Biodiversity of Spiders (Araneae) in a savanna ecosystem and the processes that influence their distribution

by

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ABSTRACT

I describe the spider biodiversity for a savanna ecosystem, assess sampling techniques, investigate surrogate measures of species richness and measure the biotic and abiotic processes affecting spider diversity.

Spiders were sampled at Makalali Game Reserve, Northern Province, South Africa from February to December 1999 using pitfall traps, sweep netting, beating and active searching. A total of 4832 individuals from 268 species (14 potentially new), 147 genera (8 endemic and 2 new records for South Africa) and 37 families (1 new record for South Africa) were recorded.

There was no overall significant difference in spider diversity among different physiognomic habitat types. However, analysing the results at a functional group level revealed that the web builders were significantly affected by the habitat type. Mopane woodland habitat type had the greatest number of web builders and general bushveld the least.

Sweeping and active searching sampled the greatest number of individuals and species respectively. I recommend a combination of at least beating and active searching, which together sampled the highest number of unique species, for efficient and cost effective surveys.

There was a significant relationship between the spider species richness and other invertebrate richness. However, the relationship is not significant when functional groups are considered separately. There was also a significant relationship between the number of species and families and species and genera. However, species level identifications remain ideal for conservation purposes. Inexperienced participants significantly overestimate the number of species. The use of surrogates is not supported by the work conducted in this study.

It is still unclear what biotic and abiotic processes or combination of processes influence spider diversity patterns at the local scale. Different spider functional groups are significantly influenced by different factors. However, habitat diversity (branches and vegetation density) was the most common factor influencing spider diversity. Predicted diversity (modelled using GIS and beta-coefficients from multiple regression analyses) was higher than measured diversity values. While further research into the role of other environmental variables is clearly required, current reserve management should aim to maximise microhabitat structural diversity.
PREFACE

The experimental work described in this dissertation was carried out in the School of Life and Environmental Sciences, University of Natal, Durban, from February 1999 to December 2000, under the supervision of Dr Robert Slotow (University of Natal) and co-supervision of Dr Tanza Crouch (Durban Natural Science Museum).

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.
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CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

The natural environment is under continuing threat from humankind primarily due to the exponential human population growth rate. Alarmingly, the growth rate is not likely to decline for several decades, with the majority of this growth occurring where most of the biological diversity is concentrated (Cincotta, Wisnewski & Engelman 2000).

As the world's population increases, so too do the demands placed on the earth's resources. With exponential growth as it is, it is unlikely that the earth will be able to sustain itself indefinitely (Norton 1986; Pearce & Moran 1994). Uncontrolled population growth leads to declines in biological diversity (McNeely 1994, Tilman 2000). Besides the profound ethical and aesthetic implications, it is clear that the loss of biological diversity has serious economic and social costs (Lovejoy 1986; Heywood 1995; Gates & Folmer 1999).

The destruction of natural habitats results in massive changes to diversity at a variety of levels throughout the world (Tilman 2000). Humans have had a close and mutually supportive relationship with their environment for tens of thousands of years and we can go as far as saying that biological diversity represents the very foundation of human existence (McNeely et al. 1995).

Some of the impacts of humans on the natural environment are irreversible, such as the extinction of species, while others are not, but the challenges of managing natural resources in a sustainable manner has clearly increased (Mooney et al. 1995). This loss of biological diversity is of major concern worldwide (Hafernik 1992; Anon 1993; Pearce & Moran 1994; Bush 1997; White Paper on diversity 1997). In the last decade, there has been a considerable increase in interest of the state of the earth's diversity. Simply looking at the increase in publications on biodiversity since 1992 highlights this. The number of publications has grown rapidly and in 1999 alone there were 705 publications (Figure 1; Institute for Scientific Information (ISI) Database 1995 - 2000).

The last decade has seen a dramatic, worldwide, increase in the attempts to describe, count and identify the earth's biological diversity (Pearce & Moran 1994; Jeffries 1997). Part of the increase has been the recognition of the value of diversity and its importance in maintaining our existence as we know it.

1.2 The value of diversity

The sheer diversity of life is of inestimable value. It provides a foundation for the continued existence of a healthy planet and our own well-being. The loss of biological diversity will
diminish the capacity of ecosystems to provide society with a stable and sustainable supply of essential goods and services (Tilman & Downing 1994; Tilman et al. 1996; Levine & D'Antonio 1999; McCann 2000; Tilman 2000). In addition to its affects on current functioning of ecosystems, many believe that ecosystems rich in diversity gain greater resilience and are therefore able to recover more readily from stresses such as drought or human induced habitat degradation (Tilman 1997; Naeem & Li 1997; Chapin et al. 2000). When ecosystems are diverse, there are a range of pathways for primary production and ecological processes such as nutrient cycling, so that if one is damaged or destroyed, an alternative pathway may be used and the ecosystem can continue functioning at its normal level. If biological diversity is greatly diminished, the functioning of ecosystems is put at risk. Thus, as species disappear, humanity loses food, energy, medicine and industrial products. As genetic diversity erodes, our capacity to maintain and enhance agricultural, forest, and livestock productivity decreases (Ried & Miller 1989, Chapin et al. 2000).

Possibly the greatest value of the variety of life may be the opportunities it gives us for adapting to change. The unknown potential of genes, species and ecosystems is of inestimable but certainly high value. Genetic diversity will enable breeders to tailor crops to new climatic conditions. In addition, there exists the potential that there are still undiscovered cures for known and emerging diseases.

There is possibly no single argument that alone provides irrefutable grounds for attempting to maintain all existing biological diversity. A more general approach, however, recognises that resource values, precautionary values, ethics, aesthetics, and simple self-interest provide an overwhelmingly powerful and convincing case for the conservation of biological diversity.

### 1.3 What is Biodiversity?

Harper & Hawksworth (1994) summarise the history of the term “biodiversity”. It was coined in the 1980’s by Wilson (1988). Since then the use of the term has gained momentum and there have been numerous studies throughout the world which attempt to and measure, quantify and describe the richness and variety of all earth living organisms (Pearce & Moran 1994; Jeffries 1997). Its widespread usage is directly related to the growing awareness of threats facing the natural environments plants and animals and our concerns over its destruction (Holloway & Stork 1991).

Biodiversity has become increasingly used as a conceptual focus for conservation policy and practice in response to one of the strongest themes underpinning the founding work on biological diversity, species extinctions, the numbers of species and extent of ecosystems (Jeffries 1997).

Although widely used, the term “biodiversity” is rarely defined (Jeffries 1997). A
widely accepted definition of the term biodiversity is the expression of the variety and variability of life forms (Ried & Miller 1989; McNeely 1994; Dippenaar-Schoeman 1998; Biodiversity Series 1993). This has further been expanded to include various levels: "The variety of life and its processes. It includes the variety of living organisms, the genetic differences among them, the communities and ecosystems in which they occur, and the ecological and evolutionary processes that keep them functioning, yet ever changing and adapting" (Ried & Miller 1989; Noss & Cooperrider 1994). Clearly biodiversity is a very complex and all embracing concept, that can be interpreted and analysed on a number of different levels and scales (Noss 1990; Pearce & Moran 1994). Usually it is considered at three different levels: genetic (within species), species (species numbers) and ecosystem diversity (Holloway & Stork 1991; Biodiversity Series 1993; Pearce & Moran 1994; Hawksworth 1995; Bush 1997).

Genetic diversity refers to the variety of genetic information contained within an organism. It occurs within and between populations as well as between species. Species diversity refers to the variety of living species both in terms of the numbers of species and their relative abundance. Ecosystem diversity refers to the variety of ecological processes present within ecosystems with respect to habitats, biotic communities, and ecological processes (Biodiversity Series 1993; Pearce & Moran 1994; Jeffries 1997). The primary focus of this study is on species diversity.

1.4 Loss of Biodiversity and Extinction

Human actions, e.g. exploitation, habitat destruction, pollution, ecosystem cascades and mismanagement, cause declines and extinctions of species in very direct ways (Jeffries 1997; Dobson 1996; Ried & Miller 1989; McNeely et al. 1995). The current rate of extinctions of the world's species highlights the urgency of the task of understanding species diversity. Presently, the number of species in the world threatened with extinction far outstrips available conservation resources, and the situation is not likely to improve (Meyers, Mittermeier, Mittermeier, da Fonseca & Kent 2000). Extinctions are now becoming increasingly common and widespread (Dobson 1996; Samways 1996). According to Hafernik (1992) the rate of species extinctions has roughly paralleled patterns of human population growth. Although, extinction of species is not a new phenomenon, Kupchella & Hyland (1993) suggest that human activities have helped to bring the rate of species extinction today close to the rates of mass extinctions of the past.

Furthermore, human activities are placing significantly more species at risk of extinction today than any time in the past as a result of forced environmental change (McNeely et al. 1995). Recent species extinctions and ecosystem collapse suggest that a new crisis may be taking place (Jefferies 1997). These concerns have been coupled with the
realisation that our knowledge of the diversity and variability of plants, animals and microorganisms and the ecosystems in which they occur is woefully incomplete (Heywood 1995). As a consequence we may be losing value species before their usefulness is discovered.

Estimates of the precise rates of the loss of biological diversity are hampered by the absence of any baseline measurement (McNeely 1994). However, it seems likely that the expansion of the human niche by various forms of conversion is geometrically related to extinctions (Pearce & Moran 1994). Over the next century the projected loss of species might be expected to be as high as 20 to 50% of the world's total which represents a rate 1 000 to 10 000 times the historical rate of extinction (Wilson 1988; Pimm et al. 1995). Pimm et al. (1995) are reluctant to give accurate predictions of the rate of extinctions because knowledge of endemic populations is insufficient. However, given that the environment is already heavily utilised by people and given the estimated population growth, the rate of the loss of biodiversity and extinctions is far more likely to increase than to stabilise (McNeely 1994).

The mass extinctions of species, if allowed to persist, would constitute a problem with far more enduring impacts than any other environmental problem. According to the evidence from past mass extinctions, evolutionary processes would not generate a replacement stock of species within less than several million years. What we do in the next few decades will determine the long-term future of the Earth's abundance and diversity of species (Meyers et al. 2000).

Increasing interest is being expressed in environmental issues. This awareness is based on the realisation that the state of the Earth's biological systems is of fundamental importance to human society and that our influence on these systems is increasing exponentially (Heywood 1995). In the light of this increased interest, there are now numerous studies underway throughout the world dedicated to describing and measuring the diversity of the earth. This study is just one of the thousands attempting to measure the biodiversity in an area.

1.5 Measurement of species diversity

Measures of biodiversity are needed to determine the "where" of in situ conservation action rather than the "how", particularly in deciding which combinations of available areas could represent and help sustain the most biodiversity value for the future.

Diversity can be defined by the following general types: alpha (α), beta (β) and gamma (γ). The alpha component refers to the within habitat diversity. This is a measure of the number of species occurring within an area of a given size. The beta component refers to the between habitat diversity. This measures the richness of a potentially interactive assemblage (turnover) of species (Bisby 1995). Gamma diversity is a measure of the total diversity within a large region. This component deals with biodiversity at the landscape level (Noss 1990).
Values for biodiversity are difficult to measure quantitatively. Additionally, there are many biological forms, complexes and parameters of diversity that can be measured (Oates & Folmer 1999). Species richness, i.e. the number of species within a region, is the most fundamental measure of diversity (Cole 1994). Often species richness is used synonymously with species diversity. However, species diversity includes some consideration of evenness and of species abundance (Pearce & Moran 1994, Magurran 1988). There are numerous indices that can be used to calculate the richness and diversity (e.g. the Shannon-Wiener index) but will not be discussed in detail here. Chapter 3 addresses the relative merits of different indices.

One area where diversity measures are useful is conservation, where the general philosophy is: species rich communities are better than species poor ones (Magurran 1988). For the purpose of this study diversity indices will be used to compare diversity patterns in the Reserve. In addition, the underlying biotic and abiotic processes influencing the diversity will be investigated through the application of a spatial information system (see below).

1.6 Factors influencing diversity

Most major terrestrial and freshwater groups are more speciose in tropical than temperate regions, at low elevations than high, and in forests than in deserts (Biodiversity Series 1993; Trevelyan & Pagel 1995; Gaston 2000). On land, diversity is also usually higher in areas of high rainfall and lower in drier areas (Gaston 2000). The richest areas are undoubtedly tropical moist forests. If current estimates of the number of species (mainly insects) comprising the microfauna of tropical moist forests are credible, then these areas, which cover perhaps 7% of the world’s surface area, may well contain over 90% of all species. These global patterns of species diversity are widely accepted throughout the world (Trevelyan & Pagel 1995; Gaston 2000).

Determining why these differences occur has long been the core objective for ecologists (Gaston 2000). The past decade has seen a proliferation of studies documenting broad-scale spatial patterns in biodiversity. However, the reasons for the large-scale geographic variation in species diversity, and in particular for the very high species diversity of tropical moist forests, are not fully understood. A host of global patterns of spatial variation in biodiversity have been explored. Some suggested causes for the differing diversity in different parts of the world can be attributed to climate, area, latitude, altitude; productivity, available resources and habitat complexity to name just a few (MacArthur 1972; Rosenzweg 1995; Trevelyan & Pagel 1995). While there is extensive literature on the patterns of diversity at a global scale, local and regional patterns of diversity have not been considered in such detail.
Understanding the patch dynamics of landscapes has been greatly facilitated through the use of spatial information systems. These systems can adequately examine the hierarchical and spatial complexity of heterogeneous ecological systems. A Geographical Information System (GIS) is a computer-based systems allowing for input, storage, manipulation, analysis and display of spatial and descriptive information (Haslett 1990; Barr & Carter 1995). Multiple data layers can be analysed and displayed (Yonzon, Jones & Fox 1991).

GIS has the capability of easily analysing and updating spatial information quickly and efficiently. It also has a wide variety of applications in research and management (Michelmore 1994). Some uses of GIS applicable to management planning include area measurements, overlay, distance measurements, attribute selection and the ability to facilitate "what if" planning (Yonzon, Jones & Jefferson 1991).

The power of GIS is especially useful when one wishes to overlay species distributions to produce maps of species richness. Maps produced using GIS provide powerful monitoring tools and can provide important regional information about species and habitat distributions (Miller 1994). By using a series of overlaid maps various aspects of spatial distribution of species can be understood (Noss & Cooperrider 1994; Barr & Carter 1995). The highly adaptable mapping and analysis system can easily cope with a wide range of geographical, ecological and biological data sets (Haslett 1990).

GIS uses two types of systems, the raster and vector-based systems. Raster-based systems record spatial information as points in a regular network of grid cells, while vector-based systems use patterns of points, lines with specific magnitudes and directions and areas to represent the data (Haslett 1990). Areas within interconnected vectors are polygons of varying shapes and sizes. Information about the contents of the polygons is stored separately as attribute files.

In the current context GIS was used to relate the diversity of spiders from a site to the biotic and abiotic processes of that site. The diversity of spiders was correlated with measures of precipitation and temperature or other environmental factors.

1.7 Conservation of Biodiversity

The conservation of biological diversity seeks to maintain the life-support system provided by nature in all its variety, and the living resources essential for ecologically sustainable development (UNEP 1992). The earth will retain its biodiversity only if humans have the presence to do so and this will only occur when humans realise the extent to which they rely on biodiversity (Tilman 2000).

Conservation of biodiversity is essential for maximising the span of existence of the human species, meeting the needs of future generations and contributing to the stability and robustness of many economic and ecological systems (Tisdell 1997; Tilman 1999). It can only
take place when our knowledge of the organisms around us is enhanced. (Hawkesworth 1991; Dippenaar-Schoeman 1998; Pearson & Caroll 1998). Increasing our knowledge of the organisms on earth is therefore essential.

Our knowledge of the world in terms of numbers of described species, especially for "megadiverse" groups such as arthropods, is remarkably limited (Coddington, Young & Coyle 1996). It is only certain groups such as birds, mammals and flowering plants that our knowledge is reasonably comprehensive (Pearce & Moran 1994; Heywood 1995). However, many species of plants and animals remain completely unknown to science. In comparison our knowledge of invertebrate species is effectively non-existent (Lovejoy 1986; Wilson 1988; Solbrig, Medina & Silva 1996; Colwell & Coddington 1994; Pearce & Moran 1994). At present approximately 1.4 million species of living organisms have been described (Lovejoy 1986).

Accurate knowledge of the number and different types of species in a given community or ecosystem is the basis for understanding how a system functions, and thus how the removal or addition of species may alter that functioning. Knowing which species are present is a prerequisite for understanding the ecological roles of critical community members - what they eat, who eats them, and how they alter the community in which they live. Not knowing how many species are in a community sorely limits the ability to predict the fate of that community under different kinds of anthropogenic stresses (U.S. National Report, 1995).

Sound conservation management depends increasingly on sound knowledge of the biology and dynamics of the species (New 1995).

The worldwide movement towards increasing the knowledge of organisms around us led to the formulation of policies to try and preserve the world's diversity. At the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro in 1992, the world community recognised the necessity of continued economic growth while at the same time maintaining the integrity of the biosphere. Through a global action plan named AGENDA 21, these nations called for increased knowledge of the Earth's biodiversity.

In November 1995 South Africa ratified the Convention on Biological Diversity (CBD) which emanated from the convention. Signatories are obligated to develop a strategic plan for the conservation and sustainable use of biodiversity. Meeting these goals will require an intensive national effort, involving three interrelated scientific missions: to discover, describe and to make an inventory of the species diversity of the world; to analyse and synthesise the information into predictive classification systems that reflect the history of life; and to organise this information in an efficiently retrievable form that best meets the needs of science and society (UNEP 1992). There are many areas of research in South Africa that are poorly covered, one of these being invertebrates. This study will contribute towards the honouring of obligations by South Africa to the Convention on Biological Diversity by
conducting more research on groups that are poorly known. This study deals with one group of invertebrates namely spiders (Araneae).

1.8 The status of invertebrate diversity

Invertebrates are the most diverse and abundant animals in most natural ecosystems but their importance in sustaining those systems is commonly not appreciated (New 1995). Determining the distribution of invertebrates is an integral part of assessing their conservation status and their possible need for management. Invertebrates, and in particular insects, can therefore not be ignored in the assessment of biodiversity (Holloway & Stork 1991).

The number of species in existence varies widely and that of insects ranges from an estimated three to 50 million (Wilson 1988). More recent assessments of available literature estimate the number of species to be closer to 10 million (Dobson 1996). The wide variation in the estimates of the number of insect species in the world arises from the variation in the method of calculation of those estimates (Hawksworth 1991; Solbrig et al. 1996). Samways (1993a) estimates that only 7 - 10% of all insect species have been described and of those, only a small percentage have enough known about their biology to allow the construction of informed conservation plans.

In the past, invertebrates were largely ignored in the design of conservation areas. Their conservation in existing parks and reserves has been incidental (De Wet & Schoonbee 1991; New 1999; Skerl & Gillespie 1999). In South Africa it was only in the 1980's that attempts were made to assess the extent to which conservation included representatives of all the indigenous fauna and flora (Pienaar 1991). Invertebrates were specifically provided for in South Africa in 1985 by the establishment of the Invertebrate Conservation Services Section by the Transvaal (now Gauteng Province) Chief Directorate of Nature and Environmental Conservation (DeWet & Schoonbee 1991).

The reluctance of using invertebrates in conservation studies is mainly because of: (1) the time constraints, (2) lack of knowledge of the taxon (taxonomy, biology and distribution), (3) unstandardised sampling methods and (4) inadequate number of experts to do the species identifications. Furthermore, invertebrates surveys generate very large samples which demand a considerable effort to process in terms of time and expertise (New 1999).

Despite the above negative aspects of working with invertebrates, they represent a group of organisms that are potentially useful when assessing the biodiversity of an area because of: (1) their generality of distribution, (2) trophic versatility, (3) rapid responses to perturbations and (4) ease of sampling (Holloway & Stork 1991).

There are too many undescribed taxa for which the expertise to identify organisms to the level of species does not exist for us to even contemplate surveying the complete diversity. At the current rate it will take several thousand years to describe all the species or
have an idea about the diversity if traditional taxonomic methods are used (McNeely et al. 1995). This is because of (1) the formal determination of species names is time consuming and, in those groups where formal taxonomy is poorly developed, may not be possible; identifications are costly and (2) there are very few professional taxonomists, especially in southern Africa (Oliver & Beattie 1993).

Both the magnitude and the urgency of the task of assessing global biodiversity require that we make the most of what we know through the use of estimation and extrapolation (Colwell & Coddington 1994). Likewise, future biodiversity inventories need to be designed around the use of effective sampling and estimation procedures especially in “megadiverse” groups such as arthropods (Colwell & Coddington 1994; Hawksworth & Kalin-Arroyo 1995).

It is in the light of this problem that other more rapid methods of diversity estimation have been suggested. The use of diversity indicators (Faith & Walker 1996; McGeoch 1998; Noss 1990), higher taxon level identification (family or genus-level) and morphospecies level (Oliver & Beattie 1993) identification as surrogate methods for species richness that may make the task of estimating global species diversity more manageable (Pearce & Moran 1994; Prance 1994; Williams & Gaston 1994; Balmford, Green & Murray 1996; McGeoch 1998). These measurements have often proved useful but limitations are often not recognised (Balmford et al. 1996a). Furthermore, other studies have emphasised inaccuracy of conclusions based on indicator species (Lawton et al 1998; Van Jaarsveld et al. 1998). Although it is very appealing to use quicker methods for biodiversity assessment the data obtained may not be adequate for conservation decision making, e.g. rare and endemic species may be missed when higher levels of identification are used.

Despite this, indicator taxa and higher taxon level identifications are being adopted more widely. This study aims to evaluate the use of indicators, higher taxon level identification and morphospecies level identification as surrogates for species richness, using spiders to test their usefulness.

1.9 Why use spiders for Biodiversity assessments?

Arachnids are an important but generally poorly studied group of arthropods that play a significant role in the regulation of insect and other invertebrate populations in most ecosystems (Russell-Smith 1999).

Previous conservation efforts in South Africa have focused on the larger vertebrates, e.g. the “big five” of Game Parks, while invertebrates were largely ignored and were only incidentally conserved in existing parks and reserves (DeWet & Shoonbee 1991; Dobson 1996). There is now a growing need to conserve all species and not only the large vertebrates (Samways 1990). Surveys of invertebrate fauna have therefore become more important,
especially in conserved areas where conservation strategies are already in place.

Spiders are among the most speciose orders of animals with more than 30,000 species described worldwide (Preston-Mafham & Preston-Mafham 1984). They are ubiquitous generalist predators and are themselves an important food source for other animals. Consequently, a very valuable component of ecosystem functioning (Dippenaar-Schoeman 1979; Nyffeler, Sterling & Dean 1994; Dippenaar-Schoeman & Jocqué 1997; New 1999; Skerl 1999). Spiders also show potential as a group to be used for higher taxonomic surveys. Oliver & Beattie (1996) found that non-specialists could be quickly trained to make remarkably accurate count of spider morphospecies. Furthermore, spiders are gaining favour in ecological studies as indicators of environmental quality as they are diverse, abundant and interact with the environment in ways that sensitively and rapidly reflect environmental stress, especially those living in specialised habitats (e.g. caves) (Uetz 1991; Abensperg-Traun et al. 1997; Churchill 1997; Churchill & Arthur 1999; Doran 1999). Downie et al. (1999) has shown that spiders are even useful for effective management of agricultural land in Scotland. They have also been shown to be important biological control agents in agricultural ecosystems (Dippenaar-Schoeman 1979; Riechert 1984; Bishop & Riechert 1990, Wise 1993; Nyffeler et al. 1994). The potential use of spiders in modelling biodiversity has been highlighted by Downie et al. (1999). They may even be a useful focal group for wholesale invertebrate conservation (New 1999).

Despite their ecological role in many ecosystems, high diversity, documented threats and the known imperilment of some species, spiders have not featured high on the priority list for conservation (DeWet & Shoonbee 1991; IUCN 1996; New 1999; Skerl 1999).

It is encouraging to know that conservation issues are shifting and spiders are featuring in some conservation efforts. However, considerable work is still needed to clarify the usefulness of spiders as indicators, relevance to high taxon surrogacy and to develop standardised sampling techniques (New 1999). This study aims to contribute towards an improved understanding of these issues.

1.10 Spiders in South Africa

In 1997, Dippenaar-Schoeman & Jocqué provided the first comprehensive overview of spider fauna and the current state of knowledge for the Afrotropical region. An inventory of the spider families, genera and species known from South Africa revealed that the araneofauna is remarkably rich when compared with some other faunas of the world. The Afrotropical region is particularly richly endowed with spiders including, 5,500 species from 71 families. This accounts for two-thirds of the known spider families for the world (Dippenaar-Schoeman & Jocqué 1997). In South Africa, 62 of the world’s 106 spider families occur here and are represented by 428 genera and approximately 2,900 species (Table 1).
Table 1: A comparative summary of the number of families, genera and species in the world and the Afrotropical Region.

<table>
<thead>
<tr>
<th></th>
<th>World</th>
<th>Afrotropical</th>
<th>Southern Africa</th>
<th>South Africa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Families</td>
<td>106</td>
<td>71 (67%)</td>
<td>63 (59%)</td>
<td>62 (57%)</td>
</tr>
<tr>
<td>Genera</td>
<td>3298</td>
<td>893 (27%)</td>
<td>613 (19%)</td>
<td>427 (12%)</td>
</tr>
<tr>
<td>Species</td>
<td>±34000</td>
<td>±5500 (16%)</td>
<td>±3800 (11%)</td>
<td>±2900 (9%)</td>
</tr>
</tbody>
</table>

Compared with the temperate regions in the Northern Hemisphere, ecological surveys of the araneofauna of tropical and subtropical regions of Africa are sparse (Dippenaar-Schoeman & Jocqué 1997, Russell-Smith 1999). Up until the early 1980's knowledge of spider diversity in South Africa had largely been based on casual collecting (Dippenaar-Schoeman; Van den Berg & Van den Berg 1989). In South Africa, most ecological studies on spiders consists of surveys in agroecosystems (Dippenaar-Schoeman 1979; Van Den Berg & Dippenaar-Schoeman 1991) and limited surveys from forest and pine plantations (Van Den Berg & Dippenaar-Schoeman 1988) and savanna (Dippenaar-Schoeman, Van Den Berg & Van Den Berg 1989).

However, in 1997 the Plant Protection Research Institute, Biosystematics Arachnida unit decided to launch the "South African National Survey of Arachnida" (SANSA) in accordance with the country's obligations to the Conservation of Biological Diversity (CBD). The main aim of SANSA is to compile an inventory of the arachnid fauna of South Africa that will provide essential information, helping with issues concerning the conservation and sustainable use of our biological diversity. There are numerous projects underway throughout South Africa which are all aimed at improving the knowledge of the arachnid fauna in South Africa (Appendix 1.1). The current study, based at Makalali Private Game Reserve, Northern Province, South Africa, will contribute to part of this wider survey of spider fauna in South Africa.

1.11 Methods for sampling spiders

There are numerous collecting techniques available for sampling invertebrates (Sutherland 1996). There are biases associated with different collecting techniques and consequently, the environment may be undersampled when only one technique is used (New 1995). Different collecting techniques can misinterpret certain components of spider assemblages. For instance, pitfall traps, which are commonly utilised for spider collecting, are effective for ground-dwelling spiders but underestimate the diversity and abundance of the plant-dwelling individuals (Green 1999).

Scientists sampling spiders for survey purposes have utilised many different methods,
e.g. pitfalls, sweep nets, beating, active searching / hand collecting and suction sampling (litter extraction). Unfortunately, there is no consensus on which technique(s) is most appropriate for spider biodiversity surveys.

Some scientists (Coddington et al. 1996; Oliver & Beattie 1993; Slotow & Hamer 2000) recognise that standardised methods are essential and stress the urgency of developing them. It is imperative to standardise and integrate the sampling techniques for biodiversity assessments because different studies can not be compared unless identical methods have been used (Coddington et al. 1996). These statements were made almost a decade ago but many studies on biodiversity continue to use unstandardised methods.

Spiders, by virtue of their small size, are able to exploit very small and specific features within the environment. Spiders are known to occupy nearly every terrestrial habitat (Preston-Mafham & Preston-Mafham 1984). For the purpose of biodiversity survey work, it is convenient to sample the spider fauna at different layers of each habitat separately (Russell-Smith 1999). For the purpose of this work, three strata can be recognised (1) the soil layer / ground layer (species active on the soil surface); (2) the field layer (species active in the grass or herb layer) and (3) the tree and shrub layer. Different methods that target these specific strata were used. The sampling techniques will be dealt with in more detail in Chapter 2.

1.12 The savanna ecosystem

It is not only certain organisms like invertebrates where more research is needed, but certain biomes have also been poorly represented in biodiversity work. One of these biomes is the savanna biome in South Africa. This study falls within this biome.

There is little consensus on the precise definition for the savanna. Savanna vegetation is characterised by a continuous graminoid stratum, with an open stratum of woody vegetation (Cole 1982; Huntley & Walker 1982). Savannas generally develop in soils of low fertility, under a regime of strongly seasonal rainfall, and are submitted to recurrent disturbances through herbivory and fire (Mooney et al. 1995). Tropical savannas are characterised by having a seasonal climate with cool dry winters and hot rainy summers (Solbrig, Medina & Silva 1996).

The savanna biome is broadly divided into three main vegetation types; shrubland, bushland and woodland, according to the density and height of the woody component of the vegetation (Low & Rebelo 1996), and the range in physiognomy and floristic diversity within savannas is considered high. The major environmental delimiting factor for the biome, is a lack of sufficient rainfall which prevents the woody component dominating, while the effects of fire and grazing maintain grass layer dominance (Low & Rebelo 1996).

Savannas are one of the world’s major biomes and cover approximately half of the African land surface, making it the most extensive African biome, but it is also one of the
biomes that has received the least ecological study (Scholes & Walker 1993). Southern Africa’s savannas, often referred to as the “bushveld”, cover 46% of the land area. In South Africa it covers one-third of the land area (Low & Rebelo 1996; Scholes 1997).

The best known feature of the African savanna fauna is the diversity and biomass of large mammals. Savannas are important in the southern African context because it is the basis of the African livestock and eco-tourism industry, making it a valuable contribution to the formal economy. One of the consequences of this is that most southern Africa savanna research is biased towards the studies on large mammals, the tree-grass interaction, fire and production ecology (Cowling, Richardson & Pierce 1997). Extensive work has been carried out in the Nylosvley Nature Reserve (Scholes & Walker 1993). However, even in this extensively studied area little work has been done on spiders. The importance of savanna ecosystems in the ecotourism industry together with a poor understanding of expected levels of diversity for this biome, warrants further investigation.

1.13 Study site: Makalali Private Game Reserve

The study was carried out at Makalali Private Game Reserve, Northern Province, South Africa (29° 09’ S, 30° 42’E), a broad-leaved savanna ecosystem. Makalali is situated close to the western border of Kruger National Park and extends over 10 000 hectares. The Reserve is the focal point for the establishment of a much larger conservation area that will embrace other private reserves in an attempt to advance the Lowveld’s green frontier towards the Drakensberg escarpment.

The area was not always populated by humans due to the existence of diseases such as sleeping sickness, malaria and blackwater fever. The introduction of vaccines has controlled these diseases and irrigation has permitted the agricultural industry to grow, particularly citrus. In recent years, however, much farmland has been turned into private wildlife reserves with either trophy hunting or ecotourism as income-generators (Butchart 1996).

Makalali was formed in 1993 by the initial purchase of 7 500 hectares of cattle ranchland, and the subsequent acquisition of adjacent farms which enlarged the Reserve to over 10 000 hectares. Part of the area had been subjected to overgrazing, but through an ongoing process of land and water rehabilitation, and the reintroduction of large mammals, the area is in the process of being reclaimed (Butchart 1996).

The Reserve is situated on the Lowveld plains (450 meters above sea level) of Northern Province, South Africa. The landscape is a combination of undulating terrain and rocky outcrops, which protrude above the bushveld. There are two dominant vegetation types in the Reserve, mixed lowveld bushveld and mopane woodland (Acocks 1975; Low & Rebelo 1996; Funston 1993). Apart from the bushveld, the vegetation is different on the rocky
outcrops and there is a narrow strip of riverine vegetation that borders the Makutswi River.

At Makalali, the habitats vary by topography and soil. Eight different habitat types are recognised in the Reserve. These include riverine areas, drainage lines, disturbed habitats (bush-cleared areas), mopane woodland, rocky outcrops and three different mixed bushveld types all with different soil types. The five habitat types that were sampled in the Reserve included mopane woodland, rocky outcrops, and the three mixed bushveld types.

Nine different plant communities within in the eight habitat type are recognised, one with two subgroups and one with three subgroups. The plant communities recognised are as follows: (1) Riparian closed woodland, (2) drainage line thicket, (3) Colophospermum mopane low closed woodland, (4) Cissus cornifolia - Commiphora africana – Lannea schweinfurthii low thicket (including two subgroups), (5) Combretum apiculatum – Acacia nigrescens low closed woodland (including three subgroups), (6) Low closed grassland, (7) Combretum apiculatum – Dalbergia melanoxylon low open woodland, (8) Combretum apiculatum – Commiphora africana low thicket and (9) Combretum apiculatum – Acacia nigrescens low closed woodland. Tree species commonly found in these plant communities are listed in Appendix 1.2. All full list of tree species occurring in the Reserve is provided in Appendix 1.3.

The Reserve has a sub-tropical climate with a wet summer and a dry winter. The average annual rainfall is 491.5 mm, but years of severe drought or above-average rainfall are not uncommon. The rainy season starts in October with the maximum rainfall falling between November and February. The daytime temperatures range from 3 °C in the winter months can reach as high as 36 °C in the summer months (Butchart 1996).

There is one large river, the Makutswi River, which runs through the Reserve and is a tributary of the Olifants River. This river bisects the Reserve almost in half and runs from west to east. Artificial water points have been created in the Reserve with some of them being supplied by borehole water, especially during the dry winter months.

The Reserve’s primary activity is ecotourism. Besides the focus on the large mammals such as lions, rhino and elephant, the game rangers at the Reserve provide the guests with information on the smaller components of the ecosystem such as invertebrates. In addition to the scientific knowledge gained from this study, the rangers were educated on the biology of the spiders occurring in the Reserve, especially large conspicuous species such as the golden orb-web spiders (Nephila sp.) and the garden orb-web spiders (Argiope sp.) which are abundant and widely distributed in the Reserve.
1.14 The focus of the current study

The present study is subdivided into four main sections: (1) a description of the species composition at the different sites, (2) an evaluation of four sampling techniques used to sample spiders, (3) an evaluation of the usefulness of surrogate methods for species richness using spiders as an example and (4) determining the underlying processes that drive the diversity at different sites through the use of GIS technology.

