been considered. Even though invertebrates eclipse all other life forms on earth in terms of sheer numbers, diversity (number of species), and biomass (dry weight), their importance to ecosystem functioning has often been overlooked or ignored (Black, Shepard & Allen, 2001).

This research project examined the impact of elephants on invertebrate diversity within the savanna biome in South Africa. In particular, the project investigated the relationship that may exist between habitat alteration by elephants in the form of pushing over trees and deposition of dung, and the utilisation of these newly created habitats by selected ground-dwelling arthropod taxa, with the aim of filling some of the gaps that exist in our understanding of the effect that elephants have on biodiversity.

This chapter briefly reviews past and present elephant numbers in South Africa, the conflict between elephants and humans, the positive and negative effects resulting from elephant feeding behaviour, and conservation of one of South Africa's keystone species. The diversity, importance and conservation status of invertebrates is highlighted. The chapter also introduces the term biodiversity, its importance, implications of loss of biodiversity and the status of biodiversity conservation in South Africa. Finally the aims and objectives of the study are presented.

Elephants in South Africa

The earliest recording of elephants (*Loxodonta africana*, Blumenbach 1797) in South Africa was in 1497 by a Portuguese navigator, Vasco da Gama at Mossel Bay on the Cape south coast (Hall-Martin, 1992). No reliable estimates of elephant numbers prior to 1652 are available for South Africa, but numbers are estimated to have been in the order of approximately 100 000 animals (Hall-Martin, 1992, Blanc, Thouless, Hart, Dublin, Douglas-Hamilton, Craig & Barnes, 2003). The decline of the South African elephant population may be divided into three eras. An increase in settlement and human population growth between 1652 and 1790 resulted in elephant numbers decreasing. From 1790 to 1870, the ivory industry and the establishment of 'professional ivory hunters' were mainly responsible for the decline in elephant numbers. Finally between 1870 and 1920, the protection of agricultural lands and crops was the overriding reason for shooting elephants. With the combination of all three factors (development, ivory trade and crop protection), the South African elephant population reached its lowest numbers of approximately 120 individuals in 1920 (Hall-Martin, 1980).

Following their decline, concern for the survival of elephants in South Africa prompted an increased focus on conservation of the species. Since then elephant numbers have changed dramatically and populations have increased mainly due to conservation and management practices. Currently it is estimated that in Africa there are approximately 470 000 elephants, with the vast majority of these located within the following five countries, Botswana, Tanzania, Zimbabwe, Zambia and South Africa (Blanc, *et al.*, 2003). In South Africa, there are approximately 13 500 elephants ([#]Ian Whyte, Pers. Comm.) of which the

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[#] Dr. Ian Whyte – Large Mammal Scientist, Scientific Services, Skukuza, Kruger National Park, South majority are located within protected areas such as national parks, provincial game reserves and smaller private game reserves (Whyte, 2004).

Conservation and management of the African elephant can only be done with a good understanding of elephants themselves – their distribution and density, their movement patterns, behaviour and particularly their impact on the ecosystems which they inhabit (Hall-Martin, 1992).

Throughout Africa and indeed South Africa, elephants within reserves have existed or exist as island populations surrounded by humans (Martin & Taylor, 1983). Generally the relationship between elephant and humans is a continual struggle over land and utilisation of the same resources in the form of food and water (Parker & Graham, 1989, Barnes, Barnes, Alers & Blom, 1991). In parts of Africa elephants and humans overlap in the habitats used (Kangwana, 1995). Where people practice agriculture, conflict arises when elephants consume and destroy cultivated crops that have been placed within their home range (Rodgers & Elder, 1977, Kangwana, 1995, Hoare, 1999). Where people's primary activity is keeping livestock the conflict revolves around the demand for grazing land and water resources (Barnes, *et al.*, 1991). Human causes of elephant mortality include poaching for ivory and meat, killing in retaliation and hostility as a result of elephant damage, sport hunting and ritual hunting. In South Africa elephant – human conflict is rare because all elephant in the country are confined to fenced areas.

Previously elephants were able to travel over long distances throughout their home range. In many areas human expansion and poaching have forced elephants to alter traditional movement patterns and concentrate within protected areas (Western, 1989, Tchamba &

Mahamat, 1992). In South Africa, increasing urban, semi-urban and agricultural development are the main factors contributing to the confinement of elephants within games reserves. The increased compression of elephants into smaller and smaller protected areas with no allowance for seasonal movement is likely to accelerate habitat destruction and loss of biodiversity in many protected areas (Pienaar, 1983). Finding solutions to these problems and balancing elephant habitat utilisation whilst maintaining biodiversity is one of the most pressing management challenges in elephant conservation (Roth & Douglas Hamilton, 1991).

The increasing elephant population in many small reserves in South Africa (Whyte, 2004) is often deemed as an immediate problem that requires drastic actions to prevent habitat and biodiversity loss (Pienaar, 1983). The debate surrounding the various options (culling, translocation, contraception) that are potentially available to reduce elephant numbers is complex and detailed discussion is beyond the scope of this thesis. However, culling is often cited as the most effective and inexpensive method to reduce elephant population numbers and a possible solution to this complex problem (Whyte & Fayrer-Hosken, 2003). Previously the decision to cull elephants was usually based on studies by biologists and game experts on the effect that elephants have on vegetation (Barnes, 1985, Ben-Shahar, 1993, Barnes, Barnes & Kapela, 1994). Continued pressure from animal rights activist organisations, which question the ethical morality of killing elephants has forced managers of conservation areas to review their policy for elephant management (Whyte, Biggs, Gaylard, & Braack, 1999). However the conservation of biodiversity and scientific findings that suggest the inter-dependence of species for ecosystem functioning forces managers to protect the ecosystem as a whole and not to preserve single species (Whyte & Fayrer-Hosken, 2003). Quantitative scientific studies are required to determine the impact of elephants on ecosystems as a whole in order to make sound, defensible elephant management decisions. In light of the high profile that elephants have locally and internationally, any measure taken by conservation authorities to control their numbers should be based on sound scientific knowledge and evidence as well as incorporating other societal values (ethical and aesthetic values), therefore allowing the decision to be more widely accepted by various stakeholders (Lykke, 1998, Whyte & Fayrer-Hosken, 2003).

Impact of elephants on biodiversity

Elephants have the ability to greatly affect the structure and dynamics of vegetation that surrounds them and they are often described as keystone species (Guy, 1981, Barnes, 1983, Lewis, 1986, Western, 1989, Jachmann & Croes, 1991, Tchamba, 1995). While several studies have recorded damage to habitats by elephants (Barnes, 1983, Ruggiero, 1993, Hiscocks, 1999, Babaasa, 2000), there are also numerous positive effects of elephants on the environment. These large, space-demanding animals play an important role in recycling nutrients back to soils and in the creation of waterholes that serve many life forms during times of drought. The leaves from upper canopies of trees are also made available to other browsers that would have otherwise been unable to gain access to the nutritious leaves (Gadd, 1997). Elephants assist in the regeneration of plant growth by being a dispersal agent of seeds (Western, 1989). Studies carried out in various reserves and national parks in Africa suggest that elephant dung is an important agent of seed dispersal for numerous plant species (Yumoto & Maruhashi, 1994, Dudley, 1999). During the long dry seasons the dung boli provide a moist, nutrient rich surface for seedpods to germinate (Dudley, 1999). Many species of birds such as crowned guinea fowl (*Numida melargris* Linn.), yellow-billed hornbill (*Tockus flavirostris* Rupp.), red-billed francolin

(*Francolinus adspersus* Waterhouse.), and smaller mammals, including baboon (*Papio ursinus* Kerr.), vervet monkey (*Cercopithecus pygerythrus* Cuvier.) and tree squirrels (*Paraxeras cepapi* Smith.) are secondary consumers of seeds located in the dung piles (Ruggiero & Eves, 1998, Dudley, 1999).

Changes brought about by elephants in the physical structure of the landscape also cause an increase in some otherwise rare species of plants such as the sedge, *Kyllinga nervosa* Steud., which is abundant in disturbed areas after rains (Keesing, 1998).

The research results of Keesing (1998) indicated that ungulates, especially elephants, play a major role in changes in small mammal diversity. Changes are brought about not through competition for food resources but rather through disturbance of habitats. Along the travel routes of elephants, vegetation is trampled and the soil surface is disturbed, which results in these pathways having different topography and moisture levels from the surrounding areas. This allows for an increased number of small mammal species to inhabit the area.

The study conducted by Musgrave & Compton (1997) in Addo Elephant National Park, South Africa, indicated that changes caused by elephants to the vegetation community affected habitat suitability for phytophagous insects. More phytophagous insects were found to feed on plants that were browsed by elephants than on plants that were not browsed. The nutritional value and palatability of foliage on *Acacia* species were much higher on trees that were severely browsed by elephants than those that were not browsed (Du Toit, Frisby & Bryant 1990). Trees that have been pushed over by elephants to gain access to young shoots or fruits provide other animals with a food source and also create a new habitat for many animals.

Elephants are not more important than any other component in the ecosystem but they are important agents of disturbance and as such create heterogeneity and thus contribute to biodiversity in the area (Whyte, *et al.*, 1999).

There has been a rapid increase in the number of studies pertaining to elephants over the past three decades, however the majority of these have focused on the follow five topics: census, distribution and status reports, ivory trade, effect of elephants on vegetation and conservation issues related to population numbers (Bossen, 1998). Studies on the effect that elephants may have on mammals and birds have been few (Herrmans, 1995, Cumming, *et al.,* 1997), and very little information exists on the effect of habitat alteration by elephants on invertebrates (Cumming, *et al.,* 1997).

Logs and branches that may be found on the ground after an elephant has fed and elephant dung provides an interesting interface between the damp depths of the soil and the drier open ground surface. Organisms inhabiting either of these environments (logs or elephant dung) may live here all the time or be transient inhabitants of the refugia (Wheater & Read, 1996). Animals living under and /or those associated with dead wood or the fungi and microorganisms that decompose the wood are termed 'saproxylic fauna' (Speight, 1989, Grove & Stork, 1999). Grove & Stork (1999) stated that there was already a large body of knowledge on temperate and boreal region saproxylic insects and the effect that disturbance (logging) has on them. Studies and information on tropical forest saproxylic insects lags far behind, but even more disconcerting is that knowledge about these insects in the savanna biome is non-existent. In light of current international efforts to develop techniques to monitor sustainable forest management for biodiversity there has recently been an increase in ecological research initiatives on saproxylic fauna (Davis, Goodwin &

Ockenfels, 1983, McComb & Lindenmayer, 1999). These priorities now need to be transferred to the African savanna biome.

The savanna biome

The savanna biome covers approximately 46% of the surface land in South Africa (Low & Rebelo, 1996). A large number of private conservation initiatives and prime state conservation areas are situated in this biome, conserving numerous charismatic species of global and national significance, including the African wild dog, black and white rhinoceros, cheetah, leopard and the African elephant. This biome also has a large number of endemic species, many of which are invertebrate species that play a critical role in the structure and functioning of the ecosystem (Keesing, 2000). The savanna biome is therefore important in terms of conservation.

Invertebrate conservation

Invertebrates are conservatively estimated to comprise about 95% of all living species (Wells, Pyle & Collins, 1983, Myers, Miltermeier, Miltermeier, da Fonseca & Kent, 2000) and in most natural ecosystems they are the most diverse and abundant organisms (New, 1995). Despite their presence in all habitats, their critical role in ecosystems processes (Savage, 1995) and more than 250 years of taxonomic research, the extent, distribution and biology of invertebrate species remains poorly known (Wells, *et al.*, 1983). The importance of invertebrates in ecological processes and as a living resource of benefit to humans should not be underestimated. These organisms provide vital ecosystem services, such as pollination, litter decomposition, nutrient cycling, soil aeration and drainage and invertebrates are a source of food for a wide variety of birds and mammals (Majer, 1978). Irrespective of their importance and the significant role they play in ecosystem functioning, studies, research opportunities and conservation strategies involving invertebrate fauna have been severely lacking.

Traditionally conservation efforts have been directed towards saving large vertebrates and their habitats. Money and energies are allocated mostly to the endangered large, charismatic species. Hence, vertebrate-centred conservation strategies continue to dominate efforts to conserve biodiversity and much less attention is given to rare or endangered invertebrate species (Wells, *et al.*, 1983). Major impediments to invertebrate conservation efforts are the poor public image that these organisms have; lack of human appreciation for their importance and an overall general disregard and dislike of invertebrates (Samways, 1993). However, there is increasing awareness of the threats to invertebrates and concern about the detrimental effects that the loss of invertebrate diversity could have on ecosystems (Black, *et al.*, 2001).

Through increasing population pressures, human activities have steadily modified wilderness areas into landscapes of settlement, agricultural lands and industrial sites that preclude the co-existence of humans with many creatures. Invertebrates are no exception. There are numerous examples of human habitat alteration, of which the most important are deforestation, agricultural activities, industrialisation and urbanisation that affect terrestrial invertebrates. Some species of invertebrates have home ranges that are so small that they could be eradicated by a single event such as building a house or the granting of a timber concession (Wells, *et al.*, 1983). Scientists anticipate the extinction of a high proportion of the world's plant and animal species within a few decades (Wells, *et al.*, 1983). It has been said that the highest number of species lost will be invertebrates, 'the little things which undoubtedly run the world' (Wilson, 1988), but which rarely gain acknowledgement.

Interest in invertebrate conservation has greatly increased since the 1970's. Many countries such as Australia, New Zealand, United States of America and several European countries have been recording threatened invertebrate species (Wells, *et al.*, 1983). Invertebrates are now included in the wildlife legislation of many countries. In South Africa, it was only in the 1980s that attempts were made to assess the extent to which conservation included representatives of all indigenous flora and fauna (Pienaar, 1991). The establishment of the Invertebrate Conservation Services Section by the Transvaal (now Gauteng Province) was the first step in acknowledging and attempting to conserve invertebrate fauna in South Africa (De Wett & Schoonbee, 1991). Conservation agencies, reserves and national parks are in the process of changing or have changed their mission statements and research objectives to include invertebrates in the conservation of biodiversity (Government Gazette, 1997, Braack, 1997).

Biodiversity: definition

The conservation of biological diversity seeks to maintain the life-support system provided by nature that is essential for maximising the existence of the human species, meeting the needs of future generations and contributing to the stability of many economic and ecological systems (Tilman, 1997). The term 'biodiversity' or 'biological diversity' was first coined by Walter Rosen at the 1986 National Forum on BioDiversity meeting held in Washington D.C. (Wilson, 1988). Biodiversity is an extremely complex concept that can be interpreted and explained in various ways (Noss, 1990, Pearce & Moran, 1994). One such interpretation is 'The number and variety of living organisms on earth, millions of plants, animals and microorganisms, the genes they contain, the evolutionary history and potential they encompass, and the ecosystems, ecological processes, and landscapes of which they are integral parts. Biodiversity thus refers to the life-support and natural resources upon which we depend.'(Noss, 1990, Armsworth, Kendall & Davis, 2004).

Genetic diversity refers to the variety of genetic information within all plants, animals and microorganisms (Soule, 1991). It occurs within and between populations as well as between species, thus enabling development of new breeds of crops, domestic animals and allowing adaptation of species in the wild to changing conditions (Noss, 1990, Armsworth, *et al.*, 2004).

A species is a 'group of plants, animals, microorganisms or other living organisms that are morphologically similar; that share inheritance from common ancestry; or whose genes are so similar that they can breed together and produce fertile offspring' (Noss, 1990, Armsworth, *et al.*, 2004).

An ecosystem consists of communities of plants, animals and microorganisms, soil, water, and the air on which they depend. These all interact in a complex way, contributing to processes on which all life forms are dependant (Noss, 1990, Armsworth, *et al.,* 2004). Ecosystem diversity refers to the variety of biotic communities and habitats (ecosystems) and the ecological processes that occur within them (Pearce & Moran, 1994, Jeffries, 1997).

In this study biodiversity is investigated at the level of species, paying particular attention to abundance of individuals representing different species and species richness, which are linked to ecological processes.

Importance of biodiversity

Biodiversity is highly valuable at all levels for producing products and commodities to meet basic human needs and for providing amenities and services to promote human health and well being (Wilson, 1988). Components of biodiversity can be given direct and / or indirect economic value.

Studies have indicated that biodiversity increases resistance of communities to diseases (Purvis & Hectare, 2000). The rapid recovery of ecosystems from stresses such as drought or human induced degradation is more evident in a biologically diverse or heterogeneous system than one that is considered to be more homogenous in diversity (Tilman, 1997, Naeem & Li, 1997).

Recreation and ecotourism is one of the most rapidly growing industries in many countries, involving 200 million people per year and earning billions of dollars per year worldwide (Primack, 2000). Locations with high biodiversity such as protected nature reserves and parks are able to generate extensive economic wealth from this resource. Hence, the loss or depletion of such a resource is not only detrimental to the ecosystem but to the economic stability of the country as well (Oldfield & Alcorn, 1991).

Direct benefits provided by biodiversity are derived from the sustainable use of resources. These include the food that we eat, medicine and industrial products that we obtain from the environment (Ehrilich & Wilson, 1991, Chaplin, Zavaleta, Eviners, Naylor, Vitousek, Reynolds, Hooper, Lavourel, Sala, Hobbie, Mack & Diaz, 2000). In many third world countries, large proportions of the population are still directly dependent on biological resources for their livelihood and existence (James, Norse, Skinner & Zhoa, 1992). There is a serious need to educate people and help them understand that there are benefits to derive from the conservation of biological diversity. People need to recognise the values of biodiversity, the consequences of loss of biodiversity and the need for its conservation.

Implications of loss of biodiversity

Habitat degradation and loss and overexploitation of natural resources driven by an ever-growing human population and greatly increased consumption levels are the primary factors behind the loss of biodiversity (Reid & Miller, 1989, Dobson, 1996, Jeffries, 1997). What is bad for biodiversity will almost certainly be bad for the human population because of its dependence on the natural environment for air, water, raw materials, food, medicines and other goods and services (Oldfield & Alcorn, 1991). There has been mounting evidence that the loss of biological diversity will have severe consequences for the prosperity of communities and environments by diminishing the capacity of the ecosystem to provide society with a suitable and sustainable supply of essential goods and services (Tilman & Dowing, 1994).

Human activities such as large-scale agriculture, industrial development, commercial logging, and deforestation have severely impacted on the biodiversity of many areas. These activities not only change the habitat for many species but also lead to a decline in overall diversity of the area. For example, clear-cutting in a southern Appalachian forest resulted in the reduction of spider abundance and in a small decrease in the number of ground-dwelling and aerial spider species (Coyle, 1981). It was suggested that the process of clear-cutting, which involved the removal of forest canopy and reduction of litter thickness, was responsible for changes in the microclimate and therefore spider abundance decreased (Coyle, 1981). A study conducted by Bloemer, Hodda, Lambshead, Lawton & Wanless, (1997) on soil nematode diversity concluded that statistically significant effects were only detected in areas where extreme disturbance (active slashing, burning and complete mechanical forest clearance) was recorded, however there was an overall trend of a decline in nematode species richness with increasing forest disturbance. Human activities place significantly more species at risk of extinction today than at any other time in the past (McNeely, Gadgil, Leveque & Redford, 1995). However, due to the lack of baseline information (McNeely, *et al.*, 1995) the exact extent of biodiversity loss is unknown.

Biodiversity status and invertebrate conservation in South Africa

South Africa is ranked as the third most biologically diverse country in the world because of the unusually high percentage of vascular plants that are unique to this country. In addition South Africa is home to an estimated 5.8% of the world's total mammal species, 8% of bird species, 4.6% of the global diversity of reptile species, 16% of the total number of marine fish, 5.5% of the world's described insect species (Government Gazette, 1997) and 6% of the global arachnid diversity (Dippenaar-Schoeman, 2001).

According to McGeoch (2002) South Africa's insect species richness is estimated at two to three times more than what is currently described and the figure for other terrestrial arthropods is probably similar. Recognition of the importance of insect conservation in the country was first established at a workshop at the 8th Congress of the Entomological Society of Southern Africa in 1991. Since then actions for the conservation and for increasing awareness of insects and other terrestrial arthropods in South Africa have drastically increased. Research has contributed to conservation action and management decisions that promote insect conservation goals. In addition, significant advances continue to be made towards improving the understanding of insects and the threats they face. Researchers, concerned public members and government, are slowly addressing many of the conservation problems faced by South Africa's invertebrates.

Broad aim and objectives

Conservation agencies in South Africa have previously concentrated their conservation efforts on larger more charismatic vertebrates, namely, the 'Big Five' species, whilst invertebrates were largely ignored (DeWet & Shoonbee, 1991, Dobson, 1996). The realisation by managers of parks and reserves that there is a growing need to conserve biodiversity in general is clearly illustrated in the vision and mission statements and overall objectives of many conservation organisations. For example, the elephant management policy for many reserves has now been modified, in that the elephant population is now to be managed according to measured impacts on biodiversity rather than on absolute numbers of elephants (Whyte, Biggs & Braack, 2003). However, little quantitative data on elephant impacts on invertebrates exist. The focus of this study was the relationship between one of South Africa's most revered animals, the African elephant and some of South Africa's least known organisms, invertebrates.

The overall aim of this project was to assess the effect that habitat alteration by elephants had on the diversity of selected ground-dwelling invertebrates. The primary focus of the project was an investigation of the additional source of refugia/habitats (logs and dung) provided by elephants through the process of facilitation for invertebrate communities. This study was divided into two main sections, namely, a descriptive section (Chapter 4) and two experimental chapters (Chapters 5 and 6). The research was carried out in two small reserves, Madikwe Game Reserve and Makalali Private Game Reserve, in the northern region of South Africa.

The objectives of the study were:

1. To determine whether there is a relationship between the level of elephant ustilisation of vegetation, the production of refugia (logs and dung) and the diversity of selected ground-dwelling invertebrates.
2. To determine the extent to which refugia (logs and dung) affect the diversity, abundance and species richness of selected ground-dwelling invertebrates.
3. To identify the community structure of selected ground dwelling invertebrates associated with logs and elephant dung.
4. To determine whether there is any spatial variation in the impact of habitat alteration by elephants on ground-dwelling invertebrate diversity, species richness and abundance.

5. To determine whether there is any temporal (in terms of seasonal change and change in community with age of dung) variation in the impact of habitat alteration by elephants on ground-dwelling invertebrates.

The study was carried out at a local, small scale, because this was considered, as an appropriate starting point for investigating a suite of ground-dwelling invertebrates, for which there was no existing relevant information, within a limited time period.

CHAPTER 2

DESCRIPTION OF THE STUDY SITES

This chapter describes the savanna biome and the two game reserves (Madikwe Game Reserve and Makalali Private Game Reserve) in South Africa where this research was undertaken.

Savanna

The savanna biome makes up approximately one fifth of the world's land surface and is the largest biome in southern Africa, occupying 36% of the area in Africa and over one-third of the area in South Africa (Scholes & Walker, 1993, Low & Rebelo, 1996). It is characterised by a grassy ground layer and a distinct upper layer of woody plants. Where the upper stratum is near the ground, it may be referred to as a shrubland, where it is dense, it is called woodland and in areas at an intermediate stage, it is referred to as bushveld (Low & Rebelo, 1996). In South Africa there are two basic categories of savanna. These are the broad and fine leafed savanna (Scholes, 1997).

The environmental factors delimiting this biome are complex: altitude ranges from sea level to 2 000 meters above sea level; rainfall varies from 235mm to 1 000mm per annum; frost may occur from 0 to 120 days per year; and almost every major geological and soil type is characteristic of the biome. A major factor that limits the upper layer from dominating is rainfall. This together with fire and herbivory keeps the grass layer dominant. Plant species within the savanna have adapted to survive fire and have either become fire tolerant or resistant (Low & Rebelo, 1996).

Although savanna is the most extensive African biome and hence extremely important, it is the least studied terrestrial system (Scholes & Walker, 1993). Much of the tourism industry in South Africa is dependent on the savanna biome and this provides employment and economic wealth for a large number of people. It is here that most of the 'Big Five' game reserves are situated and on which a large amount of ecotourism is generated. For example the privately owned Phinda Game Reserve generated US$3 million in 2000 and a single camp in Hluhluwe-Imfolozi Park generated a similar amount (*Michael Brett, Pers Comm.). Tourist statistics at South Africa's premier wildlife park, the Kruger National Park have shown a steep growth since 1994 with 954 732 visitors in 1997/1998, 933 488 in 2001/2002 (decrease attributed to the 2000 floods), but recovering to over a million people in 2002/2003 (South African National Parks, Annual Reports, 2002 – 2004), thereby illustrating the importance of this biome.

Madikwe Game Reserve

Madikwe Game Reserve covers approximately 75 000 hectares and is located between 24°38'23" S to 26°8'23" E and 24°52'13" S to 26°29'09" E, in the northern reaches of the North West Province of South Africa. The reserve is bordered by Botswana in the north, the Marico River in the east, the Dwarsberg range in the south and the Zeerust – Gabarone road in the west (Davies, 1997).

For decades the area had been used for cattle farming and arable agriculture. Largely through mismanagement and inappropriate farming practices, much of the vegetation in the area was degraded. Following land feasibility studies, wildlife based tourism was

* Michael Brett–Ecotourism Consultant, current institution: Lesotho Highlands Development, Maseru

determined to be the most viable and economical use of the land. Since 1991, the area has undergone an intensive period of development to establish itself as a premier game reserve in the North West Province. This ultimately included an extensive restocking program of species that historically occurred in the region.

Madikwe consists mainly of extensive plains, which slope gently in a north-easterly direction towards the Marico River. A low range of quartzite hills runs in an east to west direction and divides the reserve into two fairly distinctive and equal halves. The plains in the northern half of the reserve are much flatter than the more gently rolling plains in the southern areas. The Dwarsberg, which is located in the northern section of the park, is the dominant mountain range that rises approximately 200 meters above the surrounding plains. The highest point in the reserve (1328 meters above sea level) is located at Tshwene, which is at the centre of the reserve, whilst the lowest point (950 meters above sea level) is found in the extreme north-eastern corner of the reserve. It is here that the only permanent natural source of water, the Marico River, flows out of the reserve (Davies, 1997).

Madikwe Game Reserve is situated in an arid area, with the mean annual rainfall varying between 475mm in the north-eastern regions and 520mm in the southern areas of the reserve. Summer (between the months of October and April) is the rainy season and winter is extremely dry with virtually no rainfall (Davies, 1997).

A variety of soil types are found at Madikwe. Soils on the hills are predominately shallow and rocky, while those found on the base of the hills are fairly well drained (Davies, 1997). The vegetation in Madikwe is classified into four groups, namely mixed bushveld, Kalahari thornveld, arid sweet bushveld and other turf thornveld (Acocks, 1975). Zacharias (1994) classified the vegetation in the reserve into two main groups: broad-leafed communities, which were dominated by *Combretum* species and microphyllous communities, which were dominated by *Acacia* species. Davies (1997) described in detail the vegetation associated with each of the two main communities found in Madikwe Game Reserve. The distribution of the vegetation types described below is illustrated in figure 2.1.

A) **Broad-Leaved Community**

There are six sub-divisions in this vegetation classification.

1. *Combretum apiculatum* with *Vitex zeyheri* and *Tarchonanthus camphorates* which is located in shallow dolomitic soils in a central band across the reserve. Other tree species include *Grewia* species, *Ximenia americana, Rhus leptodictya, Sclerocarya caffra, Ozoroa paniculosa* and other *Combretum* species.

2. Broad-leaved mountain veld which is dominated by *Combretum apiculatum* and associated with this species is *Combretum imberbe, Combretum molle, Combretum hereroense, Diospyros lycioides, Dombeya rotundifolia, Pappea capensis* and *Spirostachys africana.*

3. *Combretum imberbe* woodland, which is found mainly in the north-eastern corner of the reserve. It is associated with *Sclerocarya caffra, Burkea africana* and several *Acacia* species.

4. Community with dominant tree species *Sclerocarya birrea, Acacia erubescens* and *Acacia tortilis,* which is located mainly in the north-central areas of the reserve. Other tree species are *Pappea capensis* and *Boscia foetida.*

5. A narrow band of mixed *Acacia* and *Combretum* veld, which runs south of the dolomite soils. Other trees include *Grewia* species, *Ziziphus mucronata* and *Euclea undulata.*

6. *Terminalia sericea* veld, which occupies a small area in the extreme north-western corner of the reserve. *Acacia erubescens* is the other species that is present.

B) **Microphyllous Communities**

This community is further divided in two categories.

1. Straight thorned *Acacias,* which is also divided into two categories:
   1.1. Mixed *Acacia* woodland, which is associated with black clay soils in the north-western areas of the reserve. The main tree species here are *Acacia nilotica, Acacia tortilis, Acacia robusta* with scattered areas having *Acacia mellifera, Acacia erubescens, Spirostachys africana, Rhus lancea* and *Grewia* and *Gymnosporia* species.
   1.2. *Acacia tortilis* and *Acacia gerrardii* located in the vleis on the heavy clays in the southern area of the reserve. *Dichrostachys cinerea* and *Ziziphus mucronata* may also be located in this area.