Chapter 2 focuses on the methods used to sample spiders for biodiversity purposes. Four different sampling techniques were used to survey spiders in this Reserve. Selected methods sampled spiders from all microhabitats (soil, field and tree layer) within the environment. The advantages and disadvantages of the various methods are explored further in this Chapter. The consensus in literature on which method or methods are best for complete sampling of the environment remains unresolved. Recommendations for standardised sampling techniques for spiders are provided.

Chapter 3 of this study focuses on providing a baseline inventory of the diversity of spiders in five representative habitats throughout the Reserve. The species composition occurring in the different habitat types is described. The diversity, evenness and richness of spiders at different sites in the Reserve is provided. Sites are compared to each other based on similarity. A checklist of spiders sampled from the Reserve is given. The species checklist list will be valuable both to the park staff as well as contributing to the wider survey on arachnids in South Africa.

Chapter 4 evaluated the use of three surrogate methods for species richness. The surrogate methods evaluated included indicators, higher taxon level identification and the use of morphospecies level identifications by non-specialists. The use of spiders as indicators for wholesale invertebrate diversity was evaluated. Some speciose families of spiders, e.g. Thomisidae and Salticidae, were evaluated as indicators of wholesale spider diversity. The higher taxon level identification (genera and family level) were evaluated as surrogates by comparing the higher level identification with the true species richness. The morphospecies level identification by non-specialists was evaluated using undergraduate students to test the usefulness of this method.

Chapter 5 focuses on the processes (biotic and abiotic) that drive the diversity at the different sites within the Reserve. A multiple regression analysis was performed to determine the best model explaining the diversity of all spiders as well as the diversity of different functional groups. The influence of these processes on the diversity was evaluated using Geographic Information System (GIS) technology. GIS has the capability of modelling relationships between environmental variables and surveyed site attributes. Maps of significant biotic and abiotic factors from the models were generated. The maps were then
overlayed to produce a predictive diversity model for the Reserve. IDRISI and ArcView were used for the GIS analysis.
CHAPTER 2

SPIDER (ARANEAE) BIODIVERSITY: RECOMMENDATIONS FOR A STANDARDISED QUANTITATIVE SURVEY METHODOLOGY

2.1 INTRODUCTION

Spiders, by virtue of their small size, are able to exploit very specific features within the environment and are able to occupy a diverse range of small niches that are not available to larger organisms (Foelix 1996). Spiders are known to occupy nearly every terrestrial habitat, from the peaks of the highest mountain ranges to the depth of the largest caves and pot-holes, from damp marsh to dry desert, anywhere in fact that they can find other arthropods to provide them with a meal. Some spiders even spend part of their life on and in water. They can also be found on coastal dunes and some can tolerate immersion in salt water while the tide is in. The only environment where spiders are absent is from the polar regions (Preston-Mafham & Preston-Mafham 1984). Spiders are an important but generally poorly studied group of arthropods that play a significant role in the regulation of insect and other invertebrate populations in most ecosystems (Foelix 1996; Dippenaar-Schoeman & Jocqué 1997).

Our knowledge of the spider fauna of the world is remarkably limited, particularly in South Africa (Dippenaar-Schoeman & Jocqué 1997). To improve our knowledge of spider fauna surveys are necessary. However, the quality of information obtained from biodiversity surveys is directly related to the sampling protocols used (Conroy & Noon 1996). Areas with low diversity may simply be a reflection of inadequate sampling (Conroy & Noon 1996; Slotow & Hamer 2000). Hence, the sampling protocol used to assess biodiversity is very important. Most previous studies recording biodiversity have used a restricted range of sampling techniques, (e.g. Coetzee et al. 1990; Van den Berg & Dippenaar-Schoeman 1991; Kromp & Steinberger 1992; Van der Merwe et al. 1996) which are likely to have provided a biased sample of the fauna as a whole (Russell-Smith 1999).

There are several issues related to biodiversity sampling that must be taken into consideration. These issues include (1) sampling for all species, (2) sampling all microhabitats, (3) repeatability and standardisation of techniques, (4) efficiency and effectiveness of techniques and (5) biases associated with different techniques.

2.1.1 Sampling for all species and all microhabitats

No single sampling technique could hope to collect all species within an area or habitat. In addition, no sampling technique evenly covers all habitats or habitat patches that occur at a site and most techniques sample a restricted component of the fauna present.
For the purpose of biodiversity survey work, it is convenient to sample the spider fauna at different layers of each habitat separately (Russell-Smith 1999). Conveniently, three strata can be recognised in savannas: (1) the soil layer / ground layer (species active on the soil surface); (2) the field layer (species active in the grass or herb layer) and (3) the tree and shrub layer. A logical progression from this is then to use different techniques that sample these different layers. Four different techniques were selected, each covering a different stratum: (1) sweep netting - targeting the field layer, (2) beating - targeting the tree and shrub layer, (3) active searching - targeting all three layers and (4) pitfall traps - targeting the ground layer.

2.1.2 Standardisation of sampling techniques

Although standard sampling techniques for biodiversity surveys have been attempted (Hammond 1990) the recommendations are not widely adopted thus making comparisons between different sites and studies virtually impossible. It is imperative to standardise and integrate the sampling techniques for biodiversity assessments because different studies cannot be compared unless identical methods have been used.

Some efforts have been made at formulating standard sampling protocols for spiders in tropical forests (Coddington et al. 1996) yet the consensus on which technique(s) is most appropriate for spider biodiversity surveys remains undetermined for savannas.

2.1.3 Efficiency and effectiveness of sampling techniques

Sampling protocols also need to be cost effective and efficient. When selecting efficient sampling techniques, it is important to select methods that are: (1) fast (because time is often restricted and expensive), (2) reliable (because they may need to be used in various areas for the data to be comparable), (3) simple and (4) cost effective (Oliver & Beattie 1993; Coddington et al. 1996; New 1995).

Work has been done to assess the efficiency of sampling techniques for spiders in tropical forests (Coddington et al. 1996), and Heathland vegetation in Australia (Churchill & Arthur 1999) but the relative efficiency of different sampling methods needs to be quantified for biodiversity work being carried out in savannas.

2.1.4 Sampling technique biases

There are numerous collecting techniques available for sampling invertebrates (e.g. sweep nets, pitfall traps, beating, active searching, suction sampling / leaf litter extraction, canopy fogging etc. (Sutherland 1996). Inevitably there are biases associated with the different collecting techniques and consequently, the environment may be undersampled when only
one technique is used (New 1995). The four main methods assessed in this study include sweeping, beating, active searching and pitfall traps.

This study provides the opportunity to assess the relative merits of these sampling techniques and to provide a standardised technique for sampling spiders in savannas. The aims of this study was to investigate the relative advantages and disadvantages of the four above mentioned collecting techniques used in spider biodiversity surveys. The objectives were (1) to determine which sampling technique or combination of techniques is best suited for spider biodiversity surveys and (2) to provide a standardised sampling protocol for spiders in savannas.

2.2 METHODS

The study was carried out at Makalali Private Game Reserve, Northern Province, South Africa (29° 09' S and 30° 42'E), a broad-leaved savanna ecosystem. Makalali is situated close to the western border of Kruger National Park and extends over 10 000 hectares. For a more detailed description of the study site and habitat types refer to Chapter 1. During a preliminary survey (February 1999) six methods were used to sample spiders in eight different habitat types within the Reserve. The methods used included: sweep netting, beating, active searching, tree bark traps, crypto trap and pitfall trapping (see below).

Five different habitat types were then selected and eight replicate sites were sampled within each habitat type in the following three periods: autumn (late February – early March 1999), spring (late October - November 1999) and mid summer (December 1999). Over the entire sampling period, sweep netting, beating, active searching and pitfall trapping was done at 40 sites throughout the Reserve (refer to Figure 2.1). These methods were selected because they sampled species from all three strata layers in each habitat (the soil/ground layer, the field layer and the tree/shrub layer).

2.2.1 Sampling techniques

Sweeping

Sweep netting was done using a sweep net, 0.6 m in diameter with a 1.2 m long handle. Sweep netting was done by sweeping through the grass and herb layer. Each sweep covered an arc of approximately 1.5 m through the vegetation on every alternate step. A sample consisted of two transects of 20 sweeps each, totalling 40 sweeps from each sampling site. Each transect was chosen from the centre of the site and the path that allowed uninterrupted sweeping was chosen. The transects were at least 10 m apart and new sweep transects were chosen in each sampling period. The contents from the sweep nets were placed into a bucket with a small amount of ethyl alcohol to kill all the invertebrates. The contents were sorted on
Figure 2.1: Sample sites within Makalali Private Game Reserve. All sites belonging to similar habitat types are coded the same colour.
the same day. Spiders and other invertebrates were separated from vegetation.

**Beating**

Beating was done by firmly striking about four branches (all with a diameter of greater than 2 cm) on a tree with a mallet (1.5 kg) approximately ten times each. Eight trees, all different species, were selected at random in all sites. In some habitat types, e.g. mopane woodland, it was not possible to sample different tree species as the habitat was dominated by a single tree species, *Colophospermum mopane*. In this case eight trees of the same species were sampled. A white beating net was held below the branches during beating. A total of 320 beats were taken from each site. The tree species, height and diameter of the branch being beaten were recorded. The spiders were then removed from the net with a pooter and placed into a sample jar (Sutherland 1996).

**Active searching**

Active searching was initially done by marking off two quadrats of 2 m x 2 m (8 m²) in each habitat. Each quadrat was selected at random and the ground, shrubs, rocks, logs and stones were thoroughly searched for spiders. Each site was searched for a total of 2 hours. In early summer (October – November 1999) the sampling protocol was changed to include eight quadrats of 1 m x 1 m each. This represented the same area searched (8 m²) as before and the same amount of time (2 hours) was spent searching but the heterogeneity included into samples was increased. Spiders were collected either using the hand to jar technique or a pooter (Sutherland 1996). Specimens from a single quadrat at each habitat type were pooled for analysis.

**Pitfall trapping**

Pitfall traps, usually straight-sided containers sunk level with the soil surface, (Sutherland 1996) were set out in each habitat. A glass test tube (25 mm diameter x 150 mm depth) was used as the pitfall trap. These were inserted into the ground so that the lip was flush with the soil surface and contained a 20 ml solution of 3 parts 70% ethyl alcohol and 1 part 30% glycerol (Samways 1996). The ethyl alcohol acted as a preserving agent and the glycerol prevented the ethyl alcohol from evaporating. They were set out in each site as a two by five grid with traps placed ten meters apart from each other. Traps were left for a period of two weeks and the contents of the pitfall traps were collected and placed into a sample bottle and later sorted. Sorting involved separating the spiders from the other invertebrates. Spiders were then sorted into morphospecies and the other invertebrates were sorted to order level.

There were several problems associated with the pitfall traps. There are wild animals in the Reserve and on two occasions the animals interfered with the pitfall traps. Firstly, at
one site during the preliminary survey (February 1999) some Blackbacked jackal (Canis mesomelas) ate the tags marking the location of the pitfalls and also tried to dig up the pitfalls. With the tags missing it made finding the pitfalls more difficult. Secondly, at another site, also during the preliminary survey, a troop of baboons (Papio anubis) removed pitfalls and managed to dislodge the contents on the ground. In addition, 25% of the pitfalls (from two sites) were flooded on the last day that they were left in the ground in the November sample and 50% (from ten sites) in the December sampling. Thus there is a high risk of loosing samples due to rain.

2.2.2 Additional spider sampling techniques

During the preliminary study (February 1999) two additional methods for spider sampling were included namely tree bark traps and crypto traps. Tree bark traps are usually made out of strips of brown corrugated paper, wrapped around the trunk of a tree and fastened with string. The traps should ideally be left for several weeks (Van den Berg & Dippenaar-Schoeman 1988). The tunnels of the paper provide a refuge for spiders. This method is biased towards species living permanently on the trunks of trees. Tree bark traps were placed on two trees in each habitat. Builders plastic (500 mm x 500 mm) was used and was attached to the trunk of the tree with string at a height of approximately 1 m. It was expected that the plastic would provide a refuge for certain bark spiders. After a week these were removed and any spiders residing under the plastic were collected.

Crypto traps are not conventionally used to sample spiders but were included in the preliminary study as they were being used for other invertebrate work (millipedes) occurring simultaneously at this Reserve. Two crypto-traps (clear corrugated plastic sheets), measuring approximately 25cm x 25cm, were buried at random positions under about two centimetres of soil. These traps were left for one week. Spiders that had taken refuge under these shelters were then collected.

Both the crypto and tree bark traps were relatively inefficient when compared to the other four methods. Very low numbers of individuals were sampled by these methods (2 and 4 individuals respectively from eight sites). They were therefore excluded from the remainder of the study.

Three additional techniques which were not employed in this study largely because of time and logistical constraints included suction sampling, leaf litter extraction and canopy fogging. Suction sampling and leaf-litter extraction methods have been used in numerous studies and have been successful (Gibson, Hambler & Brown 1992; Coddington et al. 1996; Dobyns 1997). These techniques sample species living in the litter layer and would be more appropriate for areas with a large leaf litter content e.g. forests.
Canopy fogging allows the collector to sample areas of a plant or tree that are inaccessible to a sweep net, beating or active searching. The higher canopy of trees and shrubs can be fogged with a fast-acting pesticide, such as synthetic pyrethroid. The dead specimens fall from the trees onto sheets. This method is more frequently used in forested areas where the canopy is far beyond reach and has the disadvantage of killing non-target organisms in the process.

2.2.3 Cost efficiency and effectiveness sampling techniques

For taxonomic purposes adults are often essential for species level identifications. The number of adults and juveniles sampled using the different techniques was compared. An effective method would be one that samples the greatest proportion of adults, allowing identification to the level of species. Other factors which were considered as important for a technique to be effective was the total number of individuals, species, number of unique species and number of different families sampled by each technique.

An efficient technique would sample the most individuals in the shortest space of time and at the least cost. Determining the number of species sampled per hour assessed the efficiency of the different techniques. Other important factors that were considered for the efficiency was the repeatability of the technique, the cost of the equipment need for the technique and the time investment needed for sorting of the specimens.

2.3 Data analysis

All statistical analysis was performed using SPSS. The normality of data distribution was checked by performing a Kolmogorov-Smirnov goodness of fit test. Where necessary, data that were not normally distributed was log transformed. A one way ANOVA was done to test for significant differences among the sampling technique for the species and individuals sampled. In all cases the assumptions of the ANOVA were met (Kolmogorov-Smirnov test $P < 0.05$)

2.4 RESULTS

A total of 4832 individuals from 268 species, 147 genera and 37 families were sampled in Makalali Private Game Reserve during the study period using the four different sampling techniques. Although the sampling effort was considerable not all species have been sampled.

There was a marked difference in the number of individuals and species caught by each sampling method: sweep netting (2150 individuals and 120 species), beating (885 individuals and 125 species), active searching (1450 individuals and 188 species) and pitfall traps (174 individuals and 56 species) (Figure 2.2). The greatest number of individuals (2150) were sampled using the sweep net but it is interesting to note that this method does not
sample the highest number of species. The highest numbers of species were sampled by active searching (188), followed by the beating (125). The pitfalls produced the fewest individuals and species.

There was a highly significant difference in the number of individuals sampled by different techniques, with sweeping and active searching sampling the most and pitfalls sampling the least (ANOVA: $F_{3, 146} = 78.151, P < 0.0001$). There was also a highly significant difference in the number of species captured using different techniques, with sweeping and beating sampling the most and pitfalls the least (ANOVA: $F_{3, 146} = 63.346, P < 0.0001$; Figure 2.2).

Very few families were captured by all four techniques. There was a highly significant difference in the number of families sampled among the different techniques, with active searching sampling the greatest variety of different families (32), followed by pitfalls (19), beating (18) and sweeping (16), (ANOVA: $F_{3, 146} = 53.770, P < 0.0001$; Figure 2.3). Again, although sweeping yields the highest number of individuals, the number of families represented is lowest. Further, although pitfall traps had the lowest numbers of species and individuals they yield a relatively large proportion of the total families sampled (52%). However, there are no families sampled by pitfalls that were not sampled by at least one other method (Figure 2.4).

Beating yields the greatest number of unique species for any particular method (16%) while sweeping yields a very low percentage (6.25%) that are unique to this technique (Figure 2.4).

### 2.4.1 Sampling for all species and all microhabitats

In most sampling periods the species accumulation curves indicate that a saturation level has been reached (Appendix 2.1). The same patterns are seen when sampling methods are considered separately (Appendix 2.2). However, there is some indication that the full compliment of species have not yet been found (new species are still being added) this is because there are new habitats, e.g. riverine, that would contribute towards increasing the species list. Likewise by adding a new method, e.g. fogging, the species list would increase.

### 2.4.2 Cost effectiveness and efficiency

#### Effectiveness

Juveniles comprised 85% of all spiders sampled and the remaining 25% were made up of adult males and or females (Table 2.1). Adults are important taxonomically, as the characteristics of mature specimens are often required for species level identifications. The pitfalls sampled the highest number of adults (28.5%), making them the most effective
Figure 2.2: The effect of sampling technique on the number of individuals (σ) and species (○) sampled at Makalali Private Game Reserve. The mean and 95% confidence limits are presented.
Figure 2.3: The effect of different sampling techniques on the number of families. The mean and 95% confidence intervals are presented. N = number of different families sampled with each technique.
Figure 2.4: The effect of sampling technique on the percentage of shared and unique spider families obtained from Makalali Private Game Reserve.
method, followed by active searching (13.12%), beating (10.15%) and sweeping (7.21%).

_efficiency_

Sweeping requires more time investment than alternative techniques that samples spiders alone, e.g. active searching or beating. Approximately 20 minutes were needed to complete the sweeping from each site thus requiring a total of 13.33 person hours for the entire study (excluding the time required to sort).

It took approximately 1 1/2 hours to beat eight trees in a site, totalling 60 person hours required to complete 40 sites (excluding the time required for sorting and identifying specimens). Considerably less effort is required for sorting of beating samples than sweeping as there are no other invertebrates or plant material that first need to be separated out. Approximately 80 person hours were required to actively sample the 40 sites in this study (excluding setting up quadrats and sorting of specimens) and approximately 21 hours were required for inserting and collecting of the pitfalls at each sampling period. The total number of person hours required for pitfalls for this study was 64 hours (excluding time required for sorting). Again, the sorting of the contents from the pitfalls require more effort than for a technique that samples spiders alone, e.g. beating or active searching.

The number of person hours required to sample 40 sites is summarised in Table 2.1. The efficiency of the different methods (expressed as the number of species captured per hour) was then calculated by dividing the number of species sampled by each method by the number of person hours required to complete the 40 sites. Sweeping was the most efficient method followed by active searching, beating and pitfalls.

Table 2.1: Total number of hours required to sample 40 sites using the different sampling techniques and the efficiency of each method.

<table>
<thead>
<tr>
<th>Method</th>
<th>Sweeping</th>
<th>Beating</th>
<th>Active searching</th>
<th>Pitfalls</th>
</tr>
</thead>
<tbody>
<tr>
<td>EFFECTIVENESS</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of individuals</td>
<td>2150</td>
<td>885</td>
<td>1450</td>
<td>174</td>
</tr>
<tr>
<td>Number of adults</td>
<td>155(7%)</td>
<td>90(10%)</td>
<td>191(13%)</td>
<td>51(28%)</td>
</tr>
<tr>
<td>Number of juveniles</td>
<td>1989(93%)</td>
<td>797(90%)</td>
<td>1265(87%)</td>
<td>128(72%)</td>
</tr>
<tr>
<td>Number of species</td>
<td>120</td>
<td>125</td>
<td>188</td>
<td>56</td>
</tr>
<tr>
<td>Number of unique species¹</td>
<td>6%</td>
<td>17%</td>
<td>16%</td>
<td>0%</td>
</tr>
<tr>
<td>Number of families</td>
<td>16</td>
<td>18</td>
<td>32</td>
<td>19</td>
</tr>
<tr>
<td>EFFICIENCY</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time (h)</td>
<td>13.33</td>
<td>60</td>
<td>80</td>
<td>64</td>
</tr>
<tr>
<td>Species per hour</td>
<td>9.00</td>
<td>2.08</td>
<td>2.35</td>
<td>0.88</td>
</tr>
</tbody>
</table>

¹The unique species are a percentage of the total spiders captured by a particular method.
In order to decide which method was best, the sampling requirements, repeatability and standardisation, number of habitats sampled, efficiency and effectiveness and biases, needed to be examined more carefully. To determine which methods were most efficient and cost effective it was necessary to rank the various components. The data presented in Table 2.2 are based on subjective estimates for the different methods and are rated for their efficiency and effectiveness. The efficiency assessed the species sampled per hour, expertise required, which refers to the level of difficulty of executing the task, the repeatability, which refers to the ease at which other researchers can follow the same protocols and the cost of the equipment needed to undertake the task.

Ranking the components from Table 2.1 assessed the effectiveness of the techniques. A value of 1 represents the best or most and a value of 4 represents the least or worst. The lowest overall score represents the best method. Based these results active searching was the best methods for sampling spiders followed by beating and sweeping and lastly pitfalls. A combination of sweeping, active and beating was the best.

Table 2.2: Rank values for the efficiency and effectiveness of different sampling techniques (where 1 = the highest or most efficient and 4 = the lowest or least efficient).

<table>
<thead>
<tr>
<th>Method</th>
<th>Sweeping</th>
<th>Beating</th>
<th>Active</th>
<th>Pitfalls</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>EFFECTIVENESS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of individuals</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Number of species</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Number of unique species</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Number of families</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Total adults</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Total juveniles</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td><strong>EFFICIENCY</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species per hour</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Repeatability¹</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Expertise²</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Cost of equipment</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Ease of sorting³</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>27</td>
<td>27</td>
<td>24</td>
<td>32</td>
</tr>
</tbody>
</table>

¹Repeatability = the ease at which other researchers can follow the same protocols
²Expertise = the level of difficulty of executing the task
³Ease of sorting = time investment required for sorting the samples

2.4.3 Composition of species sampled with the different methods

There was a clear difference between the spider assemblages sampled and the technique used (Figure 2.5). Additionally, the sampling techniques tend to be biased towards certain spider assemblages.
Figure 2.5: The influence of different sampling techniques on the spider functional group composition at Makalali Private Game Reserve. N = total number of species sampled with a particular technique.
Sweeping, which targeted spiders in the field layer, collected a high proportion of plant and web-dwelling individuals but very few ground-dwelling individuals. Beating, which targeted the tree layer, also sampled a high proportion of plant and web-dwellers but very few ground-dwellers (Figure 2.5). The following families were abundant in the field and tree layers: orb-web weavers (Araneidae), jumping spiders (Salticidae), crab spiders (Thomisidae), lynx spiders (Oxyopidae) and sac spiders (Miturgidae).

Active searching, targeting the ground, field and tree layer, sampled individuals from all three functional groups in almost equal proportions (Figure 2.5). This method sampled a species of barychelid, a family not previously thought to occur in South Africa (Appendix 3.3).

The pitfall traps sampled mainly ground-dwellers and also a small proportion of plant-dwellers (Figure 2.5). Ground-dwelling individuals that were abundant included flat-bellied ground spiders (Gnaphosidae), the wolf spiders (Lycosidae) and baboon spiders (Theraphosidae).

The community composition of spiders changed significantly with time. There was a significant interaction between different spider functional group and sampling period ($F_{4,119} = 5.791, P < 0.0001$) with plant-dwellers and web builders showing similar responses over time while the ground wanderers decrease considerably in the December sampling period. The drop off of ground wanderers in the December period could be a consequence of the flooding of many pitfalls and hence the lower trap catches (Figure 2.6).

A short description of the general biology and appearance of the families sampled in Makalali Private Game Reserve is presented in Appendix 3.2 and also on the CD-ROM enclosed.
Figure 2.6: The effect of sampling period on the spider guilds (where O = ground wanderers, □ = plant wanderers and △ = web builders). The mean and 95% confidence limits are presented. N is the number of sites within the sampling period. Note the low number of ground wanderers captured in December probably reflects flooding of pitfalls rather than reduced presence within the community.
2.5 DISCUSSION

2.5.1 Sampling for all species

While this study represented a major sampling effort there are undoubtedly more species in the Reserve than the 268 found (Chapter 3). Studies that include hyperdiverse groups such as arthropods can only hope to detect a portion of the species, particularly for large sites with many microhabitats. Samples may be too small and species collected are only a small portion of the total richness (Norris 1999). In addition, by including other sampling methods such as canopy fogging, leaf litter sampling and night sampling, more species would be found. Other methods were not included here due to logistical constraints. Night active sampling was not done because of the nature of the Reserve (e.g. the presence of dangerous predators like lions: Panthera leo). Sampling was also concentrated more in the western and upper eastern part of the Reserve (Figure 2.1). Further sampling, other techniques and the inclusion of the eastern and riverine habitats may extend the species list considerably.

The data from this study show that there was a significant difference in numbers of species and individuals between the different sampling techniques \( (P < 0.05) \). Green's (1999) results also showed a significant difference between different sampling methods. In this study, very few of the total number of families were captured by a single method, indicating spider families have very specialised habitats and may represent unique functional groups (Foelix 1996).

2.5.2 Sampling all microhabitats

Hammond (1990) has stressed the importance of using as wide a range of sampling techniques as possible in invertebrate diversity surveys. He convincingly shows that a combination of different techniques is needed to adequately sample the beetle diversity. By using a combination of sampling techniques the ecosystem was more adequately sampled and the chances of finding all species was greatly increased. Green (1999) supports this but in addition emphasises the need to conduct both diurnal and nocturnal sampling to get true representations of spider assemblages. As already mentioned while this may be ideal, active nocturnal sampling is not always feasible.

Different collecting techniques may misinterpret the species assemblages because of biases toward certain strata of the environment. For instance, pitfall traps, which are commonly used for spider collecting, (e.g. Uetz & Unzicker 1976, Curtis 1980; Coetzee et al. 1990) are effective for ground dwelling spiders but underestimate the diversity and abundance of the plant dwelling individuals (Green 1999). Additionally, important rare species may be missed when a single technique is used (e.g. in a study of ants Hinkley & New 1997). In a study on ants, pitfall traps were effective yet they failed to collect the full range of species...
A study done by Coddington et al. (1996) on the spiders in a Hardwood Forest has also shown that many different techniques were necessary to sample all species present. This emphasises that a combination of different techniques should be used for survey purposes. Despite this, single techniques are used in biodiversity surveys and the results are extrapolated to represent all target taxa.

For spiders, more than one trapping method was essential. This was because they occupy different layers of a habitat. Sampling for spiders would be most efficient when all three layers (ground, field and tree layer) are covered. Therefore, using only one sampling technique, especially a passive one (pitfalls), may sample only one functional group of a large taxon, whereas a range of techniques sample a much more representative spectrum of the total diversity within higher taxon (Coddington & Cowell 1994). However, the need to increase the number of sampling techniques used should be weighed in against the need to reduce the complexity in the sampling protocol to minimise species overlap (Green 1999). Furthermore, there are practical constraints to using too many techniques (e.g. managing too large samples).

2.5.3 Biases associated with different techniques.

This study showed that sampling techniques have biases for certain assemblages of species. Sweeping and beating targeted mainly plant wanderers and web builders, pitfalls targeted mainly ground and plant wanderers and active searching targeted species from all three functional groups.

There was a large overlap in the community structure sampled by sweeping, beating and active searching. Thus species living in the field layer (plant wanderers) tend to have a more general distribution and are readily sampled using different techniques. However, the families and species sampled using sweeping were not always the same as those found by beating or active searching. There are several species that were only captured by one particular method.

Sweeping was a very effective method, sampling many individuals and species. The technique has worked well for other studies, sampling spiders from the field layer and collecting large samples in a short space of time (Van den Berg & Dippenaar-Schoeman 1988; Dippenaar-Schoeman, Van den Berg & van den Berg 1989; Coetzee, Dippenaar-Schoeman & Van den Berg 1990). However, this method is biased towards invertebrates that are easily dislodged from the vegetation (Sutherland 1996). In addition, many non-target species were also captured by this method making the sorting considerably more expensive in terms of time. Furthermore, there are ethical considerations in killing all non-target invertebrate species.

Beating was used to sample species that are well-camouflaged or hidden on plants in the shrub and tree layer (Coetzee et al. 1996). Spiders can be knocked off the tree or shrub by
hitting the branch with a mallet or stick and catching the spiders in a net or sheet as they are dislodged off the branches. It is a rapid technique that results in the collection of a large numbers of invertebrates. This method catches only the target organisms which makes the sorting considerably less for this method as opposed to sweeping or pitfalls. In this study this method sampled the highest number of unique species indicating that some spider species live in more restricted environments and will only be sampled with this method. One of the obvious biases of this method is its tendency to favour species that are easily dislodged (Sutherland 1996).

Active searching involves looking for spiders in a demarcated area for a fixed period of time. The area is thoroughly searched for any spiders. One of the most important disadvantages of active searches is that it is subject to sampler bias (Norris 1999). The success of hand collecting is dependent on the skills, experience, knowledge and individual commitment of a particular worker (Chapter 4). However, searching skills are quickly acquired and different people can quickly be taught where to look and how to catch spiders so the difference among particular workers can be quickly minimised. In addition species may be scared off as the searcher approaches. However, this is a very efficient method and spiders can be sampled from the ground, field and the tree layer simultaneously (Coddington et al. 1996; Dobyns 1997). In this study, active searching not only generated the greatest diversity in terms of the family and species richness but also greatly contributed the total number of individuals. More adults were found in active searches than either the beating or sweeping methods which increased the chances of making identifications because often, adult males or females of a species are required to make species level identifications. This is also the only method that sampled a species from the trapdoor baboon spider (Barychelidae) family. This was highly significant as this family was previously not thought to occur in South Africa. This family has been recorded previously from Ethiopia and Zaïre.

Pitfall trapping is a passive sampling technique that has been used extensively in sampling invertebrate fauna for biological diversity studies (Brennan, Majer & Reygaert 1999). The appeal of pitfall trapping lies in the ease with which traps can be set and the replicability of trapping over space and time. Other advantages of this trapping technique include (1) many species can be trapped over a short time span, (2) they sample continuously and many habitats can be sampled simultaneously and (3) they yield high numbers from a range of species (Uetz 1979; Bultman et al. 1982; Topping & Sutherland 1992; Sutherland 1996; Majer 1997; Brennan et al. 1999).

Pitfalls are also commonly used by arachnologists. However, the validity of their use is questioned by some (Bultman, Uetz & Brady 1982). Although frequently used, problems in the interpretation of pitfall data have been recognised (Luff 1975; Topping & Sutherland 1992; Abensperg-Traun et al. 1997). Pitfalls are biased towards spiders that are ground
dwelling yet the data interpretation from pitfalls often assumes it to be representative of all taxa.

Majer (1978) feels that pitfalls may not be effective for species associated with soil, deep litter and vegetation. His results indicate that pitfalls alone underestimate the complete ant community and it is very likely that similar patterns would be present in spiders as some are better able to avoid being trapped.

In addition, the efficiency of trapping of invertebrates by pitfalls changes with habitat structure, either because of a dilution effect or because of the effects of movement behaviour of invertebrates. Many scientists (Curtis 1980; Sutherland 1996; Zulka, Milasowzsky & Lethmayer 1997; Russell-Smith 1999) have shown that the capture rates in pitfalls will be influenced by environmental factors such as the nature of the surrounding vegetation. The dilution hypothesis stems from the fact that the habitats with a more complex structure have more surface area available for the invertebrates to move around on, hence, the number of pitfall traps per unit area is effectively reduced. (Topping & Sutherland 1992; Melbourne 1999). Furthermore, a study done by Melbourne (1999) revealed that habitat structure was a very important determinant of the pitfall catches and the less structured a habitat the greater the pitfall catches. Capture rates in pitfalls are also dependant on the numbers of species on the ground surface at any given time (population density), on the level of species-specific activity and trap arrangement and trap size (Luff 1975, Abensperg-Traun et al. 1997; Russell-Smith 1999). The dependence on activity may result in an inaccurate (biased) sample of the total invertebrate community in an area (Uetz 1979; Brennan et al. 1999).

Different species have different susceptibility to being caught according to trap size, behaviour and the strata in which they are active (Greenslade 1993). Zulka et al. (1997) are doubtful that pitfalls effectively reflect species abundance because of the different degrees of activity between species or sexes thus no inferences can be made on the density between species or sexes. For example, certain male spiders will be very active on the soil surface when in search of a mate and the females may less mobile. This makes males more likely to be captured by pitfalls than females, but we cannot infer that males are more abundant than females as the trap catches would simply be a reflection of their relative activity.

2.5.4 Efficiency and effectiveness of techniques

When all factors (number of individuals; species; families; unique species; total adults, total immatures, species per hour, expertise required, repeatability and cost of equipment and time required for sorting) were considered active searching was the best techniques to use for sampling spiders. This method requires very little equipment, thus rendering it cost effective when funding is limited. Mesibov, Taylor & Brereton (1995) confirm the result from this study and show that active searching was more efficient than other methods like pitfall traps.
Sweep netting was shown to be a quick, low-cost, and efficient way of collecting large numbers of invertebrates, making it well suited for survey purposes. This method samples many individuals but only a small proportion of these were adults. This may have implications when trying to identify the species and the sampling efficiency of the technique may be outweighed by the time it takes to process the samples. However, by conducting sampling at different time of the year adults were often collected in later sampling efforts and the juveniles could then be identified. However, if long-term sampling is required to sample adults the method can no longer be regarded as quick and cost effective.

In this study pitfalls were efficient at sampling the highest percentage of adult individuals, increasing the chance of identification at the level of species. However, this technique performed poorly in many other respects and it was the least cost effective method overall. Pitfalls are a risky time investment and a single storm can destroy all efforts and result in a loss of samples (Figure 2.6). Animals, in these types of reserves can also be a source of risk as they may interfere with the traps. In addition, the use of pitfalls requires that the researcher either needs to remain in an area for an extended period of time, while the traps are in the ground or return later to remove the pitfalls. This has implications on the cost of travelling, especially if the study area is far away. The use of pitfalls is not recommended.

2.5.5 Repeatability and standardisation of techniques

If a trapping technique was standardised, then any competent field worker should be able to apply the standardised procedure. To standardise techniques across studies, more than one of the same techniques needs to be included in every survey. Thus standardisation will provide results which are comparable with those from other, similarly standardised trappings (New 1999). Standardisation also allows for later validation and calibration within both time and space, i.e. repeatability (Mooney et al. 1995). Furthermore, a range of methods that are standardised and integrated will provide statistically and ecologically meaningful data (Churchill & Arthur 1999). By advancing and developing standardised survey techniques, the utility of spiders as conservation tools will be enhanced (New & Gillispie 1999). The urgency of this task has been recognised by some (Coddington et al. 1996; Oliver & Beattie 1993; Slotow & Hamer 2000).

In this study, sweeping was a very repeatable method and it can easily be standardised to be incorporated into different surveys. Likewise, beating has been found to be useful for biodiversity inventories as it was a productive and repeatable method that provided comparable numbers of species (Coddington et al. 1996).

Under standard conditions hand collecting can generate useful data sets with modest effort (Mesibov et al. 1995). Slotow & Hamer (2000) also support this argument. They show that active searching methods can be repeatable and that the technique is effective, especially
for less mobile species, e.g. millipedes (Slotow & Hamer 2000). Active searching has also been used successfully in other spider studies (Coddington et al. 1996). Furthermore, hand collecting by an experienced worker will more often yield a larger species list, since pitfall trapping is targeted at surface-active invertebrates and will capture species from the deep litter layer only occasionally (Mesibov et al. 1995).

The effect of habitat structure on pitfall trap efficiency could result in biased data for studies and difficulties when comparing different habitats. This is because pitfall trap catches are representative of the activity of the spiders, who are influenced by the structure of the environment, therefore direct comparisons between different habitats is not possible as it only reflects the relative activity of individuals (Russell-Smith 1999).

Trap sizes and numbers vary from study to study and there does not seem to be any consensus on trap design. The larger the pitfall, the more the family richness increased (Brennan, Majer & Reygaert 1999). The pitfall trap size plays a key role in trapping success. Increasing the size of traps may have facilitated the capture of a new suite of families, e.g. baboon spiders (Theraphosidae) which could have avoided smaller traps. However, by increasing the size of the pitfall, the catches of non-target invertebrates would also be increased (Brennan et al. 1999). Comparability of pitfall trap data is therefore limited to studies in comparable habitats and using traps of the same size (Churchill & Arthur 1999). Greenslade (1993) stresses that pitfalls must be used with discretion, especially for comparative purposes and only when used in conjunction with other methods, e.g. hand collecting, are the results valuable.

Therefore, the best techniques are the ones that are efficient as well as cost effective. In addition, Coddington et al. (1996) have proposed that the following aspects be taken into consideration when establishing a sampling protocol: (1) protocols of particular groups should be modified as little as possible in order to yield analytically tractable data (repeatability); (2) the number of collecting methods should be minimised and methods should be selected for their efficiency and low overlap with other methods; (3) protocols should work well in plot-based and plotless sampling situations, “time spent sampling” may be a useful index of sampling intensity and (4) the sampling unit should be sufficiently large to yield adequate numbers.

2.6 CONCLUSION

A combination of at least two or more methods should be used for spider biodiversity survey work. For example, when only sweeping was used not all species or communities were adequately sampled. However, when a combination of sweeping, beating and active searching was used all functional groups and families were sampled. For spiders, different sampling methods target certain vegetative layers and or behaviours. Therefore to successfully sample
all species and all microhabitats in an environment it is essential that more than one sampling technique be used for spiders. A combination of at least beating and active searching is recommended for efficient and cost effective surveys. This combination sampled 85% of all species. While surveys including sweeping, beating and active searching would be most ideal (sampled 94% of species). These methods were fast, reliable, simple and cheap all of which fall within the criteria proposed by Coddington et al. (1996).

To standardise techniques across studies, at least one common technique needs to be included in every survey. I recommend that active searching form part of all surveys, especially on spiders. Not only does this method target all layers within the habitat but was a very efficient and cost effective method. However, there are certain drawbacks from using a combination of methods. These included overlap between different families and different methods and by adding an extra technique the time taken to sort the samples also increased considerably. Therefore the techniques chosen should try avoid too much overlap between the techniques. Additionally, there are biases associated with each technique and the researcher should be aware of these in the interpretation of the results.
CHAPTER 3

Biodiversity of spiders (Araneae) at Makalali Private Game Reserve

3.1 INTRODUCTION

In the past, invertebrates were largely ignored in conservation and were only incidentally conserved in existing parks and reserves (De Wet & Schoonbee 1991). Increasingly more people are becoming aware of the threat that biodiversity is under and there is now a growing need to conserve all species, not only the large vertebrates. However, meaningful conservation cannot take place if the species involved are not known (De Wet & Shoonbee 1991). Surveys of invertebrate fauna in conserved areas where conservation strategies are already in place are especially important. Although these areas were not originally established to conserve invertebrates, the resources are already in place for the conservation of potentially new, rare and endemic invertebrate species that could exist in these areas.

Although considerable effort has been invested in recording spider diversity in temperate habitats (Russell Smith 1999), only recently have studies on species diversity in tropical ecosystems been undertaken (Dippenaar-Schoeman & Jocqué 1997). In South Africa, most ecological studies on spiders consist of studies in agroecosystems (Dippenaar-Schoeman 1979; Van den Berg & Dippenaar-Schoeman 1988) and forest and pine plantations (Van den Berg & Dippenaar-Schoeman 1988; Van der Merwe et al. 1996). Little is known about the composition of the arachnid communities of savanna ecosystems, especially undisturbed conserved areas in South Africa (Russell-Smith 1999). In Africa, most previous work on the inventory of savanna arachnids has been undertaken for purposes other than biodiversity assessment (e.g. Russell-Smith 1981; Van Der Merwe et al. 1996). In addition, previous studies used a restricted range of sampling techniques which are likely to have provided a biased sample (Chapter 2).

Presently, most spider related research in southern Africa is carried out under the "South African National Survey of Arachnida" (SANSA), coordinated by the Plant Protection Research Institute, Biosystematics Division, Arachnida unit. SANSA was launched in 1997 in accordance with the country's obligations to the Convention for Biological Diversity (CBD). The main aim of SANSA is to compile an inventory of the arachnid fauna of South Africa. This information is essential before we can consider conservation issues and the sustainable use of our biological diversity. There are numerous spider related projects underway throughout South Africa (Appendix 1), which are all aimed at improving our knowledge of the arachnid fauna in South Africa. It is very encouraging to know that more and more spider research is being carried out in South Africa. The current study, based at Makalali Private
Game Reserve, Northern Province, South Africa, will contribute to this wider survey of spider fauna in this country. Here I present a description of the species composition, the diversity as well as a contrast between sites found in the different habitat types within the Reserve.

The aim of this study was to investigate the spider species composition in different habitat types within a savanna ecosystem and to compare sites in terms of their family and species composition. In addition, a greater understanding of the heterogeneity of diversity at the local scale could be achieved by conducting surveys within reserves. The objectives were to describe the diversity and characteristics of families found in the different habitat types, to produce dendrograms of similarity showing the relationships between sites and habitat types based on species composition and to provide a checklist of spider (Araneae) species occurring in the Reserve.

3.2) METHODS

3.2.1 Study area

The study was carried out at the at Makalali Private Game Reserve (29° 09′ S, 30° 42′E), a broad-leafed savanna ecosystem. Makalali is situated close to the western border of Kruger National Park and extends over 10 000 hectares. The Reserve is situated on the Lowveld plains (450 meters above sea level) of Northern Province, South Africa. There are two dominant vegetation types in the reserve, mixed lowveld bushveld (Type 19) and mopane bushveld (Type 10) (Acocks, 1975; Low & Rebelo, 1996).

The Reserve has a sub-tropical climate with a wet summer (average annual rainfall 491.5 mm) and a dry winter. The rainy season starts in October with maximum rainfall falling between November and February. The daytime temperature in the summer months can reach as high as 36 °C and in winter the evenings and mornings can be chilly (3° C) while the days are warm (26 °C).

Spider sampling was done throughout the Reserve from five different habitat types. These were identified subjectively based on apparent differences in vegetation type and soil characteristics (Table 3.1). Each of the five habitat types was sampled eight times giving a total of 40 sites throughout the Reserve (Figure 2.1). The habitat types sampled were three mixed bushveld types all with different soil (fine, medium and coarse sand), mopane bushveld and rocky outcrops.
Table 3.1: Characteristics of selected habitat types.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Vegetation type</th>
<th>Soil type</th>
<th>Rocks present</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 White sandy bushveld</td>
<td>Mixed bushveld</td>
<td>Coarse sand</td>
<td>No</td>
</tr>
<tr>
<td>2 General bushveld</td>
<td>Mixed bushveld</td>
<td>Medium sand</td>
<td>Yes</td>
</tr>
<tr>
<td>3 Brown sandy bushveld</td>
<td>Mixed bushveld</td>
<td>Fine sand</td>
<td>No</td>
</tr>
<tr>
<td>4 Rocky outcrop</td>
<td>Mixed bushveld</td>
<td>Coarse sand</td>
<td>Yes</td>
</tr>
<tr>
<td>5 Mopane woodland</td>
<td>Mopane</td>
<td>Loamy sand</td>
<td>No</td>
</tr>
</tbody>
</table>

3.2.2 Preliminary survey

A preliminary survey of the Reserve was undertaken in early 1999 (30th January – 8th February). Spiders were sampled from eight sites within Reserve using a wide range of trapping techniques. These included sweep netting, pitfall trapping, beating, active searching, tree bark traps and crypto traps. The four most efficient trapping techniques were then selected for the remainder of the study (Chapter 2). The techniques chosen were sweeping, beating, active searching and pitfalls. This combination of trapping techniques sampled spiders from the ground, field and the tree layer.

3.2.3 Additional sites

While the analysis of species diversity in Chapters 2, 4 and 5 are based on the five habitat types described above in this Chapter I have included species recorded from all additional collecting. Four additional sites situated in a riverine habitat were sampled. The sampling in this habitat type was conducted in December 1999 and the sampling techniques were limited to beating and active searching.

3.2.4 Sampling techniques

The four selected sampling techniques (sweeping, beating, active searching and pitfall trapping) were done at all sites throughout the Reserve (total 40). The sampling was conducted over four periods, the preliminary survey (February 1999), late summer (late February – early March 1999), early summer (October - November 1999) and mid summer (December 1999). Refer to Chapter 2 for a detailed description of the sampling techniques.

Family-level identifications were conducted by C. Whitmore with some assistance from Dr T. Crouch and species-level identification was done by Dr A.S. Dippenaar-Schoeman of the National Collection of Arachnida, Biosystematics Division of the Agricultural Research Council Plant Protection Research Institute, Pretoria. The lack of taxonomic research in Africa within certain families, e.g. Lycosidae, makes the identification to species level in
some instances impossible (A.S. Dippenaar-Schoeman 1999 pers. comm.). Species level identifications were further hampered in the case of immature specimens and juveniles. In these cases species determinations were made only in cases of absolute certainty.

3.2.5 Diversity indices

The diversity, richness, and evenness indices for spiders were calculated using the SPDIVER.BAS program of Ludwig and Reynolds (1988). A diversity index incorporates both species richness (the total number of species), and evenness (how equally abundant the species are), in a single value (Magurran 1988). A diversity index allows comparisons to be made between two habitats. Many diversity indices exist in the literature. The Shannon diversity index ($H$) is one of the most frequently used diversity indices and it is commonly used in ecological studies (Ludwig & Reynolds 1988; Magurran 1988; Wolda 1981). The Shannon index measures the average degree of uncertainty of predicting the species of a given individual picked at random from a community. The index varies from a value of 0 for communities with only a single species to high values for communities having many species, each with a few individuals. Shannon’s index was used in this study. However, to express the diversity in species units I selected one of Hill’s (1973) diversity numbers ($N_I$) for this study:

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

Where: \( H' = \) Shannon’s index

This index assumes that individuals are randomly sampled from an indefinitely large population (Magurran 1988). Here the Shannon’s index is linearly related to the number of species in the sample. It gives the number of the species that would produce the same $H'$ as the sample if each were equally common. Hill’s index measures the effective number of species present in a sample, giving a measure of the degree to which proportional abundances are distributed among the species (Ludwig and Reynolds 1988). This index is more easily interpreted than other diversity indices (Ludwig and Reynolds 1988).

Given that values for diversity indices are often difficult to interpret, species richness and evenness are often presented as separate values. In this form they provide important insights into the ecological changes that occur over time or the differences between ecological communities (Bisby 1995).

When all species in a sample are equally abundant an evenness index will be at its maximum, decreasing towards zero as the relative abundance of the species diverge away from evenness. The modified Hill’s ratio ($E_S$) was selected from existing indices of evenness.

1 Dr A.S. Dippenaar-Schoeman, National Collection of Arachnida, Biosystematics Division of the Agricultural Research Council Plant Protection Research Institute, Pretoria
This measure of evenness is the least ambiguous and is the most easily interpreted. $E5$ is independent of the number of species in the sample (Ludwig & Reynolds 1989), making it an appealing index to use.

$$E5 = \frac{(1/\lambda) - 1}{e^{H'} - 1}$$

Where $\lambda =$ Simpson's index

$H'$ = Shannon's index

The index approaches zero as a single species becomes more and more dominant and it is unaffected by species richness (Ludwig & Reynolds 1989).

Species richness ($S$) examines the number of species occurring in a habitat. Just $S$ alone, while giving insight into diversity in different habitats, can mask shifts in dominance and evenness if there is no consideration of abundance. Overall species richness is the most widely adopted diversity measure. However, shifts towards incorporating species abundance has lead to widespread use of Shannon's index ($H'$).

All statistical analysis was performed using SPSS (Norusis 1994). The normality of data distribution was checked by performing a Kolmogorov-Smirnov goodness of fit test. Where necessary, data that were not normally distributed was log transformed. A two way ANOVA was done to test for significant differences among habitat types and among the sampling period for diversity, evenness and richness.

### 3.2.6 Spider functional groups

Functional groups include species that potentially compete for jointly exploited limited resources (Polis & McCormick 1986). Spiders live in a well-defined environment with limitations set by both physical conditions and biological factors (Foelix 1996). They can be grouped into specific functional groups based on available information on their habitat preferences and predatory methods (Bultman et al. 1982). Describing the spider diversity in terms of these groups allows for greater insight into how habitat differences may be reflected in life-history strategies. For the present study two main functional groups were recognised, namely wanderers (W) and web builders (WB), with further subdivisions based on microhabitat and general behaviour (Dippenaar-Schoeman, Leroy, De Jager & Van den Berg 1999; Table 3.2).
Table 3.2: Functional group classification of spiders.

<table>
<thead>
<tr>
<th>Functional groups</th>
<th>Abbreviation</th>
<th>Functional group explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Free- and burrow-living ground wanderers</td>
<td>GW</td>
<td>Free-living spiders running on the soil surface when active including spiders living permanently or semi-permanently in burrows</td>
</tr>
<tr>
<td>Plant wanderers</td>
<td>PW</td>
<td>Spiders foraging exclusively on the plant surface</td>
</tr>
<tr>
<td>Web builders</td>
<td>WB</td>
<td>Spiders constructing webs including funnel-webs, orb-webs, retreat-webs, sheet-webs and space-webs</td>
</tr>
</tbody>
</table>

3.2.7 Site similarity

Beta (\(\beta\)) diversity is a measure of how species numbers and identities differ between communities (Magurran 1988). In this study it was used to measure how different (or similar) a range of habitats or samples were based on their spider species composition.

One of the simplest ways to measure the \(\beta\) diversity of pairs of sites is to use similarity coefficients. Several similarity indices exist but some of the oldest similarity coefficients are also the most useful (Magurran 1988). Particularly widely used are the Jaccard and Sorensen index (Magurran 1988). The Jaccard index was used for the present study. The index was calculated using the following formulae:

\[
C_{j} = j / (a + b - j)
\]

Where:
- \(a\) = total number of species in site a
- \(b\) = total number of species in site b
- \(j\) = species common to both site a and b

A value of 1 indicates complete similarity between sites and a value of zero indicates dissimilar sites that share no species. One of the greatest advantages of this index is its simplicity yet it does have the disadvantage of not taking into account any abundance of the species (Magurran 1988). The Jaccard similarity index is appropriate in the current context as the aim was simply to see how similar sites were based on the number of families and species that were shared between the different sites. The index was first calculated based on species shared between sites and then on families shared between sites.

3.2.8 Cluster analysis

An alternative approach to the measurement of \(\beta\) diversity is to investigate the degree of association or similarity of sites or samples using standard ecological techniques of ordination and classification (Southwood 1978). Ordination techniques are frequently used to investigate
the overall similarity of sites and establish major groupings. The analysis would start with a matrix giving the similarity between each pair of sites. The two most common are combined to form a single cluster. The analysis proceeds by successively clustering similar sites until they are combined in a single dendrogram (StatSoft 1999).

The term “cluster analysis” encompasses a number of different classification algorithms (Faith 1991). It is a useful data reduction technique that can be very helpful in identifying patterns and groupings of objects. The analysis begins with each object in a class by itself (StatSoft 1999). The threshold regarding the decision when to declare two or more objects to be members of the same cluster is lowered. As a result more and more objects are linked together and aggregate (amalgamate) into larger and larger clusters of increasingly dissimilar elements. A dendrogram results and the horizontal axis denotes the linkage distance (Faith 1991; StatSoft 1999). Thus, for each node in the graph (where a new cluster is formed) the criterion distance at which the respective elements were linked together into a new single cluster can be read off. Clusters (branches) resulting from the analysis can be detect and interpreted (StatSoft 1999).

The statistical analysis programme STATISTICA was used to generate dendrograms, which could then be interpreted. The unweighted pair group average linkage and the Euclidean distances were the parameters selected. The analysis was first done using families and then species present in the different sites.

A linkage or amalgamation rule determines when two clusters are sufficiently similar to be linked together. Single linkage (nearest neighbour) uses the distance between two clusters and is determined by the distance of the two closest objects (nearest neighbours) in the different clusters. Complete linkage (furthest neighbour) uses the distances between clusters and is determined by the greatest distance between any two objects in the different clusters (i.e., by the “furthest neighbours”). Unweighted pair-group average (UPGMA) uses the distance between two clusters and calculates the average distance between all pairs of objects in the two different clusters (Faith 1991; StatSoft 1999). This method is also very efficient when the objects form natural distinct “clumps”. However, it performs equally well with elongated, “chain” type clusters (StatSoft 1999).

The Euclidean distance is the most commonly selected measure of distance. It is simply a geometric distance in multidimensional space. This method has certain advantages. For example, the distance between any two objects is not affected by the addition of new objects to the analysis, which may be outliers (StatSoft 1999). However, the distances can be greatly affected by differences in scale among the dimensions from which the distances are computed (StatSoft 1999).

Similarity of spider species among habitat types were examined using the diversity indices, the Jacard similarity coefficient and the cluster analysis.
3.3 RESULTS

3.3.1 Total numbers of species and individuals

A total of 4832 individuals from 268 species, 147 genera and 37 families were sampled in Makalali Private Game Reserve during the study period (Appendix 3.1). The species checklist includes all spiders that were sampled in the Reserve including those collected outside the sampling period e.g. around the houses and riverine habitat. Table 3.3 is a summary of the species composition. Voucher specimens were preserved in 70% ethanol and deposited in a reference collection lodged with the Durban Natural Science Museum, South Africa (Accession numbers: DMSA – ARA 346 – 611).

Table 3.3: Total numbers of spider families, genera, species and individuals sampled from Makalali Private Game Reserve. GW = ground wanderers, PW = plant wanderers and WB = web builders. 1 = white sandy bushveld, 2 = general bushveld, 3 = brown sandy bushveld, 4 = rocky outcrops and 5 = mopane woodland.

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Family</th>
<th>Genera</th>
<th>Total Species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>GW</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gnaphosidae</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Lycosidae</td>
<td>6</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Zodariidae</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Theraphosidae</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Corinnidae</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Ctenidae</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Prodidae</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Liocranidae</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Oonopidae</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Palpimanidae</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Selenopidae</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Ageleidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Anapidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Barychelidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Dictynidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Idiopidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Scytodidae</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Sicariidae</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Salticidae</td>
<td>15</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>Thomisidae</td>
<td>15</td>
<td>27</td>
</tr>
</tbody>
</table>

Note: The numbers in parentheses represent the number of species or individuals from each habitat type.
### Functional group Family  Genera  Total Species  Number of species (individuals) in each Habitat type

<table>
<thead>
<tr>
<th>Family</th>
<th>Genera</th>
<th>Total Species</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Philodromidae</td>
<td>5</td>
<td>9</td>
<td>7(38)</td>
<td>4(40)</td>
<td>7(31)</td>
<td>5(18)</td>
<td>6(38)</td>
</tr>
<tr>
<td>Pisauridae</td>
<td>5</td>
<td>11</td>
<td>5(35)</td>
<td>9(50)</td>
<td>8(85)</td>
<td>7(102)</td>
<td>6(35)</td>
</tr>
<tr>
<td>Oxyopidae</td>
<td>3</td>
<td>19</td>
<td>11(77)</td>
<td>13(53)</td>
<td>16(80)</td>
<td>14(49)</td>
<td>13(31)</td>
</tr>
<tr>
<td>Sparassidae</td>
<td>3</td>
<td>5</td>
<td>3(44)</td>
<td>4(26)</td>
<td>3(17)</td>
<td>4(28)</td>
<td>5(16)</td>
</tr>
<tr>
<td>Miturgidae</td>
<td>2</td>
<td>7</td>
<td>7(33)</td>
<td>9(52)</td>
<td>5(30)</td>
<td>5(17)</td>
<td>5(16)</td>
</tr>
<tr>
<td>Clubionidae</td>
<td>1</td>
<td>2</td>
<td>1(6)</td>
<td>1(2)</td>
<td>1(2)</td>
<td>1(5)</td>
<td>1(5)</td>
</tr>
<tr>
<td>Araneidae</td>
<td>18</td>
<td>31</td>
<td>14(437)</td>
<td>19(242)</td>
<td>20(196)</td>
<td>22(288)</td>
<td>18(317)</td>
</tr>
<tr>
<td>Theridiidae</td>
<td>10</td>
<td>28</td>
<td>8(60)</td>
<td>14(58)</td>
<td>17(75)</td>
<td>13(106)</td>
<td>13(32)</td>
</tr>
<tr>
<td>Hersiliidae</td>
<td>2</td>
<td>3</td>
<td>1(1)</td>
<td>1(1)</td>
<td>1(3)</td>
<td>1(7)</td>
<td>2(3)</td>
</tr>
<tr>
<td>Linyphiidae</td>
<td>2</td>
<td>6</td>
<td>1(1)</td>
<td>1(5)</td>
<td>1(5)</td>
<td>2(5)</td>
<td>3(3)</td>
</tr>
<tr>
<td>Pholcidae</td>
<td>2</td>
<td>3</td>
<td>1(1)</td>
<td>1(1)</td>
<td>1(1)</td>
<td>1(1)</td>
<td>1(1)</td>
</tr>
<tr>
<td>Tetragnathidae</td>
<td>2</td>
<td>3</td>
<td>1(11)</td>
<td>1(3)</td>
<td>1(15)</td>
<td>2(12)</td>
<td>1(3)</td>
</tr>
<tr>
<td>Uloboridae</td>
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<td>3</td>
<td>1(5)</td>
<td>1(2)</td>
<td>1(4)</td>
<td>1(3)</td>
<td>1(3)</td>
</tr>
<tr>
<td>Deinopidae</td>
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<td>1</td>
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<td></td>
</tr>
<tr>
<td>Eresidae</td>
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<td>2</td>
<td>1(1)</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Nesticidae</td>
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<td>1</td>
<td>1(4)</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Segestriidae</td>
<td>1</td>
<td>1</td>
<td>1(1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>37</strong></td>
<td><strong>268</strong></td>
<td><strong>121</strong></td>
<td><strong>150</strong></td>
<td><strong>160</strong></td>
<td><strong>155</strong></td>
<td><strong>148</strong></td>
</tr>
</tbody>
</table>

3.3.2 Composition of spiders in Makalali Private Game Reserve

The 37 spider families recorded from Makalali Private Game Reserve represent 60% of all currently recognised spider families in South Africa (total 62 - Dippenaar-Schoeman & Jocqué 1997).

Of the 4,659 individuals sampled at the specified sites, the orb-web spiders (Araneidae) were by far the most abundant in the reserve (32%), followed by the jumping spiders (Salticidae - 18%), crab spiders (Thomisidae - 10%), nursery web spiders (Pisauridae - 7%), lynx spiders (Oxyopidae - 7%), comb-footed spiders (Theridiidae - 5%) and the small huntsman spiders (Philodromidae - 4%) (Figure 3.1). Despite the considerable sampling effort, there are probably more species present than those sampled since the species accumulation curve indicates that the asymptote has not yet been reached (Figure 3.2).

The four additional riverine sites that were sampled revealed five new species (Philodromidae: Thanatus sp. 1; Tetragnathidae: Leucauge festiva; Lycosidae: Pardosa crassipes; Salticidae: Rhene machadoi; Corinnidae: Lessertina sp.) that were not found in the other habitat types. There were 14 potentially new species collected from this Reserve.
(Araneidae: Prasonica; Chorizopes sp; Anapidae: Metanapis sp.; Ctenidae: Ctenus sp. 2; Corinnidae: Castianeira sp.; Gnaphididae: Setaphis sp, Asemesthes sp. 2; Hersiliidae: Tama sp.; Liocranid: Andromma sp.; Oxyopidae: Oxyopes sp., Hamataliwa sp.; Philodromid: Gephyra; Sparassidae: Olios sp., Panaretella sp., Thomisidae: Pherecydes sp.). There were also some genera that were new records for South Africa (Araneidae: Prasonica; Philodromid: Gephyra). A very significant find was the Sipalolasma humicola (trapdoor-baboon spider) belonging to the family Barychelidae. This family was previously only thought to occur in Ethiopia and Zaire therefore making this a new distribution record for this family in South Africa, and a vast range extension.

Some families were more widely distributed throughout the Reserve than others. Two families that were found at all sites were the lynx spiders (Oxyopidae) and jumping spiders (Salticidae). Three families that were found in 98% of the sites included: nursery web spiders (Pisauridae), the orb-web spiders (Araneidae) and the crab spiders (Thomisidae). Other families that were found in more than 75% of all sites included comb-footed spiders (Theridiidae); flat-bellied ground spiders (Gnaphosidae); small huntsman spider (Philodromidae); sac spiders (Miturgidae); large huntsmans spiders (Sparassidae) and wolf spiders (Lycosidae).

Families that were only found at a single site included: six-eyed tunnel spiders (Segestriidae); velvet spiders (Eresidae); six-eyed spiders (Sicariidae); dwarf ring-shield spiders (Anapidae); net-casting spiders (Deinopidae); mesh-web spiders (Dictyniidae); funnel-web spiders (Agelenidae) and spurred trapdoor spiders (Idiopidae). It must be noted that although these families were found at only one site the species were not necessarily rare. They may have been cryptic or have a patchy distribution and these species may not be adequately sampled. A brief description of the appearance, general biology and morphology of the dominant genera in the families collected from the Reserve is presented in Appendix 3.2. The CD-ROM enclosed contains a hyper-linked identification manual to the spiders of the Afrotropical Region with special reference to the dominant genera sampled from the Reserve. The CD-ROM was developed for the purpose of training Reserve managers and staff as well as undergraduate students.

3.3.3 Diversity, evenness and richness indices

Diversity, evenness and richness values were calculated using the SPDIV.BAS programme of Ludwig & Reynolds (1988). The statistical programme SPSS (Norusis 1994) was used for the data analysis. In all cases the assumptions of the ANOVA were met (Kolmogorov-Smirnov test $P < 0.05$). There was no overall significant difference between the diversity ($F_{4, 39} = 2.236, P = 0.094$), evenness ($F_{4, 39} = 1.689, P = 0.184$) or richness ($F_{4, 39} = 1.766, P = 0.167$) among the different habitat types. Diversity was highest in habitat type 3 (brown sandy
Fig 3.1: Family level diversity of spiders at Makalali Private Game Reserve. Percentage abundance of the different spider families (parentheses indicate the number of individuals). The following families have been included in the “other” category Tetragnathidae (75); Lycosidae (71); Theraphosidae (31); Clubionidae (30); Hersiliidae (21); Prodidomidae (19); Uloboridae (17); Linyphidae (17); Zodaridae (14); Corinnidae (14); Scytodidae (11); Ctenidae (11); Palpimanidae (10); Liocranidae (9); Pholcidae (5); Nesticidae (4); Barychelidae (4); Oonopidae (3); Idiopidae (3); Agelenidae (3); Anapidae (2); Sicariidae (1); Segestriidae (1); Eresidae (1); Dictynidae (1) and Deinopidae (1).
Figure 3.2: There are an estimated 280 species of spider present at Makalali Private Game Reserve.
Figure 3.3: The influence of habitat type, represented by the mean and ±95% confidence limits on the a) species diversity, b) species richness and c) species evenness of spiders at Makalali Private Game Reserve. N represents the number of sites in each habitat type. There were no statistically significant differences (see text).
bushveld) and lowest in habitat type 4 (rocky outcrops) (Figure 3.3a). The richness was highest in habitat type 3 (brown sandy bushveld) and lowest in habitat type 5 (mopane woodland) (Figure 3.3b). The evenness was highest in habitat type 5 (mopane woodland) and lowest in habitat type 4 (rocky outcrops) (Figure 3.3c).

When analysed by sampling period there was a significant difference for the diversity ($F_{1,39} = 16.779, P < 0.0001$; Figure 3.4a) and richness ($F_{2,39} = 10.253, P = 0.001$; Figure 3.4b) but the results were non-significant for evenness ($F_{2,39} = 2.461, P = 0.106$; Figure 3.4c). The diversity and richness follow the same patterns throughout the year, both being highest in mid summer (December).

The interaction between the sampling period and habitat type was non-significant for diversity ($F_{8,39} = 1.157, P = 0.362$), richness ($F_{8,39} = 1.408, P = 0.242$) and evenness ($F_{8,39} = 0.848, P = 0.571$). The diversity, evenness and richness follow the same patterns in the different habitat types at different times of the year.

### 3.3.4 Functional groups and families

Spiders were divided into three main functional groups: the plant wanderers, ground wanderers and the web-builders. The diversity, richness and evenness were reassessed at this level to determine if the different life strategies of spiders were influenced in any way by the habitat and or by time as these patterns may have been masked by the overall effect of a combined diversity.

Overall, the number of wandering spiders was greater than that of web builders. Plant wanderers were the most abundant and widely distributed. They comprised 48% of all spiders sampled (total individuals = 2 239). Web builders comprised 41% (total individuals = 1 916) and ground wanderers, 11% (total individuals = 501). There was no significant difference in the diversity ($F_{4,39} = 0.217, P = 0.927$), richness ($F_{4,39} = 0.226, P = 0.921$) or evenness ($F_{4,39} = 2.735, P = 0.051$) for the plant wanderers among habitat types (Figure 3.5a). There was also no significant effect of habitat type on the diversity ($F_{4,39} = 0.368, P = 0.829$), richness ($F_{4,39} = 0.898, P = 0.480$) or evenness ($F_{4,39} = 0.521, P = 0.721$) of ground wanderers (Figure 3.5b). The web builders also showed a non significant effect of habitat type on richness ($F_{4,39} = 2.243, P = 0.093$) and evenness ($F_{4,39} = 0.491, P = 0.743$). However, there was a significant effect of habitat type on the diversity of web builders ($F_{4,39} = 3.452, P = 0.022$) (Figure 3.5c).

The effect of time on community structure differed slightly from the results for the combined analysis (see previous section). The diversity of plant wanderers was not significantly affected by the time ($F_{2,39} = 1.405, P = 0.268$; Figure 3.6a) yet the richness ($F_{2,39} = 3.803, P = 0.036$) and evenness ($F_{2,39} = 5.482, P = 0.011$) were (Figure 3.6b & c). The diversity ($F_{2,39} = 15.797, P < 0.001$) and richness ($F_{2,39} = 21.102, P < 0.001$) of ground wanderers was significantly affect by the sampling period but the evenness ($F_{2,39} = 0.721, P =
Figure 3.4: The influence of sampling period, represented by the mean and ± 95% confidence limits on the a) species diversity, b) species richness and c) species evenness of spiders at Makalali Private Game Reserve. N represents the number of sites in each sampling period. See text for statistical tests.
Figure 3.5: The effect of habitat type on the a) diversity, b) richness, and c) evenness of spiders at Makalali Private Game Reserve. Spiders have been divided into guilds and (□, ○, Δ) represent the plant wanderers, ground wanderers and web builders respectively. The mean and 95% confidence limits are presented. N represents the number of sites within the habitat type.
Figure 3.6: The effect of sampling period on the a) diversity, b) richness, and c) evenness of spiders at Makatalli Private Game Reserve. Spiders have been divided into guilds and (○, O, ▲) represent the plant wanderers, ground wanderers and web builders respectively. The mean and 95% confidence limits are presented. N represents the number of sites sampled in the time period.
0.447) was not significant (Figure 3.6a,b &c). The diversity ($F_{2,39} = 10.013, P = 0.001$) and richness ($F_{2,39} = 5.390, P = 0.011$) of web builders was significantly affected by the sampling period but the evenness ($F_{2,39} = 1.067, P = 0.359$) was not significantly affected (Figure 3.6a, b & c).

The seasonal fluctuation of invertebrates was common so it is not surprising that the highest diversity and richness was seen in mid summer and lower values are recorded at other times of the year. Interestingly, there was no overall significance between the evenness and sampling period but when spiders were divided into functional groups, there was an evenness effect with time on plant wanderers. This indicated that at different times of the year different compliments of ground wanderer and web building species were dominating the environment and the abundance of these species was relatively uniformly distributed. This means for ground wanderers and web builders we were either sampling many individuals of the same species or few individuals of many different species at any particular time of the year.

While the plant wanderers differed in evenness with time and may have been influenced by the structural diversity of the habitat or its phenology. Therefore, either the plant wanderer evenness was highest when there is maximal structural diversity (mid summer) or at different times of the year there were either lots of juveniles of one species and at other times of the year fewer adult individuals of the same species. The only way to get a true habitat type effect on the diversity would be to resample the same sites at the different times of the year.

Plant wanderers

The more common plant wandering families encountered, i.e. occurring in >25% of the sites included: lynx spiders (Oxyopidae), jumping spiders (Salticidae), nursery web spiders (Pisauridae), crab spiders (Thomisidae), small huntsman spiders (Philodromidae); (Miturgidae), large huntsman spiders (Sparassidae) and leaf-curling sac spiders (Clubionidae). Plant wanderer diversity was highest in habitat type 3 (brown sandy bushveld) and lowest in habitat type 5 (mopane woodland).

Ground wanderers

The more common ground wandering spiders encountered included: flat-bellied ground spiders (Gnaphosidae) wolf spiders (Lycosidae); baboon spiders ( Theraphosidae); long-spinnered ground spiders ( Prodidomidae); dark sac spiders ( Corinnidae) and armoured spiders ( Zodariidae). The highest diversity of ground wanderers was in habitat types 1 (white sandy bushveld) and 2 (general bushveld) and lowest in habitat type 4 (rocky outcrops).
Web builders

The web building spiders are usually abundant in the field and tree layer, where they build a variety of different types of prey-catching webs. The more common web-builders included members from the following families: orb-web spiders (Araneidae), comb-footed spiders (Theridiidae), long-jawed spiders (Tetragnathidae) and hammock-web spiders (Linyphiidae). The web builders diversity was highest in habitat type 3 (brown sandy bushveld) and lowest in habitat type 4 (rocky outcrops).