2. Hooked - horned *Acacias,* which is also divided into two categories:
   2.1. Acacia mellifera with *Boscia foetida* woodlands. Other tree species that may be found in this area include *Acacia tortilis, Zizphus mucronata* and *Grewia flava.*
   2.2. Acacia erubescens group. This is a widespread and complex group that is associated with numerous other tree species. These include *Acacia mellifera, Acacia burkei, Acacia nigrescens, Boscia foetida, Boscia albitrunca, Dichrostachys cinerea, Combretum* species, *Euclea undulata, Rhus leptodictya, Ximenia americana* and *Ziziphus mucronata.*

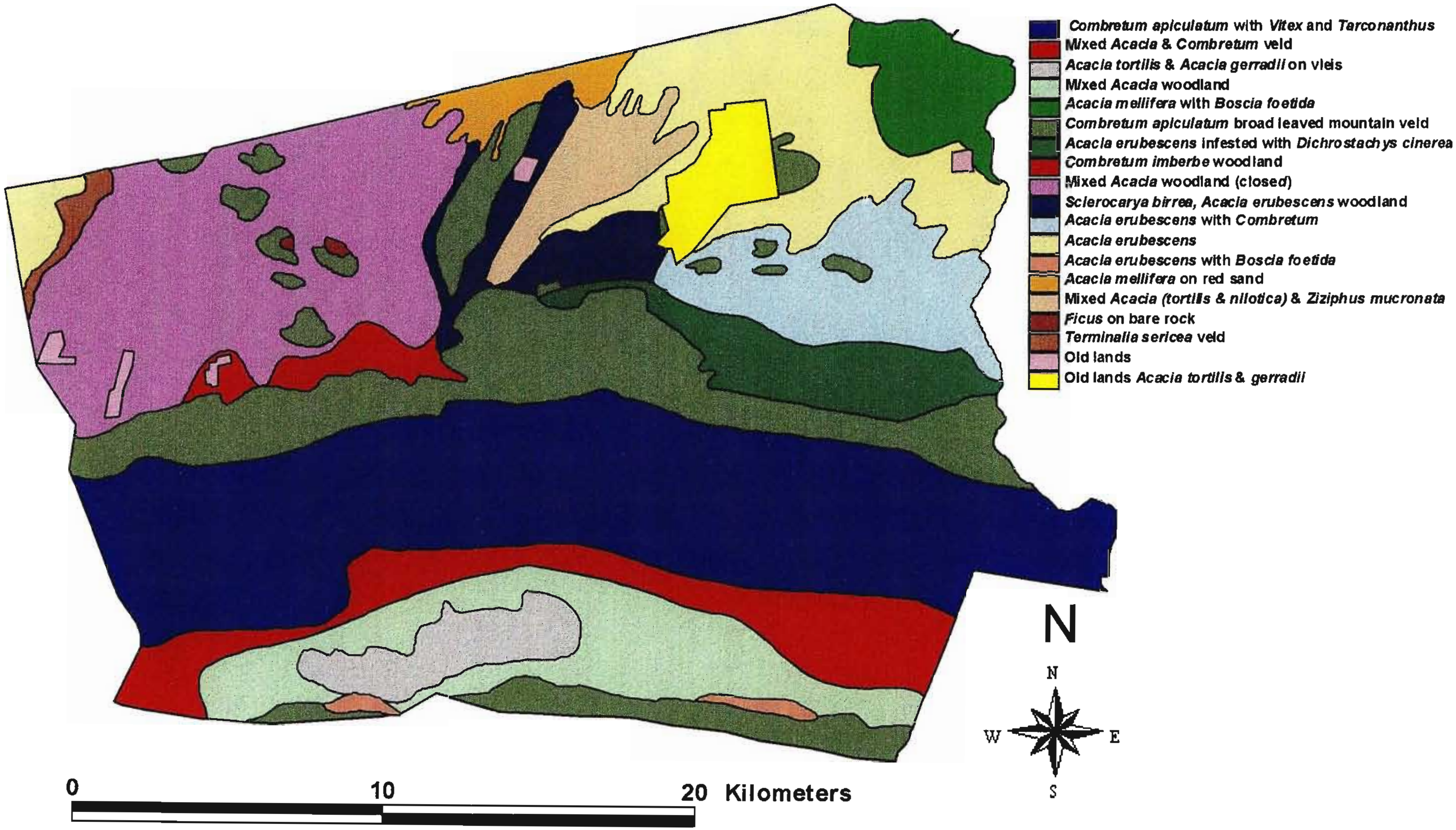


Figure 2.1. Vegetation map of Madikwe Game Reserve illustrating the distribution of the dominant vegetation communities (Davies, 1997).

Elephant re-introduction

The re-introduction of elephants into the reserve was a two-phase project. The first re-introduction project took place in 1992. Twenty-five young orphaned elephants, all of the same age, were translocated from the Kruger National Park (KNP). These elephants were all the by-products of elephant culling undertaken to control elephant numbers in KNP. The elephants were driven to Madikwe and released into bomas. Here they were allowed to settle down and become accustomed to their new environment, before being released into the reserve. The second re-introduction project took place in 1993. At this time, Gonarezhou National Park in Zimbabwe was experiencing a prolonged and severe drought and numerous efforts were being made to rescue as many drought-stricken elephants from the park as possible. One hundred and ninety-four elephants, which included entire family units, were successfully translocated from the park to Madikwe. Once again the elephants were released into bomas, in order to recover from the trauma of the capture and relocation procedure and to become accustomed to their new surroundings and the electrified fencing (Hofmeyr, 1997).

Between 1992 and 1993, a total of 219 elephants were translocated from KNP and Zimbabwe to Madikwe Game Reserve. According to the 1996 game count, the elephant population in Madikwe was approximately 255 individuals (Hofmeyr, 1997) and in 2003 the population had increased to approximately 450 individuals ([+] Markus Hofmeyr, Pers Comm.).

[+] Dr. M Hofmeyr – Head of Game Capture, Kruger National Park, Skukuza, South Africa.

The socio-economic issues surrounding the establishment of Madikwe Game Reserve

Appropriate land use, the socio-economic situation of people neighbouring the reserve, and the potential benefits to these communities were important factors taken into consideration when establishing Madikwe Game Reserve (Davies, 1997). Wildlife conservation that is linked to ecotourism and the socio-economic development of local communities can compete favourably with other forms of land use. In many rural regions of South Africa agricultural activities, however marginal, seem to provide the bulk of the income to a household. It is therefore imperative to determine if a switch to ecotourism would be a viable and better option (Davies, 1997).

Various feasibility studies conducted within areas surrounding Madikwe Game Reserve determined that communities living around the potential conservation site were poor, with few if any economic opportunities available to them and as a result they were underdeveloped (Setplan, 1991). In 1991 the majority of residents relied solely upon income generated from outside the area. This included working as migrant or domestic workers in cities. A large proportion of adults had not received adequate education and this lack of literacy skills limited their ability to find employment, which then translated into extremely low employment rates. Basic infrastructure, services and developments, such as water supply, sewerage, roads, electricity and telephones were severely lacking (Setplan, 1991).

Although economically unsustainable, more than half of the population adjacent to the reserve were involved in some way or another in agricultural activities. Most of the agricultural activity was restricted to livestock production but livestock ownership in the area seemed to be heavily skewed to a small minority of the population. This meant that if the area, which is now proclaimed for conservation were distributed among the people, only those with sufficient livestock would benefit, resulting in further discrepancies in distribution of wealth among the people (Setplan, 1991).

It was therefore concluded that establishing the conservation area created the potential for greater employment and business opportunities than current agricultural practices. Conservation and associated ecotourism constituted the only realistic and tangible option available to the communities in these remote and under developed regions in South Africa (Anon. 1993). The socio-economic impacts of establishing Madikwe Game Reserve have not been assessed.

Makalali Private Game Reserve

Makalali Private Game Reserve is currently a 33 000 hectare game farm located between 24°02'13" S to 30°35'44" E and 24°14'35" S to 30°47'54" E. The reserve is situated close to the western border of the KNP, at the foothills of the Drakensberg Mountains in the Limpopo Province of South Africa.

Makalali and its surrounding areas were unfarmable until the 1940's, mainly due to the presence of various illnesses, such as malaria. The introduction of vaccines, improved medical attention and increased awareness of the various diseases brought the sicknesses under control and the land was handed to soldiers who came back from the Second World War. The initial trend was to farm cattle but over a period of 40 years, due to low carrying capacities and unpredictable seasons, it was determined that cattle farming was not a viable option for that particular area. In recent years, many of the former cattle farms have been converted into private wildlife reserves, supporting trophy hunting and ecotourism (Butchart 1996). Makalali was initially a 7 500 hectare cattle farm that was purchased in 1993. The acquisition of neighbouring farms in 1994 extended it to over 10 000 hectares. Recently, the private game reserve once again extended its boundaries by purchasing more adjacent farms.

The reserve is situated on the lowveld plain between 300 and 500 meters above sea level. The landscape is a combination of undulating terrain and rocky outcrops. The main vegetation types are mixed lowveld bushveld and mopane bushveld (Acocks, 1975, Low & Rebelo, 1996). The Makhutswi River is a perennial tributary of the Olifants River, and is the only large river that flows through Makalali. The river runs from west to east and splits the reserve almost in half. To supplement the water shortages during the dry winter months numerous artificial watering points have been created within the reserve.

The reserve has a sub-tropical climate with wet summers and dry winters. This is a relatively dry area with an average annual rainfall of 450mm. The rainy season begins in October with maximum rainfall between November and February. Temperatures within the reserve range from 3°C in winter to above 36°C in summer.

According to Low & Rebelo (1996), the vegetation in the reserve can be classified into nine different plant communities. The tree species that commonly occur in each of the nine plant communities within Makalali Private Game Reserve were described by Druce (2000) and are listed in detail below. The distribution of the vegetation types described below is illustrated in figure 2.2.

1. **Riparian closed woodland**

   This woodland is characterized by *Flueggea virosa, Croton megalobotrys, Dichrostachys cinerea, Ziziphus mucronata, Gymnosporia buxifolia, Phoenix reclinata, Diospyros mespiliformis.* The following species are restricted to this vegetation type: *Acacia robusta, Acacia caffra, Acacia schweinfurtheii, Berchemia discolor, Combretum erythrophylum, Euclea natalensis, Ehretia rigida, Ficus sycomorus* and *Ficus ingens.*

2. **Drainage line thicket**

   The species that characterize this vegetation type are *Albizia harveyi, Lonchocarpus capassa, Commiphora glandulosa* and *Flueggea virosa. Gymnosporia buxifolia* and *Grewia* species are also abundant.

3. ***Colophospermum mopane* low closed woodland**

   This vegetation type is mainly composed of *Colophospermum mopane* trees. Other than the dominant tree species, *Euclea divinorum, Grewia* species, *Combretum hereroense, Commiphora glandulosa,* and *Dalbergia melanoxylon* are also found here.

4. ***Cissus cornifolia – Lannea schweinfurtheii* low thicket**

   This vegetation type is made up of *Cissus cornifolia, Commiphora africana* and *Lannea schweinfurtheii.* There are also two sub-vegetation types that are recognised within this community.

   4.1 *Ormocarpum trichocarpum – Dichrostachys cinerea* variant

   Ormocarpum trichocarpum, Commiphora glandulosa, Dichrostachys cinerea and *Combretum hereroense* make up this thicket.

   4.2 *Combretum apiculatum – Commiphora africana* variant

   Several *Grewia* species occupy the highest density in this community. Other species that may be located here include *Acacia exuvialis, Acacia nigrescens, Dalbergia melanoxylon* and *Lannea schweinfurtheii.*

5. ***Combretum apiculatum – Acacia nigrescens* low closed woodland**

This is the most prevalent vegetation type in the reserve, and is characterized by *Combretum apiculatum, Acacia nigrescens, Ziziphus mucronata* and *Sclerocarrya birrea.* This plant community also consists of three sub-vegetation types each with two variants.

5.1 <u>*Ziziphus mucronata – Combretum hereoense* variant</u>

5.1.1 *Dichrostachys cinerea – Acacia exuvialis* sub-variant

Extremely high densities of *Acacia exuvialis* and *Dichrostachys cinerea* characterize this vegetation type. Other species include *Acacia nigrescens, Combretum apiculatum, Combretum hereroense, Commiphora glandulosa* and *Grewia* species.

5.1.2 *Combretum apiculatum – Ziziphus mucronata* sub-variant

Combretum apiculatum and *Ziziphus mucronata* are the two dominant tree species, however *Acacia nigrescens, Combretum hereroense, Dichrostachys cinerea* and *Grewia* species may also be found here.

5.2. <u>*Combretum apiculatum – Terminalia prunioides* variant</u>

5.2.1 *Acacia nigrescens – Ormocarpum trichocarpum* sub-variant

Acacia nigrescens, Combretum apiculatum, Grewia species *Dichrostachys cinerea* and *Acacia exuvialis* are predominant in this vegetation type.

5.2.2 *Acacia exuvialis – Sclerocarrya birrea* sub-variant

Combretum apiculatum as well as *Grewia* species occur in high densities. Other important species are *Dalbergia melanoxylon, Acacia nigrescens* and *Cissus cornifolia.*

5.3 <u>*Acacia exuvialis – Strychnos madagascariensis – Dalbergia melanoxylon* variant</u>

5.3.1 *Acacia nigrescens – Acacia exuvialis* sub-variant

This community is dominated by *Acacia nigrescens* and *Combretum apiculatum.* Other species identified here are *Dichrostachys cinerea, Acacia exuvialis, Flueggea virosa, Strychnos madagascariensis* and *Ziziphus mucronata.*

5.3.2 *Strychnos madagascariensis – Combretum apiculatum* sub-variant

The tree species that are dominant in this vegetation type include *Combretum apiculatum, Strychnos madagascariensis, Balanities maughamii, Commiphora glandulosa, Grewia* species, *Acacia nigrescens* and *Dichrostachys cinerea.*

6 **Low closed grassland**

All grassland within the reserve is assigned to this vegetation type.

7. ***Combretum apiculatum – Dalbergia melanoxylon* low open woodland**

The species prevalent in this vegetation type include *Acacia exuvialis, Grewia* species, *Commiphora africana, Gymnosporia buxifolia* and *Dalbergia melanoxylon.* This vegetation type also includes areas that have been cleared to address bush encroachment.

8. ***Combretum apiculatum – Grewia* low thicket**

Combretum apiculatum and *Grewia* species are the dominant tree species. There is a relatively high density of other woody species, including *Commiphora africana, Acacia nigrescens, Gymnosporia buxifolia* and *Acacia karroo.*

9. ***Combretum apiculatum* – low closed woodland**

This woodland type is characterized by an extremely high density of *Combretum apiculatum* plants, with *Acacia nigrescens, Grewia* species, *Combretum hereroense* and *Sclerocarrya birrea* also located among the dominant species.

Conservation initiatives implemented in Makalali Private Game Reserve included erosion control, bush-clearing programs, rehabilitation of previously degraded land and renovating the network of roads. Conservation plans also included the re-introduction of large mammals that were previously indigenous to the area. A pride of lions, five white rhinos and two herds of elephants were translocated from the KNP in May 1994. This was the first ever relocation of family groups of adult elephants from the KNP. The first translocation included 13 elephants. In 1996 another 24 elephants were translocated to the reserve. In 2000 the elephant population in the reserve consisted of an estimated 56 individuals (* Audrey Delsink, Pers Comm.).

* A. Delsink – Elephant Ecologist, Makalali Private Game Reserve, South Africa.

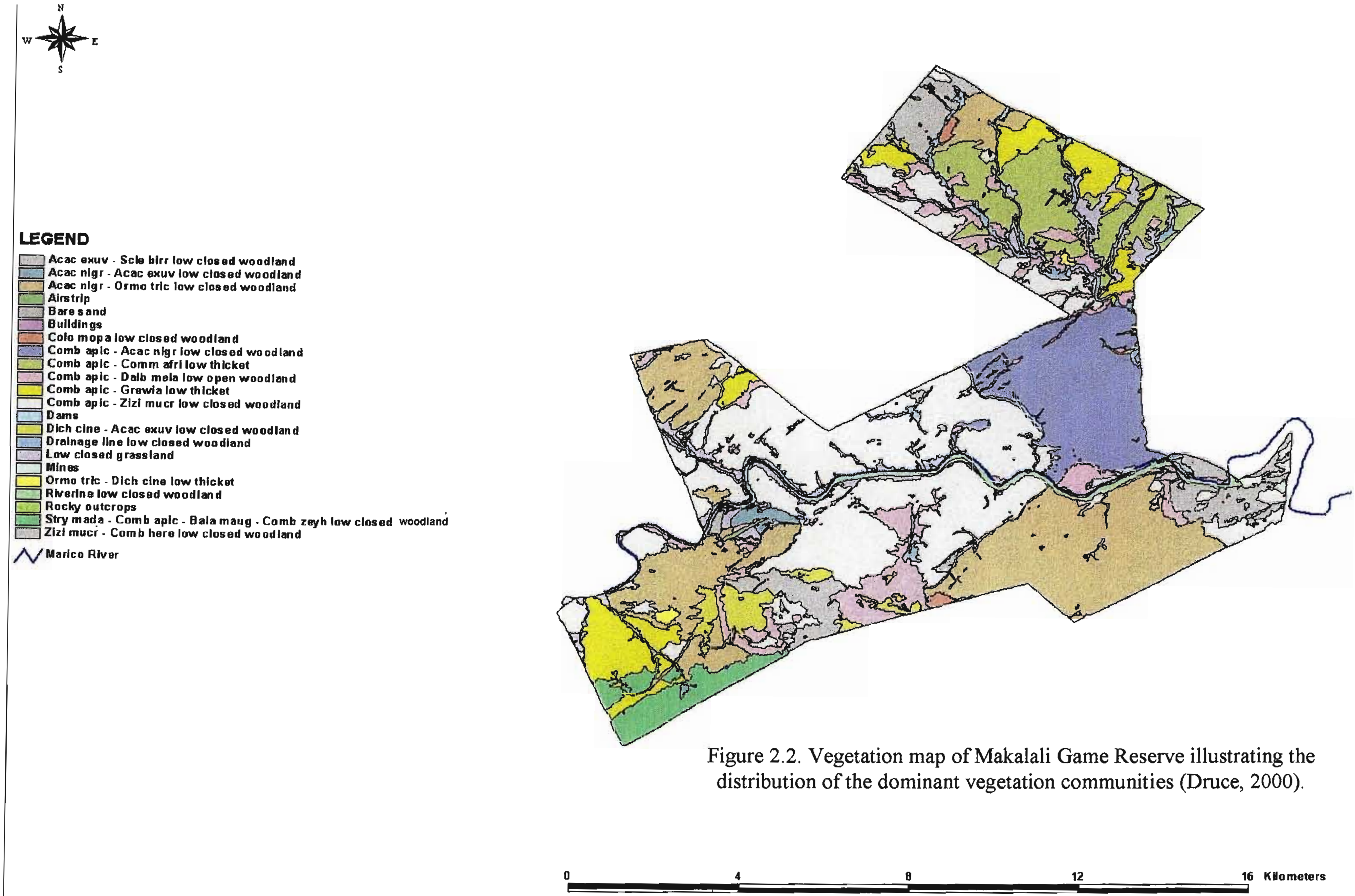


Figure 2.2. Vegetation map of Makalali Game Reserve illustrating the distribution of the dominant vegetation communities (Druce, 2000).

CHAPTER 3

INVERTEBRATES IN ECOLOGICAL RESEARCH: APPROACHES ADOPTED FOR THIS STUDY

The communities of organisms that live under logs and dung are little noticed and even less studied yet the role of such invertebrates in decomposition and soil nutrient recycling is critical. There are several reasons for the lack of research on and knowledge of invertebrates. These include the enormous diversity and abundance of invertebrates, which makes ecological research time-consuming and costly, and the lack of taxonomic expertise to identify most invertebrate groups. In order to address the neglect of invertebrates in ecological research, several approaches have been recommended. These include using a "shopping basket" approach to selecting a limited number of taxa that can be included in the study and using morphospecies identifications for speciose groups where taxonomic expertise is not available (Slotow & Hamer, 2000).

Selection of focal taxa

The "shopping basket" approach (Hammond, 1994) of selecting several taxa that represent different ecological functions was used to select taxa for this study. The focal invertebrate taxa were selected according to the following criteria: (1) invertebrates that live beneath logs and dung and are not totally dependent on dung, (therefore the dung beetle communities were not included); (2) invertebrates falling within size range for the meso and macro faunal categories (greater than 0.2mm in length) proposed by Wallwork (1970); (3) invertebrates with limited mobility which therefore excluded all flying insects and (4) invertebrates representing a range of functional groups namely predators, herbivores, detritivores and generalists. The groups that were targeted for this project were ants, centipedes, millipedes, scorpions, spiders and termites.

Ants (Class: Insecta, Order: Hymenoptera, Family: Formicidae)

The order Hymenoptera constitutes one of the largest and most specialised insect orders. There are possibly more than 100 000 described species in the world and an even greater number that are awaiting scientific description (Scholtz & Holm, 1985). In South Africa there are approximately 540 described species of ants, of which 30% are endemic to this country. There are two major groups or sub-orders of Hymenotpera: Symphyta or Sawflies, which are mostly phytophagous and Apocrita, which include bees, wasps and ants. Members of the later sub-order are highly specialised and non-phytophagous (Scholtz & Holm, 1985).

The importance of ants in the ecosystem is well recognised. Ants play important roles in seed dispersal, pollination, predation, nutrient flow and soil improvement through soil aeration (Petal, 1978). The few thousand ant species known to the world are all included in a single family, Formicidae. Ants are social insects that are dominated by the female sex, as the males take no part in the colony's daily activities (Scholtz & Holm, 1985). Nests, which provide shelter and protection, are usually built in natural cavities in wood or soil. The colonies also live in underground tunnels or in galleries within dead wood. Ants prefer soil that is moist and well shaded (Brian, 1977). The diet of ants consists of soil insects, fungi from wood and soil, seed, honeydew, sugar and fruits. However, their primary source of food is green plants (Brian, 1977).

Centipedes (Class: Chilopoda)

This is a diverse class of invertebrates, with an estimated global diversity of approximately 10 000 different species. Thus far there are about 2 500 species of centipedes that have been described throughout the world and approximately 150 of these species may be found in South Africa (Lawrence, 1987). There are four principle orders, all of which are represented in South Africa. These orders are: Geophilomorpha, Scolopendromorpha, Lithobiomorpha and Scutigeromorpha. The orders collected for this study are briefly described in Appendix 3.1.

Centipedes range in length from 10 to 300mm. They are nocturnal, and lack an impervious cuticle layer (Cloudsley-Thompson, 1968), which makes them vulnerable to desiccation and predation. They usually live in damp, dark and obscure places particularly under stones, fallen leaves or branches, under bark and in the crevices of soil. Centipedes are primarily carnivorous but a few of the Geophilomorpha will on occasion feed on plant tissue. Their diet ranges from soil-dwelling arthropods, to small mice and birds and snakes (Cloudsley-Thompson, 1968). Centipedes subdue their prey with a pair of poisonous claws called 'forcipules' (Cloudsley-Thompson, 1968, Lawrence, 1987) that release a neurotoxic poison (Lawrence, 1987).

Millipedes (Class: Diplopoda)

An estimated number of 50 000 to 80 000 species of millipedes occur globally (Schrock, 1999) of which approximately 11 000 species have been described globally (Minelli & Golovatch, 2001). A total of 552 species, distributed between 71 genera, 15 families and seven orders have been recorded in Africa south of the Zambezi and Kunene Rivers (Hamer, 1998). The orders collected in this study are briefly described in Appendix 3.2.

Millipedes play an important role in the process of soil formation (Bano, 1992). Millipedes are classified as detritis feeders, mainly feeding on decomposing plant material (Hopkin & Read, 1992), including rotting wood, as well as new roots and green leaves (Lawrence, 1987). They are known to process as much as 30% of dead organic matter per year, via the stimulation of microbial activity, which promotes decomposition (Hopkin & Read, 1992, Dangerfield & Kaunda, 1994).

Millipedes range in length from 2 to 300mm. These organisms require a relatively humid environment to live in because they lack a waxy epicutical layer (Brusca & Brusca, 1990). Most millipedes are found in damp, earthy places, wet soil and sunless forest floors with abundant decaying leaves and shreds of rotting bark. In dry areas stones, fallen branches (logs), deserted termite mounds or other debris serve as shelter against heat and aridity.

Scorpions (Class: Arachnida, Order: Scorpiones)

Worldwide there are approximately 1400 described scorpion species in nine families (McGavin, 2000). Scorpions are considered to be the most ancient terrestrial arthropod and the most primitive arachnids (Brusca & Brusca, 1990) and are often referred to as 'living but sophisticated fossils' (Polis, 1990).

The southern African scorpion fauna is well studied and speciose. The region contains approximately 8% of the world's genera and at least 10% of the world's species (Prendini, 2002). There are approximately 140 described species in South Africa, of which 80% are endemic to the country (McGavin, 2000). There are three families found in South Africa, namely Buthidae, Scorpionidae and Ischnuridae (Leeming, 2003).

Scorpions favour warm areas and become sluggish in cold weather (McGavin, 2000). Most scorpions are only active at night, hunting and feeding, and they seek refuge during the day. Scorpions have two main methods of sheltering, namely burrowing and hiding under rocks, stone or bark. In South Africa, the genus *Parabuthus* has some species that are burrowers that dig in sandy or sandy loam soil, while others seek shelter under stones, logs or other debris (Newlands, 1978). Species of another genus, *Uroplectus*, also shelter in dark crevices of trees and rocks, under bark, stones and beneath leaf litter on the ground (Newlands, 1978). The size of scorpions varies from a few centimetres to one of the largest arachnids of approximately 180mm (Brusca & Brusca, 1990).

Scorpions are easily identified by their post-abdominal sting and two chelate pedipalps. Scorpions are generalist predators, whose diet consists chiefly of spiders, insects such as flies, cockroaches, grasshoppers, crickets, and mantids, myriapods, and even some small mice (Cloudsely-Thompson, 1968).

Spiders (Class: Arachnida, Order: Araneae)

Dippenaar-Schoeman and Jocquè (1997) compiled the first comprehensive overview of the spider fauna of the Afro-tropical region, which includes approximately 5 500 species distributed among 71 families. Sixty-two of the world's 106 spider families are found in South Africa and are represented by 428 genera and about 2900 species (Dippenaar-Schoeman & Jocquè, 1997).

Arachnids are an important but generally poorly studied group of arthropods that play an important role in the regulation of insect and other invertebrate populations in most ecosystems (Russell-Smith, 1999). Although there are exceptions to every rule, spiders can be classified according to their lifestyle. Spiders can be divided into the following three groups, namely web-building spiders, plant-living spiders and ground-living spiders. For the purpose of this project, only spiders that live under or within logs and elephant dung were sampled. Ground-living or free-living spiders were mainly collected but it was not uncommon to collect spiders that are classified as plant-living that were associated with the logs and dung.

Termites (Class: Insecta, Order: Isoptera)

There are over 2500 species of termites distributed throughout the world (Uys, 2002). The family Termitidae includes about 80% of the isopteran species. This family is also the largest family of termites in Southern Africa, with 39 genera, and approximately 190 species. Other families in Southern Africa include Kalotermitidae (six genera and 11 species), Teropsidae, Hodotermitidae (with two genera each with one species) and Rhinotermitidae (three genera and seven species) (Scholtz & Holm, 1985).

Termites are a particularly important component of the soil arthropod community. In some African forests the abundance and biomass of termites is up to an order of magnitude greater than any other insect groups (Eggleton & Bignell, 1995). Termites play key roles in decomposition processes, nutrient cycling, nitrogen fixation, carbon flux, soil creation and distribution (Meyer, Braack, Biggs & Ebersohn, 1999).

Termites spend most of their life underground, inside timber or within their nests (Scholtz & Holm, 1985). They build different types of nests of varying complexities. The simplest are those of the Kalotermitidae, which are merely cavities and galleries excavated in wood (Uys, 2002). Termites feed only on matter of vegetable origin. The most common source of food is wood. Other food sources can include animal fodder, old sacks and dung from grazing wild animals (Uys, 2002).

Morphospecies identification

In order to overcome difficulties associated with the large diversity and the taxonomic difficulties of including invertebrates in research, identification to morphospecies level, instead of named species can be utilised. Morphospecies are samples most commonly identified to family level, and then separated superficially on morphological characteristics which result in recognisable taxonomic units that can be used as a measure of biodiversity (Slotow & Hamer, 2000). In several cases the identification to morphospecies level has proven to be a reliable estimate of species richness and turnover, which are consistent with the results obtained from identifications by specialised taxonomists (Oliver & Beattie, 1996). For this project the morphospecies approach was only used for one focus taxon. Spiders were identified to morphospecies level by a person experienced in the identification of spiders to family level.

There are, however, several problems associated with the use of morphospecies. These include inaccuracies in species richness counts, and the limitation that a morphospecies cannot provide any information on rarity, level of endemism, or even ecological role (Slotow & Hamer, 2000). Therefore, for this project, five of the six selected invertebrate taxa (ants, centipedes, millipedes, scorpions and termites) were identified to species level by specialised taxonomists as detailed in Chapter 4.

Measuring diversity: the use of indices

It is extremely difficult to measure biodiversity and represent this measure as a single value therefore surrogate measures of biodiversity are often used (Gaston, 2000, Purvis & Hector, 2000). These include a variety of indices based on the number of species and the abundance of each species. The use of indices does, however, result in the loss of information and many indices make assumptions about sampling that are usually difficult to meet (Purvis & Hector, 2000). It is recognised that there are numerous disadvantages to using any diversity index (Groombridge, 1992, Gaston, 2000). However of the three levels that define biodiversity, species diversity is the most commonly used method for assessment. This is based on the idea that by increasing the species diversity of an ecosystem one usually achieves greater diversity of genes, higher taxa and habitats (Purvis & Hector, 2000).

For the purpose of this study, I assessed biodiversity in terms of a species diversity index, which comprises two components, namely species richness and species evenness. Species evenness refers to how the total abundance (number of individuals) is distributed among the species, whilst species richness refers to the number of species within the community (for example, species per unit area) (Ludwig & Reynolds, 1988).

There are numerous diversity indices in the literature. To calculate species diversity in community ecology the Shannon Index (H') is most commonly used (Wolda, 1981, Ludwig & Reynolds, 1988). Ludwig and Reynolds (1988) described this index as a measure of the average degree of 'uncertainty' in predicting the species of an individual chosen at random from a community. This average uncertainty increases as the number of species increases and the distribution of individuals among the species becomes even. The index varies for communities with only a single species (index value of 0) to communities consisting of many species (high index values). The equation is as follows:

$$H' = - {}^{S*}\sum (p_i \ln p_i)$$

where H' is the average uncertainty per species in an infinite community made up of S^* species with known proportional abundance $p_1, p_2, p_3 \ldots\ldots\ldots\, p_{S^*}$.

The units for the Shannon's diversity index are not expressed in species. To accommodate for this, the Hill's diversity number, which is the number of species in a sample, is calculated with the following equation (Ludwig & Reynolds, 1988).

$$N1 = e^{H'}$$

Where, H' is the Shannon's index.

Calculation of species richness

The easiest and most straight forward manner to determine the value for species richness would be *S*, the total number of species in a community. One limitation of calculating S is that in comparative studies, the sample sizes must be equal. This was the case for this study, and therefore species richness was calculated by counting the exact number of species within a sample (*S*).