Possible abiotic and biotic factors influencing the spider diversity at the habitat types will be explored further in Chapter 5. Microhabitat influences on spider diversity at different sites will also be investigated further in Chapter 5.

3.3.5 Site similarity

Family composition varied considerably between the different habitats with no differences between the sites being immediately obvious. In order to make the interpretation of the similarity matrices simpler, only sites that shared more than 70% of their families and 30% of their species were included. Table 3.4 shows the Jaccard similarity coefficients between the different sites based on the families shared between them and Table 3.5 shows the same analysis but uses the number of species shared. The values for all similarity coefficients are presented in Appendix 3.3.

The most striking feature of these tables was that the sites analysed at family level were more similar than at the species level analysis. This was simply because families shared more characteristics at a higher taxonomic level. At the level of family there was a higher degree of similarity between sites than at the level of species but even at this higher taxon level only one site has all families in common (site 2.7 and site 5.7). The majority of sites shared at least half of the families present. Sites within the same habitat type at the family level were not more similar than sites among habitat types ($G_1 = 2.338, P < 0.001$, Table 3.4).

However, other than this there were no obvious patterns. At species level there were no sites that shared all species. The highest similarity value was 0.4, which was still less than half of the species shared. Again, sites within the same habitat type at the species level were not more similar than sites among habitat types ($G_1 = 0.121, P < 0.001$, Table 3.5).

There were several sites that shared many common families. This implies that many families have a wide distribution and do not seem to require specialised habitats.

All habitat types have at least one spider family that was unique to that habitat type. Habitat types 3 (brown sandy bushveld) and habitat type 4 (rocky outcrops) had the greatest number of unique spider families (Figure 3.7a). All habitats also had at least one unique spider species to that habitat type. Habitat type 4 (rocky outcrops) had the greatest number of
unique species followed by habitat types 5 (mopane woodland), 3 (brown sandy bushveld) and 2 (general bushveld) (Figure 3.7b).

3.3.6 Cluster analysis

STATISTICA was used to generate dendrograms based on presence / absence data for families and species. The family level analysis revealed three main clusters (Figure 3.8a). Cluster A had two sites, 4.6 and 1.3. Cluster B consisted of a combination of habitat types 3, 4 and 5 while cluster C was a combination of mainly habitat types 1 and 2 with two sites from habitat type 3 (Figure 3.9a).

At species level there were four distinct clusters (Figure 3.8b). Each cluster had sites from at least four different habitat types (Figure 3.8b). At first there did not appear to be any patterns emerging from this analysis. However, the same data was re-analysed but used the sampling period (i.e. time of year) instead of sites. The results showed that sites clustered according to sampling period (Figure 3.9b). Cluster A was the autumn sample (March 1999), cluster B was the summer sample (December), cluster C was the spring sample (October 1999) and cluster D was also an autumn sample, taken during the preliminary survey in February 1999 (Figure 3.9c).
Figure 3.7: The contribution of the five different habitat types to spider diversity where a) is the family composition and b) is the species sampled.
Figure 3.8: Dendrogram for a) families and b) species shared at different habitat types and different sampling times sites using the unweighted pair-group average (UPGAMA) and Euclidean distances. There are three main clusters (A - C) of sites for shared families (Figure 3.4a) These cluster at a habitat level. Four main clusters (A - D) are present for species shared (Figure 3.4b) and these cluster according to season. Sampling sites are coded by habitat type (1 = white sandy bushveld, 2 = general bushveld, 3 = brown sandy bushveld, 4 = rocky outcrops, and 5 = mopane woodland with the site number within the habitat after the sampling period. The letters represent the sampling period where M = late summer (March 1999), N = early summer (November 1999), D = mid summer (December 1999) and F = preliminary sample (February 1999).
Figure 3.9: The percentage of (a) families in clusters A - F, (b) species in clusters A - D and (c) the species clusters A - D according to sampling period.
Table 3.4: Jaccard's similarity coefficient between different sites based on families sharing more than 70% of their families. All values have been multiplied by 100 for ease of interpretation. The shaded area represents sites within the same habitat type.
Table 3.5: Jaccard’s similarity coefficients for the sites sharing more than 33% of their species. All values have been multiplied by 100 for ease of interpretation. The shaded area represents sites within the same habitat type.

| Site | 1.1 | 1.2 | 1.3 | 1.4 | 1.5 | 1.6 | 1.7 | 1.8 | 2.1 | 2.2 | 2.3 | 2.4 | 2.5 | 2.6 | 2.7 | 2.8 | 3.1 | 3.2 | 3.3 | 3.4 | 3.5 | 3.6 | 3.7 | 3.8 | 4.1 | 4.2 | 4.3 | 4.4 | 4.5 | 4.6 | 4.7 | 4.8 | 5.1 | 5.2 | 5.3 | 5.4 | 5.5 | 5.6 | 5.7 | 5.8 |
|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1.1  | 36  | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| 1.2  | 31  | 40  | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| 1.3  | 31  | 31  | 33  | 33  | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   |
| 1.4  | 31  | 31  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  |
| 1.5  | 31  | 31  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  | 34  |
3.4 Discussion

3.4.1 Species composition

The 37 spider families recorded from Makalali Private Game Reserve represent 60% of all currently recognised spider families in South Africa (Dippenaar-Schoeman & Jocqué 1997). The most striking result was the high diversity in this savanna biome. The number of families found here was as high or higher than numbers recorded for other biomes surveyed in South Africa (Table 3.6). Only a study done in the Nama-Karoo (Dippenaar-Schoeman, Leroy, De Jager & Van den Berg 1999) showed a higher family diversity than this current study. That study was conducted over a ten year period. The sampling for the current study was done in a single year and the spider family diversity was therefore surprisingly high. There was only one family less in the current study than the Nama-Karoo ten year study. Furthermore, we would expect the diversity in forest biomes to be higher than that of savanna but this is not supported in the literature. This study illustrates that savanna biomes are very important for the preservation of an important component of invertebrate biodiversity and are thus an essential biome to conserve.

The families that were abundant were also widely distributed throughout the Reserve. All of the abundant families have many species and many of these families are widely distributed throughout the world (Appendix 3.2).

Some families were not as cosmopolitan and were only found in a single site. Site restriction by some species should not be confused with rarity. Many of these species are cryptic or patchily distributed and they were simply not sampled adequately. Some examples include Stegodyphus dumicola and the baboon spiders (Theraphosidae). S. dumicola was only sampled in one habitat type but the distribution is known to be extremely patchy (Siebt & Wickler 1988). Nests were observed outside of the sampling area. This particular group was simply not sampled adequately because of its patchy distribution and not because the species is rare. The theraphosids (baboon spiders) were sampled from all five different habitat types but in low abundances (only 15 individuals were found throughout the Reserve). Low trap catches be a reflection on an inadequate sampling protocol for this particular taxon. Theraphosids are nocturnal and in this study night sampling could not be done. However, additional hand collecting was done and three different theraphosid species were collected from their burrows. These additional species were not found whilst sampling in the sites. Many theraphosid burrows were observed, especially in the western section of the Reserve in the white sandy and brown sandy mixed bushveld habitats (habitat types 1 and 2).
Table 3.6: Number of spider families surveyed from different biomes within South Africa.

<table>
<thead>
<tr>
<th>Biome</th>
<th>Number of families</th>
<th>Number of Genera</th>
<th>Number of Species</th>
<th>Study Duration</th>
<th>Methods used</th>
<th>Location</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nama-Karoo</td>
<td>16</td>
<td>29</td>
<td>32</td>
<td>3 years</td>
<td>Sweeping, Beating</td>
<td>Mountain Zebra National Park, Eastern Cape Province</td>
<td>Dippenaar-Schoeman 1988</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Searching</td>
<td>Karoo National Park, Western Cape Province</td>
<td>Dippenaar-Schoeman, Leroy, de Jager &amp; Van den Berg 1999</td>
</tr>
<tr>
<td></td>
<td>38</td>
<td>102</td>
<td>116</td>
<td>10 years</td>
<td>Sweeping, Beating</td>
<td>Dune Forests of Richards Bay, Kwa-Zulu Natal</td>
<td>Dippenaar-Schoeman, Wassenaar (in press)</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>41</td>
<td>49</td>
<td>1 year</td>
<td>Beating, Searching</td>
<td>Swartboskloof, Western Cape Province</td>
<td>Coetzee, Dippenaar-Schoeman &amp; Van den Berg 1990</td>
</tr>
<tr>
<td></td>
<td>33</td>
<td>-</td>
<td>136</td>
<td>1 year</td>
<td>Searching</td>
<td>Sabie, Mpumalanga Province</td>
<td>Van den Berg &amp; Dippenaar-Schoeman 1988</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>82</td>
<td>110</td>
<td>4 years</td>
<td>Sweeping, Beating</td>
<td>Makalali Private Game Reserve, Northern Province</td>
<td>Current study</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>36</td>
<td>36</td>
<td>1 year</td>
<td>Beating</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>53</td>
<td>54</td>
<td>1 year</td>
<td>Pitfalls, Bark traps</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>37</td>
<td>147</td>
<td>268</td>
<td>1 year</td>
<td>Sweeping, Beating</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
3.4.2 **Diversity, evenness and richness**

There are many environmental factors that are able to affect species diversity. Some of these factors include 1) time, 2) spatial heterogeneity, 3) competition, 4) predation, 5) environmental stability and 6) productive habitats (Rosenzweig 1995). Possible abiotic and biotic factors influencing the diversity at the different sites will be explored further in Chapter 5.

If spider family distribution were indeed affected by the habitat type alone we would expect all sites within the same habitat type to have high similarity values and share little with other sites. This was not the case and indicates that the sites are all unique. Additionally, there are many factors determining the species composition at the sites and not simply the habitat type. An alternative interpretation of this was that the habitat types classified as different at the beginning of the study may be more similar than previously thought.

Diversity values varied considerably between the different sites and habitat types did not necessarily have similar diversities. There was a no overall significant difference between the diversity, evenness or richness among the different habitat types. This was surprising because I would expect bushveld habitat types (type 1 – 4), a combination of different trees, herbs and shrubs, to have a higher diversity than the mopane woodland habitat type as this habitat type is dominated by a single tree species (*Colophospermum mopane*). However, this was not the case and although the mopane woodland appears to be a more barren habitat (floristically) it still had a rich diversity. The Barychelidae (*Sipalolasma humicola* (Benoit, 1965)) which is a new distribution record for South Africa was found in the mopane woodland habitat type. This data indicates that spiders were not limited to a particular habitat type and may be influenced by factors other than habitat type.

However, when spiders were divided according to their functional group there was a significant effect on the web builders diversity and the plant wanderers evenness of habitat types. The web building and plant wandering spiders rely on the vegetation for some part of their lives, either for finding food, building retreats or for web building. The structure of the vegetation is therefore expected to influence the diversity of spiders found in the habitat. There were many more wanderers (plant and web) sampled than ground-dwellers. This again indicates that structural diversity of the vegetation may be in some way influencing the spider diversity.

Studies have demonstrated that a correlation exists between the structural complexity of habitats and species diversity (Uetz 1979; MacArthur 1964; Pickett et al. 1991; Andow 1991; Hawksworth & Kalin-Aroyo 1995; Rosenzweig 1995). Diversity generally increases when a greater variety of habitat types are present because the more habitats there are the more
species may exist (MacArthur 1964; Ried & Miller 1989; Cook 1991; Hawksworth & Kalin-Arroyo 1995).

Early investigators recognised that the historical structure of the habitat could profoundly affect the composition of the spider community. Effects arise not only from variations in the availability of supports for anchoring webs, but also from the provision of retreats and modifications of the microclimate, which could have an effect on the spiders as well as their prey.

Uetz (1991) suggests that structurally more complex shrubs can support a more diverse spider community. Downie et al. (1999) and New (1999) have demonstrated that spiders are extremely sensitive to small changes in the habitat structure, including habitat complexity, litter depth and microclimate characteristics. Generally, as disturbance increases the spider species richness decreases. Thus the physical structure of environments has an important influence on the habitat preferences of spider species, especially web-building species (Uetz 1991; Hurd & Fagon 1992).

All habitat types had unique families and species indicating that all habitats are important if the spider biodiversity is to be conserved. Therefore, no one habitat type is less important than another and efforts should be made to conserve representatives of all habitat types within the Reserve.

Patterns of species diversity between habitat types may have been hidden at the species level because many of the species found appeared to be rare as they were only found occasionally. This may not necessarily be the case and certain species may just be more cryptic that others (see above). The dominance of samples by few species with many individuals and many species with few individuals is common in invertebrates. At the level of species, there were no sites that are completely similar. The highest similarity value was 0.4, which was still less than half of the species shared. Again, if species distributions were influenced by the habitat we would expect all sites within the same habitat type to share many species. This was not the case and sites within the same habitat type shared very few common species (Table 3.5). This indicated that species were not restricted to one habitat and other factors such as prey availability may be more important in determining spider species distributions.

At the level of species there were four distinct clusters. These clusters closely corresponded to the sampling period. This indicated that similar species were present at specific times of the year. Seasonal variation may have been a more important determinant than the habitat type alone. This provides valuable insight into sample protocols and certain species may dominate at different times of the year. Therefore, to get a true representation of the species present sampling should be conducted in all seasons. This conclusion is supported by other work being conducted in the Reserve on other invertebrates (beetles, ants and
grasshoppers) where different species dominated at different times of the year. In addition, certain species may mature at different times of the year and thus by conducting sampling throughout the year adults can be collected. The adults are taxonomically important, as they are often essential for species level determinations.

Care needs to be taken when interpreting the significance of differences between arthropod diversity indices, since not all species have been sampled. From the species accumulation curve there was some indication that the amount of new species encountered after each new sampling period was decreasing but the full compliment of species has not yet been reached. The four samples taken from the riverine area further support the fact that not all species have been found because five new species were found in this habitat alone.

3.4.5 Conservation

Considering the high spider diversity in this Reserve efforts should be continued to ensure that the area is conserved, not only for the large vertebrates (which attract considerable attention), but also for the invertebrates. There were several genera (e.g. Araneidae: Araneilla, Nemospiza; Gnaphosidae: Caponia; Miturgidae: Cheiramiona; Salticidae: Thyenula; Sparassidae: Panaretella; Theraphosidae: Brachionopus and Zodariidae: Caesetius) sampled in the Reserve that are endemic to South Africa. The following genera, Ceratogyrus, Harpactira and Pterinochilus are protected species and all three occur in this Reserve. The baboon spiders are popular as pets and are often sold on the black market and it is imperative to conserve these species. The trapdoor baboon spider (Barychelidae) was also sampled here which is the first distribution record of this species in South Africa. Efforts should be made to support reserves, as the resources are already in place for the conservation of other animals so the costs of preserving these habitat types for all species biodiversity is considerably less.

3.5 Conclusion

The ecology and diversity of the spider fauna of the Northern Province is poorly known. Except for taxonomic descriptions (Lawrence 1937, Lawrence 1938), the only ecological studies on spiders is that of Van der Merwe (1994) and Van der Merwe et al. (1996), who compared the spiders of forests, pine plantations, and grassland. The present study is therefore a significant contribution to our knowledge on spider species distribution in South Africa. This study represents new distribution records for all species recorded and 14 possibly new previously undescribed species. Two genera, Araneidae: Prasonica and Philodromidae: Gephyra, are new distribution records for South Africa. A new distribution record for the Barychelidae family was a valuable find because this family was not previously thought to occur in South Africa. The savanna habitat has an extremely diverse spider community and further research should be encouraged in this biome.
Chapter 4

ASSESSMENT OF INDICATORS, HIGHER TAXON IDENTIFICATION AND MORPHOSPECIES IDENTIFICATION BY NON-SPECIALISTS AS SURROGATE METHODS USED IN RAPID BIODIVERSITY ASSESSMENT

4.1 INTRODUCTION

Invertebrates include more than 80% of all animals (Samways 1993a), and yet are severely under-represented in studies of southern African diversity. Site biodiversity estimates that do not consider invertebrates, not only omit the greatest part of what they are attempting to measure, but also ignore major contributors to essential ecosystem processes (Wilson 1988). It has been recognised by several scientists (Samways 1994; McNeely et al. 1995) that the inclusion of invertebrates in biodiversity inventories is desirable. However, the demand on time and resources using conventional methods is immense. Complete inventories of all organisms are impractical at present because there are far too many for direct enumeration (Williams, Gaston & Humphries 1997). Furthermore, at the current rate it would take several thousand years to describe all the species or to have an idea about the diversity if traditional taxonomic methods are used (McNeely et al. 1995).

Invertebrate diversity is particularly challenging because: (1) there is a high proportion of undescribed or undetected species; (2) the formal determination of species names is time consuming and, in those groups where formal taxonomy is poorly developed, may not be possible; (3) species identifications are costly and identifying all species, even in a limited area, is thus a very expensive task. (4) species distributions are unknown; (5) professional taxonomists are few; (6) comparative sampling methods are non-standardised and (7) knowledge of responses to environmental change is generalised and limited (New 1999; Oliver & Beattie 1993; Oliver et al. 2000).

In addition, for many large-scale ecological studies the experience and resources required for species resolution are often not available and this is especially so in developing countries (Nielsen, Shiel & Smith 1998). Hence, there is often a need to trade off taxonomic resolution for ecological answers. The need to develop quicker and easier methods for describing the species of the world is clearly desirable.

In South Africa, there is a serious lack of taxonomic expertise, especially for spiders. Dippenaar-Schoeman & Jocqué’s (1997) book on African spiders is the first comprehensive guide to identifying spiders of southern Africa. However, even though a vast amount of information is covered in this guide, only identification to the level of family, and in some cases genus, can be done. Original literature and descriptions for the species are simply not readily available for the 5 500 species which are presently known to occur in sub-Saharan
Biologists are continually suggesting novel shortcuts to the identification of conservation priorities (Vane-Wright et al. 1991), and particularly, the estimation of species richness (Colwell & Coddington 1994). Some of these methods include extrapolation, species accumulation curves, parametric models or relative abundance and non-parametric methods (Colwell & Coddington 1994; Harper & Hawksworth 1994).

Another approach to resolving this problem is to find surrogates for diversity measures; quantities that are more easily determined and which correlate strongly with those measures (species richness) of biodiversity which ultimately are desired (Gaston & Blackburn 1995). The use of surrogates has long been advocated as a means of inferring the relative levels of biodiversity in different areas as expressed by species richness (Gaston & Blackburn 1995).

Three main groups of surrogates have been suggested to help overcome the problem of trying to do an inventory of the world's species: (1) the use of "indicator groups", i.e. groups whose diversity correlate with that of others (Faith & Walker 1996; McGeoch 1998; Noss 1990); (2) the use of "ecological shortcuts" to understanding natural communities such as the higher taxon approach (genus and family level identifications) (McGeoch 1998; Balmford et al. 1996a) and (3) the allocation of morphospecies by non-specialists (Trueman & Cranston 1997; New 1995; Oliver & Beattie 1996; McGeoch 1998; Balmford et al. 1996a). These surrogates all aim to accelerate the rate at which species inventories are done.

### 4.1.1 Indicators as surrogates for species richness

Indicators are species that are diverse, easily and quickly studied, are functionally significant and whose patterns of diversity are likely to be representative of many other species (Abensperg-Traun et al. 1997; Pearson & Carroll 1998). Invertebrates are often selected as indicators based on the following criteria: (1) ease and reliability of sampling, (2) abundance, (3) functional importance and (4) ability to rapidly reflect changes in the environment (New 1995).

There have been many attempts to use indicator species to predict species richness (e.g. Clark & Samways 1993; Pearson & Cassola 1992; Pearson 1994; Beccaloni & Gaston 1995; Cranston & Trueman 1997; Carroll & Pearson 1998). Taxa that have been extensively used as indicators include butterflies, dragonflies and beetles (reviewed in Samways 1994; McGeoch 1998). Some species work well across taxa but generally the same indicator cannot be used across continents (Pearson & Carroll 1998).

Some authors (New 1995; Coddington et al. 1996) propose that spiders are a potential group that could be used as indicators as they fit the categories required to be efficient indicators (diverse, easily sampled, functionally important and reflect changes in the
environment). Some scientists (Preston-Mafham & Preston-Mafham 1984, New 1999) consider spiders to be a useful focal group for wholesale invertebrate conservation. Spiders are among the most speciose orders of animals with more than 30,000 species described worldwide (Preston-Mafham & Preston-Mafham 1984). They are ubiquitous generalist predators and are themselves an important food source for other animals. Consequently, a very valuable component of ecosystem functioning (Dippenaar-Schoeman 1979; Nyffeler, Sterling & Dean 1994; Dippenaar-Schoeman & Jocqué 1997; New 1999; Skerl 1999).

More recent attention has focussed on the development of indicators of biodiversity, particularly in relation to estimates of species richness in highly diverse groups, such as invertebrates, where comprehensive species-level surveys are usually not possible (Hammond 1990; Oliver & Beattie 1996; Andersen 1997; Rodríguez, Pearson & Barrera 1998). However, recent studies have emphasised inaccuracy of conclusions based on indicator species and few studies have demonstrated a significant positive relationship between the diversities of indicator and target taxa (Lawton et al. 1998; Van Jaarsveld et al. 1998; Cranston & Trauman 1997). Abensberg-Traun et al. (1997) caution that indicators should not be used without verification of their validity.

In this study, the use of spiders as indicators of wholesale invertebrate diversity and the use of two diverse spider families (Thomisidae and Salticidae) as indicators of wholesale spider diversity was evaluated.

4.1.2 Higher taxa as surrogates for species richness

The higher taxon method involves reducing the level of identification of samples to groups above species (such as genera or family) (New 1995; Balmford et al. 1996a). Higher taxa are markedly fewer than species, and their spatial distributions tend to be proportionately better known (Gaston, Williams, Eggleton & Humphries 1995). In addition, there is a widespread correlation between family and species richness (Williams et al. 1994). This approach has become one of the more popular surrogates measures used for predicting biodiversity (Williams, Gaston & Humphries 1997).

There are several advantages to using a higher taxonomic level identification, making their use extremely tempting to many scientists. Some of these advantages include: (1) the expression of patterns of biodiversity in terms of numbers of higher taxonomic units provides a powerful way of overcoming the insurmountable resource demands (i.e. time and expertise) in obtaining equivalent data on species numbers thus making surveys more cost effective (Balmford, Jayasuriya & Green 1996b; Williams & Gaston 1994; Williams, Humphries & Gaston 1994; Gaston et al. 1995); (2) since higher taxa are more easily surveyed this method could possibly act as a reliable surrogate for patterns of species richness (Balmford, et al. 1996a; Williams & Gaston 1994); (3) this technique enables more rapid biodiversity
assessments and could be especially useful in identifying areas for conservation (Prance 1994; Balmford et al. 1996a); (4) juveniles can often be associated with adults at the higher levels and incorporated into analysis, whereas they must be ignored in species-level assessments (New 1999); (5) some source of error, such as misidentification, can be avoided and (6) by reducing the number of species within major taxa requiring taxonomic treatment (identification to morphospecies), a greater range of major taxa can be incorporated into surveys (May 1999).

In several cases this method has been very useful and proved reasonably accurate (Oliver & Beattie 1996; Balmford et al. 1996a; Balmford et al. 1996b; New 1999). Churchill (1999) has shown that family level interpretation of spiders can be as effective as species level separations. However, others feel this method should be used with caution, as the limitations are not always recognised and the data may become unreliable if used for biodiversity studies (Balmford et al. 1996a; McGeech 1998; Nielsen et al. 1998; Van Jaarsveld et al. 1998; Slotow & Hamer 2000). In addition, this method may lead to a loss of information (Roy & Foote 1997). This study will evaluate the use of two higher levels of identification (family and genus) for the purpose of spider biodiversity studies.

4.1.3 **Morphospecies identified by non-specialists as surrogates for species richness**

A more recent attempt to improve cost efficiency is the use of non-specialists (also known as biodiversity technicians (Oliver & Beattie 1993) in Australia or parataxonomists (Goldstein 1996) in Costa Rica) to sort invertebrate specimens to morphospecies (Oliver & Beattie 1993; Beattie & Oliver 1994; Cranston & Hillman 1992). These non-specialists receive little training and are used to divide species into recognisable taxonomic units (RTU’s). This method focuses specialist input at critical phases of the process. Morphospecies-level identifications are frequently used for a number of reasons: (1) morphospecies classification requires no taxonomic expertise since organisms are grouped on a like-with-like basis and can therefore be undertaken by anyone; (2) it is relatively quick and cost effective (Oliver & Beattie 1993) and (3) morphological diversity has the potential to provide a very useful biodiversity metric (Roy & Foote 1997; New 1999).

Oliver & Beattie (1997) have shown that morphospecies identified by non-specialists can provide estimates of richness and turnover consistent with those generated using species identified by taxonomic specialists. However, since species determinations of invertebrates are rarely based on characteristic features apparent to the inexperienced eye, the estimates of morphospecies are likely to be either an under or over estimation of the true level of diversity. Furthermore, juveniles, females and males often look different to non-specialists, leading to over estimation of diversity for some groups (Balmford et al. 1996a; Slotow & Hamer 2000).
Despite this, it is a standard technique. This study attempts to determine whether non-specialists, with minimal training, could produce accurate estimates of the number of spider species contained within samples, the accuracy being determined by a taxonomic specialist. The emphasis was on the estimates of species richness and not on the naming of taxa.

The aims of this study were to determine if the species richness surrogates (indicators, higher taxa and morphospecies) used were reliable for biodiversity studies, using spiders as an example. The objectives of this study were therefore to (1) investigate if spiders are reliable indicators of wholesale invertebrate diversity, (2) test the efficiency of the higher taxon method (family and genus level) as surrogates for species richness and (3) to evaluate the reliability of the use of morphospecies, sorted by non-specialists (undergraduate students), as opposed to true species in biodiversity assessment.

4.2 METHODS

Sampling was done at 40 sites throughout Makalali Private Game Reserve (Figure 2.1). This represented eight replicates of five different habitat types. The habitat types are described in detail in Chapter I and include: three mixed bushveld areas with varying soil types, rocky outcrops and mopane woodland. Four different sampling techniques (described in detail in Chapter 2) were used to capture the spiders, these included sweep netting, beating, active searching and pitfall trapping.

The selected methods sampled different layers of the environment. Sweep netting sampled spiders in the field layer, beating sampled spiders in the tree and shrub layer, pitfalls sampled ground dwellers and active searching sampled all layers.

4.2.1 Spiders as indicators

Invertebrates were sampled from the Reserve at the same sites and at the same time as the spiders using pitfall traps and sweep nets. The invertebrates were sorted first to order level by C. Whitmore and then sorted by a B.Sc. Honours student (4th year) from the University of Natal, Durban to morphospecies level. Three groups of invertebrates were selected for further analysis. These were ants (Hymenoptera), beetles (Coleoptera) and grasshoppers (Orthoptera). The diversity, richness and evenness values were calculated (Chapter 3) for all three groups combined as well as separately for ants, beetles and grasshoppers. The relationship between the diversity of spiders and that of other invertebrates was determined.

In addition, a very speciose spider family, crab spiders (Thomisidae) was evaluated for its usefulness as an indicator of wholesale spider diversity. The species richness of thomisids was correlated with all other spider species richness to determine whether a relationship existed between the two. The taxonomy of thomisids is well known in South
Africa. The group has been extensively reviewed by Dr A.S. Dippenaar-Schoeman of the National Collection of Arachnida, Biosystematics Division of the Agricultural Research Council Plant Protection Research Institute, Pretoria (Dippenaar-Schoeman 1980a; Dippenaar-Schoeman 1980b; Dippenaar-Schoeman 1983; Dippenaar-Schoeman 1984; Dippenaar-Schoeman 1985; Dippenaar-Schoeman 1986a; Dippenaar-Schoeman 1986b; Dippenaar-Schoeman 1988; Dippenaar-Schoeman 1989b). It follows from this that these groups have the potential to be used as indicators of wholesale spider diversity because (1) their taxonomy is well known, (2) there are local experts available who are able to identify these groups and (3) they are abundant and readily sampled using different sampling techniques. Therefore, should a positive relationship between the diversity of these groups and wholesale spider diversity exist, they could be used as indicators. This would facilitate quicker biodiversity assessments because sampling could be focussed towards one group and costs in terms of time and expertise would be considerably reduced. Thomisids are just one of the very diverse spider families and in order to make the results more generalised another diverse family namely jumping spiders (Salticidae) were also evaluated for their usefulness as indicators of wholesale spider diversity. The salticids are a very abundant family and are readily sampled using various techniques.

4.2.2 Higher taxa as surrogates for species richness

All specimens were sorted to family level (Dippenaar-Schoeman & Jocqué 1997) by C. Whitmore with some assistance from Dr T. Crouch, Durban Natural Science Museum. The species-level determinations were done by Dr A.S. Dippenaar-Schoeman. Data for the two levels of identification were then compared.

4.2.3 Morphospecies identified by non-specialists as surrogates for species richness

The use of morphospecies for biodiversity studies was evaluated using a range of people with limited skills and knowledge of entomology and arachnology. Four undergraduate students (1st and 2nd year Biology students) were used to sample and sort spiders from ten different sites in the Reserve. The students conducted sweep netting and active searching in the ten selected sites. Two transects of 20 sweeps each were done in each site and the contents were placed into a bucket and later sorted. Active searching was done in plots of 1 m x 1 m and each quadrat was thoroughly searched for spiders. The spiders were collected using the hand-to-jar method or a pooter (Sutherland 1996). Each individual did two plots in each site and the time spent searching was 15 to 20 minutes in each quadrat. A total of two hours was spent searching each site. Students did all the collecting and sorting of specimens without help from more experienced participants. Students sorted spiders into morphospecies, with the aid of a
dissecting microscope. The spiders were then checked by C. Whitmore and later by Dr A.S. Dippenaar-Schoeman. The two levels of identification allowed for the testing of the accuracy of this method as a surrogate for species richness.

4.3 RESULTS

4.3.1 Spiders as indicators

There was a significant positive relationship between the spider species richness and invertebrate richness (Linear regression: $R^2 = 0.112, F_{1,38} = 4.799, P = 0.035$; Figure 4.1). However, when spiders were divided according to their functional groups (plant wanderers, ground wanderers and web builders) (Chapter 3) there was no longer a significant relationship between spider species richness and wholesale invertebrate diversity. The relationship was also non significant when insect groups (ants, beetles and grasshoppers) were considered separately. (all $P > 0.05$, Table 4.1, Figure 4.2). The use of spiders as indicators for wholesale invertebrate diversity was supported but only when all invertebrates combined were considered. This implies that the relationship between insect species richness and wholesale spider species richness was not very robust.

Table 4.1: Summary table of the relationships between spider species richness and insect species richness. Note that there are no significant relationships.

<table>
<thead>
<tr>
<th>Linear regression</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ant (S) vs spider (S)</td>
<td>1.38</td>
<td>0.286</td>
<td>0.596</td>
</tr>
<tr>
<td>Beetle (S) vs spider (S)</td>
<td>1.38</td>
<td>0.507</td>
<td>0.481</td>
</tr>
<tr>
<td>Grasshopper (S) vs spider (S)</td>
<td>1.38</td>
<td>0.137</td>
<td>0.714</td>
</tr>
<tr>
<td>Insect (S) vs spider plant wanderers (S)</td>
<td>1.38</td>
<td>2.523</td>
<td>0.120</td>
</tr>
<tr>
<td>Insect (S) vs spider ground wanderers (S)</td>
<td>1.38</td>
<td>0.558</td>
<td>0.459</td>
</tr>
<tr>
<td>Insect (S) vs spider web builders (S)</td>
<td>1.38</td>
<td>0.005</td>
<td>0.943</td>
</tr>
</tbody>
</table>

There was a significant negative relationship between the thomisid species richness and all other spider richness (Linear regression: $R^2 = 0.171, F_{1,38} = 7.848, P = 0.008$; Figure 4.3a). As the thomisid species richness increases the combined species richness of other spiders decreases. Similar results were obtained for the salticids (Linear regression: $R^2 = 0.222, F_{1,38} = 10.869, P = 0.002$; Figure 4.3b). As the salticid species richness increased so the species richness of all other spiders combined decreased.

4.3.2 Higher taxa as surrogates for species richness

There was a significant positive relationship between the numbers of species and numbers of families (Linear regression: $R^2 = 0.505, F_{1,38} = 38.74, P < 0.0001$; Figure 4.4) as well as the
Figure 4.1: The use of spiders as indicators of invertebrate species richness.
Figure 4.2: The use of spider species richness as an indicator of (a) Formicidae, (b) Coleoptera and (c) Orthoptera species richness.
Figure 4.3: The use of a) thomisids and b) salticids as indicators of spider species richness.
number of species and number of genera (Linear regression: $R^2 = 0.736$, $F_{1,38} = 106.02$, $P < 0.0001$; Figure 4.3). Although both relationships were significant, the strength of the genus:species relationship was greater than the species:family relationship. The genus:species regression more closely approximated the 45° slope than the species:family regression. The two regression slopes were significantly different from one another ($t = 18.32$, df = 76, $P < 0.05$). This implies that genera were significantly better than families as surrogates for species richness. Both the genera and family level of identification overestimate the true number of species. However, at the level of family the number of species was significantly more overestimated than at the level of genera.

The answers obtained from the different levels of analysis also need to be evaluated in a biological context. The answers obtained from the different levels of identification may give very different results. This could have serious implications if the results were to be used for conservation purposes. For example, a significant difference was observed between sampling period and species (ANOVA: $F_{2,149} = 3.609$, $P = 0.030$) and genera (ANOVA: $F_{2,149} = 3.063$, $P = 0.050$) but this relationship was not significant at the level of family (ANOVA: $F_{2,149} = 1.826$, $P = 0.165$; Figure 4.5). Therefore if surveys were conducted only to the level of family the answers obtained could differ dramatically.

### 4.3.3 Morphospecies identified by non-specialists as surrogates for species richness

The number of morphospecies identified was compared to the number of true species determined (Figure 4.6). The results showed a significant overestimation of species by inexperienced participants for both sampling techniques when compared to the results for experienced participants ($F_{1,148} = 34.24$, $P < 0.001$; Figure 4.7). As experience and practice increased so fewer mistakes were made. The spiders for March and November were sorted by C. Whitmore and there was a marked decrease in the level of overestimation between March and November. The improvement was largely due to some previous training, a reference collection and a lot of practice (Figure 4.6).

There was also a significant difference between the level of overestimation between the sweep samples and the active searching samples sorted by the inexperienced participants. Twice as many individuals were sampled by sweeping than active searching (544 and 268 individuals respectively). The data indicates that as the volume of samples increase so too does the level of overestimation (Figure 4.6).

The improvement of sorting ability of students with time showed no relationship ($F_{1,8} = 2.950$, $P = 0.124$) and the students tend to consistently overestimate the number of species (Figure 4.8). However, the field sorting was only conducted over a single week and this may not be enough time to detect a significant improvement as they were still learning.
Figure 4.4: The use of higher taxa as surrogates of species richness. The genera (×) and families (□) are compared. The genera more closely approximate the 45° angle (dotted line) meaning they are better surrogates. The values represent the different sites sampled.
Figure 4.5: The seasonal effect on spider diversity at the level of family (○), genera (○) and species (△). The mean and ±95% confidence limits are presented. N = the number of sites sampled within each time period.
Figure 4.6: The effect of participants experience on their ability to sort morphospecies accurately. Any values over 0 indicate an over estimation and values below zero indicate an underestimation. The (o) and (a) symbols indicate sweeping and active searching respectively. The mean ± 95% confidence limits are presented. Less experienced participant refers to my initial sorting, more experienced participants represents previous training and sorting and inexperienced participants represents the students with no prior sorting experience.
Inexperienced participants

Experienced participants

Figure 4.7: The influence of experience on the ability of participants to accurately sort morphospecies. The number of species (□) and morphospecies (○) are compared. The mean and 95% confidence limits are presented. N represents the number of sites sorted by each participant.
Figure 4.8: The overestimation of spider morphospecies made by inexperienced participants with time. The numbers represent the number of species. Two values appear on the same day because two sites were sorted per day.
4.4 DISCUSSION

4.4.1 Indicators as surrogates for species richness

New (1999) suggested that spiders could be used as a possible focal group, which are of wide relevance to terrestrial ecosystems. This would help overcome the challenges of taxon surveys and taxonomic inadequacy. It would be convenient if the diversity of spiders (predators) correlated positively with that of other invertebrate taxa, e.g. insects (prey). However, indicator relationships cannot always be assumed, particularly when indicator and target organisms differ in their habitat associations since different factors may govern their distributions. In addition, Abensberg-Traun et al. (1997) caution that indicators should not be used without verification of their validity.

The results indicated that spiders could be used as indicators of wholesale invertebrate diversity. However, the relationship was not very robust because once the spiders were separated into different functional groups (plant wanderers, ground wanderers and web builders) and compared to different insect components (ants, beetles, grasshoppers) there was no longer any relationship.

This has implications for the designing of sampling protocols. The study done in Chapter 2 shows that different sampling techniques capture different components of the spider fauna and single techniques, e.g. pitfalls alone, will not sample the full compliment of species. Therefore, no attempt should be made to compare these groups unless all microhabitats have been sampled. Although there was a positive relationship it was not robust and thus the use of spiders as indicators is not recommended unless the researcher is certain that all functional groups have been adequately sampled. Care should be taken in the interpretation of these results as not all species have been sampled. Therefore based on the results from this study the use of indicators remains inconclusive.

Spiders as a group are difficult to identify to the level of species because of the sheer numbers of species and individuals. It takes many years to become a specialist and even then there are new species being described all the time. However, the taxonomy of certain groups within the Araneae are better known than others, e.g. Thomisids. This group is taxonomically well known and therefore has the potential to act as an indicator for wholesale spider diversity. There was a weak negative relationship between the diversity of thomisids and all other spiders. The same results was obtained for the salticids and therefore the use of one family of spiders to predict the richness of all other spiders was not valid in this study. It is unlikely that a single family would provide information about all species as different families have very different life strategies and occupy different strata in the environment. Furthermore, not enough is known about the distribution of spider species or their life histories generally to
explore this further.

4.4.2 Higher taxon method as surrogates for species diversity

The only properties required of higher taxa for estimating whole scale biodiversity are that their richness distribution can be predicted by the distribution of species richness and that the information to map their distribution is more readily acquired than for species (Williams & Gaston 1994).

Williams & Gaston 1994; Oliver & Beattie 1996 and Balmford et al. 1996b have shown a significant positive correlation between higher taxa and species richness. It could be inferred from these results that by surveying only a higher level more time is saved (Balmford et al. 1996a). Other scientists (Oliver & Beattie 1993; Skerl & Gillispie 1999) have shown that the method is cost effective and that it is possible to try and avoid misidentifications by doing a genus- or family-level analysis (Norris 1999). The results from this study confirm the work of others and a significant positive correlation between the species and families as well as the species and genera was found. From these results we may be tempted to infer that surveys at the level of genus or family are reliable as a surrogate measures for species richness.

This is unfortunately not the case. The answers obtained from different identification levels of identification give very different results. The data obtained from biodiversity surveys needs to be applied to real situations. An area may show a strong family: species correlation yet significant changes or impacts on biodiversity may only be detected at lower levels (genera or species). The example used here shows that significant differences between sampling periods are only detected at the level of species and genus but not at the level of family. Thus from a biological perspective we would need to use at least the level of genus and not family. These results are supported by Prance (1994) who recommends that if higher-taxon surveys are to be used, then genus- and not family-level identification be used.

For some groups, e.g. plants it may be possible to use higher taxon level identifications and the method works very well but for spiders specialist taxonomic expertise are required for identification even to the level of genus. The genera and species descriptions for many of the 5 500 spiders in southern Africa is simply not readily available. Therefore, for spiders, species level identifications may as well be done as the time and effort required for identification to the level of genus would be similar to that required for species identifications.

Gaston & Blackburn (1995) point out that the strength of the correlation between numbers of species and higher taxa is likely to decline rapidly towards progressively higher taxonomic levels (e.g. from genera to tribes to families; Williams & Gaston 1994). The strength of the correlation coefficients was greater for number of genera ($R^2 = 0.736$) than for...
numbers of families \( (R^2 = 0.505) \). In addition, the more species a given higher taxon represents the poorer an indicator of species richness that higher taxon becomes (Gaston & Blackburn 1995). A consequence of this is that there is a trade off between time saved by higher taxon surveys and the quality of information obtained from those surveys (Balmford et al. 1996a).

Despite a positive correlation between higher-taxa and species richness, Balmford et al. (1996a) have shown that the precision with which absolute species richness in reserves could be predicted from higher-taxon richness was surprisingly low, particularly for rich sites where surveying higher taxa rather than species would save the most time. Furthermore, the work of Van Jaarsveld et al. (1998) does not support the use of surrogate measures for the selection of reserves. Their results suggest the use of higher taxa as surrogates for species complementarity hold little promise at a scale relevant for practical conservation planning (Van Jaarsveld et al. 1998).

Therefore, although the number of higher-taxa present in an area may be easily and rapidly assessed (Williams et al. 1994; Harper & Hawksworth 1994), the results do not convey information about the total number of species which these higher taxa represent (Balmford et al. 1996a). On this basis Prance (1994) argues that when assessing biodiversity for conservation planning we need to focus our attention on species.

Not knowing the names of the species in a community severely limits the ability to compare different systems and to understand the biology and ecology of such organisms by comparing them to their better-known relatives (U.S. National Report, 1995). Species data is essential for the understanding of the ecosystem and to allow for adequate management (Goldstein 1999). Many conservationists seek short cuts to the interpretation of data believed to represent key aspects of the ecosystem. Some shortcuts have sacrificed their scientific underpinnings, to the extent that basic scientific considerations are bypassed (Goldstein 1999). Selecting conservation areas from genus- or family-level data cannot result in efficient species level conservation (Van Jaarsveld et al. 1998). While useful, the methods may downplay the role of the species and population specific requirements (Goldstein 1999).

4.4.3 Morphospecies identified by non-specialists as surrogates for species diversity

In this study measures of species richness were influenced by the level of experience of individuals conducting the sorting of material. Inexperienced undergraduate students overestimated species richness significantly when compared to more experienced participants.

Initially students were very cautious and whenever in doubt chose to separate species. Other arthropods were also included in the samples (e.g. ticks, mites and some insects). When sorting was done in the laboratory as opposed to the field students noticed that some species
that were initially thought to be different were actually the same (personal observation). Despite noticing their mistake there was still a tendency for students to keep samples separate if there was any doubt, resulting in an overestimation of species richness. Oliver & Beattie (1996) have shown that morphospecies generally provide overestimation and genus and family richness tend to underestimate actual species richness when richness is high and overestimate when richness is low (Gaston & Blackburn 1995).

In March of 1999 I considered myself a non-specialist as I had little previous experience in sorting and identifying spiders. There is clearly a large difference in the degree of overestimation made between the March and November samples. Norris (1999) acknowledges that mistakes are common when non-specialists identify specimens and the misidentifications are due to a lack of experience. In November far fewer mistakes were made indicating an improvement in the identification process. This was only after I had completed a week-long spider identification course with Dr A.S. Dippenaar-Schoeman and sorted many spiders.

The improvement may also be a result of having a reference collection, identified to the level of species, from the March sampling period with which I could compare the November specimens. The reference collection proved very valuable for this study. The amount of time required from experts was considerably less for the November and December samples. Attempts were made to identify spiders to level of species by comparing new specimens to the reference collection. The identifications were then verified by an expert. Oliver & Beattie (1993) indicate that estimates will improve as biodiversity technicians gain experience with the taxa they are sorting.

The students, however, did not show an improvement with time when sorting in the field and consistently overestimated species. This highlights the fact that non-specialists cannot be expected to do good quality work without first having some training in the groups that they are dealing with. In addition, the students made more overestimations for the sweep samples than for the active search samples. This could be attributed to the fact that twice as many spiders were captured by the sweeps than the active searching and as the volume of spiders increased so too did the level of overestimation. This highlights the care needed when selecting biodiversity technicians so that they have the appropriate level of qualification for the job. Some level of training is essential before non-specialists can be used beneficially to facilitate the process. The students used in this study represent an extreme case and are not equivalent to biodiversity technicians and it is not recommended that people at this level be used as biodiversity technicians.

These results were contrary to some other studies. Oliver & Beattie (1996) and Oliver & Beattie (1993) showed that morphospecies estimates made by biodiversity technicians may be sufficiently close to formal taxonomic estimates of species richness to be useful for the
rapid assessment of biodiversity. This contradiction may be because for their study, only mature spider specimens were used which could account for the high degree of agreement between non-specialist and specialist estimates. They acknowledge that including other life stages (e.g. juveniles) in rapid biodiversity assessment may lead to large errors (Oliver & Beattie 1993). The data also suggests that the use of morphospecies require a minimum of unambiguous morphological features that a relatively untrained individual can easily and quickly utilise.

While the morphospecies method is appealing and there are studies supporting its use, some authors are not convinced about the general applicability of the data. Goldstein (1996) expresses concern about the morphospecies approach of Oliver & Beattie (1993) and the usefulness of the data for setting conservation priorities and establishing protocols for biological monitoring. Traditionally, the role of the non-specialists (parataxonomists or biodiversity technicians) has been to help with the preliminary sorting of samples prior to their examination by specialists. This cuts down on the amount of time required by the specialist in routine general sorting, allowing more time for accurate determinations (Goldstein 1996). However, in some parts of the world, non-specialists are being used to collect and act as a substitute for, rather than a supplement to, the examination of organisms by specialists (Goldstein 1996). Any faulty estimation of the numbers and identities of species may have far reaching consequences and impede, rather than enhance, understanding, so that great care is needed to ensure the quality of the results produced (New 1995). The assumption that non-specialist personnel can replace specialist taxonomic expertise at a fraction of the cost is patently false. Biodiversity technicians, however, can play a major role in extending the efficiency of the limited number of taxonomists by effective sorting and preparation of specimens from bulk samples, and thus rendering specialists' time more effective (New 1995).

Oliver and Beattie (1993) use the approach that species richness should be the primary criterion on which both the prioritisation of natural areas for conservation and monitoring of natural communities should be based (Goldstein 1996). However, those areas that are species-rich often do not support many species that are actually of conservation concern. Hence, surrogate measures of species richness will likely overlook areas supporting rare, endemic or threatened organisms (Goldstein 1996).

McGeoch (1998) cautions that the use of morphospecies should be undertaken with great care as problems may arise when different study sites are to be compared. The morphospecies may not be assigned consistently during different surveys. This ultimately necessitates species-level taxonomy or a standardised method of classifying species. McGeoch (1998) also indicates that the quality of the data on which bioindicator predictions and conservation are made is fundamental to their accuracy. Slotow & Harner (2000) also discourage the use of morphospecies, especially for conservation planning.
Melbourne (1997) feels that rapid assessment of species assemblages may not be possible because, as illustrated by Hinkley & New (1997), new species are discovered with each new sampling period and 75% of the species present were only obtained after 3 to 5 sampling periods. This pattern was certainly reflected in this study. With each new sampling trip new species were added to the species checklist. This is not very encouraging if very rapid assessments want to be carried out since continued sampling or long-term studies would be necessary to sampling all species in the environment. Therefore, despite the widespread interests in promoting rapid biodiversity assessments, there are clear indications that this may not always be beneficial (Melbourne 1997).

4.5 CONCLUSION

Although there was a positive relationship between the spider species richness and insect species richness the use of spiders to predict wholesale invertebrate diversity was not supported. There was a significant correlation between the numbers of species and families and the number of species and genera. This relationship was stronger at the level of genus than family. It follows then that if higher taxon surveys are to be used for biodiversity assessment then estimates at the level of genus should be used. Species-level identifications remain ideal if the data are to be used for conservation. Higher taxon data should only be used in situations where there are insufficient resources available for good species data to be a realistic alternative.

The use of spider morphospecies identified by non-specialists is not recommended here. Spiders are a particularly large group and at least a week of expert training and many hours of sorting are recommended. However, the morphospecies level identifications do improve with practice (personal experience). If this approach is to be used then the same individual should sort specific groups and will thus become more experienced. If morphospecies have to be used, then a good knowledge of specific taxonomic characters of each group chosen is essential (Slotow & Hamer 2000).

Reference collections are essential and should be properly labelled and documented, and lodged at institutions with appropriate curatorial staff. This would allow for comparisons with other sites at different times and more importantly allows for specimen verification.
CHAPTER 5

BIOTIC & ABIOTIC PROCESSES DRIVING SPIDER BIODIVERSITY

5.1) INTRODUCTION

5.1.1 Patterns vs processes

Biodiversity, the variety of life, is distributed heterogeneously across the Earth (Biodiversity Series 1993; Gaston 2000). Some areas have very high diversities (e.g. tropical forests) while others are virtually devoid of life (e.g. deserts). Some suggestions as to the causes of differing global pattern of diversity in different parts of the world can be attributed to climate, area, latitude, altitude; productivity, available resources and habitat complexity to name just a few (MacArthur 1972; Rosenzweig 1995; Trevelyan & Pagel 1995). Most major terrestrial and freshwater groups are more speciose in tropical than temperate regions, at low elevations than high, and in forests than in deserts (Biodiversity Series 1993; Trevelyan & Pagel 1995; Gaston 2000). These global patterns of species diversity are well established (Trevelyan & Pagel 1995; Gaston 2000).

Determining why these differences occur has long been the core objective of ecologists (Menge & Olson 1990; Gaston 2000). The past decade has seen a proliferation of studies documenting broad-scale spatial patterns in biodiversity. While there is extensive literature on the patterns of diversity at a global scale, the underlying processes driving the local and regional patterns of diversity have not been considered in such detail.

The processes influencing groups such as mammals (Munthali & Banda 1992; du Toit 1995) and birds (MacArthur & MacArthur 1961; MacArthur 1972; Fretwell & Lucas 1970) are well studied. Far less research has been conducted on the processes influencing the diversity patterns of invertebrates and even less on spiders. In addition, our knowledge of these groups is geographically biased with the majority of the studies being conducted in northern temperate latitudes (Trevelyan & Pagel 1995).

A better understanding of processes influencing the diversity of invertebrates is clearly desirable. In addition further research is needed in poorly studied groups such as arthropods. This study focuses on one particular group, namely spiders. However, any study of biotic distribution, diversity and endemism requires the identification of pattern before the underlying processes can be defined (Turpie & Crowe 1994). The patterns of spider diversity at a localised area were investigated in Chapter 3 and the current Chapter attempts to understand the underlying abiotic and biotic processes that influence these diversity patterns.

Understanding which variables are important in determining the diversity is critical to conservation management (Trevelyan & Pagel 1995; Dekker, Van Rooyen & Bothma 1996).
By obtaining correlations between biotic variables (e.g. plant distribution) and extremes of abiotic factors (e.g. temperature, precipitation, wind, etc) an improved understanding of why natural species occur where they do can be achieved (Barr & Carter 1994). This information is essential if species are to be preserved and efforts can then be made to manage conservation areas so those beneficial processes that enhance diversity are maintained. For most animals, a suitable habitat must satisfy various physical constraints and provide sufficient prey and protection from predators (Riechert & Gillespie 1986).

5.1.2 Scale – microhabitat vs macrohabitat

In any environment both biotic and abiotic processes cause differences among communities, and both operate on a range of spatial scales. However, the relative importance of these processes in regulating community patterns appears to vary at a spatial (Menge & Olson, 1990, Samways 1994; Gaston, 2000) and temporal scale (Samways 1994; Rosenzweig 1995). As a result, species diversity patterns are dependant on a complex interplay between both large- and local-scale processes (Menge & Olson 1990).

Scale of measurement, temporal or spatial, has an important bearing on interpretation of temporal events and spatial patterns (Samways 1993b). In addition, the scale at which the analysis is carried out is critical in determining which species benefit from conservation and management decisions. For example, species endemism may not be reflected at a regional scale but only at a local scale (Erasmus, Freitag, Gaston, Erasmus & Van Jaarsveld 1999).

Patterns of species abundance and diversity generally exhibit consistent (homogenous) trends along environmental gradients at the global scale and yet when diversity patterns are considered at a local scale, the species distribution is rarely uniform (Menge & Olson 1990). The spatial patterns are in part determined by the biotic and abiotic processes of the environment (Warrick & Cypher 1998).

Therefore, in order to understand the patterns and the effects of abiotic and biotic processes on species distribution, these processes need to be analysed at different spatial and temporal scales (Samways 1993b; Erasmus et al. 1999). The development of a predictive theoretical framework of community structure will thus be hierarchical (Menge & Olson 1990). In this study multiple regression analysis was used to establish predictive models of spider diversity using microhabitat measurements of biotic and abiotic factors. The processes important in determining the spider diversity were then scaled up to give a local representation of the expected relative diversity for the entire Reserve.

5.1.3 Habitat patchiness

No natural environment is homogeneous; rather, the environment of any plant or animal population is a mosaic consisting of more or less dissimilar sub-environments. There is
heterogeneity with respect to climate, food resources, and living space. Also, the heterogeneity may be temporal with change occurring over time and/or spatial, with dissimilarity found in different areas (Rosenzweig 1995). Species cope with environmental heterogeneity in diverse ways. There is no single plan that prevails in nature. The influence of heterogeneous environments on the structure of animal communities has been discussed frequently in ecological literature (MacArthur 1962; Rosenzweig 1995; du Toit 1995).

African savannas have much spatial heterogeneity (Toit 1995). The heterogeneity results from spatial variation in soil moisture and soil nutrients, which in turn creates patchiness in the quality and quantity of vegetation and ultimately has an effect on other animals (Toit 1995). The effect of habitat patch size will be evaluated in this study by comparing different size patches and the diversity at each patch.

5.1.4 Evaluation of predictive GIS modelling approach

Understanding the patch dynamics of landscapes has been greatly facilitated through the use of spatial information systems (GIS). These systems can adequately examine the hierarchical and spatial complexity of heterogeneous ecological systems (Chapter 1). In the current context GIS was used to relate the diversity of spiders from a site to the biotic and abiotic factors of that site. The spatial information system also allowed for the testing of influences of area on diversity (i.e. patch size). We would expect larger patches to have higher diversity values.

The aim of this section of the study was to determine which abiotic and biotic factors influence the diversity of spiders (Araneae) in a savanna ecosystem. The objectives were to (1) determine the predictive model combining different processes that best explained the spider diversity, (2) to produce Reserve-wide maps of the significant biotic and abiotic factors from the models and (3) to overlay the maps to produce predictive maps of the relative diversity of spiders in the Reserve and (4) compare the actual measured diversity with the predicted diversity and (5) determine how patch size affects the diversity of spiders.

5.2 METHODS

5.2.1 Biotic & abiotic factors affecting diversity

Spider Diversity determination

The diversity of spiders (Araneae) occurring at the different sampling sites was calculated using the SPDIVVER.BAS program of Ludwig and Reynolds (1988). Shannon’s diversity index was used in this study (expressed in species units). Chapter 3 provides details on species diversity indices and their calculation. A richness and evenness index was also calculated but only the diversity index was used in this current analysis. The diversity was
calculated for all spiders as well as for the different functional groups (plant wanderers, ground wanderers and web builders) (Chapter 3). For the multiple regression model the diversity was used as the dependent variable and all other biotic and abiotic variables were the independent variables.

There was a significant seasonal effect on the diversity of spiders (Chapter 3). Therefore the effect of season was factored out before performing the multiple regression analysis. This was done by performing an ANOVA and saving the residuals. The residual values for diversity and the different functional groups were used as dependant variables in the model.

**Vegetation density determination**

The vegetation density at each site was determined by doing the point-centred quarter (PCQ) method (Sutherland 1996). A point was randomly selected and this represented the centre of four compass directions (N, S, E and W), that divide the sampling site into four quarters. The following factors were measured in each quadrant: distance to the nearest tree < 1 m high and > 2 m high, tree species, diameter, height of tree, length of canopy along the greatest length (canopy L), length of canopy perpendicular to canopy L (canopy b) and the density of canopy cover.

The above procedure was repeated five times in each site to give a total of 40 measurements in each site (20 for trees < 1 m high and 20 for trees > 2 m high). The values measured from each site were used to calculate the density of vegetation based on the following equation (Sutherland 1996):

\[
\text{Density} = \frac{1}{D^2}
\]

Where: \( D^2 \) = the mean value taken from the averaged distance of all trees

A value for the density of trees < 1 m high and > 2 m high was calculated. The two measurements were required because the functional groups of spiders maybe influenced by different size trees depending on their life strategies. The density measurements from the PCQ data from each site was used for the multiple regression analysis. These values were extrapolated to produce a Reserve-wide map (see below).

**Vegetation type**

Prior to this study (December 1998 to February 1999) students, under the supervision of David Druce of the University of Natal, Durban, undertook a vegetation analysis of the Reserve. A two kilometre wide grid was constructed in Idrisi and overlaid in a north south direction over the map of the border and roads of the Reserve. This was done to determine
where transect lines should be placed. These transect lines were then divided into smaller 50 m long transects.

A 50 m tape was placed in a north-south direction using a compass. A GPS reading was taken at the beginning, middle and end of each transect. The density of trees along the transect was noted by recording all tree species that were within 500 mm of either side of the tape measure. The transect number, species name, diameter, height and distance along the 50 m tape were recorded. The resulting data allowed for the determination of species densities and composition of woody plants within each habitat type and to separate each habitat type into vegetation types.

The density and species composition of the transects was determined by using TWINSPLAN (See Appendix 5.1 for details). Nine major plant communities were recognised, one with 2 subgroups and one with three subgroups (Appendix 1.2). The most predominant plant community is the Sclerocarya birrea – Acacia nigrescens – Combretum apiculatum – Ziziphus mucronata low closed woodland (type 5) (Appendix 5.2). Tree species commonly found in these plant communities are listed in Appendix 1.2. A full list of tree species occurring in the Reserve is provided in Appendix 1.3.

Only the vegetation types that occurred in the spider sampling sites were included in the multiple regression analysis. The types used were Cissus cornifolia – Commiphora africana low thicket, Ziziphus mucronata – Combretum hereroense low closed woodland, Combretum apiculatum – Terminalia prunoides low closed woodland, Acacia exuvialis – Strychnos madagascariensis low closed woodland and Colophospermum mopane low closed woodland.

Rainfall

Rain gauges were set up at each site as well as at other locations throughout the Reserve. Rainfall data were gathered during the sampling periods. The data collected from the sampling sites was used for the multiple regression analysis.

Additional rainfall data, collected from 11 sites scattered throughout the Reserve, were obtained during the rainy season by the Reserve staff. The mean annual rainfall was calculated for each site. These values were then extrapolated (see section 5.2.3) to produce a Reserve-wide map of rainfall.

Temperature

Air and soil temperatures were measured at all the selected sites using a minimum / maximum thermometer. One thermometer was placed in the air, tied to a branch in a tree and one was buried just below the soil surface for a period of one week. Soil temperature was taken for the duration of sampling and air temperatures were taken at regular intervals throughout the
duration of the study.

The temperature data gathered from the sampling sites were used for the multiple regression analysis. These data were also used for creating the Reserve-wide predictive maps (see below)

**Soil characteristics**

Soil samples were collected from the top 5 cm of soil at each site where active searching was conducted, as well as from the general surrounding area of each spider sampling site. Approximately five hand trowels of soil were collected from each site. These soil samples were placed in a box (standard size obtained from CEDARA – 80 mm x 90 mm x 60 mm) and sent to CEDARA Agricultural College for organic matter composition analysis. A number of agriculturally important soil variables including soil sample density (g / mL), cations (mg / L) including phosphorus, potassium, calcium, and magnesium, zinc and manganese, soil exchange acidity (cmol / L), total cations (cmol / L), acid saturation (%), pH (KCL), organic carbon (near infra-red spectroscopy - NIRS) and soil clay content (%).

Additional soil samples were collected at each site and analysed for moisture content and particle size. Soil moisture was assessed by taking five samples of soil from random areas within the site. These samples were weighed in the field and then oven dried at a constant temperature of 105 °C for 24 hours. The dried soil was then re-weighed to determine dry mass.

Soils were classified as either sand, loam or clay based on the particle-size classes. Particle size analysis was done by sieving approximately 100 g of soil from each sampling site through sieves of decreasing size (500 μm, 250 μm, 125 μm and 53 μm). The dry weight of soil left in each sieve was then weighed. The particle-size grades of the British Standards Institution were used (Hodgson 1976).

The presence of clay in soil helps prevent leaching of mineral nutrients during heavy rains. Cations (positively charged) adhere by electrical attraction to the negatively charged surface of clay particles. The cations are made available to the plant when H⁺ ions in the soil displace the mineral ions from the clay (Campbell 1987). Thus clay plays an integral part in the cation exchange capacity of soils and contributes to plant nutrition.

Not all soil variables from the CEDARA analysis were used in the multiple regression model. Only soil density, total cations, acidity, pH, Zn, Mn and clay content were used in the multiple regression analysis.

The individual cations were excluded because they are included in the cation (%) measurement. The acid saturation was also excluded as it is related to the pH of soils and is thus a duplicate measurement. Soil organic content was also excluded and this variable was
not always present in all soil samples taken. The soil moisture values calculated from the sites were also used in the multiple regression analysis.

**Aspect**

A digital elevation model (DEM) was generated from a 1:50 000 topographical contour map. The contour map of the study area was obtained from the Surveyor General, Pietermaritzburg, Kwa-Zulu Natal. The DEM was generated by a member of the School of Life and Environmental Sciences (Frank Sokalic) of the University of Natal, Durban. This was done by reprojecting the contour map from degrees to the South African LO coordinate system. This resulted in the x and y coordinates being expressed in metres. The x and y coordinate pairs making up the contours were then used as input into a program called Surfer. Surfer generates regular grids from irregularly spaced point data. The Kriging gridding method was used to generate the DEM with a cell size of 20 m by 20 m. The 20 m x 20 m grid was exported from Surfer in ASCII format and then imported into ArcView as a grid using the Spatial Analyst extension.

The aspect at each site was obtained from this DEM by using the “derive aspect” function in ArcView. Individual maps for north, south, east and west facing slopes were created by reclassing the aspect map to only include a single aspect at a time. The aspect for each site was determined by overlaying the sites onto the aspect map in ArcView. The aspect was then read off the map for each site. This variable has no actual value and therefore had to be set up as a dummy variable for the multiple regression analysis. A dummy variable was set up by having four columns for the aspect. A presence or absence matrix was then established. The column corresponding the aspect for a particular site was given a value of one and all others were zero. The zeros and ones were used in the multiple regression analysis.

**Prey biomass determination**

All insects from the pitfall traps and the sweep nets were kept (Chapter 3). These insects were sorted to level of order and divided into size classes. Body length measurements (from the head to the end of the abdomen) were recorded using a pair of callipers. The values were then used to calculate the biomass of insects. The biomass of insects (prey available to spiders) was then determined by calculating the weight (mg) from a weight versus length relationship (Rogers, Hinds & Bushbom 1975). The following equation was used to calculate the biomass:

$$W = 0.0305 L^{2.62}$$

Where:  
- \(W\) = the weight (mg)  
- \(L\) = the body length (mm)

The invertebrates were regarded as an indication of the prey base available to spiders.
(predators) in that particular site. The biomass of insects from sweep samples and pitfall traps was used in the multiple regression analysis. These values were also used to create the Reserve-wide map of biomass (see below).

Additional microhabitat data

The microhabitat of the all actively searched quadrats was recorded. The following factors were measured for each quadrat: number of trees, tree species, canopy cover (%), grass and herb cover (%), leaf litter cover (%), leaf litter thickness (cm), branch cover (%), branch size (mm), rock cover (%), rock size (mm) and slope (°).

An average value was calculated for the eight actively search sites for the above measured variables. The grass cover, leaf cover, rock cover and branch cover were determined by estimating the percentage that each factor covered in the actively searched quadrat. The leaf litter thickness, branch size and rock size in each quadrat was estimated and an average value was used for the site. The slope of the landscape was estimated by eye to the nearest 5 ° at each sampling site. The values for each site were used in the multiple regression. The microhabitat data values were extrapolated to create Reserve-wide maps of the different factors.

5.2.2 Descriptive models – multiple regression analysis

Four different models were generated that best explained the diversity of spiders in the Reserve. First a model for the diversity of all spiders was determined and then for the different functional groups (plant wandering spiders, ground wandering spiders and web building spiders) separately. A backward stepwise multiple regression analysis was used to determine the best combination of biotic and abiotic factors affecting the diversity of the four levels. The variables assessed in the models are listed in Table 5.1.

The soil variables are not directly related to spiders but were included in the multiple regression model because they could indirectly affect the diversity of spiders through the influence that these elements have on plants. For example cations, Zn, pH and soil moisture all affect the plant nutrition (Campbell 1987). Plants ultimately affect structure of the environment that could play a significant role in the diversity of spiders. Many other variables (e.g. leaf litter, branch presence and rocks presence) are also related to the structural diversity of the environment, all increasing the heterogeneity, which may ultimately influence the diversity of spiders.

The best model was determined based on the value of the adjusted $R^2$ and the numbers of significant variables. Some independent variables were removed from the model as they were redundant or autocorrelated with other variables (e.g. pH and soil acidity). The model was then rerun using several combinations. The final models were those that
maximised both statistical significance and biological sensibility.

Table 5.1: The biotic and abiotic factors assessed in the multiple regression analysis.

<table>
<thead>
<tr>
<th>Prey availability</th>
<th>Biomass sweep invertebrates (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Biomass pitfall invertebrates (mg)</td>
</tr>
<tr>
<td>Soil</td>
<td>Soil density (g/ml)</td>
</tr>
<tr>
<td></td>
<td>Cations*(cmol/L)</td>
</tr>
<tr>
<td></td>
<td>Clay content (%)</td>
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<tr>
<td></td>
<td>Soil acidity (cmol/L)</td>
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<td></td>
<td>Soil pH</td>
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<tr>
<td></td>
<td>Zn (mg/L)</td>
</tr>
<tr>
<td></td>
<td>Mn (mg/L)</td>
</tr>
<tr>
<td></td>
<td>Soil moisture (ml/g)</td>
</tr>
<tr>
<td>Temperature</td>
<td>Soil (° C)</td>
</tr>
<tr>
<td></td>
<td>Air (° C)</td>
</tr>
<tr>
<td>Rainfall</td>
<td>Total rainfall (mm)</td>
</tr>
<tr>
<td>Other microhabitat data</td>
<td>Leaf litter (%)</td>
</tr>
<tr>
<td></td>
<td>Leaf thickness (mm)</td>
</tr>
<tr>
<td></td>
<td>Branch presence (yes / no)^</td>
</tr>
<tr>
<td></td>
<td>Branch size (mm)</td>
</tr>
<tr>
<td></td>
<td>Rock presence (yes / no)^</td>
</tr>
<tr>
<td></td>
<td>Rock size (mm)</td>
</tr>
<tr>
<td></td>
<td>Slope (°)</td>
</tr>
<tr>
<td>Aspect^</td>
<td>N, NE, E, SE, S, SW, W or NW</td>
</tr>
<tr>
<td>Vegetation</td>
<td>Vegetation density &lt; 1 m</td>
</tr>
<tr>
<td></td>
<td>Vegetation density &gt; 2 m</td>
</tr>
<tr>
<td>Plant community types^#</td>
<td>Strychnos madagascariensis – Combretum apiculatum low closed woodland</td>
</tr>
<tr>
<td></td>
<td>Ziziphus mucronata – Combretum hereroense low closed woodland</td>
</tr>
<tr>
<td></td>
<td>Combretum apiculatum – Terminalia prunoides low closed woodland</td>
</tr>
<tr>
<td></td>
<td>Cissus cornifolia – Commiphora africana – Lannea schweinfurtheii low thicket</td>
</tr>
<tr>
<td></td>
<td>Colophospermum mopane low closed woodland</td>
</tr>
</tbody>
</table>

The cations represent all the cations in the soil (Ca, Mg, P, K, Na)

Created as a dummy variable and set up as a presence or absence

For certain variables (e.g. vegetation type and aspect) dummy variables had to be used. A dummy variable is simply a measure of presence or absence. For example if a site fell within a certain vegetation type it would receive a value of 1 for that site and if it did not
occur in the site it received a value of zero. At least one of the dummy variables (for vegetation type and aspect) had to be left out of the analysis each time but all combinations were tried. When the best model was obtained then the significant variables describing each model were mapped. The dependant variable was the diversity and the independent variables were the biotic and abiotic factors.

Beta ($\beta$) coefficient and B coefficients were obtained from the multiple regression analysis. The $\beta$ coefficients are the regression coefficients which result once all variables have been standardised to a mean of 0 and a standard deviation of 1 (Zar 1996; Statsoft 1999). Beta ($\beta$) coefficients allow for the comparison of the relative contribution of each independent variable in the prediction of the dependent variable. The B coefficient on the other hand represents the independent contributions of each independent variable to the prediction of the dependent variable. However, their values may not be comparable between variables because they depend on the units of measurement or ranges of the respective variables (Zar 1996; Statsoft 1999). The B coefficients were used for the generating the maps and the $\beta$ coefficients were used to make direct comparisons between variables.

5.2.3 Predictive extrapolation to a local scale

Computerised GIS maps of the topography, vegetation and hydrology were produced. The significant factor maps, resulting from the multiple regression models, were then superimposed. The resulting map indicates the relative diversity in the Reserve. Descriptive models can be used to (1) define problems; (2) organise thoughts; (3) understand data; (4) communicate that understanding; and make predictions (Fabricus & Coetzee 1992). In this study the resulting maps enabled me to make predictions about the relative diversity expected in different sections of the Reserve.