CHAPTER 4

THE EFFECT OF ELEPHANT USE OF VEGETATION ON REFUGIA PRODUCTION AND ASSOCIATED INVERTEBRATE DIVERSITY IN MADIKWE GAME RESERVE

INTRODUCTION

Ecotourism is one of the most important sources of revenue for many African countries. In South Africa this industry has been rapidly growing over the past decade. In 1986 the number of visitors to game reserves was 454,428, in 1998 this number had grown to 5,898,000 visitors. Visiting game and nature reserves was the number one activity for visitors to South Africa in 1997 (60%), rising by 2% over the previous year (South African Tourism Board, 1998). The Pilanesberg National Park in the North West Province generated over R80 million in 2001 through ecotourism and the Kruger National Park registered a turnover of R256.77 million in 2002, R318.21 million in 2003 and R392.62 million in 2004 (South African National Parks Annual Reports 2002, 2003 & 2004). In the period from 1986 until 1998 the number of visitors to game and nature reserves in South Africa has grown by 10.8% annually (South African Tourism Board, 1998). To enhance their attraction as ecotourism destination sites and thereby increase levels of tourism and hence produce higher revenues, several reserves have introduced large charismatic mammals, including lion, elephant, rhino and buffalo. A significant problem associated with these re-introductions is that these small reserves are delimited by a fence, which prevents the natural movements of mega-herbivores in response to depletion of their food resources. This can eventually have a substantial influence on the ecology of the reserve due to the system's inability to self-regulate.

In small reserves in South Africa where elephants have been introduced, their numbers are increasing rapidly (Whyte, 2004). Management decisions will have to be made as to how to manage the population increase. As yet, sufficient quantitative data detailing the influence of elephants on biodiversity of small reserves do not exist, and as such, decisions on the maximum numbers of elephants and levels of acceptable impact within the reserve are made largely on gut feel or anecdotal knowledge.

The term 'keystone' species has enjoyed enduring popularity in ecological literature since its introduction by Robert T. Paine in 1969 (Mills *et al.*, 1993). Any species may be regarded as a keystone species, by virtue of how they change the physical structure of the environment (Simberloff, 1998). Mills *et al.* (1993) stated that if a modified habitat affects the survival of many other species, the modifying species is regarded as a keystone species. There are various categories of presumed keystone species: predator, prey, plant, or modifier (Mills *et al.,* 1993).

Within the savanna biome there are many species that exert large functional effects on ecosystems, but this project focuses on the disturbances caused by the largest terrestrial species, the African elephant. Elephants are categorised as keystone modifiers whose activities through competition and facilitation can greatly affect habitat features without necessarily having direct trophic effects on other species. Given the assumed importance of keystone species, it is not surprising that biologists have advocated that these species be targeted in conservation efforts in order to maximise biodiversity protection.

In combination with other biotic and abiotic factors elephants can convert woodland into grassland and hence reduce forage for other species (Dublin, Sinclair & McGlade, 1990). Studies have illustrated that the change from woodland to a grassland vegetation community resulted in the loss of species from the system (Guy, 1981, Barnes, 1983, Jachmann & Croes, 1991, Cumming, *et al.,* 1997). However one can argue that with this change there would also be an increase in other species. For example grazer numbers should increase due to an increase in their required forage resource.

The spatial distribution of elephant utilisation of vegetation across areas is not uniform and several studies indicate that elephants use plants and habitats selectively by taking some species in greater proportions than their occurrence, and rejecting others entirely (Babaasa, 2000, Stokke & du Toit, 2002, Gadd, 2002). The impact of elephants on biodiversity could be expected to be patchy and related to the patterns of elephant use of the habitat, which is influenced by the distribution of water in the landscape (Gaylard, Owen-Smith & Redfern, 2003). This means that in areas where there is more elephant use of vegetation a greater impact on ground-dwelling invertebrates would be predicted because of a higher density of refugia (logs and dung) produced.

The distribution of invertebrates at a local scale is poorly understood, but recent (Druce, 2000) and ongoing studies in savanna habitats have shown that Beta diversity is high, and not always easily predicted by vegetation type. The exact factors influencing invertebrate community structure and fine-scale distribution of individual species are difficult to determine, but they are likely to be a complex combination of environmental and biotic factors, which in many cases is taxon specific. It is therefore important to assess impact of elephants on invertebrates in different vegetation types, spread throughout the reserve because natural patterns of invertebrate diversity, and the extent of elephant impact are likely to differ spatially. The factors influencing invertebrate community structure and species distributions at a local scale need to be well known to allow direct comparisons of areas with and without elephant populations as an approach to measuring impacts.

The temporal distribution of elephant feeding patterns within reserves varies considerably, with studies illustrating significant seasonal (wet and dry) and diurnal shifts in habitat use (Barnes, 1982, Lewis, 1986, Cerling, Passey, Ayliffe, Cook, Ehleringer, Harris, Dhidha, Kasiki, 2004). Many of the focus taxa are relatively long-lived, surviving more than a single season. Environmental conditions change seasonally, and these will influence the habitat requirements and activity patterns of ground-dwelling invertebrates. In order to determine the influence of season on elephant vegetation utilization, refugia production and therefore invertebrate species diversity potentially using this habitat niche, elephant impact, refugia production and invertebrate diversity were measured in summer (wet) and winter (dry).

If we assume that managers are attempting to manage their conservation areas for the maintenance of maximum biodiversity (Braack, 1997, Christensen, 1997, Fiedler, White & Leidg, 1997), then the issue is not simply the effect of elephants as a biotic process, but rather what the effect of that process is on the local environment and for the ecosystem as a whole. The purpose of this chapter is to contribute to improving the understanding of how elephant-produced refugia influences ground-dwelling invertebrate diversity.

The overall aim of this part of the project was to determine whether there is a relationship between the extent of elephant use of vegetation, the production of refugia and the diversity of ground-dwelling invertebrates, and to investigate spatial and temporal differences in any relationship. Assuming that an increase in elephant utilisation of vegetation results in an increase in abundance of refugia produced, I predict higher abundance, diversity and species richness of ground-dwelling invertebrates at sites with higher elephant utilisation.

This prediction was tested by investigating correlations between elephant utilisation and the number of refugia produced, and between invertebrate diversity and level of elephant utilisation. The hypothesis tested was that an increase in elephant utilisation of vegetation results in an increase in abundance of refugia and therefore an increase in ground-dwelling invertebrates. The null hypothesis stated that there is no relationship between the extent of elephant use of vegetation, production of refugia and invertebrate diversity.

The objectives of this part of the study were:

1. To use existing data to quantify spatial and temporal variation in elephant utilisation of vegetation;
2. To quantify spatial (vegetation type) and temporal (season), differences in the abundance of refugia (logs and dung) in relation to elephant usage calculated in objective 1;
3. To quantify and describe the diversity (abundance and species richness) of selected invertebrates associated with the refugia and
4. To determine whether the presence of refugia does increase ground-dwelling invertebrate species abundance, richness and diversity.

METHODS & MATERIALS

Mega-herbivore impact on vegetation transects

Between January 2000 and December 2001 elephant vegetation utilisation data were collected from Madikwe Game Reserve in the North Western Province, South Africa. The data were collected in three sampling periods: January 2000 (summer), July 2000 (winter) and January 2001 (summer). A total of 115 transects (Figure 4.1) (39 in January 2000, 42 in July 2000 and 34 in January 2001) were sampled in eight vegetation types throughout the reserve. During the first two sampling periods, transects were located randomly throughout the reserve, but stratified in different vegetation types and distance from major rivers and slope. During the third sampling period, vegetation communities that were previously not sufficiently sampled were selected.

Each transect was 50m in length and the width varied between 5m, 6m or 10m, depending on the density of the vegetation and species composition along the transect line. A nested design was used in which more abundant smaller individuals (<0.5m height) were sampled in smaller areas. In order to record usage of rare and highly selected species, larger nested quadrants were sampled within the original transect dimensions. All transects were laid parallel to the road and in an easterly to westerly orientation and the exact location was noted by recording the G.P.S location. Woody individuals within each transect were identified using field guides by Pooley (1994), van Wyk & van Wyk (1997) and van Wyk, van Wyk & van Wyk (2000).

The measurements recorded for each plant species are presented in data sheets included in Appendix 4.1, together with the code sheet used (Appendix 4.2). The species name, the height of the tree, number of live and dead stems, the diameter of the live and dead stems, the height below canopy and the canopy dimensions were recorded. If only a few leaves were present on the tree, the canopy dimensions were measured to the outer-most twigs. For multi-stemmed shrubs the average diameter of the stems were recorded.

Each plant was identified as having being utilised or not and for those trees utilised, the type of usage was recorded. Usage classifications were adopted from Walker (1976) and comprised leaf-stripping, removal of terminal twigs and branches, breaking of the main stem, pushing the tree over and debarking. To estimate the extent of canopy usage on a particular tree, the percentage foliage removed from the crown was recorded as (1) <5%; (2) 5%-10%; (3) 10%-25%; (4) 25%-50%; (5) 50%-75%; (6) 75%- 90% and (7) >90%. Trees that were pushed over or uprooted were recorded and placed in category seven. The bark condition of trees was also noted. Elephant usage of bark is characterised by stripped bark and tusk marking on the exposed sapwood. Two measurements were used to record debarking; the width of the area stripped relative to the circumference of the tree and the length of the stripped area relative to the height of the tree. Classes of bark utilisation were assigned as a percentage of the total usage on the tree: (1) <5%; (2) 5%-10%; (3) 10%-25%; (4) 25%-50%; (5) 50%-75%; (6) 75%- 90% and (7) >90%. The age of the utilisation was also estimated according to Croze (1974) as: (a) new (less than six months old): the wood scars at the point of breakage were still fresh, moist and yellowish in appearance or (b) old (greater than six months old): wood scars were dark and greyish in colour. Attempts were also made to determine the cause of the damage. The utilisation could be attributed to large mammalian herbivores, which were either classified as being elephants or other herbivores, environmental factors or an unknown agent. Finally the growth of the tree species in response to the utilisation was noted.

Elephant utilisation index calculation

The utilisation data were captured onto a spreadsheet programme and then run through a program written by Bruce Page (School of Biological & Conservation Sciences, University of KwaZulu-Natal, Durban). This program calculates the densities of utilised trees per tree species, per size class, for live and dead individuals separately. The following parameters were used for the analysis: the agent responsible for the utilisation was the elephant, all tree diameter size classes, both age classes of damage (greater than and less than 6 months old), the lowest index of damage was 1 (Appendix 4.2) and the type of utilisation was whole canopy removed, stem and branches broken and roots and bark removed.

All impact data for each tree species utilised per transect were combined to give a single elephant utilisation index of vegetation (density per hectare) for each transect. It was not intended to use the data collected on elephant utilisation of vegetation for a comprehensive analysis to quantify or discuss the ecological process of elephant herbivory in this study, but rather to calculate a single impact index to represent elephant utilisation on each transect to determine whether there is a relationship between level of elephant use, refugia production and invertebrate diversity. The impact index for the transects ranged from a minimum value of 0 density/hectare (no trees were impacted by elephants) to a maximum value of 1400 density/hectare.

Invertebrate sampling

Along each vegetation transect, within an area that ranged between 50m in length by 5m, 6m or 10m in width, elephant dung and logs that were considered to have been broken by elephants were quantified. The total area sampled was dependent on a minimum number of refugia identified, the density and thickness of the surrounding vegetation, with a smaller area sampled in the more dense vegetation stands. The designated area was actively sampled by one person, who turned over and broke open all the logs and elephant dung in the area in order to locate and collect specific invertebrates. The time spent sampling each individual log and dung pile was approximately three to five minutes or until the person sampling was satisfied that the refugia were adequately sampled. Invertebrates belonging to the six focal taxa (ants (Formicidae), centipedes (Chilopoda), millipedes (Diplopoda), scorpions (Scorpionida), spiders (Araneae) and termites (Isopoda)) were collected using the hand-to-jar technique.

Invertebrate Processing and Identification

Representative samples of invertebrates collected from logs and dung piles were kept in separate vials, labelled and preserved in 70% ethanol. Invertebrate samples were taken to the laboratory for identification. A WILD Heerbrugg (M5-93519) microscope was used to sort invertebrates to broad taxonomic groups and where possible identifications to lower levels were attempted for spiders using Dippenaar & Jocque (1997) and for millipedes and centipedes using Lawrence (1987).

Samples were sent to various specialist taxonomists for species identifications. Millipedes were identified by Dr M. Hamer (University of KwaZulu-Natal, Pietermaritzburg), centipedes by Dr M. Zapparoli (Universita della Tuscia, Italy), termites by Mrs V. M. Uys (Agricultural Research Council, Biosystematics Division, Pretoria), scorpions by Dr L. Prendini (American Museum of Natural History, New York, USA) and ants by Dr. H. D Robertson (South African Museum (SAM)). With the aid of a reference collection from Makalali Private Game Reserve, Miss C. Whitmore (University of KwaZulu-Natal) identified the spiders to morphospecies within families. Justification for identification to morphospecies level is given in Chapter 3. A reference collection for each taxon has been deposited in the appropriate institution. Centipedes, millipedes, scorpions and spiders are housed at the Natal Museum (Pietermaritzburg), termites were sent to the Agricultural Research Council National Insect Collection (Pretoria) and ants to the South African Museum (Cape Town).

The reference collections were used to develop descriptions for some species so that for further sampling sessions most specimens could be identified in the field. All millipedes and centipedes were identified if possible, counted, and only representative samples of individuals that could not be identified were collected. For the ant and termite samples, not all individuals could be counted and only presence or absence was recorded, but representative samples were taken for all termites and ants. All spiders and scorpions were collected.

Refuge sites versus non-refuge plots

During the last sampling session (January 2001) ten one meter square plots were laid out within each of the 34 elephant impact transects. The plots were randomly thrown along the vegetation transect line in areas where no logs or elephant dung were located. Two individuals actively searched the plots and all focal invertebrate groups were collected by the hand to jar method. The time spent sampling each plot was approximately two to three minutes or until the people sampling were satisfied that each plot was adequately sampled. Procedures for invertebrate processing, identification and storage are outlined above.

Calculation of diversity indices

The Shannon Index (H') was used to calculate species diversity (Wolda, 1981, Ludwig & Reynolds, 1988), which was calculated using the SPDIVER.BAS program of Ludwig & Reynolds (1988). The details pertaining to the calculation of the Shannon Index is outlined in Chapter 3.

Statistical analysis

The Statistical Package for Social Science (SPSS) (Norusis, 1994) was used for all data analyses. Data were checked for normality using the Kolmogorov-Smirnov test, and if normally distributed (Kolmogorov Smirnov test: $p > 0.05$), Analysis of Variance (ANOVA) was run to determine significant differences among independent variable classes for the relevant dependant variable. The t-test was run to determine pair-wise significant differences between groups. Data are represented as error bars, illustrating means and +/- 95% confidence intervals).

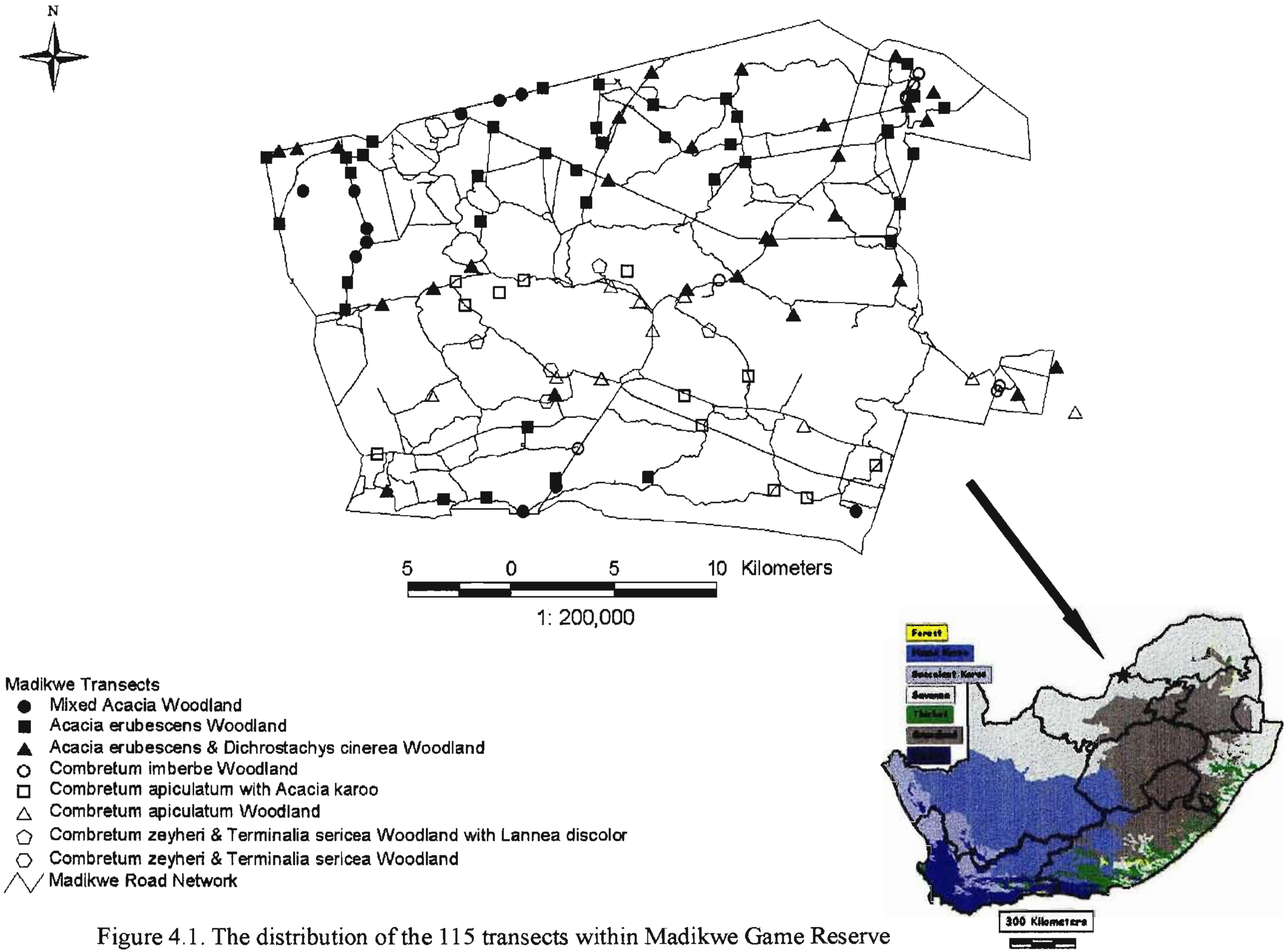


Figure 4.1. The distribution of the 115 transects within Madikwe Game Reserve

RESULTS

Elephant impact analysis

An elephant utilisation index value was calculated for each transect within the reserve. In all cases the assumption of the ANOVA were met (Kolmogorov-Smirnov test $P > 0.05$). The variation in elephant utilisation of vegetation for the two seasons and the proportion used across vegetation types is represented as error bar graphs (Figures 4.2a & 4.2b). There was no overall significant difference between elephant utilisation indices in different seasons (summer = wet & winter = dry) ($F_{1,114} = 1.803$, $P = 0.182$) (Figure 4.2a).

There was an overall significant difference in the elephant utilisation index among vegetation types ($F_{6,114} = 2.475$, $P = 0.02$) (Figure 4.2b). Significant difference of impact was noted between the *Combretum imberbe* woodland (CIW) and Mixed *Acacia* woodland (MAW), *Acacia erubescens* woodland (AEW) and *Acacia erubescens* and *Dichrostachys cinerea* woodland (AED) (t-test: $P = 0.006$, $P = 0.041$, $P = 0.041$ respectively) (Figure 4.2b). There is a clear distinction in the utilisation by elephants of the *Combretum* woodland and *Acacia* woodland, with the *Acacia* veld type being more heavily used than the *Combretum* woodlands.

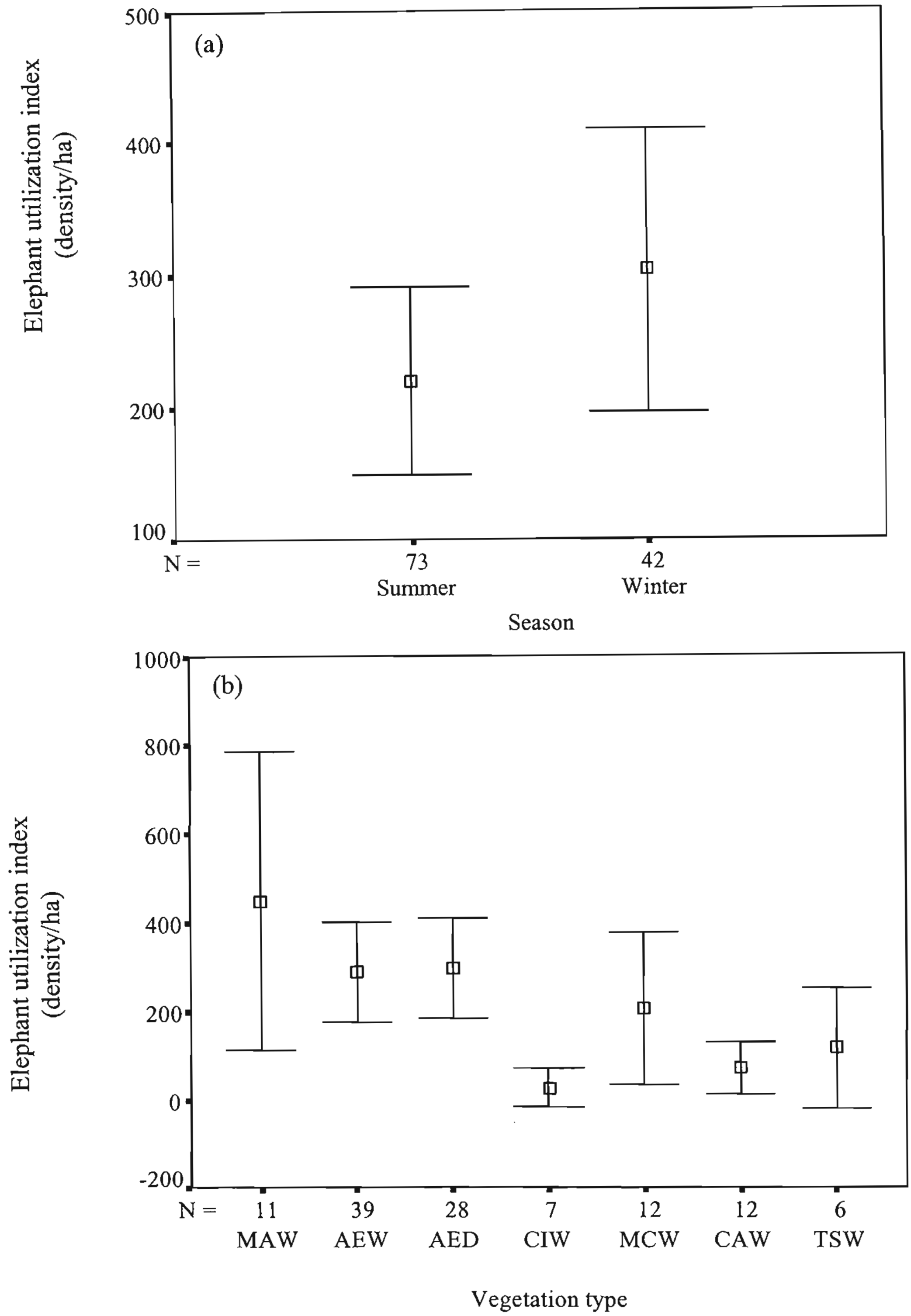


Figure 4.2. The effect of (a) season and (b) vegetation type on the elephant utilisation index in Madikwe Game Reserve. Data are illustrated by means and +/- 95% confidence levels. Vegetation type codes are as follows, Mixed *Acacia* woodland (MAW), *Acacia erubescens* woodland (AEW), *Acacia erubescens* and *Dichrostachys cinerea* woodland (AED), *Combretum imberbe* woodland (CIW), Mixed *Combretum* woodland (MCW), *Combretum apiculatum* woodland (CAW) and *Terminalia sericea* woodland (TSW). Detailed descriptions of the vegetation type codes are given in Appendix 4.1. N = the number of samples used in the analysis.

Refugia production

A total of 499 individual refugia components comprising 274 logs and 225 dung piles were sampled in the 115 transects. In all cases the assumption of the ANOVA were met (Kolmogorov-Smirnov test $P > 0.05$). There was no overall significant difference between the vegetation types for refugia production. The production of refugia by elephants was significantly higher in winter than in summer for the combined types of refugia (logs and dung) ($F_{1,114} = 26.552$, $P = 0.00$) and the pattern was the same for the individual refugia components (logs $F_{1,114} = 26.123$, $P = 0.00$; dung piles $F_{1,114} = 6.236$, $P = 0.01$) (Figure 4.3).

The prediction that with increasing elephant utilisation there would be an increase in the number of refugia produced was tested. The unstandardised residuals from a univariate analysis between vegetation types and total number of refugia was determined to remove the effect of habitat. These residuals were used as dependant variables to test the effect of elephant utilisation index and the individual refugia components (Figure 4.4). There was no relationship between elephant utilisation and the number of refugia produced for logs and dung combined. The individual refugia components also showed no relationship with respect to elephant utilisation.

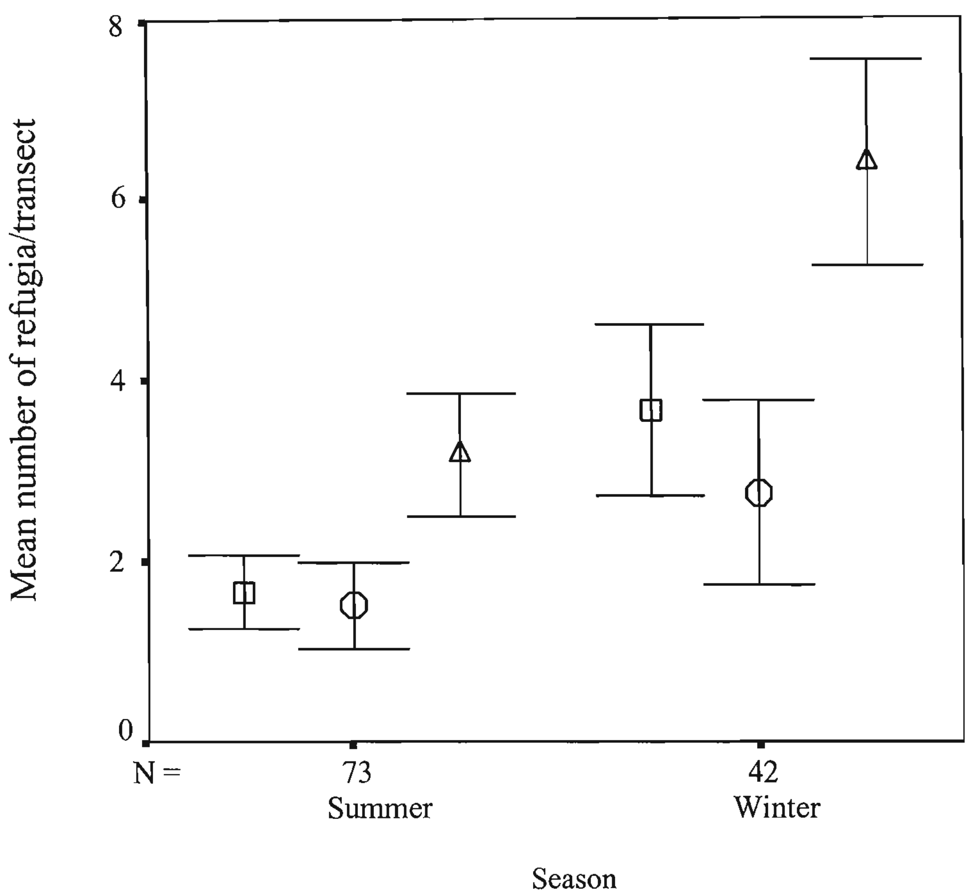


Figure 4.3. The effect of season on the mean number of refugia per transect, illustrated as combined refugia (log and dung) (Δ) and the individual number of logs (□) and dung (○). Data are illustrated by means and +/- 95% confidence levels. N = the number of transects sampled.

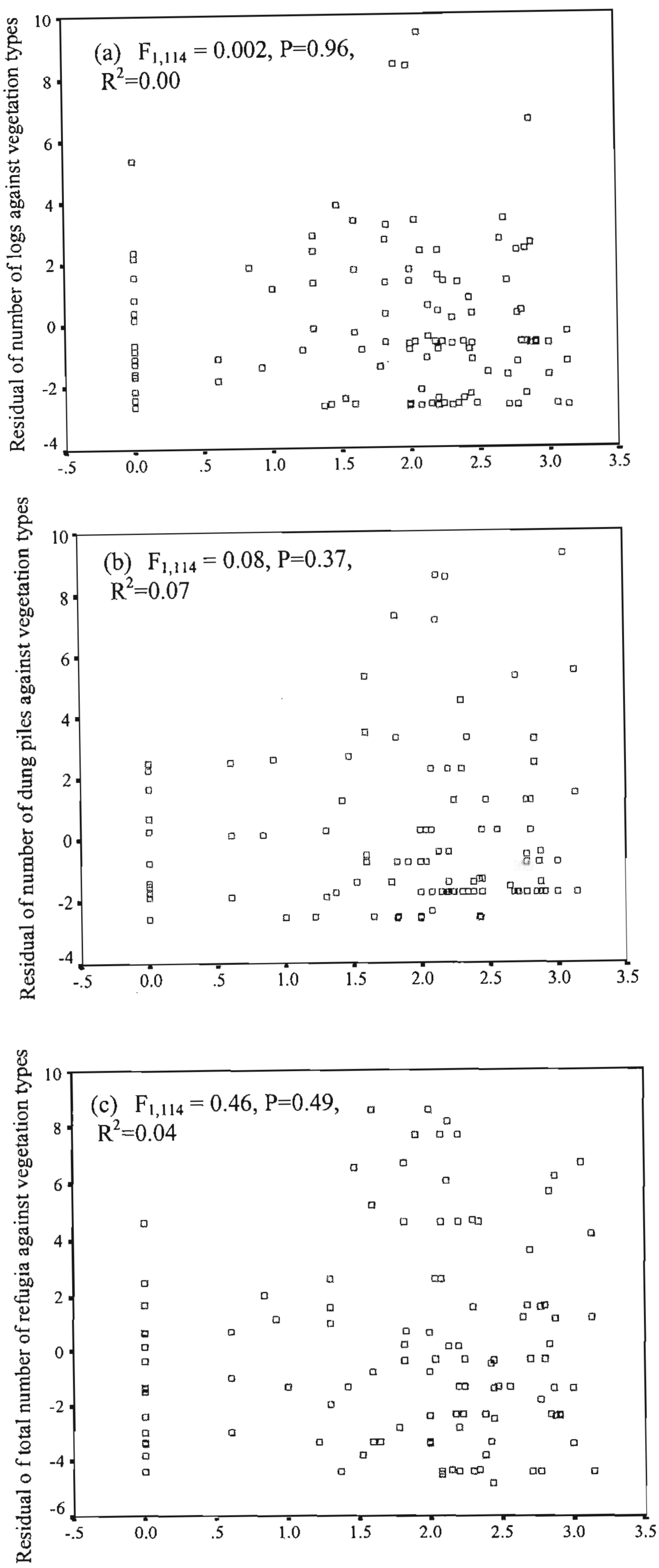


Figure 4.4. The effect of elephant utilisation on the number of (a) logs, (b) dung piles and (c) total number of refugia (both logs and dung combined). The effect of different vegetation types on the number of refugia produced is factored out by calculating the residuals (difference between observed and expected values) between the two variables.