The maps were created in the following way: an Excel spreadsheet was composed containing the longitude and latitude values that corresponded to the sampling sites. Different factors measured at the site were also included in the spreadsheet as separate fields. This matrix was saved as a text (tab delimited file) and imported into CARTLINX as nodes. The resulting node map was then exported as an ArcView .shp file and displayed in ArcView.

Maps for the individual factors were created by displaying the node map, created in Cartalinx, and the DEM map. The map was first reprojected in meters to make it compatible with the DEM map. The interpolate function in ArcView was used to extrapolated a selected factor, e.g. leaf litter thickness, to create a Reserve-wide map. The entire Reserve was not used in the analysis because many of the factors measured are simply microhabitat variables that could not be extrapolated with confidence. A buffer map was therefore created which
excluded any areas in the Reserve that fell beyond 1.250 km from any site. All variables used in the multiple regression model were extrapolated in this manner.

The only exceptions were maps of the rainfall, vegetation type and soil characteristics maps, e.g. soil density, cations, clay, Zn, Mn, and pH. More substantial data were available for these variables. The data obtained for rainfall over the sampling period were used for the multiple regression model and the rainfall data gathered by the Reserve staff throughout the rainy season was used for the mapping purposes. Additional soil data was gathered from various points in the Reserve allowing a more confident representation of the data over a wider area of the Reserve.

Patch size and species diversity

A patch can be defined as a non-linear surface area differing in appearance from its surrounds (Samways 1994). The effect of patch size on diversity was investigated by extracting summary statistics of spider species diversity that corresponded to the area covered by different vegetation types. This was done using the “zonal summary” function in ArcView. The vegetation type map was used as the theme and the predicted spider diversity grid map was used to extract the species diversity values that corresponded with different areas. The resulting table was exported as an Excel file. A correlation analysis was performed on these values to determine the relationship between area and species diversity.

5.3 RESULTS

5.3.1 Predictive Models

Spider diversity

The variables that best explain the diversity of all spiders is presented in Table 5.2. The significant variables are presented in the upper half of the table while the non-significant variables from the model are presented in the lower half of the table. This applies to all tables presented in this section. In order to simplify the regression model the variables that were non-significant or had low tolerances were removed. The tolerance is defined as $1 - R^2$ for the respective variable with all other variables currently in the equation (Crawley 1993). The variables that were excluded from this model included soil acid saturation, soil MN content, rainfall, rock size, branch size, soil density, S, W, clay and *Ziziphus mucronata* – *Combretum hereroense* low closed woodland vegetation type.

The variables that significantly positively influenced spider diversity were soil moisture and the presence of north facing slopes. Variables that significantly negatively influenced the spider diversity were *Strychnos madagascariensis* – *Combretum apiculatum* low closed woodland, vegetation density >2 m, invertebrate biomass (sweeps), slope, leaf
thickness (mm), soil temperature (°C) and rock presence.

Table 5.2: The processes affecting the diversity of spiders at Makalali Private Game Reserve. R = 0.82, R² = 0.67, Adjusted R² = 0.44, F(16,23) = 2.93, P < 0.01.

<table>
<thead>
<tr>
<th>Variable</th>
<th>BETA</th>
<th>B</th>
<th>t(23)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>14.78</td>
<td>3.11</td>
<td>0.005</td>
<td></td>
</tr>
<tr>
<td><em>Strychnos madagascariensis – Combretum apiculatum</em> low closed woodland</td>
<td>-0.67</td>
<td>-2.82</td>
<td>-3.72</td>
<td>0.001</td>
</tr>
<tr>
<td>Vegetation density &gt;2 m</td>
<td>-0.61</td>
<td>-12.96</td>
<td>-3.14</td>
<td>0.005</td>
</tr>
<tr>
<td>Invertebrate biomass (sweeps)</td>
<td>-0.61</td>
<td>-1.09</td>
<td>-2.85</td>
<td>0.009</td>
</tr>
<tr>
<td>North</td>
<td>0.49</td>
<td>1.88</td>
<td>2.81</td>
<td>0.010</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.49</td>
<td>-2.58</td>
<td>-2.57</td>
<td>0.017</td>
</tr>
<tr>
<td>Leaf thickness (mm)</td>
<td>-0.51</td>
<td>-1.90</td>
<td>-2.46</td>
<td>0.022</td>
</tr>
<tr>
<td>Soil temperature (°C)</td>
<td>-0.43</td>
<td>-0.39</td>
<td>-2.30</td>
<td>0.031</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>0.31</td>
<td>0.20</td>
<td>2.14</td>
<td>0.043</td>
</tr>
<tr>
<td>Rock presence</td>
<td>-0.45</td>
<td>-1.49</td>
<td>-2.06</td>
<td>0.051</td>
</tr>
<tr>
<td>Soil acidity</td>
<td>-0.30</td>
<td>-10.92</td>
<td>-1.99</td>
<td>0.058</td>
</tr>
<tr>
<td>Grass cover</td>
<td>0.33</td>
<td>0.03</td>
<td>1.86</td>
<td>0.076</td>
</tr>
<tr>
<td>Vegetation density &lt;1 m</td>
<td>0.30</td>
<td>1.05</td>
<td>1.82</td>
<td>0.081</td>
</tr>
<tr>
<td>Soil pH</td>
<td>0.41</td>
<td>0.92</td>
<td>1.76</td>
<td>0.092</td>
</tr>
<tr>
<td>Leaf cover (%)</td>
<td>-0.24</td>
<td>-0.03</td>
<td>-1.68</td>
<td>0.107</td>
</tr>
<tr>
<td>East</td>
<td>-0.22</td>
<td>-1.18</td>
<td>-1.55</td>
<td>0.136</td>
</tr>
<tr>
<td><em>Colophospermum mopane</em> low closed woodland</td>
<td>-0.25</td>
<td>-1.01</td>
<td>-1.02</td>
<td>0.318</td>
</tr>
</tbody>
</table>

Ground wandering spider diversity

The variables explaining the diversity of ground wandering spider diversity are presented in Table 5.3. The variables that were excluded from this model included soil density, MN, soil acid saturation, *Colophospermum mopane* vegetation type, rock size, south, west and *Ziziphus mucronata – Combretum hereroense* low closed woodland vegetation type. These variables were non significant and had low tolerance values. Soil moisture is the only significantly positive variable influencing ground wandering spider diversity. Invertebrate biomass (sweeps), leaf litter thickness, vegetation density (<1 m) and soil Zn content significantly negatively influenced the ground wandering spider diversity.
Table 5.3: The biotic and abiotic processes affecting the diversity of ground wandering spiders at Makalali Private Game Reserve. $R = 0.77$, $R^2 = 0.60$, Adjusted $R^2 = 0.44$, $F_{11,28} = 3.76$, $P < 0.002$.

<table>
<thead>
<tr>
<th>Variable</th>
<th>BETA</th>
<th>B</th>
<th>$t_{(28)}$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-3.61</td>
<td>-0.63</td>
<td>0.535</td>
<td></td>
</tr>
<tr>
<td>Soil moisture</td>
<td>0.55</td>
<td>0.47</td>
<td>3.72</td>
<td>0.001</td>
</tr>
<tr>
<td>Invertebrate biomass (sweeps)</td>
<td>-0.72</td>
<td>-1.74</td>
<td>-3.44</td>
<td>0.002</td>
</tr>
<tr>
<td>Leaf thickness (mm)</td>
<td>-0.69</td>
<td>-3.51</td>
<td>-3.35</td>
<td>0.002</td>
</tr>
<tr>
<td>Vegetation density (&lt; 1 m)</td>
<td>-0.51</td>
<td>-2.38</td>
<td>-3.11</td>
<td>0.004</td>
</tr>
<tr>
<td>Soil ZN content</td>
<td>-0.40</td>
<td>-1.61</td>
<td>-2.37</td>
<td>0.025</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.31</td>
<td>-2.19</td>
<td>-1.73</td>
<td>0.094</td>
</tr>
<tr>
<td>Air temperature</td>
<td>0.24</td>
<td>0.32</td>
<td>1.53</td>
<td>0.137</td>
</tr>
<tr>
<td>Soil cation content</td>
<td>0.34</td>
<td>0.15</td>
<td>1.47</td>
<td>0.152</td>
</tr>
<tr>
<td>Soil acidity</td>
<td>0.21</td>
<td>10.34</td>
<td>1.43</td>
<td>0.164</td>
</tr>
<tr>
<td>Branch presence</td>
<td>-0.20</td>
<td>-0.86</td>
<td>-1.31</td>
<td>0.201</td>
</tr>
<tr>
<td>Soil clay content</td>
<td>0.23</td>
<td>0.10</td>
<td>1.20</td>
<td>0.242</td>
</tr>
</tbody>
</table>

**Web building spider diversity**

The variables explaining the diversity of web building spider diversity is presented in Table 5.4. The variables that were excluded from this model included soil density, rock cover, acid saturation, soil clay content, rainfall, south, west, MN, rock size, pH and *Ziziphus mucronata* – *Combretum hereroense* low closed woodland vegetation type. These variables were non-significant and had low tolerance values.

Web building spiders are significantly positively influenced by branch size and the *Cissus cornifolia* – *Commiphora africana* – *Lannea schweinfurtheii* low thicket plant community type. The soil temperature, branch presence, east facing slopes and leaf thickness had a significant negative influence on the web building spider diversity.

**Plant wandering spider diversity**

The variables explaining the diversity of plant wanderer spider diversity are presented in Table 5.5. The variables that were excluded from this model included soil density, soil acid saturation, clay, south, west and *Ziziphus mucronata* – *Combretum hereroense* low closed woodland vegetation type. These variables were non-significant and had low tolerance values.

Plant wandering spiders were significantly positively influenced by vegetation density < 1 m, soil pH, the presence of a north facing slope and soil moisture. The variables that significantly negatively influence the plant wandering spider diversity were soil cation content, vegetation density (> 2 m), rock size, leaf cover, *Cissus cornifolia* – *Commiphora africana* – *Lannea schweinfurtheii* low thicket and invertebrate biomass (sweeps).
Table 5.4: The biotic and abiotic processes influencing the diversity of web building spiders in Makalali Private Game Reserve. \( R = 0.82, R^2 = 0.67, \text{Adjusted } R^2 = 0.58, F_{8,31} = 7.72, P < 0.00001. \)

<table>
<thead>
<tr>
<th>BETA</th>
<th>B</th>
<th>( t_{(21)} )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>23.08</td>
<td>4.73</td>
<td>0.000</td>
</tr>
<tr>
<td>Vegetation density (&gt; 2 m)</td>
<td>-0.52</td>
<td>-13.06</td>
<td>-4.55</td>
</tr>
<tr>
<td><em>Cissus cornifolia – Commiphora africana – Lannea schweinfurtheii</em> low thicket</td>
<td>0.48</td>
<td>3.03</td>
<td>4.42</td>
</tr>
<tr>
<td>Soil temperature</td>
<td>-0.57</td>
<td>-0.61</td>
<td>-4.36</td>
</tr>
<tr>
<td>Branch presence</td>
<td>-0.38</td>
<td>-1.42</td>
<td>-3.39</td>
</tr>
<tr>
<td>East</td>
<td>-0.36</td>
<td>-2.28</td>
<td>-3.23</td>
</tr>
<tr>
<td>Branch size</td>
<td>0.32</td>
<td>1.93</td>
<td>2.67</td>
</tr>
<tr>
<td>Leaf thickness</td>
<td>-0.24</td>
<td>-1.07</td>
<td>-2.13</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>0.23</td>
<td>0.18</td>
<td>1.94</td>
</tr>
</tbody>
</table>

Table 5.5: The biotic and abiotic processes affecting the diversity of plant wandering spiders in Makalali Private Game Reserve. \( R = 0.83, R^2 = 0.69, \text{Adjusted } R^2 = 0.44, F_{17,22} = 2.83, P < 0.01. \)

<table>
<thead>
<tr>
<th>BETA</th>
<th>B</th>
<th>( t_{(22)} )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>3.98</td>
<td>0.36</td>
<td>0.724</td>
</tr>
<tr>
<td>Vegetation density (&lt; 1 m)</td>
<td>0.60</td>
<td>5.30</td>
<td>3.34</td>
</tr>
<tr>
<td>Vegetation density (&gt; 2 m)</td>
<td>-0.54</td>
<td>-29.29</td>
<td>-2.97</td>
</tr>
<tr>
<td>Rock size</td>
<td>-0.79</td>
<td>-6.10</td>
<td>-2.90</td>
</tr>
<tr>
<td>Soil pH</td>
<td>0.95</td>
<td>5.46</td>
<td>2.82</td>
</tr>
<tr>
<td>Soil cation content</td>
<td>-0.78</td>
<td>-0.65</td>
<td>-2.62</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>0.36</td>
<td>0.59</td>
<td>2.58</td>
</tr>
<tr>
<td>North</td>
<td>0.43</td>
<td>4.17</td>
<td>2.34</td>
</tr>
<tr>
<td>Leaf cover</td>
<td>-0.35</td>
<td>-0.13</td>
<td>-2.28</td>
</tr>
<tr>
<td><em>Cissus cornifolia – Commiphora africana – Lannea schweinfurtheii</em> low thicket</td>
<td>-0.37</td>
<td>-5.09</td>
<td>-2.27</td>
</tr>
<tr>
<td>Invertebrate biomass (sweeps)</td>
<td>-0.38</td>
<td>-1.75</td>
<td>-2.21</td>
</tr>
<tr>
<td>Soil MN content</td>
<td>-0.31</td>
<td>-5.33</td>
<td>-1.99</td>
</tr>
<tr>
<td><em>Colophospermum mopane</em> low closed woodland</td>
<td>-0.34</td>
<td>-3.48</td>
<td>-1.53</td>
</tr>
<tr>
<td><em>Combretum apiculatum– Terminalia pruinoides</em> low closed woodland</td>
<td>-0.22</td>
<td>-3.43</td>
<td>-1.51</td>
</tr>
<tr>
<td>Soil temperature</td>
<td>-0.25</td>
<td>-0.57</td>
<td>-1.35</td>
</tr>
<tr>
<td>Soil ZN content</td>
<td>0.23</td>
<td>1.75</td>
<td>1.29</td>
</tr>
<tr>
<td><em>Strychnos madagascariensis – Combretum apiculatum</em> low closed woodland</td>
<td>-0.27</td>
<td>-2.86</td>
<td>-1.27</td>
</tr>
<tr>
<td>Branch presence</td>
<td>-0.16</td>
<td>-1.28</td>
<td>-0.99</td>
</tr>
</tbody>
</table>
5.3.2 Predictive maps

All significant variable maps from the descriptive model were overlayed to produce a predicted diversity map for the Reserve. The map calculator function in ArcView was used and the following regression equation was used for spider diversity: \( Y \) (spider diversity) = 

\[
(14.78) + \left( \text{Vegetation density} > 2 \text{ m} \right)(-12.96) + \left( \text{Strychnos madagascariensis} - \text{Combretum apiculatum} \text{ low closed woodland} \right)(-2.82) + \left( \text{Invertebrate biomass (sweeps)} \right)(-1.09) + \left( \text{North} \right)(1.88) + \left( \text{Slope} \right)(-2.58) + \left( \text{Leaf thickness} \right)(-1.90) + \left( \text{Soil temperature} \right)(-0.39) + \left( \text{Soil moisture} \right)(0.20) + \left( \text{Rock presence} \right)(-1.49) \times \text{Makalali buffer base map}.
\]

The base map was used to exclude all values falling outside of the Reserve borders. The resulting map is presented as hot and cold spots of diversity in the Reserve (Figure 5.1). Blue areas on the map represent relatively low diversities and red areas correspond with relatively high diversities. All variable maps used to produce the final predictive map are presented in Appendix 5.2 – Appendix 5.5.

Spider diversity is highest in the south western section of the Reserve and the diversity is relatively uniformly distributed. Areas of very high and very low diversity are more patchily distributed.

The regression equation used for ground wandering spiders was: \( Y \) (ground wanderers diversity) = 

\[
(-3.61) + \left( \text{Soil moisture} \right)(0.55) + \left( \text{Invertebrate biomass (sweeps)} \right)(-0.72) + \left( \text{Leaf thickness (mm)} \right)(-0.69) + \left( \text{Vegetation density} \right)(< 1 \text{ m})(-0.51) + \left( \text{Soil ZN content} \right)(-0.40) \times \text{Makalali base map} (\text{Figure 5.2}).
\]

The ground wandering spiders are relatively uniformly distributed with a small patch of relatively low diversity along the southern fenceline of the Reserve.

The regression equation used for web building spiders was: \( Y \) (web building spider diversity) = 

\[
(23.08) + \left( \text{Vegetation density} \right)(> 2 \text{ m})(-0.52) + \left( \text{Cissus cornifolia} - \text{Commiphora africana} - \text{Lannea Schweinfurthii} \text{ low thicket} \right)(0.48) + \left( \text{Soil temperature} \right)(-0.57) + \left( \text{Branch presence} \right)(-0.38) + \left( \text{East} \right)(-0.36) + \left( \text{Branch size} \right)(0.32) + \left( \text{Leaf thickness} \right)(-0.24) \times \text{Makalali base map} (\text{Figure 5.3}).
\]

The web building spider diversity is not uniformly distributed in the Reserve. The south western section of the Reserve has the highest relative diversity while the north eastern section has a much lower predicted web building spider diversity.

The regression equation used for plant wandering spiders was: \( Y \) (plant wandering spider diversity) = 

\[
(3.98) + \left( \text{Vegetation density} \right)(< 1 \text{ m})(0.60) + \left( \text{Vegetation density} \right)(> 2 \text{ m})(-0.54) + \left( \text{Rock size} \right)(-0.79) + \left( \text{Soil pH} \right)(0.95) + \left( \text{Soil cation content} \right)(-0.78) + \left( \text{Soil moisture} \right)(0.36) + \left( \text{North} \right)(0.43) + \left( \text{Leaf cover} \right)(-0.35) + \left( \text{Cissus cornifolia} - \text{Commiphora africana} - \text{Lannea Schweinfurthii} \text{ low thicket} \right)(-0.37) + \left( \text{Invertebrate biomass (sweeps)} \right)(-0.38) \times \text{Makalali base map} (\text{Figure 5.4}).
\]
Figure 5.1: The relative diversity of spiders at Makalali Private Game Reserve as represented by the soil moisture, the presence of north facing slopes, *Strychnos madagascariensis* – *Combretum apiculatum* low closed woodland, vegetation density >2 m, invertebrate biomass (sweeps), slope, leaf thickness (mm), soil temperature (°C) and rock presence. Blue areas are representative of low diversities while red areas represent high diversities. Moderate diversity is represented as grey.
Figure 5.2: The relative diversity of ground wandering spiders at Makalali Private Game Reserve as represented by soil moisture, invertebrate biomass (sweeps), leaf litter thickness, vegetation density (< 1 m) and soil Zn content. Blue areas are representative of low diversities while red areas represent high diversities. Moderate diversity is represented as grey.
Figure 5.3: The relative diversity of web building spiders at Makalali Private Game Reserve as represented by the branch size, *Cissus comifolia* – *Commiphora africana* – *Lannea schweinfurtheii* low thicket plant community type, soil temperature, branch presence, east facing slopes and leaf thickness. Blue areas are representative of low diversities while red areas represent high diversities. Moderate diversity is represented as grey.
Figure 5.4: The relative diversity of plant wandering spiders at Makalali Private Game Reserve as represented by the vegetation density < 1 m, soil pH, presence of a north facing slope, soil moisture, soil cation content, vegetation density (> 2 m), rock size, leaf cover, Cissus comifolia – Commiphora africana – Lannea schweinfurthii low thicket and invertebrate biomass (sweeps). Blue areas are representative of low diversities while red areas represent high diversities. Moderate diversity is represented as grey.
The plant wandering spider diversity is also highest in the south western section of the Reserve. There are two patches of low diversity in the middle section of the Reserve.

**Actual vs predicted diversity**

The actual measured spider diversity at the different sites is presented in Figure 5.5. This map was created to compare how the predicted and actual diversities differed. The actual diversities are presented as coloured symbols. These symbols are colour coded showing red for high diversity and blue for low diversities. Some areas correspond to the measured diversities but generally, the predicted diversity is higher than the actual measured diversity (Figure 5.5).

A possible reason for the difference is that the predicted maps are only based on the significant variables from the models and other non-significant variables that also contribute to the model were not mapped. In addition, not all the variation has been accounted for (only 44% in some cases) and there may be other unknown factors influencing the actual diversity.

For the functional groups the same patterns are seen as for all the spiders. In some areas the predicted and actual diversities are similar and in other areas they are not. The models that had more of their variation explained (higher R² values) by the biotic and abiotic processes used in the multiple regression model more closely approximated the predicted maps (Figure 5.5).

**Patch size and diversity**

There is a significant relationship between the diversity and the area (r = 1.61, P = 0.008). As the patch size increases so does the diversity Figure 5.6. The relationship is not very robust and there is a lot of variation in the data (R² = 0.03). There are many more small patches than large patches in the Reserve and the diversity is high even in the smallest patch (400 m²).

**Vegetation type**

Only two vegetation types, *Cissus cornifolia – Commiphora africana – Lannea schweinfurtheii* low thicket and *Strychnos madagascariensis – Combretum apiculatum* low closed woodland, significantly influence the diversity of spiders. The *Strychnos madagascariensis – Combretum apiculatum* low closed woodland negatively influences the diversity of all spiders. This plant community is located exclusively in the south western section of the Reserve and is not very common (Appendix 5.2). The *Cissus cornifolia – Commiphora africana – Lannea schweinfurtheii* low thicket vegetation type has a positive effect on the web building spiders but a negative effect on the plant wandering spiders. This plant community type is found mainly in the northern section of the Reserve. Plant wanderers may favour larger leafed trees. Additionally, the negative effect on plant wanderers may be a
Figure 5.5: The (a) actual measured diversity (range = 4.55 to 13.98) and predicted diversity of spiders at Makalali Private Game Reserve. The coloured dots correspond to the diversity found at the site. Low diversity is represented by dark blue, medium by grey and high diversity by red. Shades of blue or red represent intermediate diversity. Map (b) compares the actual (range = 6.29 to 25.68) and predicted relative diversity for plant wanderers.
Figure 5.5: The (c) actual measured diversity (range = 0.00 - 14.29) and predicted diversity of ground wandering spiders at Makalali Private Game Reserve. The coloured dots correspond to the diversity found at the site. Low diversity is represented by dark blue, medium by grey and high diversity by red. Shades of blue or red represent intermediate diversity. Map (d) compares the actual (range = 3.00 - 13.45) and predicted relative diversity for web building spiders.
Figure 5.6: The effect of patch size on the spider diversity at Makalali Private Game Reserve.
reflection of flower presence. At the time of sampling the trees were not flowering. Flowers are important for plant wanderers as flowers attract other insects providing them with prey (Wise 1993). The type of vegetation is less likely to have a direct effect on the spider diversity than the actual structure of the habitat.

**Aspect**

The models indicate that north and east facing slopes significantly influence the diversity of spiders. The north facing slopes positively influence the diversity of all spiders and plant wanderers. This may indicate that plant wanderers select for areas that receive more intensive sunlight. However, there is very little other evidence for this relationship in the literature. Web building spiders are negatively influenced by east facing slopes thus indicating that web building spiders do not select areas that receive morning sun. Web spiders are known to orientate themselves in such a way as to avoid thermal stress (Riechert & Gillespie 1986). The aspect is a difficult factor to interpret but the effect of temperature is the most likely explanation.

**Soil moisture and soil temperature**

Spiders are positively influenced by the soil moisture and areas that are slightly moister have a greater diversity of spiders. The soil temperature had a negative effect on the web building spiders. This indicates that areas with less shading (thus soils become hotter) would have less web building spiders.

**Other microhabitat variables**

The leaf litter thickness had a negative effect on the diversity of spiders. This does not necessarily indicate less diversity but may be a reflection of the ability of the searcher to find spiders in areas of high leaf cover and thickness. The increase in leaf litter allow for more niches in which spiders may hide and the results could indicate spiders are simply found less frequently in areas of high leaf litter. Rock presence and rock size also negatively influences the diversity of spiders. This may just be a reflection of a reduced vertical microhabitat in which spiders are able to construct webs. However, for ground wandering spiders we would expect an increase in rocks to provide a greater variety for constructing retreats (and this was not so).

The branch size had a positive influence on web building spiders. The presence of large branches may create a more complex environment on which to anchor their webs.

**Biomass invertebrates**

Spiders were not positively affected by the presence of prey. The prey availability may not be
such an important determinant of diversity of spiders. Biomass of invertebrates from sweep samples has a negative effect on spider diversity.

**Slope**

The slope has a significant negative effect on the spider diversity. Steeper slopes had lower spider diversities. Steeper slopes have higher run-off rates and therefore the soil in these areas may not be suitable for building of retreats (at least for ground wanderers).

### 5.4 DISCUSSION

Only recently have studies on species diversity in tropical ecosystems been undertaken (Russell-Smith 1999). While most studies have been on spider diversity in tropical forests (reviewed by Russell-Smith & Stork 1994), much less is known about the composition of arachnid fauna of African ecosystems (Russell-Smith 1999).

In South Africa, apart from taxonomic descriptions (Lawrence 1937, Lawrence 1938), the only ecological studies on spiders is that are those of Van der Merwe (1994) and Van der Merwe et al. (1996), who compared the spiders of forests, pine plantations, and grassland. Other previous spider related research has focussed on either (1) determining the diversity and richness in localised areas (Van den Berg & Dippenaar-Schoeman 1988; Dippenaar-Schoeman et al. 1989; Coetzee et al. 1990; Van der Merwe et al. 1996; Dippenaar-Schoeman et al 1999), (2) generating checklists of species (Dippenaar-Schoeman 1988; Dippenaar-Schoeman & Wassenaar in press) or (3) their usefulness in agroecosystems (Dippenaar-Schoeman 1979; Riechert 1984).

**Processes affecting spider diversity**

At present it is very unclear what biotic and abiotic processes or combination of processes influence spider diversity patterns at the local scale. Considerable effort has been invested in recording the spider diversity in temperate habitats and some attempts have been made towards understanding which environmental processes contribute towards the diversity of spiders. Some of the processes that have been suggested to influence the spider diversity include leaf litter (Uetz 1979; Bultman et al. 1982), habitat structural diversity (Hurd & Fagan 1992; Gibson et al. 1992; Kromp & Steinberger 1992; Greenstone 1984) and prey availability (Greenstone 1984; Nyffeler et al. 1994).

Extreme temperatures, both hot and cold, are the most extensively documented abiotic mortality factor for spiders (Wise 1993). High temperatures have been shown to negatively affect spiders because thermal stress prevents the spider from being active (Janetos 1986; Wise 1993). Thus the thermal environment limits foraging activities to certain periods of the day (Riechert & Gillespie 1986). However, the temperature influences different species
in different ways and some spiders actually select warmer areas in order to enhance egg
development (e.g. some lycosid species) (Wise 1993).

The extent to which habitat choice for spiders is an active process or passive,
probabilistic endeavour is simply not known (Janetos 1986). This study therefore makes a
significant step towards understanding processes driving spider diversity at the local scale. At
this scale the variables that were important in determining spider diversity include vegetation
density, soil moisture, vegetation type, branch size, soil pH and aspect. Most of these
processes affect the vegetation in some way thus indicating that vegetation structure could
play a key role in determining spider diversity.

These results are supported by other studies that have demonstrated that a correlation
exists between the structural complexity of habitats and species diversity (Uetz 1979;
Rozenweig 1995). Diversity generally increases when a greater variety of habitats are present
because the more habitats there are the more species may exist (MacArthur 1964; Ried &
Miller 1989; Cook 1991; Hawksworth & Kalin-Arroyo 1995). Habitat structural diversity has
also been suggested to be the main driving factor for the rich diversity seen in the tropics
(Rosenzweig 1995).

Early investigators recognised that the historical structure of the habitat could
profundly affect the composition of the spider community (Uetz 1979). Effects arise not only
from variations in the availability of supports for anchoring webs, but also from the provision
of retreats and modifications of the microclimate, which impact spiders in numerous families
(Uetz 1979; Greenstone 1984). Quantitative approaches have uncovered correlations between
(1) structural diversity of the vegetation and the species diversity of web-spinning spiders
(Greenstone 1984), (2) amount of vegetation and the activity or abundance of web spiders
(Wise 1993), (3) density of foliage on conifer branches and the size and distribution of
spiders, (4) presence of flowering herbs and densities of spiders foraging for pollinating
insects (Wise 1993), (5) nature of the substrate and the microclimate distribution of particular
species of wandering spiders (Greenstone 1984), (6) depth and complexity of the leaf litter
and the species diversity of the cursorial spider community (Uetz 1979; Greenstone 1984;
Wise 1993; Green 1999; Russell-Smith 1999).

Uetz (1991) suggests that structurally more complex shrubs can support a more diverse
spider community. Downie et al. (1999) and New (1999) have demonstrated that spiders are
extremely sensitive to small changes in the habitat structure, including habitat complexity,
litter depth and microclimate characteristics and generally as disturbance increases the spider
species richness decreases. Some spiders have been shown to select for different size shrubs
(larger shrubs as they increase in size) which relates to better supporting structures for larger
webs (Lubin, Ellner & Kotzman 1993). Thus the physical structure of environments has an
important influence on the habitat preferences of spider species, particularly web building species (Uetz 1991; Hurd & Fagon 1992; Bradley 1992). Janetos (1986) has shown that, for web builders, physical supports for the architecture of the web are the most important criteria needed for a habitat to be suitable. However, the habitat suitable does change with habitat and species (Janetos 1986).

The availability of prey has been shown to be important for certain spider species (reviewed by Janetos 1986; Riechert & Gillespie 1986) and other animals (Warrick & Cypher 1998), yet in this study spiders were not positively affected by the presence of prey. The prey availability, although important for some species, may not be such an important determinant of diversity of spiders. These results confirm that of other scientists (Lubin et al. 1993). They showed that the prey availability was not an important factor determining the habitat selection of a desert widow spider (Latrodectus revivensisi). Many spiders are able to survive long periods of starvation, primarily by waiting for prey rather than actively searching for it, and also by lowering their basal metabolic rate in the absence of enough prey to support growth and reproduction (Wise 1993). In addition, some spider foraging patterns seem to compensate for food limitation, e.g. the sit-and-wait strategies of many spiders are an adaptation to a shortage of prey.

Therefore, food is not likely a limiting factor for all spider populations in all years or habitats. A high prey biomass would more likely influence the growth rate of spiders rather than their actual diversity. The results here also confirm those of Greenstone (1984) and Bradley (1993) who found that spider diversity could not be predicted by prey availability.

The effect of leaf litter on spider diversity in this study is contrary to others. Uetz (1979) showed that more spiders were present in areas of greater litter depth. The leaf litter effect may not be evident here as the sampling techniques used in this study may not adequately sample the spiders from the litter layer. The negative effect of leaf litter depth on spiders may not necessarily indicate less diversity but may be a reflection of the ability of the searcher to find spiders in areas of high leaf cover and thickness. The increase in leaf litter allow for more niches in which spiders may hide and the results could indicate that spiders are simply found less frequently in areas of high leaf litter.

**Patch size**

Patch size was not a significant determinant of spider diversity. Even the smallest area (400 m²) had a high diversity and increasing the area does not add much more to the diversity. Ritchie & Olff (1999) have shown that the well known responses of biological diversity to different factors (e.g. species area) can arise from simple constraints on how organisms acquire resources. Therefore many other factors could be accounting for the high diversity in
some areas but it is not simply the size of the patch. This has implications for conservation as even small patches can make a significant contribution towards conserving spiders in the savanna.

Functional group differences

None of the maps for the functional groups are exactly alike thus indicating that the processes affecting the different functional groups differ at different sites. This indicates that spiders inhabit many different niches within the environment and it is very difficult to identify one or a few variables that are responsible for influencing the diversity. The only common variable between all three functional groups is the vegetation density. However, the vegetation density affects the different functional groups in different ways. These differences are not surprising as spiders occupy many different layers within the environment.

It is unlikely that single factors operate alone to limit population densities. More probably the resource that limits population growth is that which is in most limited supply at a particular time. It is thus difficult to isolate all the factors that might limit spider population densities (Riechert & Gillespie 1986).

Furthermore, none of the models are fully explained by the processes evaluated in the models. This indicates that the predictive maps can only be interpreted as relative diversities and certain areas will be relatively high while others will be relatively low. In addition, all the adjusted R² values are relatively low therefore the variables significant here do not account for all the variation in the spider diversity. Thus knowing the abiotic variable that may influence the spider diversity will not allow an accurate prediction of the spider diversity without taking into consideration many other unknown factors, e.g. competition between species, habitat disturbance (Gibson et al. 1992; Zulka et al 1997; Downie et al. 1999); successional age (Bultman & Uetz 1982; Gibson et al. 1992; Hurd & Fagon 1992; Dippenaar-Schoeman & Wassenaar in press) and predators (e.g. birds, lizards, other spiders and wasps) (Wise 1993).

Riechert & Gillespie (1986) state that the dynamic of habitat choice and utilisation are complex and difficult to analyse. They conclude that a spiders behaviour at any point in time represents a compromise between the many needs and selection pressures felt by the spider at that time in its life cycle. Understanding the suite of adaptations involved in habitat choice and utilisation requires knowledge of the history of local populations, an understanding of the relationships between spider population densities and the availability of important resources and a knowledge of the sensory capabilities of a particular species. This knowledge for the spiders at Makalali Private Game Reserve is simply not available.
Furthermore, there is some indication that the processes influencing spider diversity change over time (Uetz 1979; Bultman & Uetz 1982). This makes predicting processes important in for enhancing spider diversity extremely difficult.

This has implications for conservation, as many different variables need to be considered in order to conserve all functional groups of spiders. No one process can be deemed more important than another as the processes may change over time.

5.5) **CONCLUSION**

In this study those environmental variables that were measured did not accurately describe the processes influencing all aspects of spider diversity. The structural diversity of habitats appears to be the most significant variable influencing spider diversity. To maximise spider diversity the structural diversity of the habitat must be maintained. Spiders are an extremely diverse group that inhabit all parts of the earth and it is unlikely that all variables accounting for their diversity have been considered in this study.

Biodiversity with all its component interactions and processes (e.g. genes, species, biotopes, communities, ecosystems and landscapes) is immensely complex (Samways 1993b). At present we do not have the wisdom to attempt to conserve the details of this complexity. In addition, different variables are important for different functional groups. The varying factors responsible for the high diversity in the different functional groups suggests that finding requirements for the survival of a single species is simply not all-embracing enough for realistic conservation of so many spider species. Landscape conservation and appropriate management is a more realistic approach (Samways 1993b; Samways 1994).
CHAPTER 6

SUMMARY

The research presented in this thesis includes a description of spider biodiversity for a savanna ecosystem, an assessment of available sampling techniques for spiders, an investigation into surrogate measures of species richness and a study of the processes affecting this diversity.

The present study, conducted at Makalali Private Game Reserve, has made a significant contribution towards increasing our knowledge of spider species distributions in the savanna. This biome has an extremely high spider diversity. A total of 4,832 individuals from 268 species, 147 genera and 37 families were sampled during the study period. Considering the high spider diversity in this Reserve, efforts should be continued to ensure that the area is conserved, not only for the large vertebrates (which attract considerable attention), but also for the invertebrates.

No previous work on spiders has been conducted in this area thus the study represents new distribution records for all species recorded and 14 suspected previously undescribed species. Several genera that are endemic to South Africa occur in this Reserve which further highlights the importance of maintaining the conservation status of this biome. The protected homed baboon spider, Ceratogyrus bechuanicus Purcell, 1902, also occurs in this Reserve. The trapdoor baboon spider (Barychelidae) represents a new distribution record for South Africa. Given the unexpectedly high diversity of spider in the savanna biome further research should be encouraged. Efforts should also be made to support reserves, as the resources are already in place for the conservation of other animals (large mammals in many cases).

The sampling techniques used in this study highlight several factors: (1) a combination of at least two or more methods should be used for spider biodiversity survey work, (2) for spiders, different sampling methods target certain vegetative layers and or functional groups, (3) sweeping and active searching is recommended for efficient and cost effective surveys and (4) active searching needs to be included in all surveys to allow for standardisation between different sites and studies.

The use of surrogates for species richness in biodiversity studies is not satisfactory. The simple time efficient methods are not always the most favourable. Although there is a positive relationship between the spider species richness and insect species richness the use of spiders to predict wholesale invertebrate diversity was not supported. Higher taxon methods (family or genera) are an improvement. However, the relationship is stronger at the level of genus than family. It follows then that if higher taxon surveys are to be used for biodiversity assessment then estimates at the level of genus should be used. Species-level identifications remain ideal if the data is to be used for conservation purposes. Higher taxon data should only
be used in situations where there are insufficient resources available for good species data to be a realistic alternative. The use of spider morphospecies identified by non-specialists is not recommended here. Spiders are a particularly large group and at least a few days of training and many hours of sorting are recommended. However, the morphospecies level identifications do improve with practice. If this approach is to be used successfully then the same individual should sort specific groups and will thereby gain greater experience. Additionally, should morphospecies identifications be unavoidable, then some knowledge of specific taxonomic characters associated with the group is essential. Reference collections are critical to allow comparisons with other similar studies. They should be properly labelled, documented, and lodged at a recognised institution.

From this study it is clear that no single variable, or even a suite of variables, accurately describes the processes influencing all aspects of spider diversity. The structural diversity of habitats seems to be the most significant variable influencing spider diversity. To maximise spider diversity the structural diversity of the habitat must be maintained. Spiders are an extremely diverse group that inhabit all parts of the earth and it is unlikely that all variables accounting for their diversity have been considered in this study. Different variables are important for different functional groups. The varying factors responsible for the high diversity in the different functional groups suggests that finding requirements for the survival of a single species is simply not all-embracing enough for realistic conservation of so many spider species. Further research in this area is recommended, especially the impact of disturbance, e.g., burning and bush clearing, on spider diversity. No habitat is less important than another is and landscape conservation should be encouraged in this Reserve.
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Appendix 1.1: A summary of the current spider related research in South Africa carried out under the SANSA project.

SANSA is an umbrella project dedicated to the unification and enhancement of biosystematic research on Arachnology in South Africa. The following projects are currently being conducted under the auspices of SANSA. All of these projects contribute to our knowledge of spiders in South Africa.

1) Catalogues and checklists including: (a) a checklist and catalogue of the spiders of South Africa, (b) a list of the type specimens in the National Collection of Arachnida and (c) a check list of introduced arachnid species in South Africa.

2) Surveys of the following major biomes: (a) Forests - Ngome State Forest (Plant Protection Research Institute (PPRI) and the University of Pretoria), (b) Coastal Dune Forests - Richards Bay rehabilitated forest (PPRI and the University of Pretoria), (c) Nama-Karoo - Karoo National Park, Mountain Zebra National Park and Swartberg Nature Reserve (PPRI - registered project), (d) Woodland Arid Savanna - Kruger National Park (PPRI-registered project), Nylsvley Nature Reserve, the western part of the Soutpansberg (PPRI and the University of Venda); Loskopdam Nature Reserve (W. Croucamp - University of the Witwatersrand) and the current project in Makalali Private Game Reserve (University of Natal and Durban Natural Science Museum) and (e) Grassland - Roodeplaat Dam Nature Reserve and Rustenburg Nature Reserve.

3) Research is being conducted out in the following agro-ecosystems: (a) avocado and macadamia nuts (PPRI with ARC-Institute for Tropical and Subtropical Crops), (b) cotton (PPRI), (c) citrus (PPRI with ARC-Institute for Tropical and Subtropical Crops and CAPESPLAN), (d) tomatoes (PPRI for Tomato Producers Organization) and (e) sunflowers (PPRI)

4) Other more general projects occurring in South Africa include: (a) spiders associated with termites: *Hodotermes mossambicus* (PPRI) and *Trinervitermes trivoides* (University of the Free State and PPRI), (b) Spiders associated with caves (J. Myburg - MEDUNSA), (c) spiders of the Western Cape (N. Larson & South African Museum), (d) spiders of Kwa-Zulu Natal (T. Crouch - Durban Natural Science Museum), (e) observation on general behaviour and distribution a few Mygalomorphae spider species (M. Paulsen) and (e) a survey of introduced (alien) species (PPRI).
Appendix 1.3: Plant communities occurring in Makalali Private Game Reserve.

1 Riperian low closed woodland

This vegetation type is restricted to the banks of the Makhutswi river and ranges in width from approximately 10m to 60m either side of the river. It contains 47 species, the largest variety of woody plant species in a single vegetation type in the Conservancy. Trees common in this woodland include: *Fluegga virosa* (White-berry bush), *Croton megalobotrys* (Large Feverberry), *Dichrostachys cinerea* (Sickle bush), *Ziziphus mucronata* (Buffalo thorn) and *Gymnosporia buxifolia* (Common spike thorn), while *Phoenix reclinata* (Wild Date Palm) and *Diospyros mespiliformis* (Jackalberry) also occur in relatively high densities. There are a number of species that are restricted to this vegetation type. They include *Acacia robusta* (Brack thorn), *Acacia caffra*, *Acacia schweinfurtheii* (River climbing thorn), *Berchemia discolor* (Brown ivory), *Combretum erythrophylum* (River Bushwillow), *Euphorbia* species, *Euclea natalensis* (Natal guarri), *Ehretia rigida* (Puzzle bush), *Ficus sycamorus* (Sycamore Fig) and *Ficus ingens* (Red-leaved rock fig).

2 Drainage-line low thicket

This plant community is found in and along the drainage lines in the Conservancy, most of which are found in the North eastern section. Tree species common in this plant community include *Albizia harveii* (Common false-thorn), *Loncocarpus capassa* (Apple-leaf), *Commiphora glandulosa* (Tall common corkwood), *Flueggea virosa* (White-berry bush), *Gymnosporia buxifolia* (Common spike thorn) and *Grewia*.

3 Colophospermum mopane low closed woodland

This plant community is distinguished by *Colophospermum mopane* trees, which are by far the predominant woody plant in this vegetation type. This woodland is restricted to a few small, isolated pockets along the southern fenceline in Makalali and in the northern eastern section of the Reserve. Other species such as *Grewia* species, *Euclea divinorum* (Magic guarri), *Combretum hereroense* (Russet bushwillow), *Commiphora glandulosa* (Tall common corkwood) and *Dalbergia melanoxylon* (Zebrawood) are also present in this plant community but in low densities.

4 Cissus cornifolia - Commiphora africana – Lannea schweinfurtheii low thicket

This plant community is predominantly found in the North eastern section of the Conservancy, although there are a few small patches occur in Makalali. The distinguishing tree species in this plant community include: *Cissus cornifolia* (Bushman’s grape),
Commiphora africana (Hairy corkwood) and Laneea schweinfurthii (False marula). Two sub-vegetation types are recognised in this low thicket.

4.1 Ormocarpum tricocarpum – Dichrostachys cinerea low thicket

Dichrostachys cinerea (Sickle bush) is the dominant species in this thicket, although Grewia species are also found in fairly large densities. Other species that are present in this vegetation type include Ormocarpum tricocarpum (Caterpillar bush), Combretum apiculatum (Red bushwillow), Loncocarpus capassa (Apple-leaf), Gardenia volkensi (Savanna gardenia) and Spirostachys africana (Tambotie).

4.2 Commiphora africana – Combretum apiculatum low thicket

The Grewia species occupy the highest density of woody plants in this vegetation type, although the relatively high densities of Combretum apiculatum (Red bushwillow) and Commiphora africana (Hairy corkwood) distinguish this thicket from the other thickets. Other important species in this vegetation type include Acacia exuvialis (Flaky thorn), Acacia nigrescens (Knob thorn) and Dalbergia melanoxylon (Zebrawood).

5. Combretum apiculatum – Acacia nigrescens low closed woodland

This is the most prevalent plant community in Makalali. It is found in large areas throughout the Reserve. The large proportion of Combretum apiculatum (Red bushwillow) and Acacia nigrescens (Knob thorn) separate this vegetation type from others.

5.1 Ziziphus mucronata – Combretum hereroense low closed woodland

5.1.1 Dichrostachys cinerea – Acacia exuvialis low closed woodland

Extremely high density of Acacia exuvialis (Flaky thorn) and the presence of Dichrostachys cinerea (Sickle bush) are common in this plant community. Acacia nigrescens (Knob thorn), Combretum apiculatum (Red bushwillow) and Combretum hereroense (Russett bushwillow) are also prevalent, while Grewia species and Commiphora glandulosa (Tall common corkwood) are also present.

5.1.2 Combretum apiculatum – Ziziphus mucronata low closed woodland

The common tree species in this plant community are Combretum apiculatum (Red bushwillow) and Ziziphus mucronata (Buffalo thorn). Other tree species occurring in this plant community include Acacia nigrescens (Knob thorn) and Grewia species, Combretum hereroense (Russett bushwillow) and Dichrostachys cinerea (Sickle bush).
5.2  *Combretum apiculatum – Terminalia prunioides* low closed woodland

This plant community is distinguished by the high density of *Combretum apiculatum* (Red bushwillow) and the presence of *Terminalia prunioides* (Lowveld cluster-leaf).

5.2.1  *Acacia nigrescens – Ormocarpum tricocarpum* low closed woodland

This plant community is found only in the northern section of the Makalali Conservancy. Apart from the high diversity of *Combretum apiculatum* (Red bushwillow), it also contains a relatively high density of *Acacia nigrescens* (Knob thorn) and *Grewia* species as well as *Acacia exuvialis* (Flaky thorn) and *Dichrostachys cinerea* (Sickle bush).

5.2.2  *Acacia exuvialis – Sclerocarya birrea* low closed woodland

This subgroup is found mainly in the northern section, but is also found in the south eastern section of the Reserve. *Combretum apiculatum* (Red bushwillow) is found in high densities as well as *Grewia* species. Other important species include *Dalbergia melanoxylon* (Zebrawood), *Acacia nigrescens* (Knob thorn) and *Cissus cornifolia* (Bushman’s grape).

5.3  *Acacia exuvialis – Strychnos madagascariensis – Dalbergia melanoxylon* low closed woodland.

5.3.1  *Acacia nigrescens – Acacia exuvialis* low closed woodland

Although this plant community is also dominated by *Acacia nigrescens* (Knob thorn) and *Combretum apiculatum* (Red bushwillow), it is distinguished from other vegetation types by the presence of *Acacia nigrescens* (Knob thorn) and *Acacia exuvialis* (Flaky thorn) *Dichrostachys cinerea* (Sickle bush), *Ziziphus mucronata* (Buffalo thorn), *Combretum hereroense* (Russett bushwillow), *Flueggea virosa* (White-berry bush) and *Strychnos madagascariensis* (Black monkey orange).

5.3.2  *Strychnos madagascariensis – Combretum apiculatum* low closed woodland

This plant community is found in the south western corner of the Makalali section near the main gate. The dominant and distinguishing species in this community type are *Strychnos madagascariensis* (Black monkey orange) and *Combretum apiculatum* (Red bushwillow). Other species which occur in this vegetation type in high densities include *Acacia exuvialis* (Flaky thorn), *Acacia nigrescens* (Knob thorn) and *Dalbergia melanoxylon* (Zebrawood).

6.  Low closed grassland

There are not many areas that can be classified as grassland in Makalali. There are many areas
that are bush encroached, preventing the dominance of grassland in certain areas. The grass is particularly important for the grazing herbivores. Bush clearing projects have been initiated for the removal of *Dichrostachys cinerea* (Sicklebush) and various *Acacia* and *Grewia* species. The bush clearing creates a mosaic of habitats for a diversity of herbivores and also improves game viewing (Butchart 1996). Low densities of the following woody plants are found in this community type: *Grewia* species, *Acacia exuvialis* (Flaky thorn), *Combretum apiculatum* (Red bushwillow), *Commiphora africana* (Tall common cork wood), *Acacia nigrescens* (Knob thorn) and *Ziziphus mucronata* (Buffalo thorn).

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

Most of the aerial cover in this community type is provided by grass, with a relatively low density of woody plants, most of which are shrubs under 1.5m in height. The species that are prevalent in this vegetation type include *Acacia exuvialis* (Flaky thorn), *Grewia* species, *Commiphora africana* (Tall common cork wood) and *Dalbergia melanoxylon* (Zebrawood).

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

This community type is dominated by high densities of *Combretum apiculatum* (Red bushwillow) and *Grewia* species. Other woody species, also occurring at relatively high densities include *Commiphora africana* (Tall common cork wood), *Acacia nigrescens* (Knob thorn), *Gymnosporia buxifolia* (Common spike thorn) and *Acacia karroo* (Sweet thorn).

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

This community type is characterised by an extremely high density of *Combretum apiculatum* (Red bushwillow) plants. *Acacia nigrescens* (Knob thorn) and *Grewia* species also occur here but in much lower densities. Other important species present in this community type include *Combretum hereroense* (Russett bushwillow) and *Sclerocarya birrea* (Marula).
### Appendix 1.3: Checklist of tree species at Makalali Private Game Reserve (107 species)

<table>
<thead>
<tr>
<th>Scientific names</th>
<th>Common names</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acacia burkei</em></td>
<td>Black monkey thorn</td>
<td>Mimosoideae</td>
</tr>
<tr>
<td><em>Acacia caffra</em></td>
<td>Common hook thorn</td>
<td></td>
</tr>
<tr>
<td><em>Acacia erubescens</em></td>
<td>Blue thorn</td>
<td>Mimosoideae</td>
</tr>
<tr>
<td><em>Acacia exauvialis</em></td>
<td>Flaky thorn</td>
<td></td>
</tr>
<tr>
<td><em>Acacia gerradii</em></td>
<td>Red thorn</td>
<td></td>
</tr>
<tr>
<td><em>Acacia karroo</em></td>
<td>Sweet thorn</td>
<td></td>
</tr>
<tr>
<td><em>Acacia nigrescens</em></td>
<td>Knob thorn</td>
<td></td>
</tr>
<tr>
<td><em>Acacia nilotica</em></td>
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**REFERENCES**

Appendix 3.1: Check list of all spider species collected at Makalali Private Game Reserve.
The guild that the different families belong to have been indicated. GW = ground wanderers, 
PW = plant wanderers and WB = web builders. Genera containing potentially new species are 
indicated by (†), while new distribution records of the genera are indicated by (‡). Species 
that were not found in sites but were included in additional sampling are indicated by (*).
Species determinations have been done as far as possible. Some could not be determined and 
have been left at the genera level.

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<th>Family, genus, species</th>
<th>Guild</th>
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<td>Stegodyphus tentoriicola Purcell, 1904</td>
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<td><strong>Gnaphosidae:</strong></td>
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<td>Asemesthes ceresicola Tucker, 1923</td>
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<td>Camillina biaflaga Tucker, 1923</td>
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<td>DMSA - ARA 400</td>
<td>Camillina corrugata (Purcell, 1907)</td>
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<td>Caporia sp. 1</td>
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<td>Drasodes sp. 1*</td>
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<td>Echemus erutus Tucker, 1923</td>
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<td>Setaphis arcus Tucker, 1923</td>
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<td>Setaphis subtilis (Simon, 1897)</td>
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<td>Oxyopes pallidecoratus Strand, 1906</td>
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<td>Oxyopes schenkelii Lessert, 1927</td>
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<td>Ikuma palpimanus transvaalicus Simon, 1893</td>
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<td>22. Philodromidae:</td>
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<td>Hirriusa sp.</td>
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<td>Suemus punctatus Lawrence, 1938</td>
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<td>Tibellus minor Lessert, 1919</td>
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### 23. Pholcidae: |
| DMSA – ARA 477 | Smeringopus peregrinus Strand, 1906 |
| DMSA – ARA 478 | Smeringopus atomarius Simon, 1910 |
| DMSA – ARA 479 | Spermophora peninsulae (Lawrence, 1964) |

### 24. Pisauridae: |
| DMSA – ARA 480 | Chiasmopes lineatus (Pocock, 1898) |
| DMSA – ARA 481 | Chiasmopes sp. 2 |
| DMSA – ARA 482 | Chiasmopes sp. 3* |
| DMSA – ARA 483 | Cispius sp. 1 |
| DMSA – ARA 484 | Cispius sp. 2 |
| DMSA – ARA 486 | Perenethis sp. |
| DMSA – ARA 487 | Perenethis sp. 2 |
| DMSA – ARA 488 | Pisauridae sp. 1* |
| DMSA – ARA 489 | Pisauridae sp. 2 |
| DMSA – ARA 490 | Thalassius margaritatus (Pocock, 1898) |

### 25. Prodidomidae: |
| DMSA – ARA 491 | Theuma parva Purcell, 1907 |
| DMSA – ARA 492 | Theuma sp. 2 |
| DMSA – ARA 493 | Prodidomus flavipes (Lawrence, 1952) |

### 26. Salticidae: |
| DMSA – ARA 494 | Aelurillus sp. 1 |
| DMSA – ARA 494 | Aelurillus sp. 2 |
| DMSA – ARA 495 | Baryphus ahenus Simon, 1902 |
| DMSA – ARA 496 | Blaor sp. 1 |
| DMSA – ARA 497 | Cosmophasis quadrinaculatus Lawrence, 1942* |
| DMSA – ARA 498 | Heliothanas debilis (Simon, 1901) |
| DMSA – ARA 499 | Hyllus argyrotoous Simon, 1902 |
| DMSA – ARA 500 | Hyllus brevitaris Simon, 1902 |
| DMSA – ARA 501 | Hyllus sp. 3 |
| DMSA – ARA 502 | Hyllus sp. 4 |
| DMSA – ARA 503 | Hyllus sp. 5 |
| DMSA – ARA 504 | Hyllus sp. 6* |
| DMSA – ARA 505 | Langona sp. 1 |
| DMSA – ARA 506 | Langona sp. 2 |
| DMSA – ARA 507 | Myrmarachne sp. |
| DMSA – ARA 508 | Natta chiorogasta (Simon, 1901) |
| DMSA – ARA 509 | Portia sp. 1 |
| DMSA – ARA 510 | Rhene sp. 1 |
| DMSA – ARA 511 | Rhene machadoi Berland & Millot, 1941* |
| DMSA – ARA 512 | Salticidae sp. 1 |
| DMSA – ARA 513 | Salticidae sp. 2 |
| DMSA – ARA 514 | Salticidae sp. 3 |
| DMSA – ARA 515 | Salticidae sp. 4* |
| DMSA – ARA 516 | Salticidae sp. 5 |
| DMSA – ARA 517 | Stenaelurillus sp. 1 |
| DMSA – ARA 518 | Stenaelurillus sp. 2 |
| DMSA – ARA 519 | Thyene natali Peckham, 1903 |
27. Scytodidae:  
DMSA – ARA 520  Thyene sp. 1  
DMSA – ARA 521  Thyene sp. 2  
DMSA – ARA 522  Thyene sp. 3  
DMSA – ARA 523  Thyene sp. 4  
DMSA – ARA 524  Thyenula ogdeni (Peckham & Peckham, 1903)

28. Selenopidae:  
DMSA – ARA 525  Anyphops rubicundus (Lawrence, 1940)*  
DMSA – ARA 526  Selenops radiatus Latreille, 1819*

29. Segestriidae:  
DMSA – ARA 530  Ariadna sp.

30. Sicaridae:  
DMSA – ARA 531  Loxosceles spiniceps (Lawrence, 1952)  
DMSA – ARA 532  Loxosceles sp.*

31. Sparassidae:  
DMSA – ARA 533  Olios sp. 1  
DMSA – ARA 534  Olios sp. 2  
DMSA – ARA 535  Olios sp. 3†  
DMSA – ARA 536  Panaretella sp. 1†  
DMSA – ARA 537  Pseudomicrommata longipes (Bösenberg & Lenz, 1895)

32. Tetragnathidae:  
DMSA – ARA 538  Leucauge thomeensis Krauss, 1960  
DMSA – ARA 539  Leucauge festiva (Blackwall, 1866)*  
DMSA – ARA 540  Nephila sp.

33. Theraphosidae:  
DMSA – ARA 541  Brachionopus sp.  
DMSA – ARA 542  Ceratogyrus bechuanicus Purcell, 1902*  
DMSA – ARA 543  Harpactirella sp.*  
DMSA – ARA 544  Pterinochilus nigrofulvus (Pocock, 1898)

34. Theridiidae:  
DMSA – ARA 545  Achaearanea sp. 1  
DMSA – ARA 546  Achaearanea sp. 2  
DMSA – ARA 547  Achaearanea sp. 3  
DMSA – ARA 548  Achaearanea sp. 4  
DMSA – ARA 549  Argyrodes convivans Lawrence, 1937  
DMSA – ARA 550  Argyrodes sp. 2  
DMSA – ARA 551  Argyrodes sp. 3*  
DMSA – ARA 552  Dipoena sp. 1  
DMSA – ARA 553  Enoplognatha sp. 1  
DMSA – ARA 554  Enoplognatha sp. 2  
DMSA – ARA 555  Enoplognatha sp. 3  
DMSA – ARA 556  Episinus sp. 1  
DMSA – ARA 557  Latrodectus geometricus C.L. Koch, 1841  
DMSA – ARA 558  Latrodectus renivulvatus Dahl, 1902  
DMSA – ARA 559  Phoroncidia sp.  
DMSA – ARA 560  Phoroncidia sp. 1  
DMSA – ARA 561  Theridiidae sp. 1  
DMSA – ARA 562  Theridiidae sp. 2*  
DMSA – ARA 563  Theridiidae sp. 3  
DMSA – ARA 564  Theridiidae sp. 4*  
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<td>Monaes quadrituberculatus Lawrence, 1927</td>
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<td>Simorcus zuluanus (Lawrence, 1942)</td>
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<td>Synema decens (Karsch, 1878)</td>
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<td>Thomisus congolensis Comellini, 1957</td>
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<td>Thomisus daradioides Simon, 1890</td>
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<td>Thomisus granulatus Karsch, 1880</td>
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<td>Thomisus scrupes Simon, 1886</td>
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<td>Thomisus spiculatus Pocock, 1901</td>
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<td>Caesetius sp. 1</td>
</tr>
<tr>
<td>DMSA - ARA 604</td>
<td>Capheris fitzsimonsi Lawrence, 1936*</td>
</tr>
<tr>
<td>DMSA - ARA 605</td>
<td>Capheris sp. 2</td>
</tr>
<tr>
<td>DMSA - ARA 606</td>
<td>Capheris sp. 3</td>
</tr>
<tr>
<td>DMSA - ARA 607</td>
<td>Capheris sp. 4</td>
</tr>
<tr>
<td>DMSA - ARA 608</td>
<td>Cydrela sp.</td>
</tr>
<tr>
<td>DMSA - ARA 609</td>
<td>Diore delacatulus (Law, 1936)</td>
</tr>
<tr>
<td>DMSA - ARA 610</td>
<td>Diore sp.</td>
</tr>
<tr>
<td>DMSA - ARA 611</td>
<td>Ranops sp.</td>
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</table>
Appendix 3.2: A brief description of the general appearance, biology and dominant genera of spider families sampled in Makalali Private Game Reserve. The families have been listed alphabetically. Genera containing potentially new species are indicated by (†), while new distribution records of the genera are indicated by (‡). Species that are endemic to South Africa are indicated by (*).

Any reference to the Afrotropical region includes the following regions: Africa south of the Sahara; islands off the east coast of Africa, namely Madagascar, the Mascarenes, the Comoros, the Seychelles and adjacent small islands (Aldabra, Mauritius and Reunion); Islands off the west coast, namely St. Helena, Ascension, Cape Verde, São Tomé, Principe and Annobon; The southern part of the Arabian peninsula (Yemen), including the islands of Socotra; the Canary islands and other islands of the Macaronesian Archipelago (Dippenaar-Schoeman & Jocqué 1997)

Family AGELENIDAE (funnel-web spiders)
The Agelenidae, represented by 43 genera and about 600 species occur worldwide. Eleven genera are known from the Afrotropical Region, all belonging to the subfamily Ageeleninae (Dippenaar-Schoeman & Jocqué 1997). These spiders resemble wolf spiders. They are usually dark grey to mottled brown, with the abdomen decorated with a reddish-brown folium and a series of yellow to white spots or bands. The legs are long and narrow toward the extremities and are hairy with spines (Leroy & Leroy 2000). The carapace is long and narrow in front with the eyes (equal size) situated in two procurred rows. The abdomen is oval and tapers posteriorly. They have two elongated posterior spinnerets tapering at the ends (Dippenaar-Schoeman & Jocqué 1997).

The funnel web of agelenids is very characteristic, consisting of a flat, slightly concave silk sheet with a funnel-shaped retreat at one end, close to the soil surface (Preston-Mafham & Preston-Mafham 1984). Agelenids are common in the African savanna but owing to their sedentary life-style, are not often collected during general surveys (Dippenaar-Schoeman & Jocqué 1997).

Only one genus was sampled from this Reserve, Olorunia and was sampled from one site only in habitat type 2 (General bushveld). This genus lives permanently on a large, sheet-like web with a funnel retreat made close to the substrate (Filmer 1991). The distribution of this genus in the Afrotropical region is Zaïre and South Africa (Dippenaar-Schoeman & Jocqué 1997).

Family ANAPIDAE (dwarf ring-shield spiders)
The Anapidae, represented by 32 genera and about 146 species, occur worldwide. Five genera
are known from the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Anapids are cryptozoic spiders usually found in forested areas. Some free-living species are found in the moss and leaf litter layers. Their abdomens are covered with two or three scuta (Filmer 1991). They generally have a raised carapace and the first leg of the male spider is very long and has two small apophyses. The booklungls are replaced by tracheae and the anterior median eyes are usually reduced (Dippenaar-Schoeman & Jocqué 1997).

Only one genus, *Metanapis*, was found in the Reserve. The species found in the Reserve is potentially new. This genus was also found in only one site in the Reserve in a rocky outcrop habitat type. This genus is found in Kenya, Zaire and South Africa (Dippenaar-Schoeman & Jocqué 1997).

**Family ARANEIDAE (orb-web spiders)**

The Araneidae are a large family comprising more than 4000 species in 156 genera, 65 of which occur in the Afrotropical region (Dippenaar-Schoeman & Jocqué 1997). Several subfamilies are recognised. Araneids are a diverse group of orb-web weavers occupying a wide range of habitats (Preston-Mafham & Preston-Mafham 1984; Leroy & Leroy 2000). Their most prominent characteristics are three tarsal claws and the third leg always being the shortest. They form an important component of the spider fauna of the grass and herb layer (Dippenaar-Schoeman & Jocqué 1997).

The araneids were the most abundant family in the Reserve (1546 individuals) and were widely distributed. They were found in all habitat within the Reserve. The genera sampled from the Reserve included: *Araneilla, Araneus, Argiope, Caerostris, Chorizopes* (including one potentially new species), *Cyclosa, Cyphalonotos, Cyrtophora, Hypsacantha, Lipocrea, Nemoscolus, Nemospiza, Neoscona, Pararaneus, Prasonica* (including one potentially new species), *Pycnacantha, Singa*.

Members of the subfamily Araneinae are diverse in morphology as well as behaviour. The genus *Singa* comprises small spiders characterised by a shiny body decorated with spots or lines. They are commonly known as pyjama spiders. They live on low plants where their small orb-webs frequently go unnoticed (Filmer 1991). The web of *Cyclosa* (garbage line spiders) is usually built in shrubs and is common in open woodland (Filmer 1991). The stabilimentum often consists mainly on the prey remains attached in a vertical line to the centre of the web. The abdomen of *Cyclosa* has a distinct caudal tubercle protruding beyond the spinnerets. The abdomen is usually silver-grey with the first pair of legs longer than the others (Dippenaar-Schoeman & Jocqué 1997).

*Nemoscolus* build a small conical or coiled retreat that is made of material such as soil particles, silk and vegetable matter. The web lacks a stabilimentum. The genus *Chorizopes* is known as a specialised predator of spiders, invading webs and killing other
araneids. In the genera *Araneus* and *Neoscona* (hairy field spiders) the abdomen is usually wider than it is long, raised near the anterior, oval or triangularly oval in outline, and often overhanging the carapace. Colour varies from cream to brown to black, usually with distinct patterns dorsally. The eyes are set in two rows, with lateral eyes almost contiguous (Dippenaar-Schoeman & Jocqué 1997).

The members of the genus *Argiope* are easily recognised by their large size and brightly coloured abdomens. The abdomen usually has a yellow background decorated with darker bands, and the edge of the abdomen is often scalloped. They are diurnal spiders encountered in the hub of their orb-webs during the day. The webs are often provided with a stabilimentum consisting of zigzag silk bands (Filmer 1991).

Only one genus, *Pycnacantha* (hedgehog spider), was found from the subfamily Cyrtarachninae. This is a nocturnal araneid that live in grass and low vegetation that hangs suspended from a u-shaped trapezium, catching moths that are in full flight. The abdomen of this spider is covered with numerous sharp spines, giving it an appearance of a hedgehog (Filmer 1991).

*Cyrtophora* (tent web spiders) are widely distributed throughout the world. The abdomen is usually longer than it is wide, and high, with distinct, blunt tubercles. The colour varies from cream to black with white markings (Filmer 1991). They construct unique webs resembling that of Linyphiidae. The webs consist of a fine-meshed sheet, similar to the enlarged central area of the orb-webs, but made of dry silk and arranged horizontally (Dippenaar-Schoeman & Jocqué 1997).

Members of the subfamily Gastercanthinae are brightly decorated with yellow, red or black and white patterns. The abdomens are shiny and dorsally flattened and has a number of spiny projections laterally and posteriorly. The bright red, orange, yellow, white and black on the abdomen render this spider unmistakable (Filmer 1991; Leroy & Leroy 2000). *Hypsacantha* and *Caerostris* were the two genera sampled here that belong to the Gastercanthinae subfamily. In *Caerostris* (bark spiders), the abdomen is covered with horny protuberances that are grey-brown in colour, resembling tree bark or thorns of trees (Filmer 1991).

Araneids were very widely distributed in the Reserve, occurring in 97% of sites sampled. The genera sampled from this Reserve are found in the following regions: *Araneilla*: South Africa; *Araneus*: throughout Afrotropical region; *Argiope*: throughout Afrotropical region; *Caerostris*: throughout Afrotropical region including the Comoros; *Chorisopes*: (including one potentially new species) Madagascar and South Africa; *Cyclosa*: throughout the Afrotropical region including the Seychelles; *Cyphalonotus*: East, Central and Southern Africa; *Cyrtophora*: throughout the Afrotropical region; *Hypsacantha*: East, Central and Southern Africa; *Lipocrea*: East, Central and Southern Africa; *Nemoscolus*: Gabon, Mali,
Zaïre and South Africa; *Nemospiza*: South Africa; *Neoscona*: throughout the Afrotropical region and Madagascar; *Pararaneus*: throughout the Afrotropical region and Madagascar; *Prasonica*: West, East, Central Africa, Madagascar, Seychelles and South Africa; *Pycnacantha*: Cameroon, Central Africa, Namibia, South Africa and Madagascar; *Singa*: Tanzania, Zaïre and southern Africa (Dippenaar-Schoeman & Jocqué 1997).

**Family BARYCHELIDAE (trap-door baboon spiders)**

The Barychelidae are represented by 41 genera and occurs worldwide. The Afrotropical Region have ten genera in two subfamilies (Dippenaar-Schoeman & Jocqué 1997). Barychelids are smaller than the theraphosids (baboon spiders). They live in silk-lined burrows usually closed with a trapdoor. The apical segment of their posterior lateral spinnerets are shorter than the rest. They only have two claws, with the scopulae on the tarsi of the first and second legs well developed and iridescent. The carapace and legs are uniformly setose. The carapace is as high in the front of the fovea as it is behind (Filmer 1991; Dippenaar-Schoeman & Jocqué 1997).

Only one genus, *Sipalolasma*⁸, was sampled from the Reserve. They have a clypeus and their eight eyes are situated in a rectangular group slightly further back on the carapace. The thoracic fovea is a deep circular pit. Most species live in silk lined burrows in the ground. The burrow often has a "Y" formation (Filmer 1991). This is a new distribution record for this family in South Africa. The genus was previously only thought to occur in Ethiopia and Zaïre (Dippenaar-Schoeman & Jocqué 1997). The barychelids were recorded from three sites, all different habitat types (2, 3 and 5) but in low abundances (3 individuals).

**Family CLUBIONIDAE (leaf-curling sac spiders)**

The Clubionidae are represented by 25 genera of which five in the subfamily Clubioninae occur in the Afrotropical region (Dippenaar-Schoeman & Jocqué 1997). Clubionids are free-living, nocturnal hunters commonly encountered in sac-like retreats on foliage during the day. They are two clawed spiders. They are aggressive and use their front legs to detect and grab prey. They have long legs with scopulae on the tarsi (Filmer 1991). Their eyes are small and are situated in two transverse rows (Filmer 1991; Dippenaar-Schoeman & Jocqué 1997). While many of the species within this family are drab in colour, there are some brightly coloured species and also some species are incredibly good ant (Formicidae: Hymenopetra) mimics (Preston-Mafham & Preston-Mafham 1984).

One genus, *Clubiona*, was found in the Reserve and was sampled all five different habitat types. *Clubiona* usually has the forth leg the longest (Filmer 1991). They are frequently encountered on crops and they may play an important role in agroecosystems (Dippenaar-Schoeman 1979; Riechert 1984). This genus is distributed throughout the
Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Clubionids were found in 30% of sites sampled.