The unstandardized residuals of the regression between elephant utilisation and number of refugia produced (logs and dung combined) were tested for seasonal (temporal) and vegetation (spatial) differences. This analysis was also performed separately for logs and for dung refugia. There was a significant effect of season on refugia (measured as the unstandardized residuals of the regression of elephant utilisation) and for the two refugia types combined ($F_{1,114} = 24.511$, $P = 0.019$) and the individual refugia components (logs $F_{1,114} = 15.945$, $P = 0.00$, dung $F_{1,114} = 5.628$, $P = 0.00$) (Figure 4.5), there was significantly higher production of refugia during the winter than in summer.

Invertebrate diversity

A total of 456 individuals from four classes (Arachnida, Chilopoda, Diplopoda and Insecta) and ten orders (Araneae, Scorpiones, Geophilomorpha, Lithobiomorpha, Scolopendromorpha, Spirostreptida, Sphaerotheriida, Polydesmida, Hymenoptera and Isoptera) were collected from under refugia. The order Araneae made up 24%, Hymenoptera 30%, Isoptera 27% and Scorpiones > 1% of the total, whilst the classes Diplopoda and Chilopoda made up 11% & 7% respectively (Figure 4.6). Data are presented as total number of individuals from all transects, refuge substrates and vegetation types combined, for the respective order or class. Only one family each was collected from the orders Hymenoptera, Isoptera and Scorpiones. Eighteen families were collected from the order Araneae, whilst the Diplopoda and Chilopoda had four and two families respectively. A list of species from the focal taxa collected from Madikwe Game Reserve is presented in Appendix 4.3.

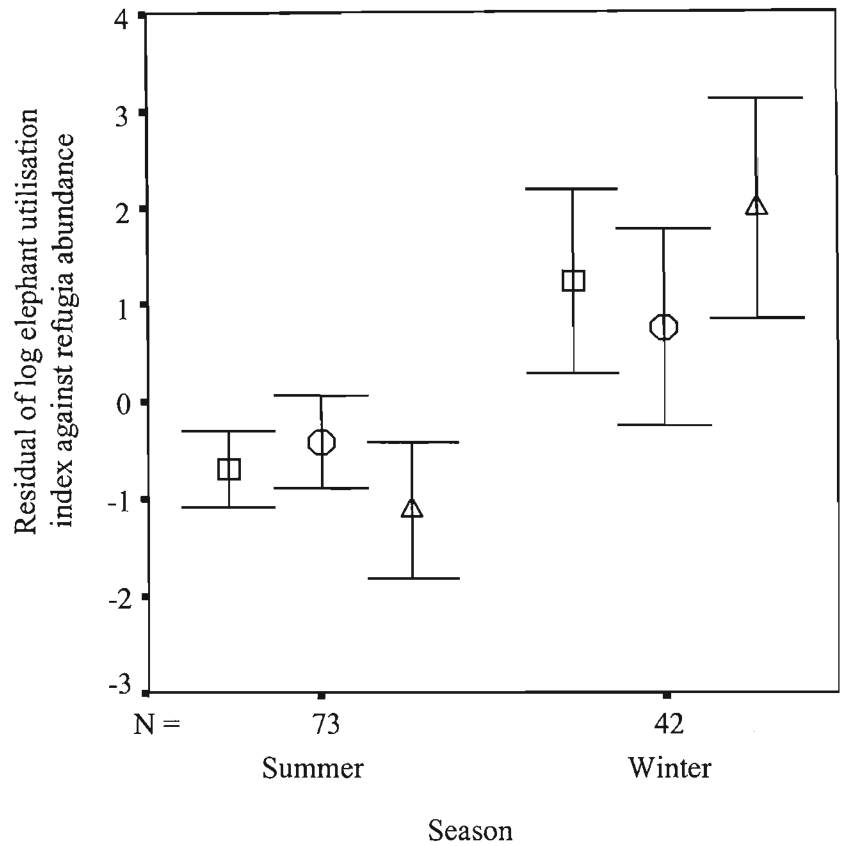


Figure 4.5. The effect of season on the refugia production (measured as the unstandardized residual from the regression between elephant utilisation and the individual components logs (□), dung (○) and total refugia produced (△)). Data are illustrated by means and +/- 95% confidence intervals. N = the number of samples in the analysis

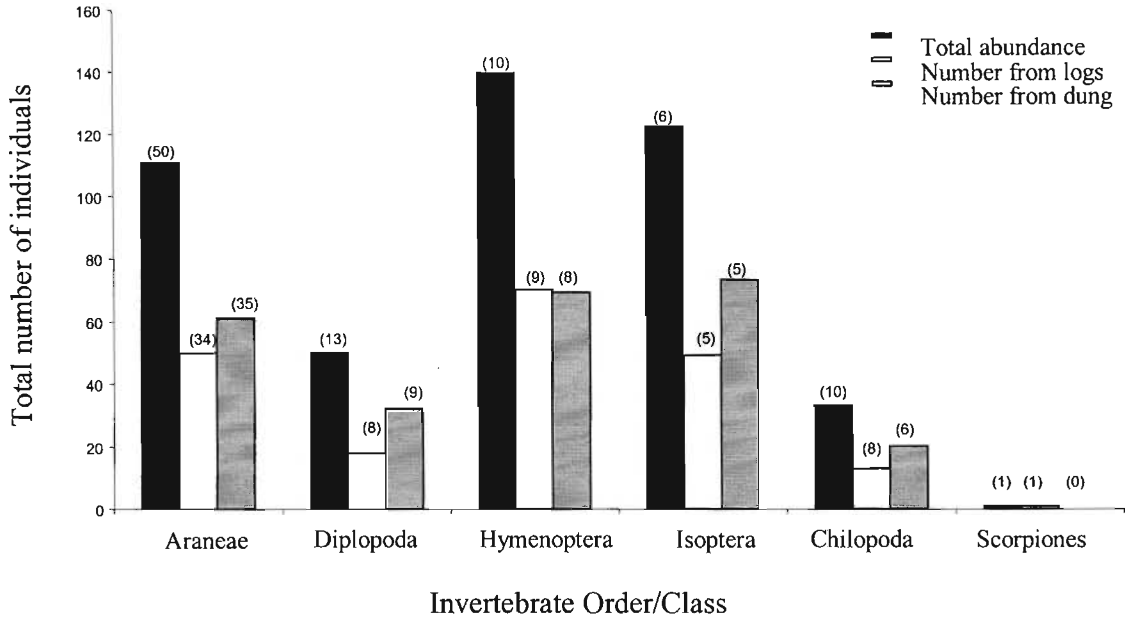


Figure 4.6. Number of invertebrate individuals collected from all transects and vegetation communities, for both types of refugia combined and for the individual components (logs and dung). The height of the bar denotes the abundance and the number of species is given in parentheses.

Refugia effect on invertebrates

The total abundance, species richness and diversity of invertebrates collected under the two types of refugia combined were tested for seasonal and vegetation differences.

There were significant differences between seasons for total abundance (ANOVA: $F_{1,114} = 9.402$, $P = 0.003$), species richness (ANOVA: $F_{1,114} = 19.770$, $P = 0.00$) and species diversity (ANOVA: $F_{1,114} = 22.658$, $P = 0.00$) (Figure 4.7), with more invertebrates sampled in summer than winter.

To determine the effect of elephant utilisation of vegetation on invertebrate abundance, species richness and diversity, the effect that vegetation types may have on abundance, richness and diversity of invertebrates was removed. There was no relationship between invertebrate species richness, diversity and abundance, (expressed as the unstandardized residuals of the regression between vegetation type and invertebrate abundance, richness and diversity) and elephant utilisation (Figure 4.8). The invertebrate species sampled at sites where elephant utilisation index was zero suggests that these logs were on the ground as a result of some other agent (fire or the natural senescence of the tree).

Refugia sites versus non-refugia plots

A total of 154 invertebrate individuals from two classes (Arachnida and Insecta) and two orders (Araneae and Hymenoptera) were collected from the additional plots without refugia. In comparison, 125 invertebrate individuals distributed among four classes (Arachnida, Chilopoda, Diplopoda and Insecta) and seven orders (Araneae, Geophilomorpha, Lithobiomorpha, Scolopendromorpha, Spirostreptida, Hymenoptera and Isoptera) were collected from under refugia sites (logs and dung) along the same transect lines (Figure 4.9). Only one family each was collected from the orders Hymenoptera and Isoptera. Nine families were collected from the order Araneae, three families from the class Diplopoda and two families from the class Chilopoda. Although the total abundance of invertebrates combined was slightly higher in the plots without refugia, greater species and family level richness was recorded from under the refugia. Exception was noted in the Araneae where four more species and in the Hymenoptera where five more ant species were recorded at sites without refugia (Figure 4.9).

The data for invertebrate abundance, species richness and diversity for the refuge sites and the additional plots (without refugia) were normally distributed (Kolmogorov - Smirnov test: $P > 0.05$). There was no significant difference between the abundance and diversity of invertebrates collected from under the refuge sites and sites without refugia. However there was a significant difference in the species richness ($F_{1,67} = 4.266$, $P < 0.043$) between the two sampling sites, with higher invertebrate species richness at sites with refugia (40 species) than those without refugia (30 species) (Figure 4.10).

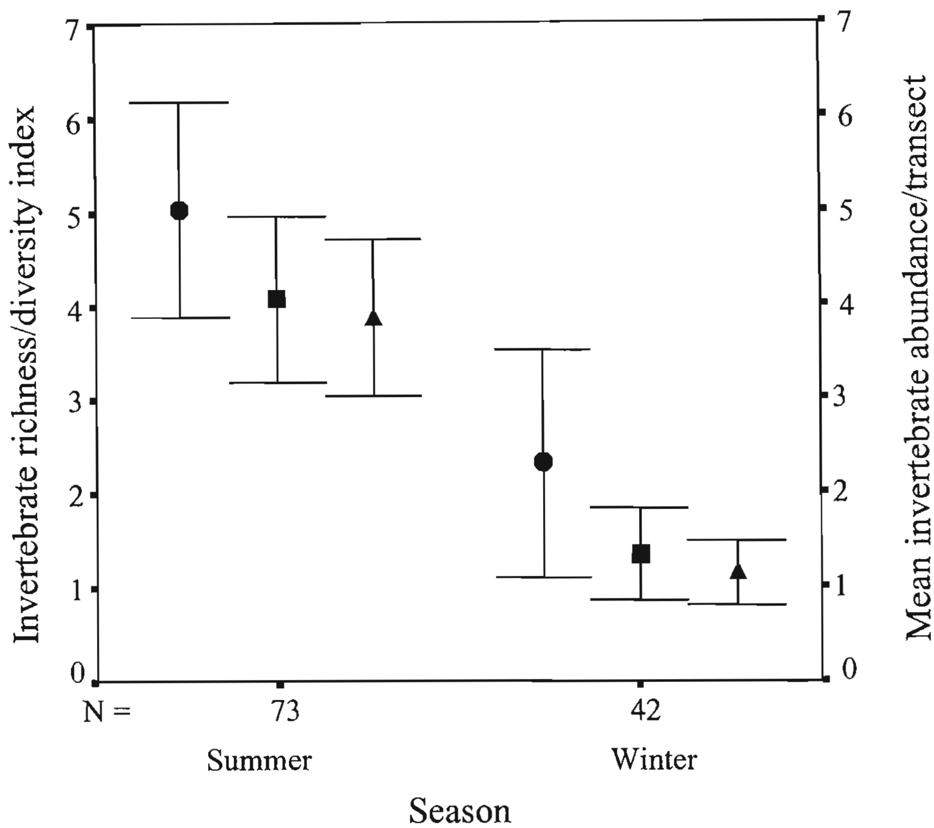


Figure 4.7. The effect of season on invertebrate abundance (mean number of individuals/transect) (●), species richness (■) and diversity (▲) under the two types of refugia (log and dung) for all transects, irrespective of vegetation type. Data are illustrated by means and +/- 95% confidence intervals. N = the number of transects sampled for the analysis.

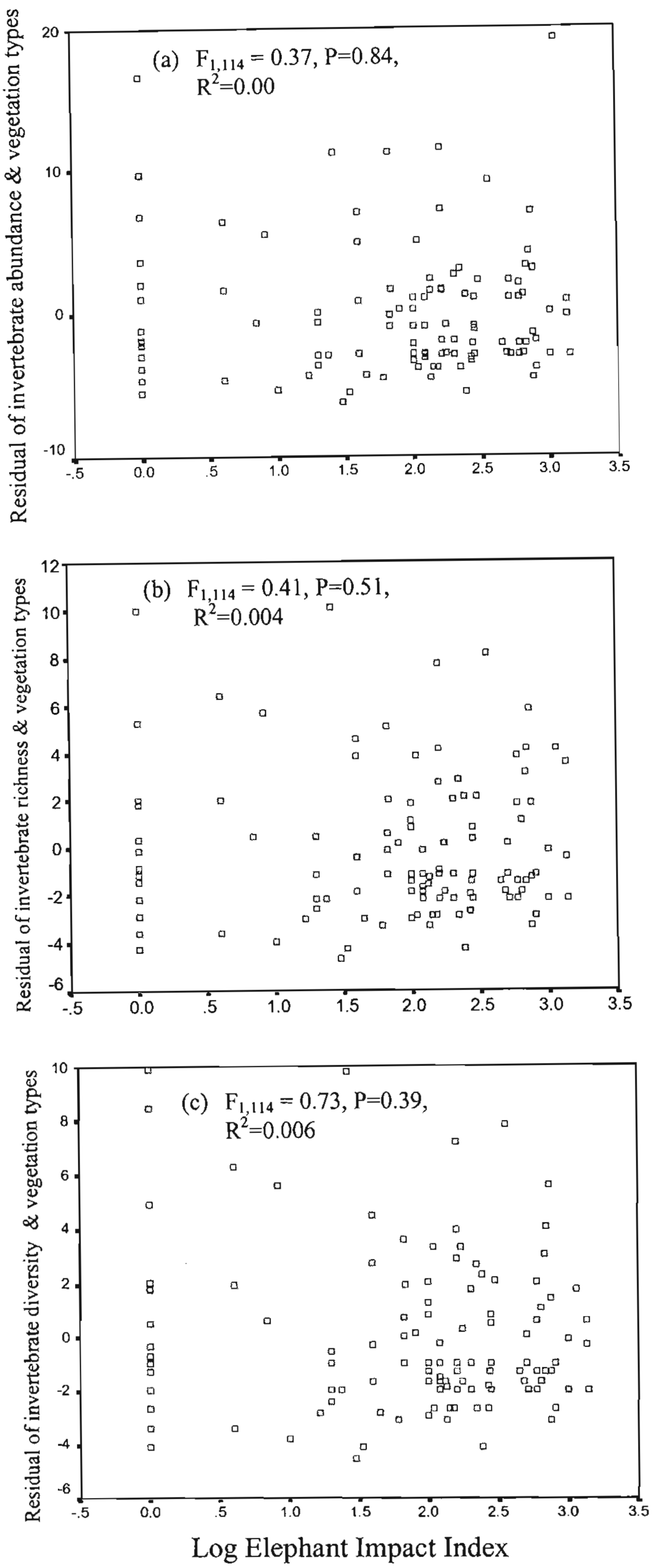


Figure 4.8. Relationship between invertebrate (a) abundance, (b) richness and (c) diversity and log of elephant index. The effect of vegetation type is factored out by calculating the residuals (difference between observed and expected values) of vegetation types and invertebrate abundance, richness and diversity.

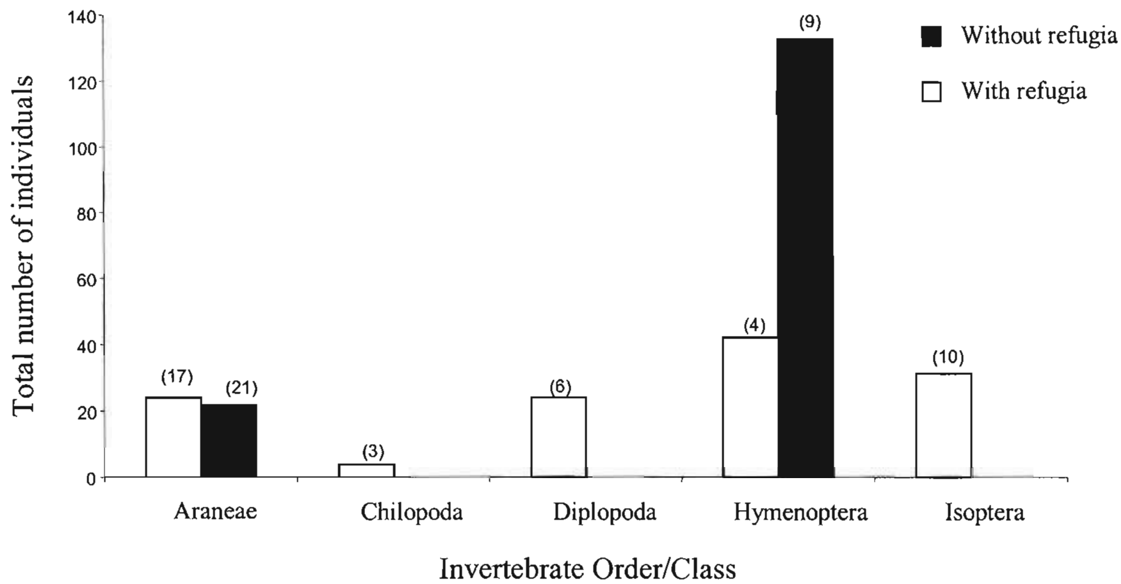


Figure 4.9. Taxonomic distribution of the total number of invertebrates collected from all plots with refugia and plots without refugia, from 34 transects, irrespective of vegetation type. The height of the bar denotes the abundance and the number of species is given in parentheses.

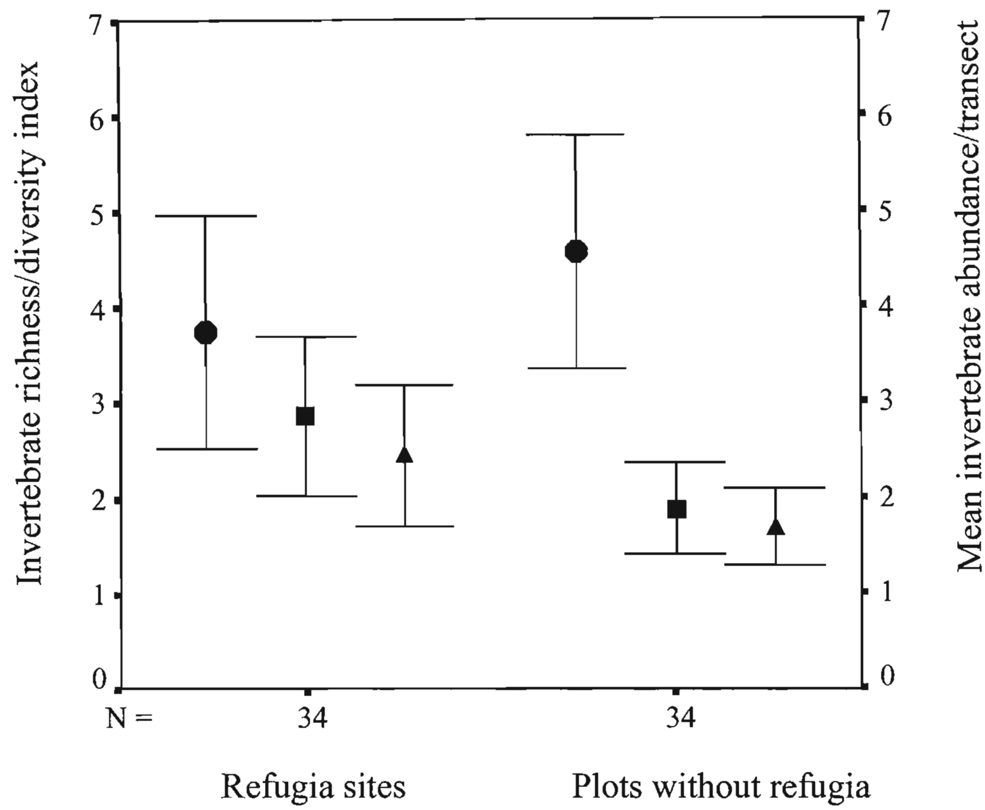


Figure 4.10. The effect of refugia on invertebrate abundance (●), species richness (■) and diversity (▲) sampled from 34 transects, irrespective of vegetation types. Data are illustrated by means and +/- 95 % confidence intervals. N = the number of transects sampled for the analysis.

DISCUSSION

Since the re-introduction of elephants into Madikwe, the population has been steadily increasing (Hofmeyr, 1997). Due to the small size of the park and the fact that a fence delimits its boundaries, the elephant population of Madikwe cannot self-regulate their numbers. It is envisioned that at some stage management will have to intervene and control elephant numbers. The high profile of elephants within the international community, and their importance for ecotourism in national parks and reserves, means that any management strategy for population control will have to be transparent and be able to stand up to careful scrutiny. Therefore any management action should be supported by sound scientific data and principles, hence understanding the impacts of elephants on biodiversity as a whole and not just a few species is crucial.

Results obtained from this study did not support the hypothesis of increasing refugia production and higher ground-dwelling invertebrate diversity with increasing elephant disturbances. However the results from the study clearly demonstrated that elephant disturbance (utilisation of vegetation), refugia production (logs and dung piles) and invertebrate diversity utilising the refugia as an additional habitat resource did vary temporally and spatially across the reserve.

The temporal variation of impact by elephants on biodiversity is influenced by the season. This is linked to habitat selection by elephants in response to seasonal changes, which has been documented elsewhere in Africa (Ben-Shahar, 1993, Lewis, 1986, Barnes, 1982, Short, 1983). The diet of elephants in African savanna systems is dominated by grasses, which often comprise approximately 60% of vegetation, in comparison to the diet of elephants inhabiting rain forests, where fruits are an important resource (White, Tutin & Fernandez, 1993). In wooded savannas grasses are generally equally important as woody material in the wet season but elephants have been shown to display seasonal dietary preference by utilising more woody vegetation in the winter months (dry season) than in the summer months (wet season) (Hiscocks, 1999, Ben-Shahar, 1993, Barnes, 1982). Although this seasonal shift in their feeding patterns was not significant in this study, the refugia production as a result of their impact on vegetation did vary seasonally, with a significantly higher proportion of logs being generated in winter than in the summer months. The palatability, nutritional value and availability of grasses are much higher in summer than in winter (Barnes, 1982, De Boer, Ntumi, Correia & Mafuca, 2000), therefore the diet of elephants reflects the availability of green and nutrient rich grasses within their habitat in summer. This seasonal use of habitat is an important mechanism of survival and optimum utilisation of resources available. The higher facilitation of logs in winter as a result of the seasonal shift in elephant diet suggests that the impact on invertebrate diversity would also vary seasonally.

The results from the study demonstrated that invertebrate populations are also influenced by seasonal patterns with higher invertebrate abundance, species diversity and richness in summer (January/February sampling) than in winter (June/July sampling). This is despite the fact that refugia were more abundant in winter, and that dry, cold environmental conditions in winter should mean that invertebrates are less active and more dependant on refugia than in the wet, warm season. The reasons for the higher invertebrate richness, diversity and abundance in summer may simply be because there are more species and individuals. Such seasonal changes in invertebrate abundance have been confirmed by other studies (Goge, 2000, Koen & Crowe, 1987). In savanna environments, millipedes are more active in summer during the rainy season than in winter (Lawrence, 1984, Dangerfield & Telford, 1991). The activity patterns of scorpions are closely related to environmental factors such as temperature, humidity and wind. When conditions are favourable, usually with the first rains of the summer months, hundreds of scorpions may emerge (Leeming, 2003). Seasonal variation among spiders was also noted by Dippenaar-Schoemann, van der Berg and van der Berg (1989) who recorded higher abundance of spiders during the summer months when temperatures and rainfall were higher. Similar results were also observed for ground-dwelling spiders by Russell-Smith (1981).

The production of refugia and invertebrate diversity, abundance and richness did not vary spatially across the reserve. However, the utilisation of vegetation by elephants did vary spatially. The higher indices of impact within the *Acacia* veld than in the *Combretum* veld is characteristic of the difference in the nutrient quality between the two vegetation communities, with higher nutrient content recorded from fine leafed *Acacia* woodlands than broad leafed *Combretum* woodland (Scholes & Walker, 1993, Scholes, Scholes, Otter, & Woghiren, 2003). The vegetation type may also influence the production of refugia, and may explain the lack of a relationship between elephant use index and density of refugia. Although data do not exist, it is possible that feeding patterns (stripping, browsing, breaking branches) are influenced by tree species and fewer or more logs are produced in certain vegetation types. This requires further investigation.

Many species have been referred to as keystone species, and the African elephant is classified as a keystone herbivore because the foraging strategy of this species often causes drastic habitat modifications (Simberloff, 1998, Mills, *et al.,* 1993). These changes are usually characterised as being destructive or detrimental to the landscape rather than being regarded as a benefit that provides additional and valuable resources to smaller organisms in the ecosystem. Trees that are pushed over or branches that are broken by elephants provide a source of cover and suitable habitats for continued existence of invertebrates and other ground-dwelling species (Gadd, 1997, Keesing, 1998, Whyte, *et al.*, 1999).

Results from this study showed that more invertebrate individuals were collected from plots without refugia than from plots with refugia. However, the abundance of a single group, ants, which dominated the collection in the plots without refugia, was responsible for the skewed results with respect to invertebrate numbers. Significantly more invertebrate species were collected from under refugia, hence species richness and diversity were much greater under logs and dung than in plots without refugia, and more unique species that require specific habitat (centipedes and millipedes) were found associated with the refugia.

Organisms inhabiting dead wood are becoming increasingly threatened (Speight, 1989). However it is only recently that these organisms have been gaining attention and recognition as organisms deemed worthy of saving (Grove & Stork, 1999, Berg, Gustatsson, Hollingback, Jonsell, & Wesier, 1995). A widely recommended method to enhance the diversity of saproxylic species in managed forests is to leave a certain amount of decaying wood associated with cuttings (Martikainen, Sitonen, Punttila & Rauh, 2000, Marra & Edmond, 1998). In savanna biomes increasing the number of decaying wood sites can be achieved through disturbances brought about by elephant utilisation of vegetation and hence an increase in the available habitat for saproxylic organisms.

Logs and dung are used by many species of vertebrate and invertebrates as cover (salamanders and bears), foraging sites (termites) and sites for attracting mates (Martikainen, *et al.*, 2000). Some species use the spaces in between the bark and wood (snakes) and others occur in spaces under the log (millipedes and centipedes). The availability of logs is important not only for providing additional habitats for invertebrates but dying, dead and fallen trees also provide nursery sites for germination and subsequent growth of plants, and they store nutrients that can be further cycled through the system (McComb & Lindenmayer, 1999).

While the importance of undisturbed habitats for particular invertebrate species is clear, this work has shown that disturbed habitats do have a part to play in providing a rich mosaic of microhabitats suitable for numerous ground-dwelling invertebrates. Although no clear link emerged between increasing disturbance by elephants and abundance of refugia, the importance of the disturbance (utilisation) by elephants as a facilitative process in providing logs and dung as an additional habitat refuge for many specialised ground-dwelling invertebrate taxa was demonstrated. In order to fully understand the specific role that elephants play in the production of additional refugia as microhabitats for ground-dwelling invertebrates, an examination of the refuge abundance and associated species diversity before and after elephant introduction to a site would be ideal.

CHAPTER 5

THE EFECT OF REFUGIA (LOGS AND ELEPHANT DUNG) ON GROUND DWELLING INVERTEBRATE DIVERSITY AT MAKALALI PRIVATE GAME RESERVE

INTRODUCTION

During the last three decades few mammals have received as much attention from biologists as the African elephant. In the 1960's and 1970's the debate centred on localised overpopulation and the effect of this on ecosystems within national parks (Douglas-Hamilton, 1973, Barnes, 1983). In the 1980's and 1990's it was the increased poaching activities and the ivory trade that stirred debate (Parker & Graham, 1989) and in the 21st century the debate returned to rapidly increasing elephant population numbers in protected areas, but this time with the added controversies over methods of population reduction, namely culling, and the need to conserve biodiversity rather than the protection of a single species. However, the impact of elephants on biodiversity is poorly known.

Elephants are a major component of the savanna ecosystem (Guy, 1981, Barnes, 1983, Lewis, 1986, Jachmann & Croes, 1991, Tchamba, 1995) and it has been continually stressed that they are an important species for ecotourism in Africa (Hachileka, 2003). Given their high international profile, and the importance of tourists (international and local) to the funding of conservation parks and the tourism industry in South Africa, management strategy with respect to these animals will have to stand up to careful scrutiny.

In the last decade many protected elephant populations in South Africa have shown signs of continual increase due to unchecked natural population growth (Whyte, 2004). Currently, elephant management strategies are based on the perception that elephants have a negative impact on the environment in which they live (Cumming, *et al.,* 1997) and according to this principle their impact could be detrimental to the long-term conservation of the environment (Cumming, *et al.,* 1997, Whyte, *et al.*, 1999). This poses a dilemma for conservation agencies that wish to maintain habitat and species diversity and are therefore compelled to reduce the impact of elephants in order to abide by their mission statements of maintaining and conserving biodiversity and environmental integrity (Braack, 1997, Christensen, 1997).

Unfortunately much of the research that influences policy makers is based on the effect that elephants have on vegetation (Barnes, 1985, Ben-Shahar, 1993, Barnes, *et al.*, 1994). Elephants do damage trees, but this may be part of the natural processes, and may actually increase the vigour of the environment. Few studies have shown the short-term effects of elephants on biodiversity (Dublin, *et al.*, 1990), although Cumming, *et al.* (1997) does illustrate the negative impact that elephants have on biodiversity (which includes fauna and not only flora) of the environment in the long-term.

Elephants should be viewed as a keystone species and consumer of woody vegetation in the savanna ecosystem by virtue of how they change the physical structure of the environment they inhabit (Simberloff, 1998). Through the process of competition and facilitation, this keystone modifier of the ecosystem can both positively and negatively influence biodiversity of an area. Facilitation by elephants can take place through addition of dung and logs, which can provide a food source (Cole, 1977, Scholtz & Holm, 1985, Deshmukh, 1989) or possible refuge sites for ground-dwelling invertebrates. The impacts of elephant feeding behaviour cannot be assessed or managed without considering the impacts on all components of biodiversity, or in isolation from the potential positive contribution to biodiversity.

Ground-dwelling invertebrate species composition, diversity, species richness and abundance have been found to differ in different vegetation types in Makalali Game Reserve (Druce, 2000, Whitmore, 2000). In order to encompass this variation in the study, the experiment was replicated within three vegetation types in the reserve. This has implications for developing an understanding of spatial distribution of the impact of elephants on ground-dwelling invertebrates, and for any effort to quantify the impacts at a landscape scale.

The overall aim of this part of the study was to determine the importance of refugia (logs and dung) generated by elephants as an additional habitat refuge for selected ground-dwelling invertebrates. The objectives of this part of the study were:

1. To identify the ground-dwelling invertebrate community associated with refugia;
2. To determine the impact of refugia (logs and dung) on the diversity, species richness and abundance of ground-dwelling invertebrates;
3. To determine whether invertebrate diversity, species richness and abundance associated with refugia differ according to vegetation type and

4. To compare invertebrate community structure in different vegetation types and different types of refugia (logs vs dung).

The hypotheses investigated in this chapter were:

1. The presence of refugia (logs and elephant dung) increases ground-dwelling invertebrate abundance, diversity and species richness;
2. Invertebrate diversity, species richness and abundance associated with refugia will differ in each of three vegetation types, with the more heterogeneous habitats having higher species richness, abundance and diversity; and
3. The type of refuge (logs or dung) will have an effect on invertebrate communities, with logs being inhabited by a different community to that inhabiting dung, and the invertebrate community associated with logs in different vegetation types more similar than the communities from logs and dung in the same vegetation type.

The null hypothesis states that there would be no difference in invertebrate abundance, diversity and species richness in sites with and without refugia and across the three vegetation types, and that there will be no difference in the communities associated with logs and dung. The hypotheses were tested by comparing plots with refugia added to plots from which refugia had been cleared.

METHOD AND MATERIALS

The experiment was set up in the Makalali Private Game Reserve in the Limpopo Province, South Africa in July 2000. Data were collected in November 2000 and February 2001.

Experimental set up of refugia

Dung

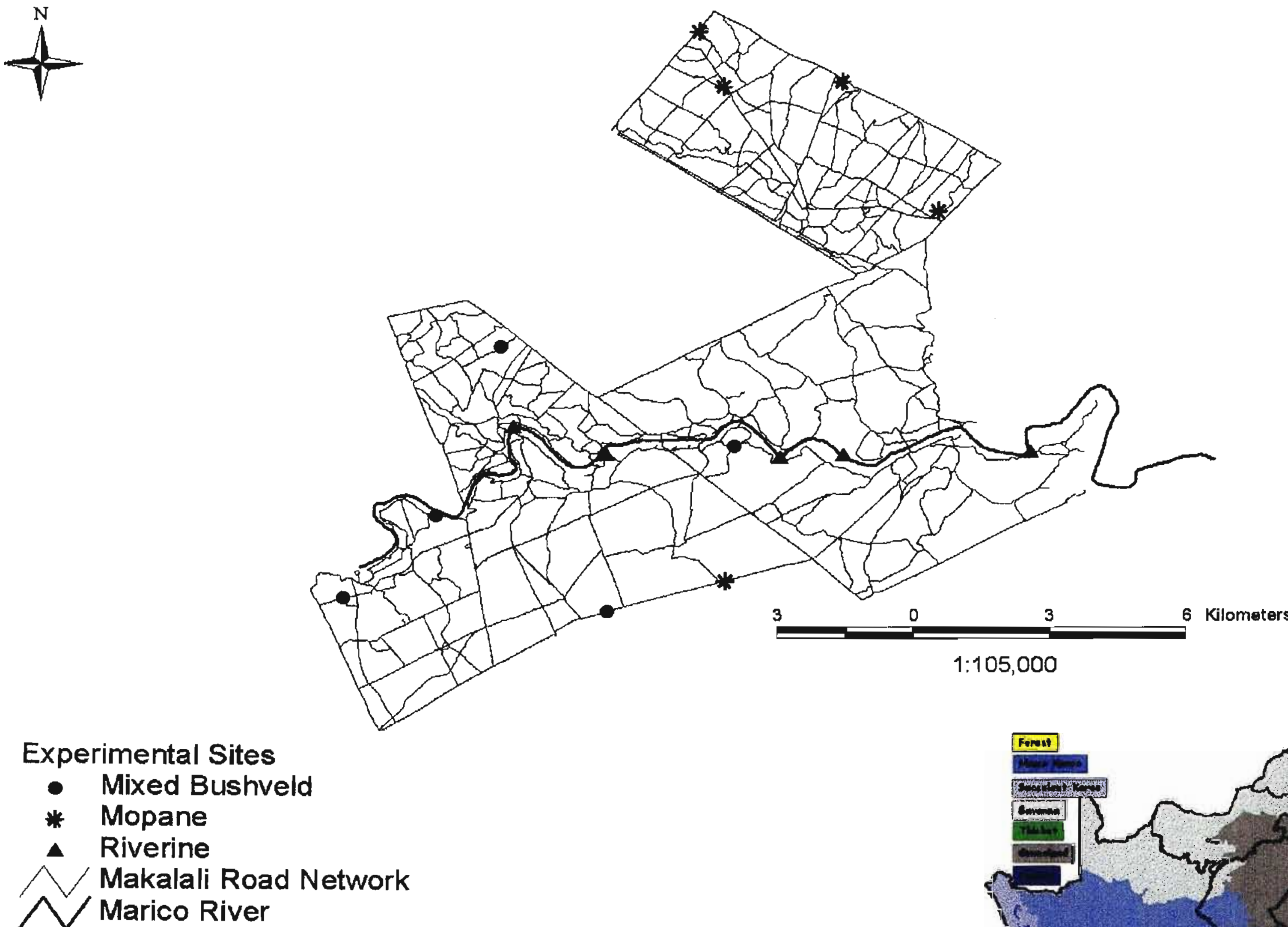
Fresh elephant dung was required for this experiment. The use of freshly deposited dung ensured that prior to the experimental set up no invertebrates, apart from dung beetles and flies (which were excluded from the analysis for this chapter) were present in the dung. Collection of the dung involved locating the elephants within the reserve, following and recording their movements for an extended period of time (usually early morning till mid afternoon). This provided an approximate position where freshly deposited elephant dung could be located. Once the elephants had moved away from the area, and it was safe to enter on foot, freshly deposited dung (approximately less than six hours old) was located and collected. The dung was stored in plastic bags for not longer than three hours.

Five sites were selected in three habitat types, which gave a total of 15 sampling sites throughout the reserve (Figure 5.1). The three habitat types selected were mixed bushveld, riverine and mopane woodland. Using two 50m measuring tapes, 20m x 20m plots were measured out at each of the three vegetation types. Metal pegs were used to mark the corners of each plot. To enable the relocation of the plots, the GPS location of each plot and each peg was recorded and a description of each plot location and the orientation of the plots were noted. Nine dung piles were placed in each of the plots, resulting in a total of 45 dung piles distributed among five plots each within three vegetation types, providing a total of 135 experimental dung piles.

Logs

Twelve *Combretum apiculatum* trees were cut down in various areas of the reserve. The trees were cut into 90 logs of approximately the same length of 50cm and a minimum diameter of 10cm. This tree species was selected because results obtained from Druce (2000), indicated that five tree species, *Sclerocarya birrea*, *Albizia harveyi*, *Colophospermum mopane*, *Combretum hereroense* and *Combretum apiculatum* were the most common tree species consumed by elephants in the reserve. Four of the five tree species were not commonly found in the reserve. *C. apiculatum* provided an ideal test log species because this tree was consumed by the elephants and it was extremely abundant in the reserve.

Five sites were selected in two habitat types, which resulted in a total of 10 sampling sites throughout the reserve (Figure 5.1). The two habitat types selected were mixed bushveld and riverine woodland. The third vegetation type (mopane) was not used as an experimental site for logs because *C. apiculatum* is not naturally found in this vegetation community. Placement of logs at these sites would not simulate the natural dynamics within the environment. Nine logs were placed in each of the plots, resulting in a total of 45 logs distributed among five plots, within two habitat types, providing a total of 90 experimental logs.



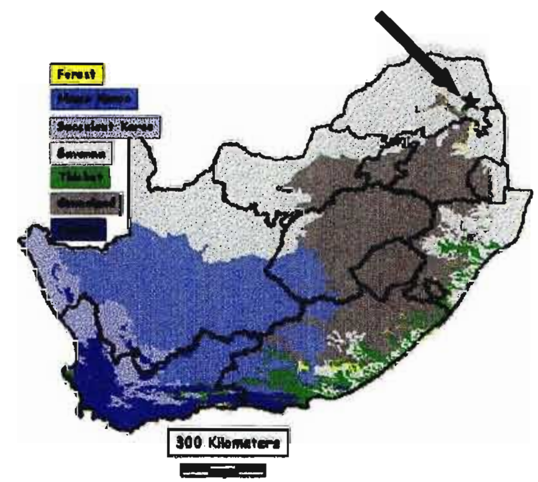


Figure 5.1. Distribution of the experimental sites within Makaklali Private Game Reserve. The log sites were only placed within the mixed bushveld and riverine vegetation type and the dung sites were within all three vegetation types.

Dung and Log placement

Within each 20m x 20m plot logs or elephant dung were placed in a 3 X 3 grid system (Figure 5.2). The refugia were placed 1m away from the boundary of the plot and each refuge was 9m away from the other. In order to standardise the area of the experimental dung pile, each dung pile was loosely packed into a wooden frame with an area of 30cm x 30cm and a height of 10cm.

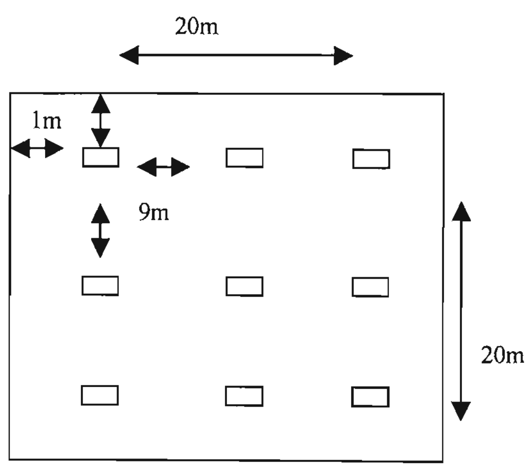


Figure 5.2. The position of the refugia within the 20m x 20m experimental plot.

Control sites

Control plots were also set up in June 2000. These plots were set up in exactly the same manner as the log and dung plots, but all logs and elephant dung piles were completely cleared by hand from within the plots. There were 15 control sites in each of the three vegetation types giving a total of 45 sites that were laid approximately 10m away from each experimental plot.

Invertebrate sampling strategy

Sampling for invertebrates was carried out in two sessions (November 2000 & February 2001). Due to the rate of decomposition of the dung and the potential loss of refugia by the end of the experiment, the number of experimental logs and dung piles that were sampled differed during the two sessions. This was also done to maximise the number of invertebrates sampled. In November 2000 (four months after experimental set up), six of the nine logs and elephant dung piles at each plot were sampled. In February 2001 (seven months after experimental set up), where possible all nine logs and elephant dung piles at each plot were sampled.

Sampling was conducted by placing a wooden frame (0.5m x 0.5m x 0.1m) over the log or dung pile being sampled. The area contained within the wooden frame was searched and invertebrates from the six focal groups (Chapter 3) were collected from under the experimental refuge. The log or dung was then placed back in its original position. The area around the dung or log and within the frame was also searched. This involved turning over all litter material, rocks and branches that were within frame. All samples were collected by the hand to jar method and were processed and stored as outlined in Chapter 4. Each plot was searched until the designated area had been satisfactorily sampled. The average time spent sampling each plot ranged between 20 and 30 minutes. During the first sampling session (November 2000) all individuals that looked different were collected for identification by the relevant taxonomists (Chapter 4). In February 2001 only representatives of taxa that had not been previously sampled or for which identification was uncertain were collected. Abundance was recorded for all species. This was done to reduce the impact that this project may have on the diversity and abundance of specific organisms within the area.

The control plots were sampled by placing the wooden frame in approximately the same nine locations used for the log and dung experimental plots (Figure 5.2). These positions were selected by pacing out one meter from the boundary of the plot and sampling and then pacing out another nine meters and then laying down the frame and sampling. Sampling involved turning over all litter material and rocks in the wooden frame, and collecting and recording target invertebrate in the same way as in the log and dung plots. To make certain that only ground-dwelling or bark-dwelling spiders and not aerial spiders were sampled, a height restriction of 50cm above the ground was placed on the search.

Statistical analysis

The species diversity and species richness indices for the six invertebrate taxa were calculated using the SPDIVER.BAS program of Ludwig & Reynolds (1988).

The statistical programme SPSS (Norusis 1994) was used for data analyses. The normality of data distribution was checked by performing a Kolmogorov-Smirnov goodness of fit test. If data were normally distributed, a two way Analysis of Variance (ANOVA) was run to determine significant differences between various testing variables (Kolmogorov Smirnov test: $P > 0.05$). ANOVA was done to test for significant differences for the abundance, species richness and species diversity of invertebrates between the three treatments (control, dung & log) and three vegetation types (mixed bushveld, mopane & riverine).

Beta (β) diversity or differentiation diversity is a measure of how different or similar a range of habitats or samples are in terms of variety (Magurran, 1988). This may be measured in terms of species change along a gradient or within different communities (Magurran, 1988). This is a simple measure of the extent to which two habitats have species (or individuals) in common. Several similarity indices are available, which have been formulated in a number of different ways (Magurran, 1988). The Jaccard index and Sorensen index are the two most frequently used indices (Southwood, 1978). For this analysis the Jaccard's coefficient was calculated with the statistical package SPSS.

This coefficient is defined by the following equation:

$$C_j = j/(a + b - j)$$

where, j is the number of species in common to the two samples, and a and b are the total number of species in each sample (Southwood, 1978). Sites that are completely similar will have a value of 100 (all species the same), and 0 if the sites are completely dissimilar (no shared species). In this study the Jaccard's coefficient was used to measure how different or similar the species composition of the six focal taxa were within the three vegetation types and refugia sites.

RESULTS

A total of 402 invertebrate individuals from 71 species, 41 genera, 26 families and seven orders were sampled from beneath the two experimental refuge substrates (Figure 5.3). Only one family each was collected from the orders Hymenoptera and Isoptera. Sixteen families were collected from the order Araneae, whilst six families from the class Diplopoda, and a single family from the class Chilopoda were collected. Of the 402 individuals, 31 individuals could not be identified to either genus or morphospecies level. These individuals contributed to the abundance calculations but were omitted from the species totals for each taxon.

The distribution of the abundance of individuals within the respective genera or families, collected for each focal taxon, for all refuge substrates and vegetation types combined is illustrated in Figures 5.4 a-e. There were 137 ant individuals distributed among 8 genera (Figure 5.4a), three individuals from a single centipede family (Figure 5.4b), 58 millipedes from five families and 12 species (Figure 5.4 c), 155 spiders from 16 families and 45 species (Figure 5.4 d) and 49 termites from three genera and species (Figure 5.4 e) that were recorded. A list of all species from the focal taxa collected from Makalali Private Game Reserve is presented in Appendix 5.1.

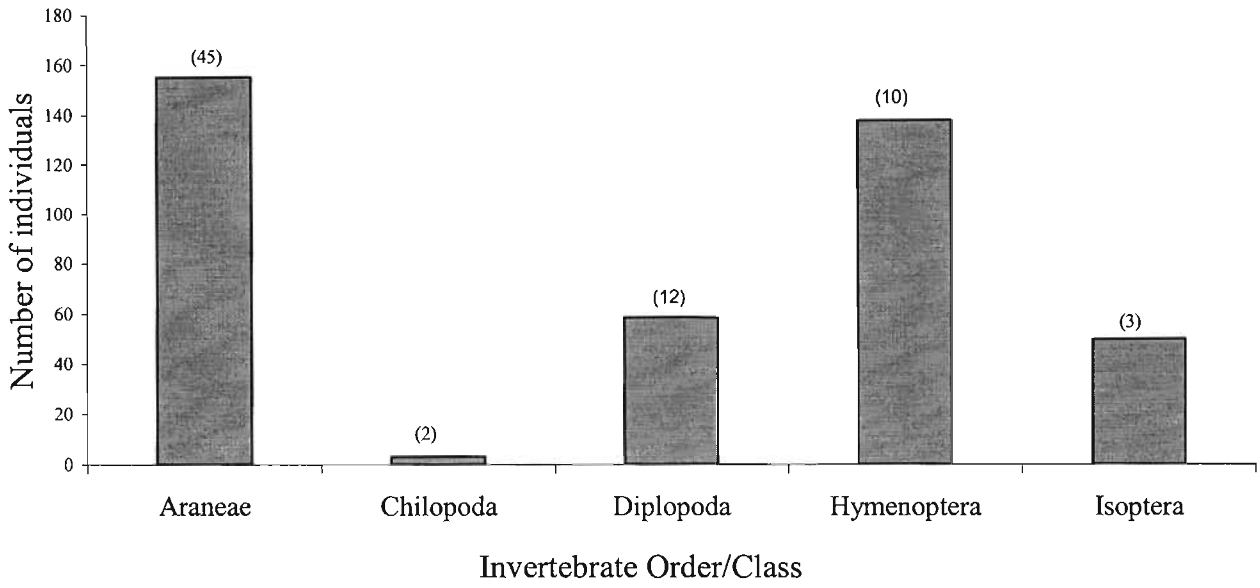


Figure 5.3. Taxonomic distribution of the total number of individuals collected during the experiment for all refugia substrates and vegetation types combined. A total of 402 individuals were sampled. The height of the bar denotes the abundance of individuals for each taxon and the number of species is given in parentheses.

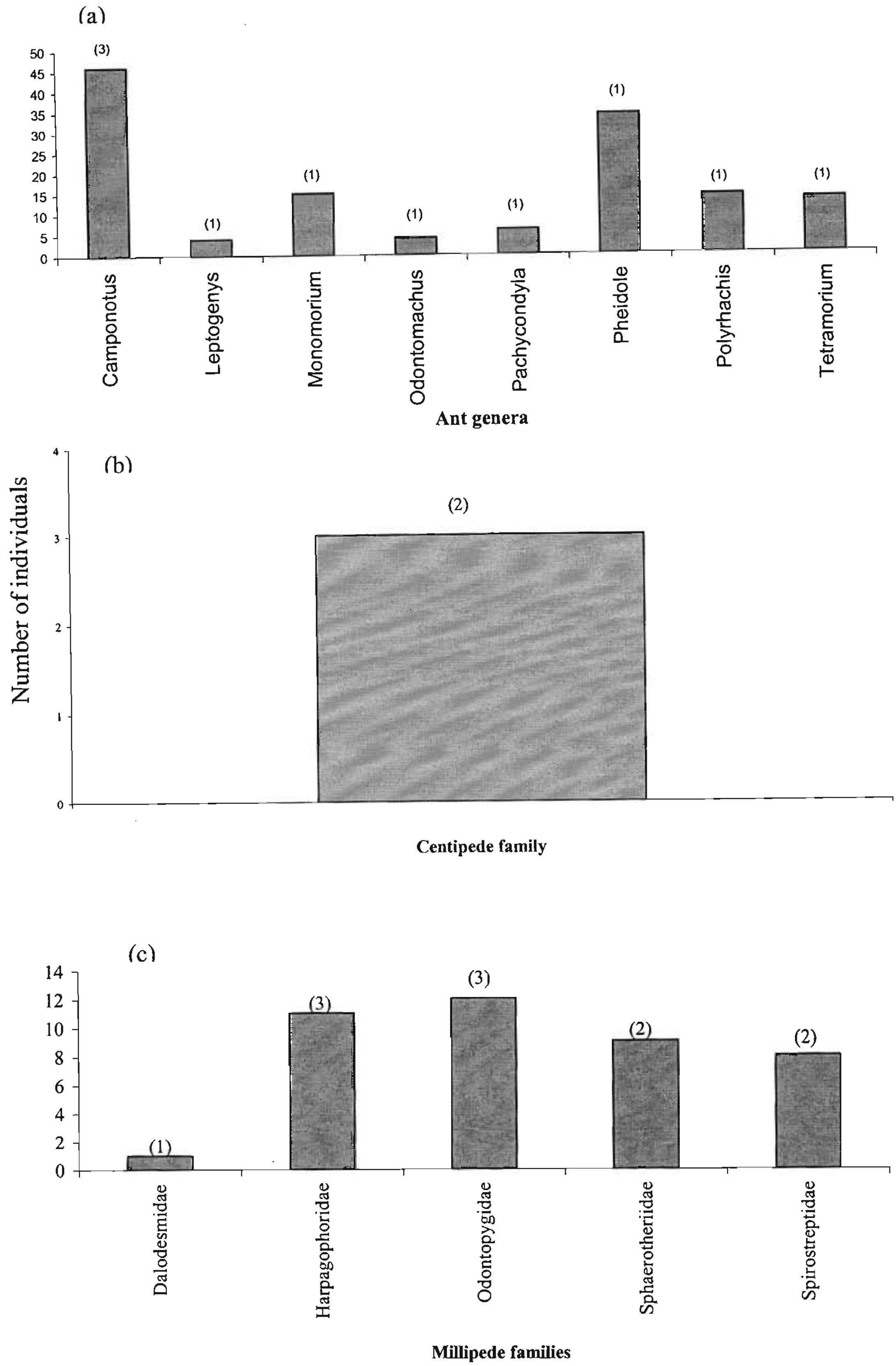


Figure 5.4.1. Taxonomic distribution of the number of individuals collected from under all refuge sites and vegetation types combined for the following taxa (a) ants (total = 137, (b) centipedes (total = 3) and millipedes (total = 58). The height of the bar denotes the abundance and the number of species is given in parentheses.

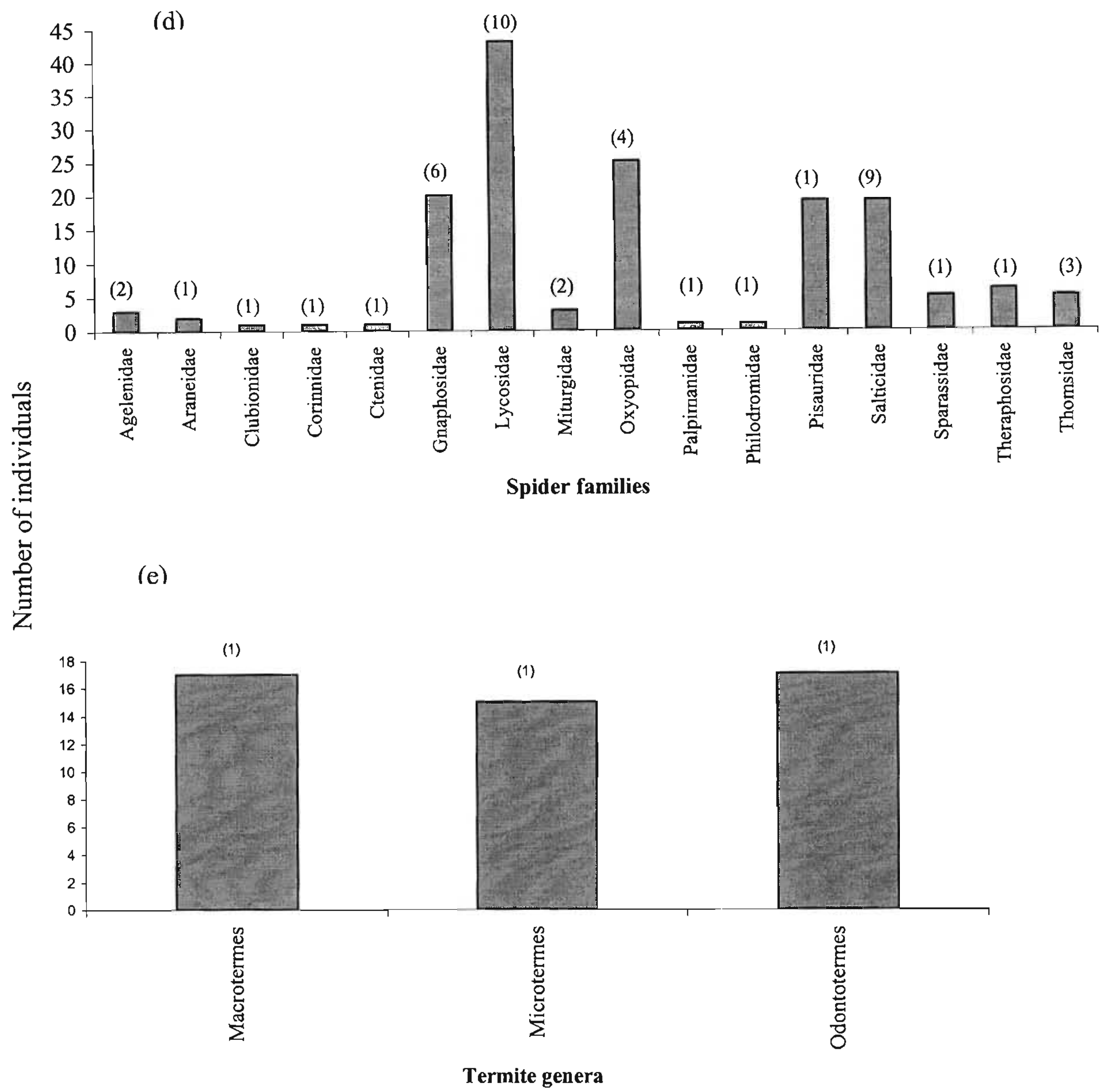


Figure 5.4.2. Taxonomic distribution of the number of individuals collected from under all refuge sites and vegetation types combined for the following taxa (d) spiders (total = 155) and (e) termites (total = 49). The height of the bar denotes the abundance and the number of species is given in parentheses.

There were significant differences in invertebrate abundance (ANOVA: $F_{1,14} = 8.53$, $P = 0.005$, species richness (ANOVA: $F_{1,14} = 9.79$, $P = 0.003$) and diversity (ANOVA: $F_{1,14} = 7.88$, $P = 0.007$) associated with refugia (logs and dung) between the different vegetation types (Figure 5.5). From the 402 individuals sampled from under refugia, 194 individuals were collected in the mixed bushveld vegetation type followed by 133 individuals from the riverine woodland and 75 individuals from the mopane woodland plots. The species richness and diversity also followed similar trends of highest values within the mixed bushveld vegetation type followed by the riverine woodland and then mopane woodland.

There were significant differences in invertebrate abundance (Univariate ANOVA: $F_{1,16} = 179.56$, $P < 0.05$), species richness (Univariate ANOVA: $F_{1,16} = 462.25$, $P < 0.05$) and diversity (Univariate ANOVA: $F_{1,16} = 221.07$, $P < 0.05$) between the plots with logs and control plots (Figure 5.6). Similar results of significant differences in invertebrate abundance (Univariate ANOVA: $F_{1,24} = 37.29$, $P < 0.05$), species richness (Univariate ANOVA: $F_{1,24} = 32.69$, $P < 0.05$) and diversity (Univariate ANOVA: $F_{1,24} = 29.57$ $P < 0.05$) were obtained between the plots with dung and the control plots (Figure 5.7). The refuge plots (log and dung) always had a higher invertebrate abundance, species richness and diversity than the control plots (without any refugia).

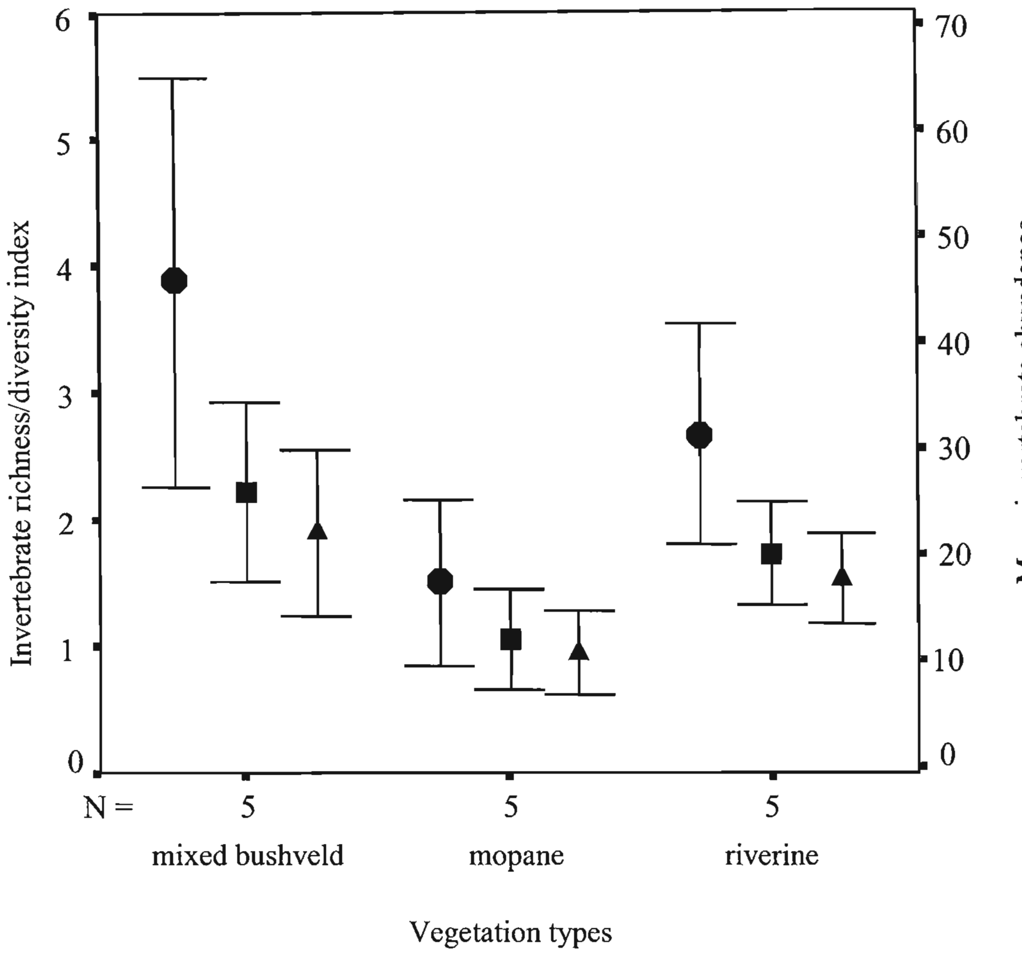


Figure 5.5: The effect of the vegetation type on abundance (●), species richness (■) and diversity (▲) for all plots and refugia types (logs and dung) combined. Data are illustrated by means and +/- 95% confidence intervals. N = the number of sites sampled in each vegetation type.

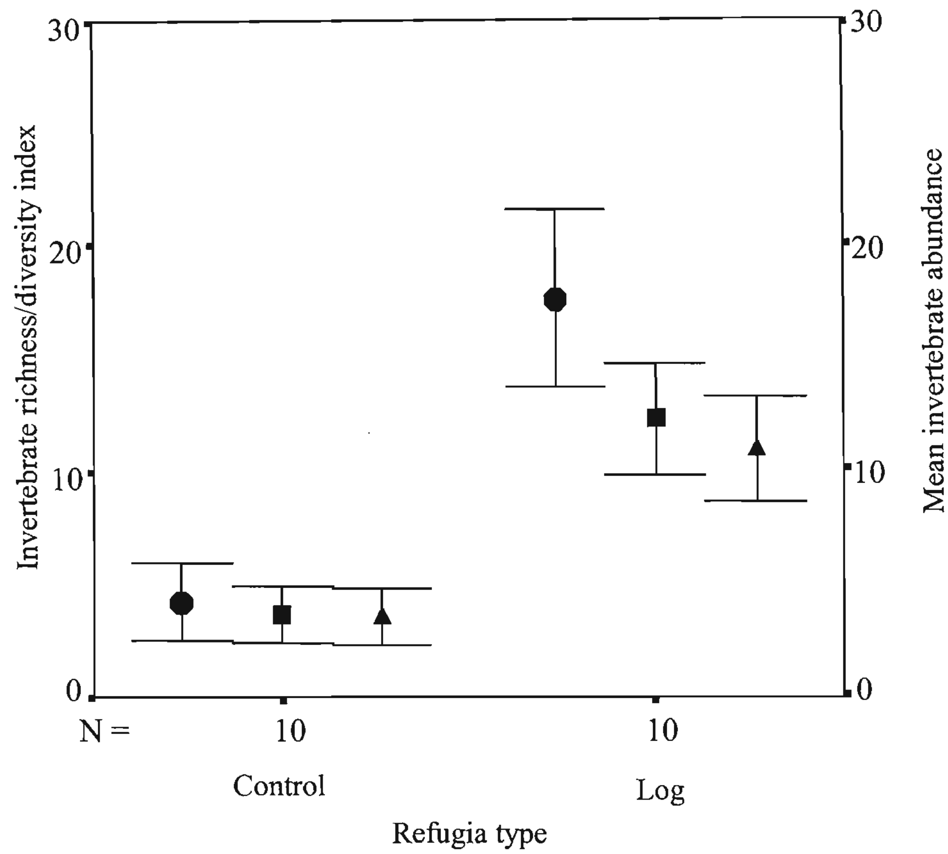


Figure 5.6. The effect of the log refugia on invertebrate abundance (●), species richness (■) and diversity (▲) for all plots and the two vegetation (mixed bushveld and riverine) types combined. Data are illustrated by means and +/- 95% confidence intervals. N = the number of plots sampled for the analysis.

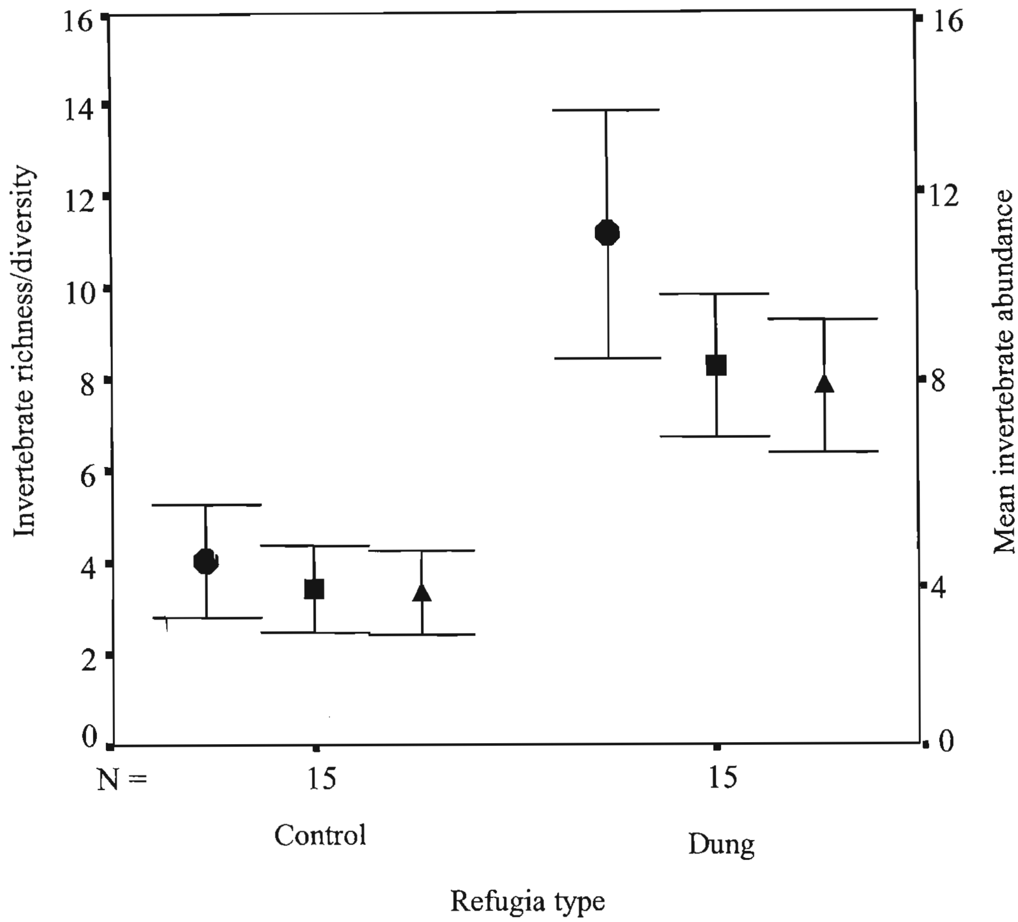


Figure 5.7. The effect of the dung refugia on invertebrate abundance (●), species richness (■) and diversity (▲) for all plots and the three vegetation types combined. Data are illustrated by means and +/- 95% confidence intervals. N = the number of plots sampled for the analysis.

The degree of similarity of the invertebrate communities utilising the refugia in the different vegetation types was tested using the Jaccard's similarity coefficient. Species composition differed considerably between vegetation types and between refuge types with no relationship being immediately obvious. In order to make the interpretation of the similarity matrices simpler, only sites that shared more than 25% of their species were included. Table 5.1 shows the Jaccard similarity coefficients for the different vegetation types and refugia based on the invertebrate species shared between them. Table 5.2 shows the same analysis but illustrates the similarity between sites within the different vegetation type irrespective of the refuge treatments. The values for all similarity coefficients are presented in Appendices 5.2 and 5.3.

The invertebrate species compositions of the log and dung sites were more similar to each other than to the control sites. However, the low level of similarity suggests that there is no typical community associated with either logs or dung. There were more unique (collected only from a specific treatment) species, families and groups at the refugia sites than in the control sites (Figure 5.8). Three different species of spiders were unique to the control sites (Corinnidae-sp1, Gnaphosidae-sp5 and Lycosidae-sp3). Fifteen species were unique to the dung refugia, with 11 of these species belonging to eight spider families (Appendix 5.4) and the remainder of the unique species comprised millipedes and one centipede.

There were also 15 species unique to the log refugia, with 13 of these species belonging to nine spider families (Appendix 5.4). The other invertebrates that were unique to logs were millipedes.

To investigate the possible influence of the different vegetation types on invertebrates utilising the refugia, the treatment effect (addition of refugia) was removed from the analysis. The five replicates of each of the vegetation types were used to calculate the Jaccards's similarity coefficients (Table 5.2). Using the initial limit of 25% as the cut off point for similarity, the sites within the mopane vegetation type showed very low similarity to the other two vegetation types (mixed bushveld and riverine) with respect to invertebrate species that utilised the refugia. Fewer than 50% of species were shared between any of the vegetation types, which indicate that there is a large amount of spatial heterogeneity in ground-dwelling invertebrate communities, even at a small scale.

The highest abundance of invertebrates and number of unique species sampled were from the mixed bushveld vegetation type, followed by riverine and then mopane woodland (Figure 5.9). A list of the unique species within vegetation types is given in Appendix 5.5.

Table 5.1: Jaccard's similarity coefficient based on number of species shared (25% or higher) between all sites within the three vegetation types (mixed bushveld – MB, mopani – MOP and riverine – RIV) and the three treatments (Control – C, Dung – D and Log – L). A value of 100 represents complete similarity and 0 represents different species. All values have been multiplied by 100 for ease of interpretation. The shaded areas represent sites within the same vegetation type and treatment.

Sites	MB C	MOP C	RIV C	MB D	MOP D	RIV D	MB L	RIV L
MB C	X							
MOP C		X						
RIV C			X					
MB D	35			X				
MOP D	33			35	X			
RIV D	31		26	39	35	X		
MB L	26			35	33	25	X	
RIV L	27			42	42	35	33	X

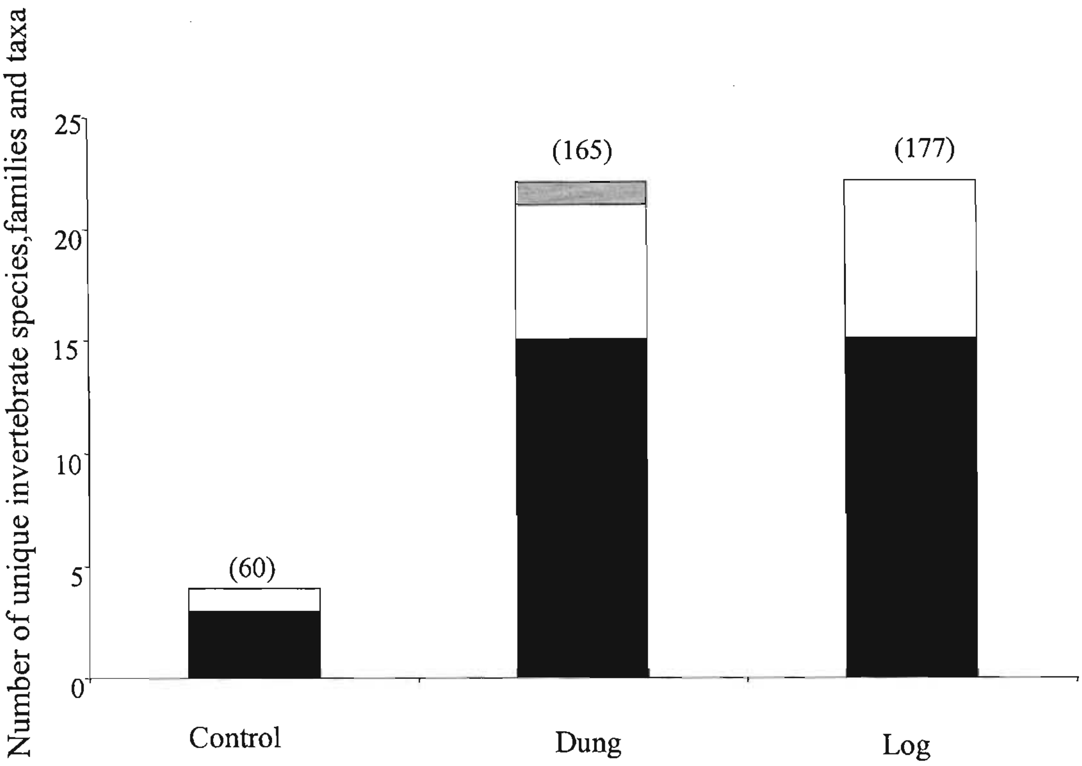


Figure 5.8. The number of unique invertebrate species (black), families (white) and taxa (grey) associated with each treatment. The total number of individuals collected for each treatment at all sites and vegetation types combined is given in parentheses.

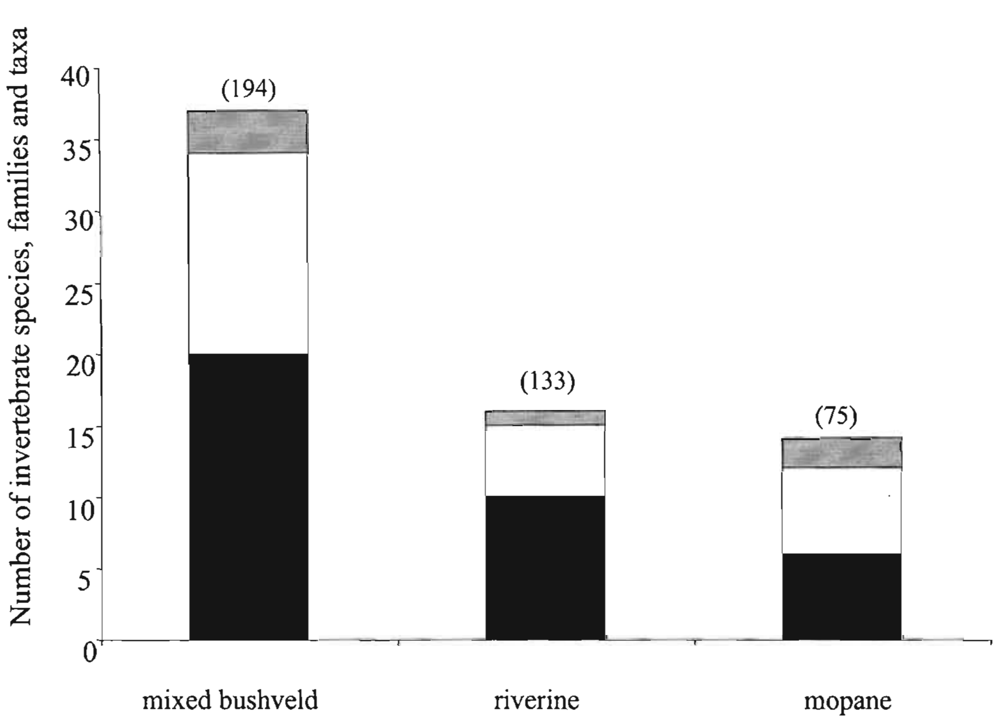


Figure 5.9. The number of unique invertebrate species (black), families (white) and taxa (grey) associated with each vegetation type, irrespective of treatment. The total number of individuals collected for each vegetation type at all sites and treatments is given in parentheses.

DISCUSSION

There is an increasing body of literature that has identified woody debris and dung as a critical habitat component for a number of vertebrate, invertebrate and microbial organisms (Marra & Edmonds, 1998). The vast majority of information that identifies the importance of decaying wood for food, shelter or a habitat niche for these organisms has focussed on the forest biome in the northern hemisphere (Berg, *et al.*, 1995, Martikainen, *et al*, 2000, Lemdahl, 2002, Sverdrup-Thygeson, & Ims, 2002). This level of interest and research on these saproxylic organisms needs to be translated to the African savanna biome.

The ecological functions of dead wood and dung include nutrient cycling, provision of structural habitat and essential food for a wide variety of plants and animals and creating ideal conditions for seed germination (Anderson & Coe, 1974, Cole, 1977, Davis, 2002, Jankielsohn, 2002). The wood adds complexity to forest floors, increasing ground to surface and below-ground heterogeneity (McComb & Lindenmayer, 1999). The presence of these refuge sites enhances the diversity of soil organisms by increasing the physical, structural, and chemical heterogeneity of the ground. In addition woody debris and dung may also be critical to the maintenance of biological properties on the forest floor by contributing to soil organic matter, maintaining soil stability and increasing soil moisture levels (Marra & Edmonds, 1998). Although soil organisms were not a focus of the current study, millipedes, ant and termites all do play a role in soil maintenance. This suggests that the presence of the refugia enhances ecosystem functioning in the savanna.

The results from the experiments carried out in the current study clearly supported the stated hypothesis of increasing invertebrate diversity with increasing refugia at individual sites (log and dung plots) across the three vegetation types sampled. This was illustrated by plots where logs and dung piles were added having significantly higher invertebrate abundance, species richness and diversity than the control plots, where log and dung piles were actively removed for all three vegetation types sampled.

The logs and dung piles provide an environment that is damp, cool and moist, which are ideal conditions for many ground-dwelling invertebrates (Lawrence, 1987). There are many specialised invertebrates such as millipedes and centipedes that require and utilise logs and dung as refuge habitats. Logs serve as a shelter for millipedes in the dry season (Lawrence, 1984) and are therefore an important refuge for species inhabiting the savanna environment. Scorpions are obligated to regulate their body temperatures and when they are cold, they are sluggish and vulnerable to predation (Leeming, 2003). Shelters are therefore of major importance to the survival of scorpions, which often exploit shelters such as rocks, logs and surface debris (Leeming, 2003). This suggests that there are specialised invertebrates utilising logs and dung refuge sites as essential habitat niches, while more generalist species occurred in the control sites which lacked logs and dung.

Other studies that support the idea that woody debris is important for invertebrates include Berg *et al.*, (1995) and Sverdrup-Thygeson & Ims (2002), which both showed that clear-cutting in many forests in Sweden was the most common factor threatening all invertebrate taxa that were investigated. It was determined that the most common consequence of clear-cutting was the decrease in decaying wood available to organisms which reduced suitable habitats, resulting in a decrease in these organisms.

Woody debris is not important exclusively for invertebrate species. Lohr, Gauthreaux, & Kilgo (2002) investigated coarse woody debris as an important structural characteristic for avian communities within pine forests. Their results indicated that removal of what they classified as down coarse woody debris and snags reduced the total breeding bird and resident species abundance, breeding bird diversity and breeding species richness. The territories of particular bird species were reduced by the removal of snags. In a concurrent study Horn (2000) found that arthropod abundance was reduced at all sites where the woody debris was removed, which can be translated to a reduction in potential prey abundance for the birds.

Although not focussed on for this project, dung beetles are important to ecosystem health and functioning, through the removal of animal waste (dung) and recycling of nutrients to the soil (Davis, 2002, Jankielsohn, 2002). There are approximately 50 genera and 780 species in southern Africa alone (Scholtz & Holm, 1985). Elephant dung is important for dung beetles. In parts of South Africa some dung beetle species are heavily dependant on elephant dung and have gone extinct in areas where elephants have been removed (*Clarke Scholtz, Pers Comm). Elephant dung is also an important micro-habitat for millipedes because of the suitable conditions for them to lay their eggs and house the early larval stage produced after hatching (Lawrence, 1966).

In this study, three spider morphospecies were unique to the control sites. These three morphospecies are members of the families Gnaphosidae, Lycosidae and Corinnidae. The former two families were also sampled under the refugia sites. However the family Corinnidae was only sampled at the control site. These spiders are described as wandering

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spiders that are encountered within leaf litter and hence do not readily utilise the refugia as a habitat niche (Dippenaar & Jocque, 1997).

The unique spider families collected from under dung piles (Ctenidae, Sparassidae and Theridiidae) and log sites (Miturgidae, Oxyopidae, Palpimanidae and Philodromidae) are described as wandering, ground-living spiders that inhabit plants, small retreats and burrows within the soil surface (Dippenaar & Jocque, 1997). The conditions provided by the logs and dung piles are ideal microhabitats for these spiders and it is possible that the species recorded are favourably influenced by the refugia generated by elephants.

Elephant generated refugia is not the only source of refugia available for ground dwelling invertebrate species to inhabit (Gardiner, 1995). However, no attempt was made to separate the origins of logs and it was presumed that elephants, through their feeding behaviour, may facilitate or increase the density of refugia by adding to those already present due to other agents. The provision of additional habitats (logs and elephant dung) available for use by the focal taxa increased the biodiversity of the study sites (log and dung plots), but also possibly for several other taxa, such as dung beetles, which were not considered in this study.

The results of this study showed a significant spatial variation between invertebrate abundance, species richness and diversity between the three vegetation types, with the more heterogeneous habitat supporting a higher diversity of invertebrates. Due to the higher number of plant species (Druce, 2000), the mixed bushveld vegetation type is considered to be a heterogeneous habitat, whilst mopane vegetation type is considered to be the most homogeneous habitat as it is dominated by a single species (*Colophospermum* *mopane*) and has minimal grass cover, which may explain the low invertebrate diversity and number of unique species. These results are also supported by other studies on specific invertebrate taxa that have demonstrated a correlation between the complexity of habitats and species richness (Dangerfield & Telford, 1992, Druce, 2000, Whitmore, 2000). Diversity generally increases when a greater variety of habitats are present because the more habitats there are the more species may exist (Reid & Miller, 1989). This suggests that the influence of elephants on ground-dwelling invertebrates, through their facilitation of refugia sites, does vary spatially (different vegetation types), with their influence being highest in more heterogeneous and plant diverse habitats across the reserve.

Logs and elephant dung do increase biodiversity in the sense of contributing to ecosystems and diversity at various taxonomic levels. Elephants are obviously a major contributor to the production of dung and logs in any savanna reserve, and this positive contribution to biodiversity should be considered together with other impacts on biodiversity in the debate on elephant populations in fenced reserves in South Africa. Continuing to ignore the role that elephants may play in contributing to this component of biodiversity will severely hamper any rational plan to conserve these distinctive and highly threatened microhabitats within the African savanna ecosystem.

CHAPTER 6

TEMPORAL CHANGES IN THE INVERTEBRATE COMMUNITY ASSOCIATED WITH ELEPHANT DUNG AT MAKALALI PRIVATE GAME RESERVE

INTRODUCTION

Studies on elephant dung have usually been centred on the use of dung as an indirect census method for counting elephants when direct observation of animals is not possible (Barnes & Jensen, 1987, Barnes, 1993). This census method is usually used when estimating populations within African forests, where visibility is most often limited and where one cannot traverse very easily on the terrain. However, elephant dung studies have expanded to include dropping counts to investigate population size, age structure of herds and their movements (Wing & Buss, 1970, Jachmann & Bell, 1984), the chemical composition of dung (Weir, 1972) and dung decomposition and its role in nutrient cycling (Anderson & Coe, 1974).

Dung piles do not decay at a constant rate. Decomposition of elephant dung is brought about by three principal factors: dung beetles, termites and mechanical disturbances such as rain, trampling, foraging for insects by birds, and fire (Jachmann & Bell, 1984). Initially the decomposition process is slow and then as time progresses, it accelerates (Barnes & Barnes, 1992). Decomposition is a complex process, which is affected by numerous factors. Dung piles deposited on the streams of banks or in gulleys can be washed away overnight by rain, but dung that remains moist due to contact with marshy ground can remain apparently fresh for longer periods. Dung exposed to direct sunlight can be baked dry, become fossilised and maintain its form for a year or more (White, *et al.,* 1993). Dung beetles (Scarabeidae) and termites (Termitidae) are important decomposers of dung piles (Scholtz & Holm, 1985, Jankielsohn, 2002). Other animals, for example African civet (*Viverra civetta* Schreber) and squirrels (*Funisciurrs lemniscatus* LeConte) forage in elephant dung piles for seeds and insects. Another factor, which has an effect on decomposition of dung, is the diet of the elephants. Diets of elephants showed marked seasonal variation, primarily in fruit content, since the availability of fruit is low in dry seasons. Dung containing increased proportions of fruit remains was consequently less fibrous and hence tend to decay faster (White, *et al.,* 1993).

The utilisation of elephant dung by invertebrates has mainly concentrated on dung beetles (Davis, 2002, Jankielsohn, 2002). Very few studies have been done to determine the use of elephant dung as a potential habitat site for other invertebrate taxa and the changes that take place within these invertebrate communities over time. The idea of succession came about when the emphasis of research was on descriptions of static communities (Pickett & McDonnell, 1989). The realisation by Cowles (1899) that communities were dynamic systems was a major change in ecology. Succession is synonymous with community change in composition and structure and is assumed to be orderly, directional and predictable (Pickett & McDonnell, 1989). The term succession in its simplest definition is the alteration of the environment or habitat by earlier communities to their detriment, which favours later successional assemblages (Pickett & McDonnell, 1989).

There are numerous environmental factors that effect the spatial and temporal distribution of organisms (Menge & Olson, 1990) and there is increasing evidence that seasonality or changes in the local habitat conditions are important factors influencing site selection by insects (Eggleton & Bignell, 1995). Although a habitat may be suitable for a particular organism at a given time, the conditions favouring that particular species may change, making the habitat less desirable for the initial inhabitant, but suitable for another species.

Previous studies conducted at Makalali Private Game Reserve have shown that micro-habitat conditions are important for habitat selection by invertebrates, with moisture content of the potential habitat being one of the more important characteristics (Druce, 2000). Moisture levels of dung should therefore influence the invertebrates associated with elephant dung of different ages. The study by Druce (2000) also showed different invertebrate communities associated with different vegetation types at Makalali Game Reserve, and this spatial diversity could influence the community associated with dung, and the extent of change as dung ages. This means that any effort to quantify the relationship between elephant dung and invertebrate diversity should consider both spatial variation in this impact, and temporal changes in the invertebrate community.

The aim of this chapter was to investigate temporal changes in the fauna of selected invertebrates that use elephant dung as a refuge site.

The hypothesis that the composition of ground-dwelling invertebrate communities changes at various stages of dung decomposition was tested. The null hypothesis suggests that there would be no change in invertebrate community composition structure with increasing age of dung.

The objectives of this part of the study were:

1. To identify and describe the ground-dwelling invertebrate communities using the different ages of dung as a refuge site;
2. To determine the extent to which the community (at higher taxon and species levels) of the focal groups changes in dung of different ages and
3. To compare ground-dwelling invertebrate species abundance, richness and diversity between the different ages of dung.

Although dung beetles are a critical component of invertebrate communities using elephant dung, they were not one of the focal groups for this part of the study. The reason for their exclusion was that this project focussed on ground-dwelling invertebrate species that live beneath the dung and use it as a refuge. Most dung beetle species are totally dependent on dung for their survival (Scholtz & Holm, 1985, Davis, 2002) and were therefore not included in any detail in this project.

METHOD AND MATERIALS

Collection of elephant dung

Fresh elephant dung was required for the set up of this experiment. This meant that prior to the experimental set up, very few or no obvious invertebrates were present in the dung. The dung was collected as detailed in Chapter 5.

Experimental Set-up

This experiment required samples of elephant dung of known age at sites that could be located at various time intervals. In June 2000 (between the 15^{th} and 20^{th}) fresh elephant dung was placed at three sites in each of five vegetation types, namely *Combretum apiculatum* and *Grewia* low thicket, *Acacia nigrescens* and *Ormocarpum trichocarpum*, *Combretum apiculatum* and *Ziziphus mucronata*, *Strychnos madagascariensis* and *Combretum apiculatum* subvariant and *Colophospermum mopane* woodland, which resulted in 15 sites throughout Makalali Private Game Reserve (Figure 6.1). One pile of fresh elephant dung was placed at each of the 15 sites. In order to keep the area of the experimental dung pile constant throughout the project, a wooden frame with an area of 90cm x 90cm and a height of 10cm was used to construct the pile of dung at each of the sites. The GPS readings, locations and descriptions of the sites were recorded. A metal peg was hammered into the ground near each of the dung piles, which allowed the experimental dung piles to be located and identified in terms of the sequence of the dates that the dung was placed.

In November 2000 (between the 15th and 20th), January 2001 (between the 27th and 30th), February 2001 (between the 19th and 20th) and February 2001 (between the 23rd and 24th) one pile of fresh elephant dung was placed at each of the 15 sites following the same procedures as before. The experimental dung piles at each site were placed approximately two to three meters away from other piles, which meant that eventually each of the 15 sites had five piles of dung, with each pile representing a different age.

Sampling

Invertebrate sampling was conducted in February 2001. At this time five sets of elephant dung of five different ages were sampled. These ages were eight months, three months, three weeks, twelve days and four days. Sampling of all dung piles at the 15 sites was done over a period of two days. All invertebrates from the focal taxa for this study were collected. Estimated numbers of earthworms, beetle larvae and dung beetles were also recorded. All samples were collected by the hand to jar method. Storage of samples, invertebrate processing and identification were conducted as outlined in Chapter 4. No time limit was allocated to sampling each of the 15 sites. Each site was searched until each of the five different ages of dung had been satisfactorily sampled. The average time spent sampling each site ranged between 25 and 30 minutes (+/- 5 to 6 minutes for each dung pile).

Analysis

The diversity index and species richness values were calculated as outlined in Chapter 4.

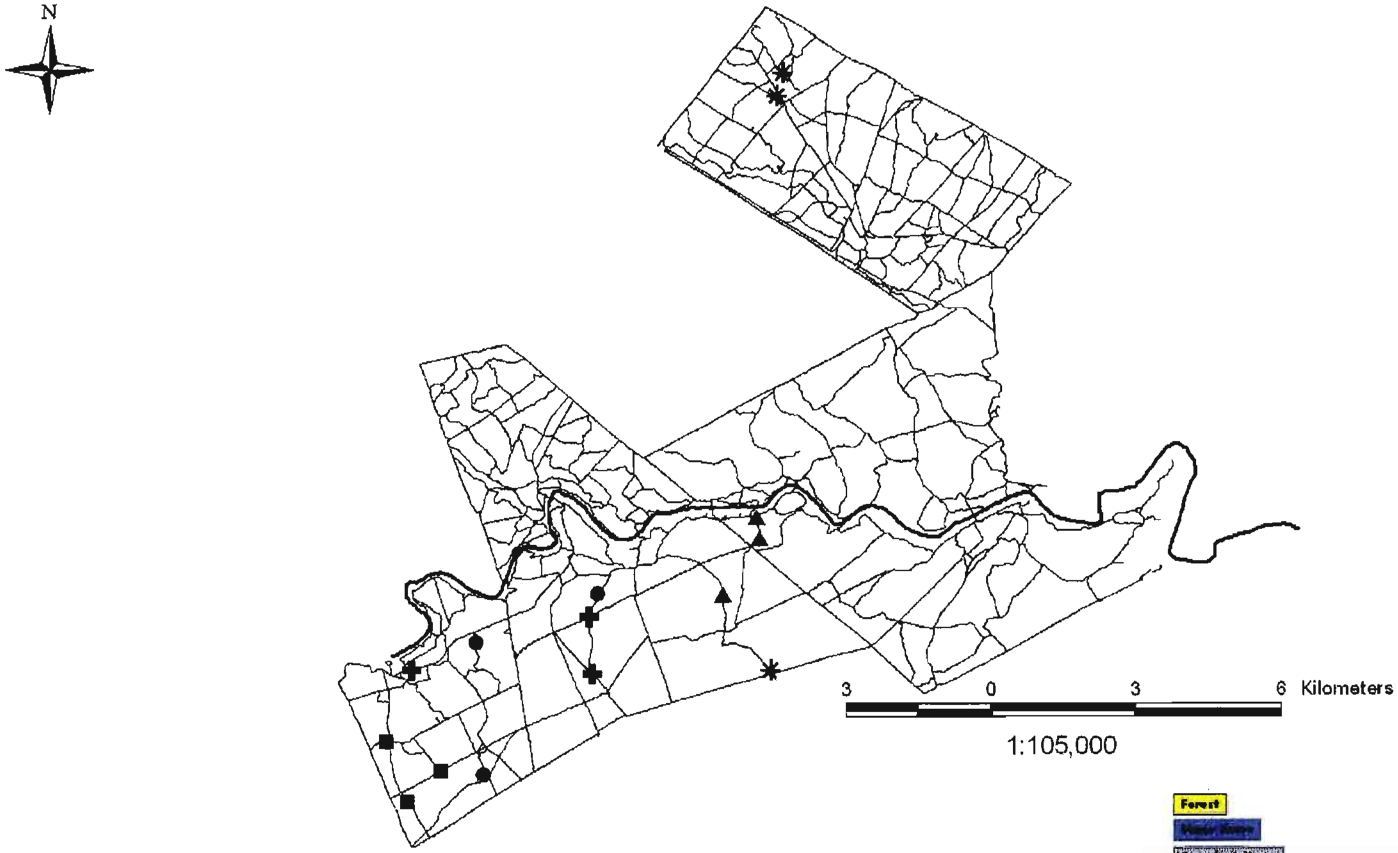
Changes in invertebrate species and higher taxon composition sampled from the five different dung ages were calculated with the following equation, with results expressed as a percentage community change of invertebrate species or higher taxa within each age class (Diamond, 1969):

$$\%\text{Community change (t)} = 100 - [(a + b) / (c + d - e)]$$

where *a* is the number of taxa in the first sample but not in sample *t* (hence must have gone "extinct" or removed in the interim from the site), *b* is the number of taxa in sample *t* but not in the first sample (species or higher taxa that had "immigrated" or added under their own power), *c* is the number of taxa present in the first sample, *d* is the number of taxa present in sample *t* and *e* is the number of taxa occurring in both samples (Diamond, 1969). All figures and calculations of percentage change begin at approximately 4 days (0.5 weeks) after placement of the dung, since there was no colonization of the dung by the focal invertebrate taxa before this time period, and sampling continued up to 32 weeks (the oldest age of dung). Invertebrate community calculations were done for the change in number of higher taxa and the number of species over the various age classes of dung. For each calculation the percentage change in either taxa or species communities was calculated in comparison to the following age class.

The statistical programme SPSS (Norusis 1994) was used for all data analysis. All data were checked for normality using the Kolmogorov-Smirnov test. If data were normally distributed (Kolmogorov Smirnov test: $P > 0.05$) Analysis of Variance (ANOVA) was run to determine significant differences among independent variable classes for the relevant dependant variables.

To best illustrate the relationship between abundance of individuals of the different taxa with respect to the age of elephant dung, the best fit of different types of regression using SPSS was produced. The regression line with the highest r^2 value tested was taken as the regression that best describes the relationship between increasing age of elephant dung and ground-dwelling invertebrate abundance.



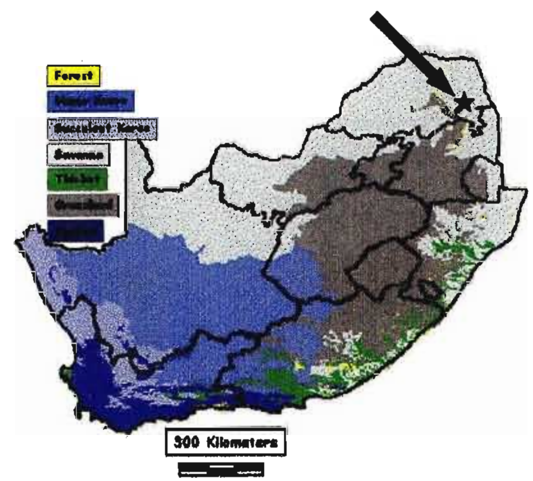


Figure 6.1. Distribution of the experimental elephant dung piles for the community change study within Makaklali Private Game Reserve.

RESULTS

Abundance and diversity of ground-dwelling invertebrates in different ages of dung

A total of 84 individuals distributed among three classes (Arachnida, Insecta and Diplopoda) and five orders (Araneae, Hymenoptera, Isoptera, Spirostreptida and Sphaerotheriida) were sampled from the five age classes of dung in five vegetation types during this experiment (Figure 6.2). A single family was collected from the orders Hymenoptera and Isoptera. Five families were collected from the order Araneae, and three families from the class Diplopoda. The list of species identified for each taxon is given in Appendix 6.1.

Percentage change for invertebrate groups & species

The percentage change for classes and orders showed a rapid decline from the first two age classes of sampling (four days and two weeks) towards zero, with no change in invertebrate community structure within the dung after four weeks. Thereafter there was a steady increase in the number of classes and orders that colonised the dung during the following two (12 and 32 weeks) age classes (Figure 6.3).

The percentage change of invertebrate species with respect to age classes also showed a sharp decline initially from the first age class (four days) to the two week old dung, but then recovered to the initial change in community percentage (approximately eighty-percent) after four weeks (Figure 6.3). The opposite trend was observed at the 12-week time interval, with an increase in the number of species but a decrease in the species that were utilising the dung. Finally there was an increase in the number of species and higher taxa from the penultimate age (12 weeks) to the final age (32 weeks) of dung.

When the percentage change of higher taxa from two to four weeks was zero, there was a rapid increase in the percentage species change at the same time (Figure 6.3). This suggests that although there was no change in the higher-level richness of invertebrate groups present, the species that colonised the dung had changed. Three species of spiders (*Lycosidae*-sp.1 & 6, *Gnaphosidae*-sp.8), a millipede (*Spinotarsus*-sp.3) and one ant species (*Campontus cinctellus)* colonised the dung at this stage.

The distribution of the percentage of the focal invertebrate groups utilising the dung over the 32 week time period is illustrated in Figure 6.4. The majority of the millipedes were located within dung that was between two and four weeks old, whilst the spiders and termites increased as the dung got older. Although not included in these analyses, earthworms and dung beetle adults and larvae were only present in dung piles that were less than four weeks old.

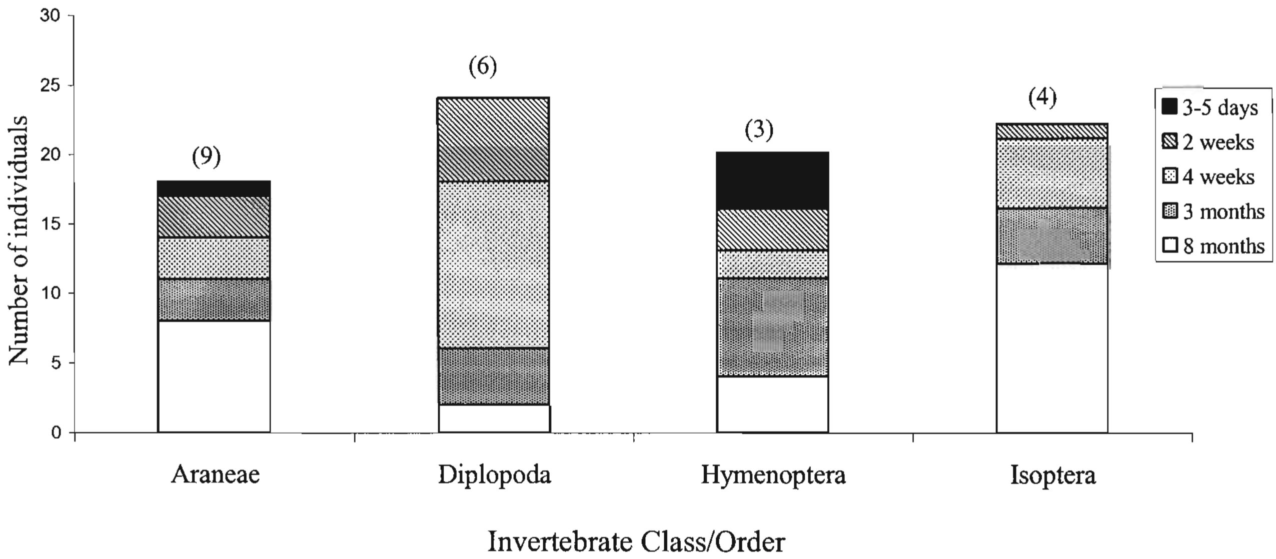


Figure 6.2. Ground-dwelling invertebrates collected for all five age classes of dung for all sites in the five vegetation types. The number of individuals is illustrated by the height of the bar and the number of species identified is given in parentheses.

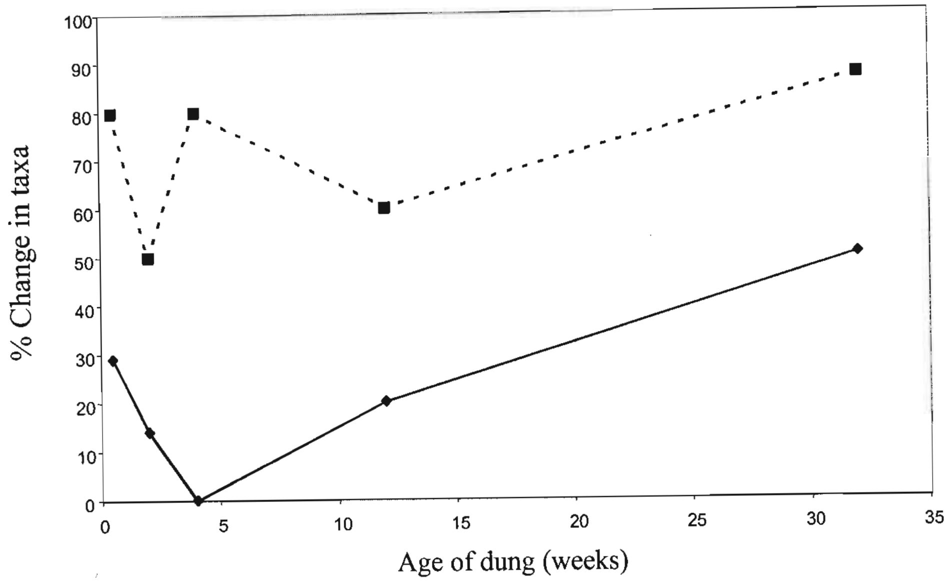


Figure 6.3. The percentage change in invertebrate classes and orders (solid line) and species (broken line) between five different ages of elephant dung across all five vegetation types.

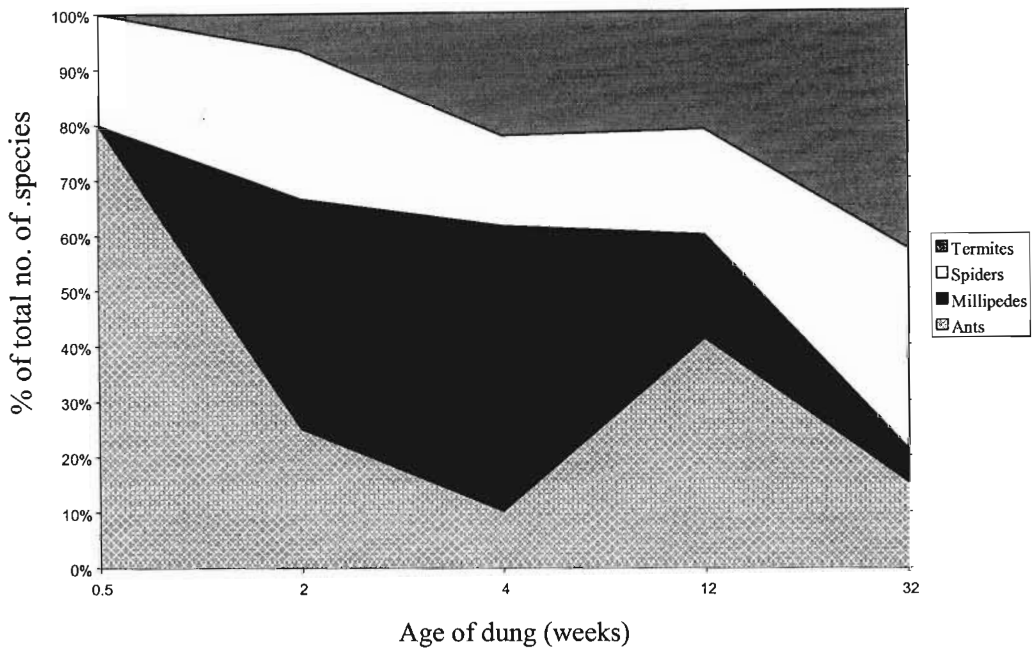


Figure 6.4. Changes in invertebrates community associated with dung of different ages, expressed as the percentage of the total number of species of the focus taxa (data from five vegetation types combined).

Species richness, diversity & abundance

There was a significant positive relationship between invertebrate abundance (Inverse regression: $R^2 = 0.89$, $F_{1,3} = 24.74$, $P = 0.01$), species richness and diversity (Logarithmic regression: $R^2 = 0.97$, $F_{1,3} = 106.87$, $P = 0.002$) and age of dung (Figure 6.5). Within three days of placing the dung at each site, there was colonisation of the substrate. All three parameters showed a rapid increase from the three day-old dung with mean species richness and diversity continuing to increase over the sampling period. The mean abundance of invertebrates sampled also increased, however the number of invertebrates slowly levelled off at the end of the sampling period.

Response of individual taxa to the age of dung

Various curve estimation regression analyses were performed for the four taxa to determine the relationship between abundance of each individual taxon and the age of elephant dung (Figures 6.6a–d). There was a significant positive relationship between the cumulative abundance of spiders (Linear regression: $R^2 = 0.89$, $F_{1,3} = 26.38$, $P = 0.01$) (Figure 6.6a) and of termites (Linear regression: $R^2 = 0.93$, $F_{1,3} = 43.79$, $P = 0.007$) (Figure 6.6b) and increasing age of elephant dung. Termites were not present within the fresh dung piles (three days old to two weeks old), but their abundance gradually increased as the dung became older. The number of spiders utilising the dung increased as the dung aged. A single spider (Lycosidae-sp7) was collected from the three day-old dung, however the specimen was collected on top of rather than under the dung and members of the family Lycosidae are described as free-living, wandering spiders.

The changes in cumulative abundance of millipedes and of ants were related to the age of dung by cubic regressions (Figures 6.6c & d). There was no significant relationship between the cumulative abundance of millipedes (Cubic regression: $R^2 = 0.99$, $F_{1,3} = 49.93$, $P = 0.1$) and of ants (Cubic regression: $R^2 = 0.99$, $F_{1,3} = 75.21$, $P = 0.08$) with age of dung. However both taxa displayed similar trends of having the their highest abundance when the dung was between two and four weeks old and decreasing in numbers as the dung became older.

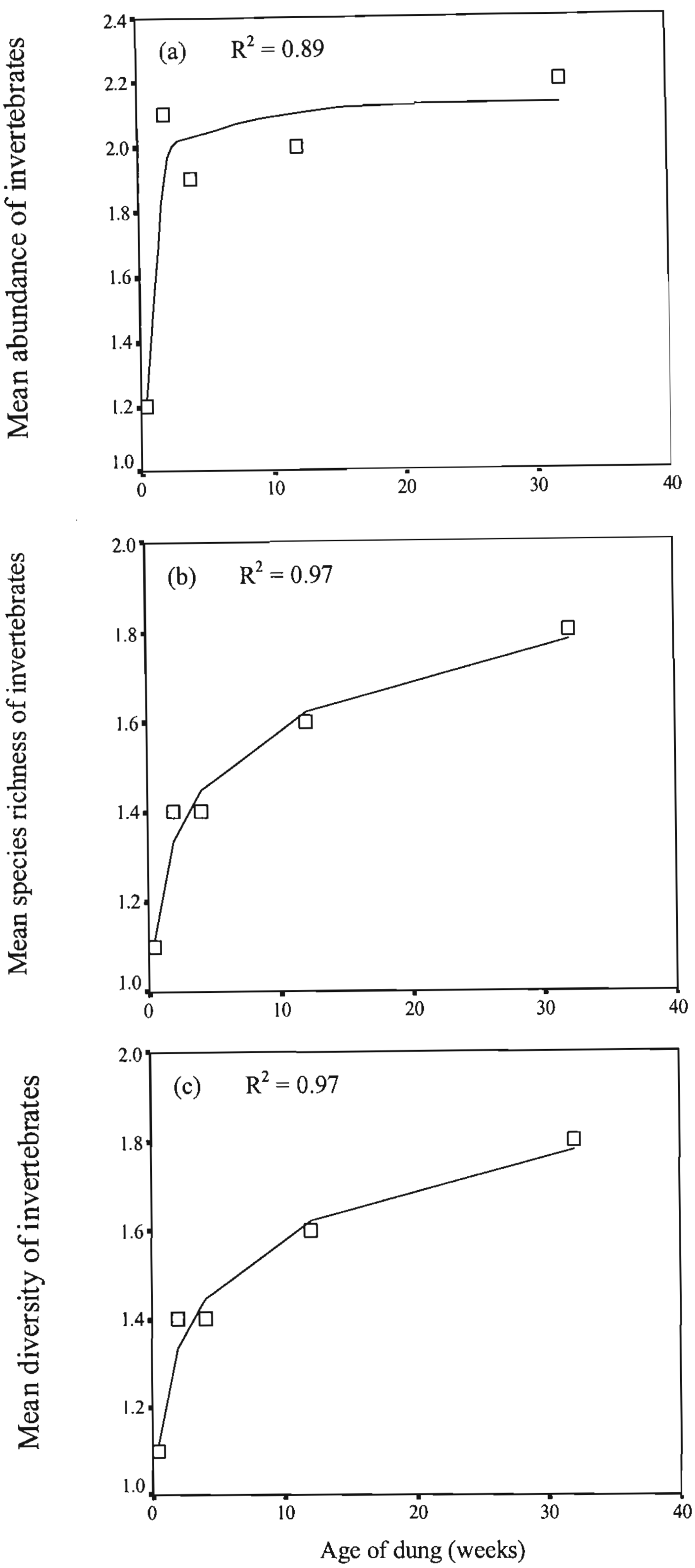


Figure 6.5: The effect of age of dung on invertebrate (a) abundance (Y = 2.14 (-0.45/t); (b) species richness (Y = 1.22 (0.16*ln (t)) and (c) diversity (Y = 1.22 (0.16*ln (t)) expressed as regression curves. The squares denote the observed means for all sites and vegetation types combined for each time sequence and the line is the best curve fit.

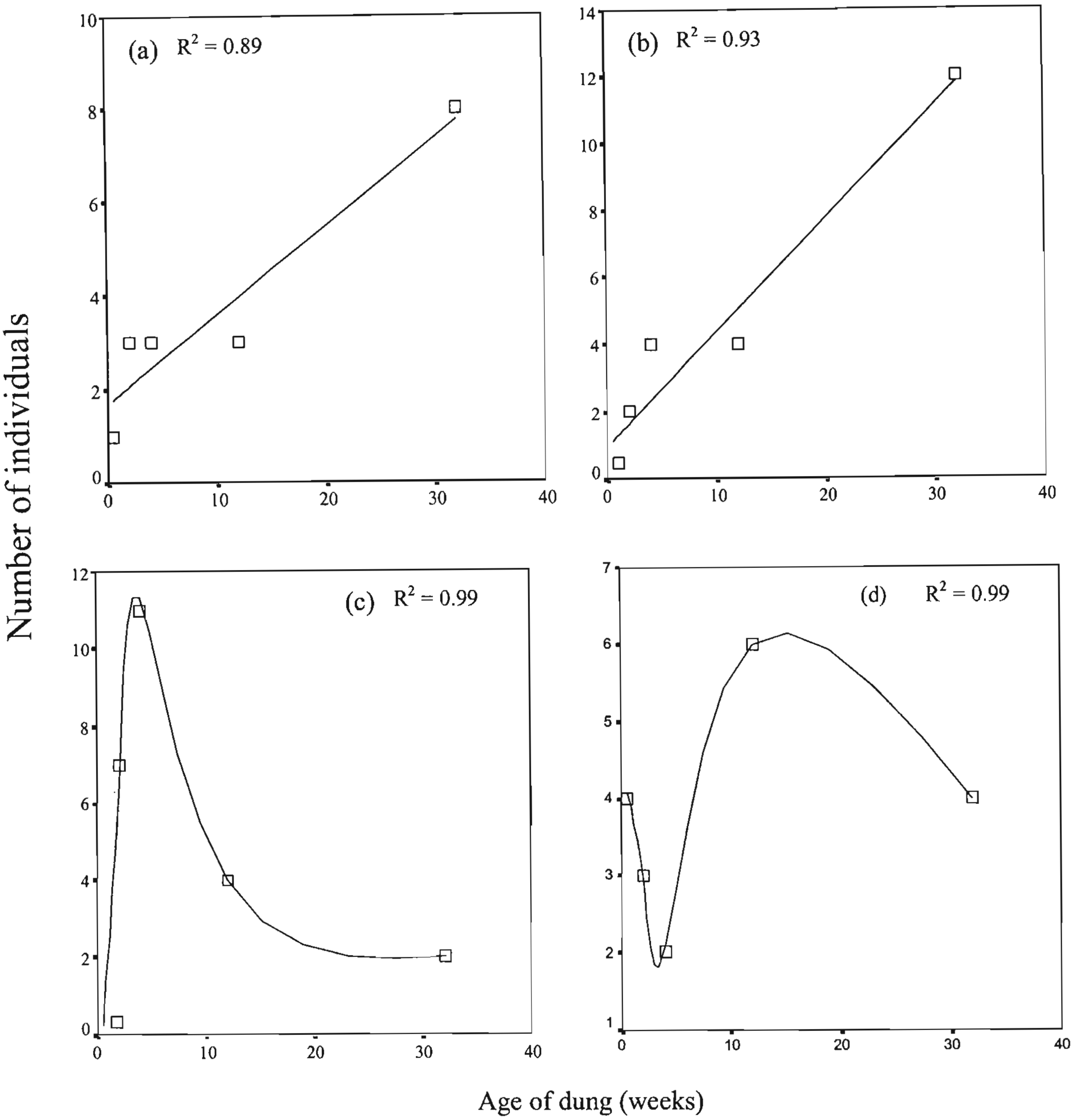


Figure 6.6. The curve estimation regression between (a) spiders ($Y = 1.68 + (0.19 * t)$; (b) termites ($Y = 0.98 + (0.34 * t)$; (c) millipedes ($Y = -2.31 + (5.44 * t) + (-0.56 * t^2) + (0.12 * t^3)$ and (d) ants ($Y = 4.63 + (-1.18 * t) + (0.15 * t^2) + (-0.004 * t^3)$ with age of elephant dung. The squares denote the cumulative abundance observed all sites and vegetation types combined for each time sequence and the line is the best curve fit.

DISCUSSION

In natural ecosystems, litter fall and the feeding activities of herbivores are the two main processes by which minerals contained in the above ground parts of plants are returned to the soil (Anderson & Coe, 1974). Therefore the excreta of all animals are crucial components of the cycle of nutrients and energy in the ecosystem (Cole, 1977, Jankielsohn, 2002). In addition to this important role in nutrient cycling, elephant dung is also an important source of food for many smaller animals, the site of seed dispersal of plants and a habitat refuge for invertebrates (Jankielsohn, 2002).

The results obtained from this experiment supported the hypothesis that ground-dwelling invertebrate community composition changes with dung of increasing age.

The main macrofaunal groups involved in decomposition within the savanna biome are termites, millipedes, dung beetles, coleopteran larvae, ants and cockroaches (Scholes & Walker, 1993). Five of these six faunal taxa were sampled at the dung sites in this project. The colonisation of fresh dung (two to three days old) by dung beetles illustrates the point that consumption of fresh elephant dung is the speciality of dung beetles (Scholes & Walker, 1993). Dung beetles will immediately come to a fresh dung pile and are very selective in the type and age of dung that they use and remove (Scholes & Walker, 1993, Anderson & Coe, 1974). The amount of moisture in the dung is an important selection criterion for dung beetles (Scholtz & Holm, 1985). Fresh dung is moist and wet, so it would stick together in a ball. The drier the dung the more easily it falls apart. Moisture levels of dung are also important to hydrate the eggs and raise the young (Scholtz & Holm, 1985, Jankielsohn, 2002).

Coleopteran larvae and millipedes were among the first groups to be sampled at the relatively fresh dung piles (up to four weeks old). These groups require a moist damp habitat away from the heat to live in and the elephant dung at four weeks had sufficient moisture to support these taxa (Lawrence, 1966). With time, as the dung became older, the moisture levels decreased, which reduced the appeal of the dung as a refuge site, and resulted in a decrease in the abundance of beetle larvae and millipedes. It is also likely that beetles matured in the dung pile, and left when their needs, the habitat conditions associated with the dung, and their mobility changed.

As the dung got older the invertebrate assemblages that dominated the dung piles changed with ants, spiders and termites being the most abundant invertebrates. Due to the lack of moisture and hence drier conditions, the microclimate of the three and eight month old dung was more suitable for the termite species that include dry dung as part of their diet (Scholes & Walker, 1993). The dominance of termites within older, drier dung piles is also supported by Cole (1977), who showed that there were higher numbers of termites within older and drier dung piles than any of his other treatments (fresh dung, dung liquid or dung that water was added to). His study also pointed out the importance of termites in the removal of elephant dung during the dry season, because the activity of coprophagous beetles decreased whilst the activity of termites increased. The number of spider individuals sampled in the different ages of dung did not change considerably. This suggests that spiders may have been sampled opportunistically and were most likely present at the dung piles in search of prey rather than using the dung as a refuge site.

Small changes in temperature, humidity, moisture content or any other conditions within specialised habitats such as dung have more of an effect on invertebrates than would be felt by larger creatures (Kirby, 1992). Invertebrates are in general much more sensitive to habitat changes than plants or vertebrates (Kirby, 1992). Many invertebrates, particularly the rarer ones, are highly specialised and have precise habitat requirements. Wingless invertebrates have limited powers of dispersal and their small size makes them incapable of travelling any distance. Many spend much of their lives within microhabitats that may seem trivial for other species, hence the importance of these refuge sites such as logs and elephant dung within the savanna biome for invertebrates.

This project demonstrated that once the dung is available, there are many invertebrate communities that use the dung at various stages of decomposition, suggesting that changes in the microclimate of elephant dung piles are important for a variety of invertebrate communities that potentially use the dung as a refuge site. This is relevant because it means that any debate on the impact of elephants, or monitoring of invertebrates associated with dung as part of management activities, needs to consider the temporal changes in the fauna associated with dung, and to recognise that elephant dung is a dynamic system, which is important for the conservation of invertebrate communities.

CHAPTER 7

SUMMARY & CONCLUSION

Within fenced parks and reserves in South Africa, the success of elephant protection has contributed to a steady increase in elephant population numbers. The feeding behaviour of elephants inflicts structural changes on individual plants, which may influence single-species dynamics, plant densities and vegetation communities (Dublin *et al.,* 1990). These changes have resulted in concerns about the negative impacts elephants may have on the ecosystem (Cumming *et al.,* 1997, Whyte *et al.,* 2003). Perceived negative consequences of such impacts have prompted considerations of artificial reduction of elephant numbers in order to limit the effect on the ecosystem.

It is accepted that many factors outside of science such as societal values and ethics, inform high level decision making, even on scientific issues. However, invoking a sound scientific argument remains one of the most politically safe and technically sound options when complex or risky decisions have to be made. If science is to be used as the main basis for making decisions on elephant management strategy within protected areas, managers need to consider the impacts of elephants in terms of variation over space and time and influences on biodiversity as a whole and not just the most common and easily measured parameter, i.e. vegetation.

Conservation organisations' primary goal is the conservation of biodiversity rather than that of single species preservation (Whyte, *et al.*, 1999, 2003). Many ecologists realise that savanna biomes are not stable ecosystems where tree densities and species composition are in equilibrium but rather that the savanna biome is a dynamic ecological system, in which elephants play a critical role as keystone species (Gillson & Lindsay, 2003). Elephants are not more important than any other component of biodiversity, but they are considered major ecosystem drivers (Whyte, *et al.*, 1999). The effects of elephant management on biodiversity is therefore of paramount importance, particularly as there is a paucity of in-depth studies on the impact of elephants on smaller, less charismatic species, such as invertebrates.

In light of the essential ecological services that invertebrates provide, conservation of these organisms should be of paramount importance to people. However, invertebrates are largely marginalised from conservation activities because of: a lack of awareness of their ecological significance, the perception that invertebrates are too diverse, abundant and poorly known to allow their inclusion in biodiversity conservation activities and because of the lack of capacity and expertise to include invertebrates in biodiversity conservation programmes (Samways, 1993). Thus continued research, education and awareness programmes, and active conservation initiatives are essential to ensure viable populations of invertebrates in order to maintain ecosystem functions, and to conserve the large proportion of biodiversity.

The research conducted for this thesis was at the microhabitat level, which may be considered a small scale within the broader landscape. However, since the ground-dwelling invertebrates included in this study are flightless, they are likely to be influenced by environmental factors (season and vegetation communities) at this scale. This scale was therefore considered a logical starting point for a study of the impact of changes to the environment at the microhabitat level on invertebrates.

In this study, an attempt to link the effect of refugia on invertebrate diversity to the production of refugia by elephants was carried out. Elephant usage of habitat was assigned an index of utilisation, refugia generated as a result of utilisation were recorded and ground-dwelling invertebrates at each site were sampled. This project should be considered as the first step in assessing invertebrate use of refugia provided by elephants at a small scale. For future studies, it may be useful to scale such a project up and to compare invertebrate diversity before and after the introduction of elephants to an area. Alternatively, such studies could include comparisons of diversity in areas with and without elephants. However, the areas would need to be replicated (at least three sites with a fence line contrast or three area where elephants are to be introduced). The time and elephant density required for impacts to be measurable at a large scale are unknown, but would need to be determined, so additional sites with different durations of elephant habitation and different elephant densities should be investigated as well. Vegetation types may also influence impacts and therefore replicates within different vegetation communities need to be factored in. In addition, a sound understanding of the distribution of invertebrates and those environmental factors structuring communities at the study area are necessary to avoid confusing impacts of elephants with trends determined by other factors, such as previous land use (conservation land, cattle farm) and differences in factors such as vegetation, altitude, aspect and soils. Thus a study of the impacts of elephants on invertebrates at a large scale is likely to be a long-term and costly undertaking.

The aim of this project was to assess the effect that habitat alteration by elephants has on the diversity of selected ground-dwelling invertebrates. Habitat alteration in this study was considered as the provision of logs and dung by elephants as potential refuge niches for invertebrates. Elephant habitat alteration, refugia production and the associated refugia use by ground-dwelling invertebrates were investigated in terms of spatial (vegetation types) and temporal (season and age of dung) variation across the two reserves.

Results from the study showed that a wide range of unique invertebrate species specialise in exploiting decomposing wood and elephant dung as a habitat niche and are dependent on these refuge sites for their survival. The results obtained from this study illustrated higher invertebrate diversity, abundance and species richness in areas with refugia than in areas without refugia, which demonstrated the importance of the two refuge substrates (logs and elephant dung) for maintaining saproxylic biodiversity.

This project showed that the impact of elephants on vegetation types, the resultant production of refugia (logs and dung) and the associated ground-dwelling invertebrates that used the refugia varied spatially across different vegetation types in the two reserves. Significant spatial variation in elephant utilisation of vegetation at Madikwe Game Reserve was identified with use being heaviest in the fine-leafed nutrient rich *Acacia* veld and lowest in the broad-leafed nutrient poor *Combretum* woodlands (Scholes, *et al.,* 2003).

Spatial differences in invertebrate abundance, species richness and diversity associated with the refugia were observed between the three vegetation types sampled at Makalali Game Reserve. Habitats classified as heterogeneous have been shown in a number of studies to contain greater diversity of organisms (Dangerfield & Telford, 1992, Siemann, 1998). When compared to homogeneous habitats, those that are considered to be heterogeneous have many more microhabitats within the system and hence can support greater numbers of species (Druce, 2000, Whitmore, 2000). The same conclusion was drawn from this study, with the refugia within the mixed bushveld habitat supporting the highest levels of invertebrate diversity, compared to the more homogeneous mopane vegetation type.

In addition to spatial variation in elephant impact on vegetation, the study at Madikwe Game Reserve also showed strong temporal variation in utilisation of woody vegetation by elephants, with higher production of logs in winter than in summer. The temporal variation of invertebrate abundance, species richness and diversity associated with the refugia was higher in summer than in winter. Although not quantified, it was observed that within the low elephant impact areas, other agents of disturbances, such as fire or the natural senescence of trees could potentially contribute to refugia production. In order to fully isolate and understand the role that elephants play in refugia production, this project should ideally be replicated in an area with no elephants but again natural differences will need to be considered in invertebrate communities.

The impacts of elephants on invertebrates did not only vary seasonally, but the age of elephant dung also strongly influenced the invertebrate community. Dung beetles were the first group of invertebrates to colonise the dung. As the microclimate of the dung changed with time, conditions became ideal for other invertebrate communities. Over the eight-month period, dung beetle communities were followed by millipedes that used the dung for egg laying and desiccation avoidance (Lawrence, 1966). The abundance of spiders did not vary significantly with age of dung. This suggests that the spiders were opportunistically sampled and were most probably not using the dung as a refuge site but rather as a potential site for capturing prey. Finally, as the microhabitat of the dung became drier, the ant and termite communities were able to utilise the dry elephant dung (Scholes & Walker, 1993) at the end of the experiment.

To guide management decisions regarding elephant/vegetation interactions and the resultant consequences for biodiversity as a whole rather than just for vegetation, the following factors need to be taken into account: the role or combination of biotic and abiotic factors needs careful consideration in the context of ecosystem function and interaction with elephant impacts, all impacts must be interpreted within a spatial and temporal framework and not just as a point in time assessment and while managers feel a sense of urgency to deal with the "problem" immediately, an informed decision will needs to integrate temporal and spatial studies on as many components of biodiversity influenced by elephants, and all possible outcome scenarios should be investigated with modelled with supporting data from studies such as this.

The impacts of elephants on biodiversity are complex and cannot be seen in isolation from other ecosystem processes and drivers such as rainfall, fire and surface water availability. There is evidence that suggests that in areas where their dispersal is confined, elephants can both reduce diversity and play a role in creating habitat for certain species, thereby helping to maintain and promote greater diversity. Results from this study support the latter scenario, that refuge substrates such as logs and dung facilitated by elephant disturbance on vegetation maintains diverse saproxylic fauna that is distinct from fauna associated with other habitat elements. Hopefully, the results from this study will provide additional and alternative scientific information that will assist conservation managers to resolve elephant management issues in a way that complies with the mandate of conservation organizations and with the National Environmental Management: Protected Areas Act, 2003 (ACT No. 57 OF 2003).

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Appendix 3.1

Brief description of the three centipede orders sampled in this project

Geophiolomorpha consists of 16 genera with 72 species in Southern Africa. Representatives from this order are elongated, worm like, organisms with 31 to about 181 pairs of legs. Known as 'earth-dwellers' these centipedes are very seldom seen on the surface of the ground or exposed to the surface. Earth centipedes live largely in loose soil or damp mould into which they may burrow (Lawrence, 1984). They are predominately carnivorous but certain species will on occasion feed on plant material (Eason, 1964).

There are ten South African genera that make up Scolopendromorpha. A single species is found in four of the genera. Two of the genera, *Cryptops* and *Cormocephalus* have comparatively large number of species, with 12 and 23 species respectively. Members of this order have approximately 21 to 23 pairs of legs. They have a wide range of prey, ranging from mice, toads, small geckoes, snakes insect and spiders to small birds (Lawrence, 1934, Cloudely-Thompson, 1958).

Lithobiomorpha are soft-bodied organisms with 15 pairs of legs. They are classified as carnivorous feeders, occasionally consuming soft-bodied creatures (worms and slugs) and larvae, however insects form the bulk of their diet. They are found under stones and are therefore referred to as 'stone-dweller'. In South Africa they are most frequently located under rotting wood or in forest leaf litter (Lawrence, 1984).

Appendix 3.2

Brief description of the three millipede orders sampled in this project (Lawrence, 1987).

Polydesmida

Individuals from this order are easily distinguished by their moderate size and the comparatively few segments that they have. Eyes are absent throughout the entire order. Of all the diplopod orders, Polydesmida is the richest in species and has the greatest diversity of colour and form. They are described as light-avoiding creatures that retreat into crevices in wood or under bark. Their habit of burrowing into soil and feeding upon woody material plays an important role in breaking soil and vegetation hence assisting in the formation of humus.

Sphaerotheriida

Members of this order are also known as 'pill-millipedes' or *Sphaerotherium*, meaning 'round-animal'. The action of rolling into a ball when threatened is an adaptation that ensures that all the vulnerable parts of the organism are safely hidden beneath the hard covering of its armour-like exterior. Individuals are sedentary in habit, unrolling at night to feed on woody debris, decaying and living parts of plants and during the daylight hours seeking refuge in damp shady places.

Spirostreptida

These are commonly referred to as 'thousand-legs' or 'shongololos'. They are elongated worm-like millipedes with a large number of segments. Individuals from this order are the most common of all millipedes whose habitat ranges from gardens to open bushveld.

Adults of this group are often described as scavengers and corprohages that show very little discrimination in their choice of food. Spirostrepids are usually found in damp earthy places, wet soils, among decaying leaves and under pieces of rotting bark.

Appendix 4.1

Sample of the data sheet used for mega-herbivore browsing study at Madikwe Game Reserve, 2000

Site Number: ________________ **Orientation:** ______ **Date:** ______________ **Locality:** ______________________________

Transect / Nest No.: ________________ **Dimensions:** ______ **m by** ______ **m**

Sample Stratum: ________________ **Community Description :** ____

Scribe: ________________ **Latitude:** ________________

Metricians: ________________ **Longitude:** ________________ **Page** ____ **of** ______ **pages**

Species Code	Num. Live Stms.	Num. Dead Stms.	Diam/s. (cm)	Old Diam. (cm)	Hght. (m)	HBC (m)	D1 (m)	D2 (m)	St.	Typs.	C/R Util. Inds.	Brk. Rem. Inds.	Ages	Agts.	G.R.	DCon	UCon	RCon	PD	Dist A	Dist L	Dist R
xxxx xxxx x	xx	xx	xxx.xx	xxx.xx	xx.xx	xx.xx	xx.xx	xx.xx	xx	xx	x	x.x	x	xx	x	x	x	x	x	xx.xx	xx.xx	xx.xx

Appendix 4.2

The codes and their explanation used for the vegetation sampling at Madikwe Game Reserve, 2000.

State of the Individual (St.)

Code	Description
01	Normal Growth
02	Live – Leaves all Lost during Winter
10	Coppice Growth from Larger (Older) Dead Stem
11	Coppice Growth from Accumulated Browsing of Young Plant
12	Coppice Growth from Repeated Fire
13	Coppice Growth from Repeated Moisture Stress
14	Cut Down – Still Living
20	Senescent
30	Tree Dead - Main Stem Partially Broken
31	Tree Dead - Main Stem Completely Broken (Pollarded)
32	Tree Dead - Main Stem Pushed Over (Partially Uprooted)
33	Tree Dead - Main Stem Debarked
34	Tree Dead - Main Stem Intact. Accumulated Branch Removal
35	Tree Dead – Debarking and Branches / Stems Removed
50	Tree Dead – Intact – Cause of Death Unknown
51	Tree Dead – Intact – Killed By Moisture Stress
52	Tree Dead – Intact - Dead From Shading
53	Tree Dead – Intact - Dead From High Light
54	Tree Dead – Killed By Combination Of Moisture Stress and Branch Removal
55	Tree Dead – Killed From Combination of Shading and Branch Removal
56	Tree Dead Killed by Fire
60	Tree Dead – Totally Uprooted
70	Top Kill – Drought Dieback
71	Top Kill - Frost Dieback
72	Top Kill – Dieback From Debarking
80	Windfall

Type

01	Whole Plant Utilized
02	Whole Branches Removed from Canopy
03	Branch Ends Removed
04	Leaves Stripped
05	Bark Removed
06	Roots Removed
07	Accidental Damage
08	Dieback of Main Upright Branches/Stems from Top Down
09	Dieback of Branches/ Branch Ends from Shade
10	Main Stem/s Cut/Eaten Back

Canopy Volume, Root Volume, Leaf Volume Utilization Index (C/R Ut.Ind.)

Code	Description
0	0 % of Volume Removed
1	1 % - 10 %
2	11 % - 25 %
3	26 % - 50 %
4	51 % - 75 %
5	76 % - 90 %
6	91 % - 99 %
7	100 %

Debarking – Circumference (Brk.)

	Percentage of Circumference
1	1 % - 10 % Of The Circumference Of The Stem Removed
2	11 % - 25 %
3	26 % - 50 %
4	51 % - 75 %
5	76 % - 90 %
6	91 % - 99 %
7	100 %

Debarking - Stem Height (Brk.)

	Percentage of Stem Height
1	1 % - 10 % of height of stem
2	11 % - 25 % of height of stem
3	26 % - 50 % of height of stem
4	51 % - 75 % of height of stem
5	76 % - 90 % of height of stem
6	91 % - 100 % of height of stem
7	Whole stem plus branches

Agent (Agt.)

Code	Description
1	Elephant
2	Giraffe
3	Kudu
4	Eland
5	Black Rhinoceros
6	Other Browsers
7	Human
8	Moisture Stress
9	Flooding
10	Shading
11	High Light
12	Fire
13	Frost
14	Wind
15	Accidental
16	Unknown
17	Insects

Age of Utilization (Age)

Code	Description
1	< 6 months
2	> 6 months

Growth Responses (G.R.) to Branch Removal, Stem Breaking and Debarking

Code	Description
1	Coppice Growth
2	No Coppice Growth - Vigour Appears Unaffected
3	No Coppice Growth - Vigour Appears Reduced (Tree Dying)
4	Tree Dead

Continuation (UCon.)

Code	Description
1	Canopy Removal, Stem Breakage, Bark Removal on Same Tree
1	Canopy Removal On Same Tree, But of Different Age or Type
1	Canopy Dimensions On Next Line Are New Dimensions After Felling

Continuation (DCon.)

Code	Description
1	Stem Diameter And Number Of Stems On Next Line Are From The Same Individual

Appendix 4.3

Species list of all invertebrates collected at Madikwe Game Reserve, North Western Province, South Africa.

Species determinations have been done as far as possible. Identifications that were not possible have been left at either genera level or taken down to morphospecies level.

Focal group	**Family**	**Genus**	**Morpho/species**
Ants	Formicidae	*Camponotus*	sp
	Formicidae	*Camponotus*	*cinctellus*
	Formicidae	*Camponotus*	*vestitus*
	Formicidae	*Leptogenys*	*furtiva*
	Formicidae	*Monomorium*	*junodi*
	Formicidae	*Odontomachus*	*troglodytes*
	Formicidae	*Pachycondyla*	*caffraria*
	Formicidae	*Pheidole*	sp
	Formicidae	*Polyrhachis*	*schistacea*
	Formicidae	*Tetramorium*	*setuliferum*
Centipedes	Scolpendridae	*Cormocephalus*	*anceps segnis*
	Henicopidae		gen sp.
	Henicopidae	*Lamyctes*	*africana*
	Henicopidae	*Lamyctes*	*sinuta*
	Henicopidae	*Lamyctes sp.*	*gr sinuta*
	Henicopidae	*Lamyctes*	sp
	Scolpendridae	*Rhysida*	*afra afra*
	Scolpendridae	*Scolopendra*	*morsitans*
	Geophilomorpha		sp
Millipedes	Dalodesmidae	*Gnomeskelus*	sp
	Harpagophoridae	*Zinophora*	*diplodonta*
	Odontopygidae		juv
	Odontopygidae	*Chaleponcus*	*spathulatus*
	Odontopygidae		sp2
	Odontopygidae		sp1
	Spirostreptidae		juv
	Spirostreptidae		sp1
	Spirostreptidae	*Doratogonus*	*rugifrons*
	Spirostreptidae		sp2
	Spirostreptidae	*Lophostreptus*	sp
	Spirostreptidae	*Synophryostreptus*	*punctatus*
	Spirostreptidae	*Lophostreptus*	n. sp

Focal group	**Family**	**Genus**	**Morpho/speceies**
Scorpions	Scorpionidae	*Opistophthalmus*	*fitzsimonsi*
Spiders	Ammoxenidae		1,2,3
	Araneidae		2,3,4
	Caponiidae		1
	Ctenidae		2,3
	Gnaphosidae		1,2,3,4,5,6,7
	Lycosidae		1,2,3,4,5,6,7
	Miturgidae		1,3
	Oxyopidae		1,3,6
	Palpimanidae		1
	Pisauridae		4
	Prodidomidae		1,2,3,4
	Scytodidae		1,2
	Sparassidae		4
	Telemidae		1,2
	Tetragnathidae		1
	Theraphosidae		3,4
	Thomisidae		1,2,4,5,7,8
	Zodariidae		2,3
Termites	Macrotermitinae	*Macrotermes*	*michaelseni*
	Macrotermitinae	*Odontotermes*	*latericius*
	Macrotermitinae	*Macrotermes*	*vitrialatus*
	Macrotermitinae	*Allodontermes*	*rhodesiensis*
	Macrotermitinae	*Odontotermes*	*badius*
	Macrotermitinae	*Hodotermes*	*mossambicus*

Appendix 5.1

Species list of all invertebrate collected at Makalali Private Game Reserve, Limpopo Province, South Africa.

Species determinations have been done as far as possible. Identifications that were not possible have been left at either genus level or taken down to morphospecies level.

Focal group	**Family**	**Genus**	**Morpho/species**
Ants	Formicidae	*Camponotus*	sp
	Formicidae	*Camponotus*	*vestitus*
	Formicidae	*Camponotus*	*cinctellus*
	Formicidae	*Leptogenys*	*furtiva*
	Formicidae	*Monomorium*	*junodi*
	Formicidae	*Odontomachus*	*troglodytes*
	Formicidae	*Pachycondyla*	*caffraria*
	Formicidae	*Pheidole*	sp
	Formicidae	*Polyrhachis*	*schistacea*
	Formicidae	*Tetramorium*	*setuliferum*
Millipedes	Dalodesmidae	*Gnomeskelus*	sp
	Harpagophoridae		juv
	Harpagophoridae	*Zinophora*	*diplodonta*
	Harpagophoridae	*Zinophora*	sp
	Harpagophoridae	*Zinophora*	*similis*
	Odontopygidae		juv
	Odontopygidae	*Chaleponcus*	*acanthophorus*
	Odontopygidae	*Spinotarsus*	sp1
	Odontopygidae	*Spinotarsus*	sp2
	Odontopygidae	*Spinotarsus*	sp3
	Spirostreptidae		juv
	Spirostreptidae		juv sp1
	Spirostreptidae	*Doratogonus*	*rugifrons*
	Spirostreptidae	*Bicoxidens*	*brincki*
	Spirostreptidae	*Lophostreptus*	sp
	Spirostreptidae	*Triaenostreptus*	sp
	Spirostreptidae	*Lophostreptus*	*rugosotriatus*
	Sphaerotheriidae	*Sphaerotherium*	juv
	Sphaerotheriidae	*Sphaerotherium*	sp1
	Sphaerotheriidae	*Sphaerotherium*	sp2

Focal group	**Family**	**Genus**	**Morpho/speceies**
Termites	Macrotermitinae	*Macrotermes*	*michaelseni*
	Macrotermitinae	*Odontotermes*	*latericius*
	Macrotermitinae	*Macrotermes*	*vitrialatus*
	Macrotermitinae	*Allodontermes*	*rhodesiensis*
	Macrotermitinae	*Odontotermes*	*badius*
	Macrotermitinae	*Hodotermes*	*mossambicus*
Spiders	Agelenidae		1, 2
	Araneidae	*Argiope*	1
	Ctenidae	*Ctenus*	sp
	Gnaphosidae		1,3,4,5,6,8
	Lycosidae		1,2,3,4,5,6,7,8,9
	Miturgidae	*Cheiracanthium*	*furculatum*
	Miturgidae	*Cheiracanthium*	sp
	Oxyopidae	*Hamataliwa*	sp
	Oxyopidae	*Oxyopes*	sp
	Oxyopidae	*Oxyopes*	1,2,3
	Palpimanidae	*Iheringia*	*biplagiata*
	Philodromidae	*Tibellus*	*minor*
	Pisauridae	*Perenethis*	sp
	Salticidae		1,2,3,4,5,6,8,9,10
	Sparassidae	*Olios*	sp
	Theraphosidae	*Pterinochilus*	sp
	Thomisidae	*Heriaeus*	*crassispinus*
	Thomisidae	*Heriaeus*	*transvaalicus*
	Thomisidae	*Runcinia*	*flavida*
Centipedes	Scolpendridae	*Cormocephalus*	*westwoodi dispar*
	Oryidae		sp1
	Scolpendridae	*Cormocephalus*	*buttneri*
	Scolpendridae	*Scolopendra*	*morsitans*

Appendix 5.2

Jaccard's similarity coefficient for the number of species shared between all sites within the three vegetation types (mixed bushveld – MB, mopane – MOP & riverine – RIV) and the three treatments (Control – C, Dung – D & Log – L). A value of 100 represents complete similarity and 0 represents different species. All values have been multiplied by 100 for ease of interpretation. The shaded areas represent sites within the same vegetation type and treatment.

Sites	MB C	MOP C	RIV C	MB D	MOP D	RIV D	MB L	RIV L
MB C	X							
MOP C	22	X						
RIV C	18	12	X					
MB D	35	14	17	X				
MOP D	33	18	18	35	X			
RIV D	31	15	26	39	35	X		
MB L	26	15	16	35	33	25	X	
RIV L	27	16	23	42	42	35	33	X

Appendix 5.3

Jaccard's similarity coefficient for the number of species shared between all sites within the three vegetation types (mixed bushveld – MB, mopane – MOP & riverine – RIV). A value of 100 represents complete similarity and 0 represents different species. All values have been multiplied by 100 for ease of interpretation. The shaded areas represent sites within the same vegetation type. The numbers represent the site number within a particular vegetation type.

Sites	MB 1	MB 2	MB 3	MB 4	MB 5	MOP 1	MOP 2	MOP 3	MOP 4	MOP 5	RIV 1	RIV 2	RIV 3	RIV 4	RIV 5
MB 1	X														
MB 2	27	X													
MB 3	26	31	X												
MB 4	24	27	25	X											
MB 5	23	30	24	26	X										
MOP 1	11	16	13	11	21	X									
MOP 2	13	29	22	18	22	15	X								
MOP 3	16	17	25	35	26	14	24	X							
MOP 4	14	23	22	24	10	5	14	13	X						
MOP 5	9	23	18	8	22	15	11	24	4	X					
RIV 1	12	26	28	22	11	6	10	5	18	10	X				
RIV 2	26	38	33	35	23	20	26	30	21	16	29	X			
RIV 3	16	21	18	21	16	21	17	21	10	17	7	32	X		
RIV 4	19	33	23	25	19	9	32	30	36	16	15	46	28	X	
RIV 5	11	18	29	28	17	17	13	13	29	18	17	35	26	25	X

Appendix 5.4

The invertebrate groups, families and species unique to each of the treatments,(sites with no refugia (control) and sites with refugia (logs and dung)) that was sampled during the experimental trial at Makalali Private Game Reserve.

Substrate	Taxa	Family	*Genus*	Species
Control	Spider	Corinnidae		sp1
Control	Spider	Gnaphosidae		sp5
Control	Spider	Lycosidae		sp3
Dung	Spider	Agelenidae		sp2
Dung	Spider	Ctenidae	*Ctenus*	sp
Dung	Spider	Gnaphosidae		sp4
Dung	Spider	Sparassidae	*Olios*	sp
Dung	Spider	Lycosidae		sp1
Dung	Spider	Lycosidae		sp2
Dung	Spider	Lycosidae		sp7
Dung	Millipede	Odontopygidae	*Spinotarsus*	sp2
Dung	Spider	Salticidae		sp2
Dung	Spider	Salticidae		sp5
Dung	Centipede	Scolpendridae	*Cormocephalus*	*anceps segnis*
Dung	Centipede	Scolpendridae	*Scolopendra*	*morsitans*
Dung	Millipede	Spirostreptidae	*Triaenostreptus*	sp
Dung	Spider	Theridiidae	*Zeonina*	sp
Dung	Spider	Thomisidae	*Runcinia*	*flavida*
Log	Spider	Agelenidae		sp1
Log	Spider	Araneidae	*Argiope*	sp1
Log	Spider	Miturgidae	*Cheiracanthium*	*furculatum*
Log	Spider	Miturgidae	*Cheiracanthium*	sp
Log	Spider	Gnaphosidae		sp3
Log	Millipede	Harpagophoridae	*Zinophora*	*diplodonta*
Log	Millipede	Harpagophoridae	*Zinophora*	sp
Log	Spider	Oxyopidae	*Hamataliwa*	sp
Log	Spider	Palpimanidae	*Iheringia*	*biplagiata*
Log	Spider	Philodromidae	*Tibellus*	*minor*
Log	Spider	Salticidae		sp4
Log	Spider	Salticidae		sp8
Log	Spider	Salticidae		sp9
Log	Spider	Thomisidae	*Heriaeus*	*crassispinus*
Log	Spider	Thomisidae	*Heriaeus*	*transvaalicus*

Appendix 5.5

The invertebrate groups, families and species unique to each of the three vegetation types irrespective of treatment sampled during the experimental trial at Makalali Private Game Reserve.

Vegetation type	Taxa	Family	Genus	Species
Mixed Bushveld	Spider	Agelenidae		sp1
Mixed bushveld	Spider	Agelenidae		sp2
Mixed bushveld	Spider	Araneidae	*Argiope*	sp1
Mixed Bushveld	Spider	Miturgidae	*Cheiracanthium*	sp
Mixed Bushveld	Centipede	Scolpendridae	*Cormocephalus*	*anceps segnis*
Mixed Bushveld	Spider	Ctenidae	*Ctenus*	sp
Mixed bushveld	Spider	Gnaphosidae		sp3
Mixed Bushveld	Spider	Thomisidae	*Heriaeus*	*crassispinus*
Mixed Bushveld	Spider	Thomisidae	*Heriaeus*	*transvaalicus*
Mixed bushveld	Spider	Palpimanidae	*Iheringia*	*biplagiata*
Mixed Bushveld	Spider	Lycosidae		sp7
Mixed Bushveld	Spider	Salticidae		sp1
Mixed bushveld	Spider	Salticidae		sp2
Mixed Bushveld	Spider	Salticidae		sp4
Mixed bushveld	Spider	Salticidae		sp5
Mixed bushveld	Spider	Salticidae		sp6
Mixed Bushveld	Millipede	Sphaerotheriidae	*Sphaerotherium*	sp2
Mixed Bushveld	Millipede	Odontopygidae	*Spinotarsus*	sp2
Mixed bushveld	Spider	Theridiidae	*Zeonina*	sp
Mixed bushveld	Millipede	Harpagophoridae	*Zinophora*	*diplodonta*
Mopane	Spider	Corinnidae		sp
Mopane	Spider	Gnaphosidae		sp4
Mopane	Spider	Lycosidae		sp1
Mopane	Spider	Sparassidae	*Olios*	sp
Mopane	Spider	Thomisidae	*Runcinia*	*flavida*
Mopane	Millipede	Spirostreptidae	*Triaenostreptus*	sp
Riverine	Spider	Miturgidae	*Cheiracanthium*	*furculatum*
Riverine	Spider	Oxyopidae	*Hamataliwa*	sp
Riverine	Spider	Lycosidae		sp2
Riverine	Spider	Lycosidae		sp3
Riverine	Spider	Lycosidae		sp4
Riverine	Spider	Lycosidae		sp9
Riverine	Spider	Oxyopidae	*Oxyopes*	sp1
Riverine	Spider	Salticidae		sp8
Riverine	Spider	Salticidae		sp9
Riverine	Spider	Philodromidae	*Tibellus*	*minor*

Appendix 6.1

Species list of all invertebrate collected for the invertebrate community composition change experiment at Makalali Private Game Reserve.

Species determinations have been done as far as possible. Identifications that were not possible have been left at either genus level or taken down to morphospecies level.

Focal group	**Family**	**Genus**	**Morpho/speceies**
Ants	Formicidae	*Camponotus*	sp
	Formicidae	*Camponotus*	*cinctellus*
	Formicidae	*Pheidole*	sp
Millipedes	Odontopygidae	*Chaleponcus*	*acanthophorus*
	Odontopygidae	*Spinotarsus*	sp1
	Odontopygidae	*Spinotarsus*	sp3
	Odontopygidae	*Spinotarsus*	juv
	Sphaerotheriidae	*Sphaerotherium*	sp1
	Sphaerotheriidae	*Sphaerotherium*	sp2
Spiders	Gnaphosidae		6,7,8
	Lycosidae		1,6,7
	Miturgidae		1
	Theraphosidae		2
	Thomisidae		3
Termites	Macrotermitinae	*Macrotermes*	*michaelseni*
	Macrotermitinae	*Allodontermes*	*rhodesiensis*
	Macrotermitinae	*Odontotermes*	*badius*
	Macrotermitinae	*Hodotermes*	*mossambicus*

Appendix 6.2

Elephant dung illustrating the different quantity of fruit content during each season of collection at Makalali Private Game Reserve.

(a) Dung that was collected in summer (February), which clearly shows the large amount of fruit that was already present in the dung.

(b) Dung that was collected in winter (July). The fruit content is extremely low.