Family CORINNIDAE (dark sac spiders)
The Corinnidae are a fairly large family represented by 51 genera, 22 of which occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Corinnids are wandering spiders that are frequently encountered in semi-arid habitats and leaf litter in forested areas (Dippenaar-Schoeman & Jocqué 1997). They build silk retreats in rolled-up leaves and in plant debris. The egg-sacs are shiny and disk-shaped and are attached to the substrate. Some corinnids are known to mimic ants (Formicidae; Hymenoptera) or, occasionally, velvet ants (Mutillidae: Hymenoptera) (Dippenaar-Schoeman & Jocqué 1997).

Three genera were found in the Reserve. These included Castianeira; Corinnomma and Trachelas. The Castianeira movements are ant-like, involving rapid movements with jerky pauses and sudden changes in direction. While walking, the abdomen moves up and down and the front legs are held in the air to mimic the antennae of ants (Dippenaar-Schoeman & Jocqué 1997). Trachelas usually occur in dry, hot areas, usually at the base of plants. They move slowly and resemble palpimanids (Dippenaar-Schoeman & Jocqué 1997). Corinnids were sampled from all five different habitat types and occurred in 28% of all sites sampled. The genera sampled in the Reserve are distributed in the following regions: Castianeira: throughout the Afrotropical Region and Madagascar; Corinnomma: Ethiopia and South Africa; Trachelas: East, West, Southern Africa and Madagascar (Dippenaar-Schoeman & Jocqué 1997).

Family CTENIDAE (wandering spiders)
The Ctenidae are represented by 28 genera, nine of which occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Ctenids are nocturnal, wandering spiders, hunting their prey on foliage and on the soil surface (Preston-Mafham & Preston-Mafham 1984). They resemble wolf spiders and are marked with cryptic colours (Filmer 1991). Their legs are strong, with stout spines, and the tarsi have two claws and scopulae. The eyes are in three rows (2:4:2). When running the front legs are usually held off the ground. They are the most abundant nocturnal spiders in rainforests (Dippenaar-Schoeman & Jocqué 1997). The ctenid female deposits her egg sac on the substrate or carries it between the chelicerae and palpi.

Anahita and Ctenus were the only ctenid recorded from the Reserve. The Anahita genus was found in all five habitat types and occurred in 23% of all sites sampled, while Ctenus was found in all habitat types except type 5 (mopane woodland). The genera are distributed in the following Afrotropical Regions: Anahita: East, West, Central Africa, Madagascar and Comoros; Ctenus: throughout the Afrotropical Region (Dippenaar-Schoeman
Family **DEINOPIDAE (net-casting spiders)**

Deinopidae are a small family found in tropical and subtropical regions of the world. The 60 recognised species occur in four genera, three of which are known from the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Deinopids are usually referred to as stick spiders on account of their shape or ogre-faced spiders on account of the pair of enormous eyes that they possess (Preston-Mafham & Preston-Mafham 1984). They live in low vegetation and construct a small expandable web that they cast over their prey. They hunt in low bushes and shrubs. The spider hangs head down above the substrate, supported by a scaffold of non-sticky silk. The web corners are held by the front two pairs of long legs. By moving the legs the size of the web can be varied and swung onto the prey. It uses its hind legs to wrap the prey (Filmer 1991; Leroy & Leroy 2000).

One genus, *Deinopia*, was sampled from the Reserve. The genus was only found in habitat type 3 and at one site. *Deinopia* (ogre faced spiders) are usually blackish, coated with white hairs. The posterior median eyes are set far forward and are greatly enlarged. They make their web after nightfall and await prey during the dark hours. During the day it can be found pressed flat against the bark or branch with the two long pairs of front legs stretched forwards and the back legs grasping the twig firmly (Filmer 1991). The genus is found in the following Afrotropical Regions: East, West, Central and Southern Africa (Dippenaar-Schoelman & Jocqué 1997).

Family **DICTYNIDAE (mesh-web spiders)**

The Dictynidae are represented by more than 350 species in 47 genera, 10 of which are known to the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Little is known about the dictynids of the Afrotropical region. Most dictynids of the subfamily Dictyninae live in a nest consisting of a retreat and a web. The web consists of parallel threads criss-crossed with cribellate silk to form a ladder structure. The retreat is made within the mesh. Webs are usually constructed on the stems and leaves of plants, but some species construct their webs on walls. Some dictynid species are ground-dwelling while others live in the intertidal zone.

These small spiders have a wide cribellum and a uniserate calamistrum but are generally recognised by their unique webs (Filmer 1991). The abdomen may slightly overlap the carapace and is usually decorated with light and dark patterns. The carapace is distinctly high and usually clothed in white hairs. The eyes are arranged in two straight rows and are almost the same size. The anterior median eyes are dark and the rest of the eyes appear pearly white. The chelicerae are long and indented (Preston-Mafham & Preston-Mafham 1984; Dippenaar-Schoeman & Jocqué 1997).
One genus, *Mashimo*, was sampled from the Reserve. The species was in habitat type 3 and was only found at a single site. The distribution in the Afrotropical Region for this genus is Zambia and South Africa (Dippenaar-Schoeman & Jocqué 1997).

Family **ERESIDAE** *(velvet spiders and social spiders)*

The Eresidae are represented by ten genera and 110 species in two subfamilies. Both subfamilies occur in the Afrotropical Region where nine genera are represented. The Eresidae include groups with very diverse lifestyles and are either ground dwelling or plant dwelling. They are corpulent cribellate spiders with a characteristic carapace bluntly rounded in the front, a round to oval abdomen and they usually have thick short legs. The cribellum is situated ventrally just anterior to the spinnerets in the form of a cream band. The median eyes are set close together while both pairs of lateral eyes are set far apart. (Preston-Mafham & Preston-Mafham 1984; Dippenaar-Schoeman & Jocqué 1997).

The only species found here belonged to the genus *Stegodyphus*. Most species are solitary except the social *Stegodyphus dumicola* that occurs in throughout southern Africa, and *Stegodyphus mimosarum* that occurs along the eastern regions. The latter two species are the most commonly encountered resulting in the misleading common names, community nest or social spiders, being used to describe the entire genus (Filmer 1991).

Although the eresids were only sampled from one habitat type and occurred in one site, their distribution is wider than it appears. Many of the *Stegodyphus* nests occur along fence lines and high in trees and were therefore simply not sampled. This genus is found throughout the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997).

Family **GNAPHOSIDAE** *(flat-bellied ground spiders)*

The Gnaphosidae are a large family comprising about 141 genera and 1 500 species in six families worldwide. Forty-one genera and about 323 species occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Gnaphosids are free-living ground dwellers, with only a few living on plants. Most of the ground dwelling species construct a silk retreat under stones or surface debris within which they remain during non-active periods. Some gnaphosids attach their egg-sacs to the substrate whereas others spin complex egg-sacs in their retreats (Dippenaar-Schoeman & Jocqué 1997). Gnaphosids catch their prey using speed, force and agility. Their eyesight is poor and their prey is perceived by tactile or chemotactic stimuli. Surveys in the Afrotropical Region have shown that gnaphosids are more common in dry habitats. They are occasionally encountered in wet fields but very rarely in dense forest (Dippenaar-Schoeman & Jocqué 1997).

They are dull coloured spiders and some genera have markings on the abdomen. They have hairs on the abdomen which may glisten (Filmer 1991). The shape of the carapace is
variable – ovate to narrow. The eyes are in two rows, commonly both procurred, with the posterior median eyes in some species oval and set at an angle. The chelicerae are robust and they have dark fangs curving inwards and overlapping. The spinnerets are cylindrical and are markedly parallel to and separate from each other (Filmer 1991; Dippenaar-Schoeman & Jocqué 1997).

Eight genera of Gnaphosidae were sampled. These included *Asemesthes; Camillina*; *Caponia; Drasodes; Echemus; Setaphis†; Zelotes and Trachyzelotes*. *Camillina* construct a retreat of soft silk under large stones on relatively flat ground. *Asemesthes and Zelotes* are often found in association with termites. Gnaphosids were widely dispersed in the Reserve and were sampled from all habitat types and occurred in 90% of the sites sampled.

The genera sampled from this Reserve are found in the following Afrotropical regions: *Asemesthes*: Ethiopia, Angola, Namibia, South Africa; *Camillina*: East Africa, Niger, South Africa, Seychelles, Madagascar and Cape Verde; *Caponia*: South Africa; *Drasodes*: Ivory Coast, East Africa, Namibia, South Africa, Madagascar, St. Helena; *Echemus*: Ethiopia, Guinea-Bissau, South Africa, Principes; *Setaphis*: throughout the Afrotropical Region and Cape Verde; *Zelotes*: West, East Africa, Namibia, South Africa; *Trachyzelotes*: Senegal, Ethiopia, South Africa, Yemen (Dippenaar-Schoeman & Jocqué 1997).

**Family HERSILIIDA (long-spinnered spiders)**

The Hersiliidae are a family with worldwide distribution that comprise five genera and about 85 species. Three genera occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Hersiliids have diverse life-styles, ranging from wandering tree-dwellers to ground-dwelling web-builders (Leroy & Leroy 2000). Their flattened bodies allows them to lie adpressed to bark without casting shadows or enables them to hide in cracks. They are extremely fast runners and are occasionally encountered on walls and lichen-covered rocks. Body colour varies widely within species but they are often cryptically coloured to match their substrate. They generally have two long spinnerets protruding well beyond the posterior of the abdomen. Their eyes are in two recurved rows situated on a large protuberance at the front of the carapace (Dippenaar-Schoeman & Jocqué 1997).

Two genera, *Hersila* and *Tama†*, were found in the Reserve. *Hersila* occurs on tree-bark where its mottled appearance camouflages it well (Filmer 1991). They do not spin webs, but will attack pedestrian prey. *Tama* are usually found under stones where they build irregular webs similar to those of pholcids (Dippenaar-Schoeman & Jocqué 1997; Filmer 1991). *Tama* build a retreat with a circular wall of closely woven webbing plastered with small stones, chips and vegetable debris. The outside wall is concave and smooth, while the inside is decorated with a mass of fine strands and small stone chips. The hersiliids were sampled from all habitat types except habitat type 5 but occurred in just 7.5% of the sites.
sampled. The genera sampled from the Reserve are found in the following Afrotropical regions: *Hersila*: throughout the Afrotropical region, Madagascar; *Tama*: Namibia, South Africa (Dippenaar-Schoeman & Jocqué 1997).

**Family IDIOPIDAE (spurred trap door spiders)**

Idiopids are represented by 19 genera and about 200 species in three subfamilies. Two subfamilies are known to the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Idiopids are trap door spiders that cover their burrows with wafer-type or cork-type lids. Idiopids use their rastellum to excavate their burrows. The burrows are made in a variety of microhabitats, frequently on open grass plains where the soil is soft. The burrows are closed with a single trapdoor, hinged with silk on the side (Filmer 1991). They are usually medium-sized to very large (8 - 33 mm) mygalomorph spiders with three claws and a rastellum. Their anterior lateral eyes are close together at the edge of the clypeus, well forward of the other eyes that are set on a tubercle. The tarsi and metatarsi of the first leg have numerous lateral spines and all tarsi of the male show scopulae (Dippenaar-Schoeman & Jocqué 1997; Leroy & Leroy 2000).

Only one genus, *Idiops*, was found in the Reserve. This genus was restricted to a single site from habitat type 1. The burrows of *Idiops* are usually made in open grassy plains with a gentle slope. The lid is usually cork-like and varies in shape from round to D-shaped, and the dorsal side is usually covered with grass or debris. This genus is distributed in the following regions: East Africa, Zaïre and southern Africa (Dippenaar-Schoeman & Jocqué 1997).

**Family LINYPHIIDAE (hammock-web spiders)**

The Linyphiidae are a large family, comprising 472 genera and more than 4000 species. Seventy six genera occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Linyphiids spin delicate sheetwebs between branches of trees or shrubs, in tall grass and sometimes close to the ground. Spiders are suspended upside-down under the sheet and they have no retreat. Prey is bitten through the sheet from below. It is then pulled through the sheet before being consumed (Dippenaar-Schoeman & Jocqué 1997). In the Afrotropical region, linyphiids are much more abundant at higher altitudes than in lowlands, possibly as a result of interference competition with ants (Dippenaar-Schoeman & Jocqué 1997).

Two genera were sampled, *Ostearius* and five other, as yet, undetermined linyphiid species. The linyphiids were found in all habitat types, occurring in 30% of all sites sampled. Members belonging to the subfamily Linyphiinae are all small spiders. Their eyes are in two rows with the anterior median eyes often darker than the rest. The abdomen tends to be globose and usually shiny black to dark brown. The *Ostearius* genus is a cosmopolitan
species and occurs in the following Afrotropical regions: Kenya, Tanzania, Angola, Cameroon, South Africa, Namibia and St. Helena (Dippenaar-Schoeman & Jocqué 1997).

FAMILY LIOCRANIDAE (spiny-legged sac spiders)
The Liocranidae are represented by three subfamilies and 41 genera, 11 of which occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Liocranids are free-living, ground-dwelling spiders with several genera commonly found in dense forest litter. They are small to medium-sized (3 - 15 mm) with two claws and eight eyes. The posterior and median spinnerets have cylindrical gland spigots (Dippenaar-Schoeman & Jocqué 1997).

Two genera that were found in the Reserve were Andromma and Rhaeboctesis. Andromma are commonly found in association with ants and termites. Liocranids were found in all habitat types except mopane woodland (habitat type 5) and occurred in 18% of all sites sampled. The genera sampled from the Reserve are distributed in the following Afrotropical regions: Andromma: Ivory Coast, Cameroon, Ethiopia, Kenya, Zaire, Burundi and South Africa; Rhaeboctesis: Namibia, South Africa (Dippenaar-Schoeman & Jocqué 1997).

Family LYCOSIDAE (wolf spiders)
The Lycosidae are represented by 96 genera and more than 3 000 species. The Afrotropical Region has a rich fauna with 51 genera in seven subfamilies (Dippenaar-Schoeman & Jocqué 1997). Lycosids are wandering spiders usually found on the ground but with some species occurring on plants. Most species hunt during the day, but some of the larger species are nocturnal (e.g. *Lycosa*) (Leroy & Leroy 2000). Lycosids have a very characteristic eye pattern, the eyes are arranged in three rows (4:2:2). The anterior four eyes are very small and either straight or slightly procurred, the two larger posterior medians are situated on the vertical front of the carapace; and the smaller posterior lateral eyes are above and to the sides of the head (Dippenaar-Schoeman & Jocqué 1997). The abdomen is oval and has brown, orange, grey and black chevron patterns (Preston-Mafham & Preston-Mafham 1984; Filmer 1991).

The genera sampled from the Reserve included: *Evippomma, Lycosa, Pardosa, Trabea, Zenonina* and seven undetermined species. *Pardosa* are commonly found on the soil surface as well as on plants and could play an important role in integrated pest control (Dippenaar-Schoeman & Jocqué 1997). *Pardosa* are smaller members of the family and are creamy brown to black (Filmer 1991). Some species of *Pardosa* are semi aquatic and are frequently encountered on the banks or stony beds of rivers and ponds and run with great agility on the surface of the water. Members of *Lycosa* are known as burrowing wolf spiders, living in silk lined burrows. They are pale cream in colour, with chevrons on the abdomen. Their chelicerae are red and are displayed when they are threatened (Filmer 1991). The genus *Zenonina* is...
characterised by a triangular abdomen and frequently has a white patch above the spinnerets. The setae on the body surface are replaced by iridescent scales (Dippenaar-Schoeman & Jocqué 1997). Lycosids were found in all habitat types, occurring in 75% of the sites sampled.

The genera sampled from the Reserve are found in the following Afrotropical regions:

**Evippomma**: Burkina, Faso, Senegal, Tanzania, Ethiopia, Sudan, Southern Africa; **Lycosa**: Sierra Leone, Ivory Coast, Chad, Zaire, South Africa, Madagascar, St. Helena; **Pardosa**: throughout the Afrotropical region; **Trabea**: Zaire, Tanzania, Malawi, South Africa; **Zenonina**: Ethiopia, Angola, Namibia, South Africa (Dippenaar-Schoeman & Jocqué 1997).

**Family MITURGIDAE (forest floor and sac spiders)**

The Miturgidae have 18 genera of which 11 are known from the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Miturgids are free-living spiders commonly found on the forest floor. Only members of the subfamily Machadoniinae occur in our Region and they form an essential part of the spider fauna in South African forests (Dippenaar-Schoeman & Jocqué 1997). This group includes spiders with both two and three tarsal claws, as well as those without a cribellum. They have short robust legs (Filmer 1991). The carapace shows bands of colour and the abdomen varied faint markings from spots to chevrons (Filmer 1991; Dippenaar-Schoeman & Jocqué 1997).

The two genera sampled from the Reserve included *Cheiracanthium* and *Cheiramiona*. Members of *Cheiracanthium* are known as sac spiders owing to the sac-like retreats that they construct on vegetation. *Cheiracanthium* plays an important role in agroecosystems throughout the world (Dippenaar-Schoeman & Jocqué 1997). They are aggressive feeders and are frequently found in houses where they construct their silk retreats in folds in fabric. This genus includes a number of medically important species (Prins & Le Roux 1986). The bite of *Cheiracanthium* spp. is not very painful and often the victim is not even aware of being bitten. The venom is cytotoxic, and the area around the bite may become inflamed and swollen. An irregular lesion with a central haemorrhagic vesicle develops. Sloughing of dead tissue in the centre may leave an ulcerating wound. The bite may also produce symptoms similar to tick-bite fever 2 - 3 days after delivery of the bite. The lesion takes two weeks to heal (Prins & Le Roux 1986).

Miturgids were found in all habitat types and were widely distributed throughout the Reserve occurring in 82% of sites sampled. The *Cheiracanthium* genus is found throughout the Afrotropical Region while the *Cheiramiona* genus is endemic to South Africa (Dippenaar-Schoeman & Jocqué 1997).

**Family NESTICIDAE (scaffold-web spiders)**
The Nesticidae are a small family represented by seven genera, two of which occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Nesticids resemble and are closely related to Theridiidae but have more robust legs (Filmer 1991). They also use viscid silk to wrap their prey, suggesting that the two families are sister groups. They are very small to medium spiders (2 - 6 mm). Their first pair of legs is significantly longer than the other three pairs. The abdomen is greyish and pale yellow-white and in some species has short fluffy hairs (Dippenaar-Schoeman & Jocqué 1997).

Only one species from an undetermined genus was found in the Reserve. This species was not very widely distributed. It was found exclusively in habitat type 3 and was collected at only three sites. Genera within this family occur in Tanzania, Zaïre, Southern Africa, Seychelles, St. Helena and São Tomé (Dippenaar-Schoeman & Jocqué 1997).

Family OONOPIDAE (dwarf six-eyed spiders)
The Oonopidae, represented by 54 genera and about 267 species, are widely distributed in the tropics. Two subfamilies occur in the Afrotropical Region which includes 26 genera (Dippenaar-Schoeman & Jocqué 1997). Oonopids are nocturnal, ground-dwelling hunters that actively pursue their prey. They occur in a variety of habitats such as dry duneland, forested areas, buildings, bird's and termite nests and the webs of other spiders. During the day they hide under stones and plant debris, humus and leaf litter. Some oonopids are found in association with dry material, for example hay sheds (Dippenaar-Schoeman & Jocqué 1997). They even occur in dry insect collections where they probably prey on mites. Oonopids either have soft abdomens (subfamily: Oonopinae) covered in fine, pale hairs or abdomens that are covered with a hard shield or scutum (subfamily: Gamasomorphinae) (Filmer 1991).

The two species of oonopids that were found in the Reserve included: a Gamasomorpha sp. and an unidentified Oonopidae sp. Species from the subfamily Gamasomorphinae are usually small armoured oonopids with two chitinous scutes or shields covering the dorsal and ventral sides of the abdomen. The eyes are all light in colour and arranged in a compact group (Filmer 1991). Oonopids were found in three habitat types (3, 4 and 5) and were sampled from three sites. The Gamasomorpha genus occurs in the following Afrotropical regions: Kenya, Tanzania, South Africa, Seychelles, Mauritius, Fernando Poo, São Tomé and St. Helena (Dippenaar-Schoeman & Jocqué 1997).

Family OXYOPIDAE (lynx spiders)
Oxyopids are a family comprised of nine genera, four of which are known to the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Oxyopids are mainly plant dwelling spiders commonly found on grass, shrubs and trees. They are also known as lynx spiders because of the manner in which prey is hunted (Preston-Mafham & Preston-Mafham 1984). Oxyopids
hunt both by day and night and have good vision which enables them to quickly detect prey. They actively search for prey on plants by leaping from leaf to leaf. Prey is caught with the legs, and often by jumping a few centimetres or more into the air to seize a passing insect or by executing small jumps in pursuit of prey flying over plants. Oxyopids feed on moths of the families Noctuididae, Geometridae and Pyralidae, as well on a wide range of agricultural pests in agroecosystems (Riechert 1984; Dippenaar-Schoeman & Jocqué 1997). Oxyopids are generally recognised by having long spines that stand out at a 90° angle to the leg surface. They also have a high angular carapace that is flattened in the front with a wide clypeus and a distinctive hexagonal eye pattern. The abdomen tapers to a point (Dippenaar-Schoeman & Jocqué 1997).

The three genera of oxyopids sampled here were *Hamataliwa*, *Oxyopes* and *Peucetia*. Members of *Peucetia*, with their bright green colour, usually occur on green foliage, resembling the colour of the host plant. *Peucetia* is able to change colour to blend in with the colour of the plant on which it occurs (Dippenaar-Schoeman & Jocqué 1997). *Oxyopes* and *Hamataliwa* are smaller in size than *Peucetia*. The *Oxyopes* are common on plants and are usually inactive at night, hanging from a dragline attached to the underside of a leaf. They vary in colour from yellow-green to dull brown. *Hamataliwa* is a drab brown colour, but it is easily recognised as a member of the family by its typical spines, and as a member of the genus by little tufts of hair growing out above the eyes (Filmer 1991). Oxyopids were very widely distributed in the Reserve, occurring in all habitat types and sites sampled.

The genera sampled from the Reserve occur in the following Afrotropical regions: *Hamataliwa*: Senegal, Niger, East Africa, Zaire, Namibia, South Africa; *Oxyopes*: throughout the Afrotropical region; *Peucetia*: throughout the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997).

**Family PALPIMANIDAE (palp-footed spiders)**

The Palpimanidae are represented by 13 genera, ten of which are known from the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Palpimanids are slow moving spiders. Most species are ground dwelling and easily collected in pitfall traps. They are found during the day in small, irregular sac-like retreats under stones. They have a sclerotised carapace, sub-oval in outline. The carapace and legs are red in colour. The abdomen is ovate, with the cuticle leathery and the epigastic region sclerotised, forming a scute that circles the peduncle (Filmer 1991). When walking the greatly enlarged and armoured front legs are held up in the air. The tibiae, metatarsi and tarsi bear thick prolateral scopulae composed of spade shaped setae. Some of the larger palpimanids may prey on some trap door spiders. In Southern Africa, palpimanids occupy a wide variety of habitats, from extremely arid regions in Namibia to densely forested areas (Dippenaar-Schoeman & Jocqué 1997).
Two genera which were found in the Reserve included *Diaphorocellus* and *Ikuma*. *Diaphorocellus* usually has a purplish abdomen with light spots on the dorsal aspect. The posterior median eyes are triangular and subcontiguous (Filmer 1991). *Ikuma* are slow moving nocturnal hunters, preying on insects and other spiders (Leroy & Leroy 2000). Their posterior median eyes are round and widely separated (Filmer 1991). During the day they are founds under rocks in retreats of sticky silk. The palpimanids were found in all habitat types except habitat type 1 and occurred in 20% of all sites sampled.

The genera sampled from the Reserve are distributed in the following Afrotropical regions: *Diaphorocellus*: Namibia, South Africa; *Ikuma*: Namibia, South Africa (Dippenaar-Schoeman & Jocque 1997). These genera are endemic to southern Africa.

**Family PHILODROMIDAE (small wandering crab spiders)**

The Philodromidae are represented by 30 genera, eight of which occur in the Afrotropical Region (Dippenaar-Schoeman & Jocque 1997). Philodromids are free-living hunters commonly found on plants (Preston-Mafham & Preston-Mafham 1984; Leroy & Leroy 2000). Their movements are erratic and using their claw tufts and scopulae they are able to move around swiftly. In general philodromids have slightly dorsal-ventrally flattened bodies with slender, laterigrade legs and claw tufts are present. Most species have an elongated to oval abdomen, often with chevron type markings. There are teeth on the promargin of the chelicerae and the eyes are positioned in two recurved rows (Dippenaar-Schoeman & Jocque 1997).

Five genera were found in Makalali these include the *Gephyrota†‡*, *Hirriusa*, *Philodromus*, *Tibellus* and *Suemus*. *Hirriusa* spp. live on the soil surface and owing to their reddish brown colour, blend in with their surroundings. Members of *Hirriusa* often occur in high numbers in areas infested by harvester termites. Members of *Tibellus* are plant-dwelling, commonly found on tall bushes and grass. Their elongated, straw-coloured bodies, with dark longitudinal lines, as well as their posture, render them inconspicuous in dry grass. *Philodromus* occur on tree trunks, in low bushes and herbs. They are grey to brownish-yellow in colour and move about rapidly on plants, usually capturing prey by lying in ambush with legs extended (Dippenaar-Schoeman & Jocque 1997).

Philodromids were widely distributed in the Reserve, occurring in all habitat types and 90% of sites sampled. The genera found in the Reserve are distributed in the following Afrotropical regions: *Gephyrota*: Ivory Coast, Cameroon, South Africa; *Hirriusa*: Namibia, South Africa; *Philodromus*: Niger, East Africa, Sudan, Zaire, Namibia, South Africa, Bioko (part of Equatorial Guinea), St. Helena; *Tibellus*: throughout the savanna regions but absent from Madagascar; *Suemus*: Sierra Leone, East Africa, South Africa (Dippenaar-Schoeman & Jocque 1997).
Family **PHOLCIDAE** *(daddy-long-leg spiders)*

The Pholcids are a fairly large family comprising 39 genera and about 500 species worldwide. The Afrotropical Region has 13 genera from 5 subfamilies (Dippenaar-Schoeman & Jocqué 1997). They live in tangled spacewebs consisting of different configurations. Some are irregular with long threads criss-crossing in an irregular fashion, or the centre of the web consists of a large, more compactly woven sheet, with a network of irregular threads above and below (Filmer 1991). Pholcids characteristically vibrate the web rapidly when disturbed. The female carries the egg sac with her chelicerae. Several species are widely distributed and are commonly found in human habitations (Preston-Mafham & Preston-Mafham 1984). These spiders are delicate with very thin long legs (Dippenaar-Schoeman & Jocqué 1997; Leroy & Leroy 2000).

The two genera sampled in the Reserve were *Smeringopus* and *Spermophora*. *Smeringopus* have a cylindrical abdomen with a chevron pattern. *Spermophora* has a more globular abdomen (Filmer 1991). The eye pattern of *Smeringopus* is distinct. There are two sets each of three contiguous eyes, on either side of the carapace, raised on slight tubercles, with two smaller anterior median eyes in the centre front of the carapace. In *Spermophora* the anterior median eyes are absent (Filmer 1991; Dippenaar-Schoeman & Jocqué 1997).

Pholcids were found in all habitat types but occurred at only one site in each of the different habitat types. The genus *Smeringopus* is found throughout the Afrotropical Region including São Tomé and Madagascar and *Spermophora* is found in Kenya, Tanzania, Zaire, Congo Republic, South Africa, Comoros and Madagascar (Dippenaar-Schoeman & Jocqué 1997).

Family **PISAURIDAE** *(nursery-web and fishing spiders)*

The Pisaurididae are a large family and 32 of the 54 genera occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Pisaurids have diverse life-styles, some live in webs and others are free-living hunters. They have slender bodies and long legs (Preston-Mafham & Preston-Mafham 1984 & Leroy & Leroy 2000). The elongated abdomen shows symmetrical patterns of black on rufous-brown to grey background. The long legs have numerous spines. There are three claws on each tarsi and a colulus is present. Pisaurid females carry their eggs in their chelicerae. Just before the young emerge, the female constructs a framework of silk, known as a nursery web, in which the eggs are deposited. After emerging from the egg-sac the young remain in the nursery until dispersal commences (Dippenaar-Schoeman & Jocqué 1997).

The four genera that were sampled from Makalali were *Chiasmopes, Cispius, Perenuthis* and *Thalassius*. *Cispius* live on leaves and make a small retreat. They are active hunters that pursue their prey in leaps and bounds across the substrate (Filmer 1991). They
are commonly found in grasslands and open forests. *Thalassius* spp. are fish-eating spiders, and inhabit the fringes of freshwater pools. They can walk well on water as well as on land. The front legs are used in a sensory capacity much like the antennae of insects that are held in the air while the hind legs are dragged along. They hunt on the surface of the water, preying only on small fish, tadpoles, freshwater shrimps, insects and small toads. They dive into the water to grab their prey (Preston-Mafham & Preston-Mafham 1984; Filmer 1991). Pisaurids were widely distributed in the Reserve, occurring in all habitat types and 98% of sites sampled.

The genera sampled from the Reserve are distributed in the following Afrotropical regions: *Chiasmopes*: East, Central Africa, Namibia, South Africa; *Cispius*: throughout the Afrotropical region; *Perenethis*: East, Central Africa, Namibia, South Africa; *Thalassius*: throughout the Afrotropical Region including Madagascar (Dippenaar-Schoeman & Jocqué 1997).

Family **PRODIDOMIDAE** (long-spinnered ground spiders)

The Prodidiomidae are represented by 27 genera of which 12 occur in the Afrotropical Region. Three subfamilies are recognised, two of which occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Very little is known about the behaviour of prodidomids. They are free-living, nocturnal ground-dwellers, hiding during the day under stones or debris on the ground. They are more commonly found in the warm, dry regions of the Afrotropical Region. They are generally very small to medium-sized (1.5 - 9 mm) with two claws and eight eyes. Their anterior spinnerets are further forward than gnaphosids and they have gland spigots bearing long plumose setae (Dippenaar-Schoeman & Jocqué 1997).

Two genera, *Theuma* and *Prodidomus*, were found in the Reserve. Some species of *Prodidomus* have been found to be associated with ants (Dippenaar-Schoeman & Jocqué 1997). Prodidomids were found in all habitat types except type 3 and occurred at 30% of all sites sampled. The genera sampled from the Reserve are distributed in the following Afrotropical regions: *Theuma*: Namibia, South Africa; and *Prodidomus*: Guinea-Bissau, Senegal, East, Central and southern Africa, Ascension (Dippenaar-Schoeman & Jocqué 1997).

Family **SALTICIDAE** (jumping spiders)

This is the largest spider family comprising more than 5000 species worldwide. The Afrotropical Region has a rich fauna that includes 111 genera (Dippenaar-Schoeman & Jocqué 1997). Salticids are diurnal, cursorial hunting spiders with well-developed vision. With their large eyes and complex retinas they have unique resolution abilities, unparalleled in animals of similar size. Generally males have ornate pedipalps and all have a squarish
chephalothorax that is as large or larger than the abdomen. The anterior median eyes are larger than the remaining eyes. Most salticids do not spin a capture web or use silk to catch prey. Silk is only used to build sac-like retreats in which to moult, oviposit and sometimes mate, or which they occupy during periods of inactivity. The retreats are small, made of densely woven silk and attached to various substrates (Preston-Mafham & Preston-Mafham 1984; Dippenaar-Schoeman & Jocqué 1997; Leroy & Leroy 2000).

Salticids made up a large proportion (18% - 839 individuals) of spiders sampled in the Reserve and were also widely distributed, occurring in all habitat types and all sites. The 14 genera sampled from the Reserve included Aelurillus, Baryphus, Blanor, Cosmophasis, Heliophanus, Hyllus, Langona, Myrmarachne, Natta, Portia, Rhene, Stenaelurillus, Thyene, Thyenula*.

The Portia spp. belongs to the subfamily Spartaeinine and these spiders are renowned for their hunting skills. Prey may be caught outside the web during hunting raids, or in the web of the prey itself, which is stalked by means of aggressive mimicry when the salticid imitates the signal emitted by males of the prey. They generally prey on other spiders and have the ability to move over cribellate and ecribellate silk. (Dippenaar-Schoeman & Jocqué 1997). The males of this genus are referred to as dandy because of its elaborate pedipalps and black hairs on its body and upper legs (Filmer 1991).

Myrmarachne is a large genus comprising 106 species that resemble ants, both in behaviour and morphology. The spiders do not prey on ants but the resemblance affords these spiders a measure of protection. These salticids have rather unique abilities, e.g. they are very efficient in catching moths and some eat the eggs of other spiders (Dippenaar-Schoeman & Jocqué 1997).

The members of the Cosmophasis genus are behavioural mimics that exhibit aggressive mimicry. They have been observed mimicking Camponotus ants in the sand dunes of the Namibia desert (Dippenaar-Schoeman & Jocqué 1997).

The genera sampled from the Reserve occur in the following Afrotropical regions: Aelurillus: West Africa, Ethiopia, Tanzania, Sudan, Chad, South Africa, Yemen; Baryphus: throughout the Afrotropical Region including São Tomé; Blanor: Kenya, Zaïre, Zimbabwe, South Africa, Yemen, Cape Verde; Cosmophasis: West Africa, Ethiopia, Sudan, Zaïre, Namibia, South Africa, Bioko; Heliophanus: West, East and southern Africa, Yemen, Seychelles; Hyllus: throughout Afrotropical Region including Madagascar, Seychelles, Comoros, Yemen; Langona: throughout the Afrotropical region; Myrmarachne: throughout the Afrotropical Region including most islands, Yemen; Natta: West and East Africa, Zaïre, Mozambique, South Africa, Madagascar; Portia: throughout the Afrotropical Region including Madagascar; Rhene: Senegal, Guinea, Ethiopia, South Africa; Stenaelurillus: Senegal, East Africa, Zaïre, South Africa; Thyene: throughout the Afrotropical Region
including Madagascar, Annobon, São Tomé, Yemen; *Thyenula*: endemic to South Africa (Dippenaar-Schoeman & Jocqué 1997).

**Family SCYTODIDAE (spitting spiders)**

The Scytodidae are represented by a single genus, *Scytodes*, which includes 56 Afrotropical species (Dippenaar-Schoeman & Jocqué 1997). Scytodids are nocturnal, cursorial spiders that have a specialised way of catching prey. They are the only spiders known to possess prosomal glands that produce silk (Preston-Mafham & Preston-Mafham 1984). These enormous, specialised glands consist of two parts: an anterior part that produces venom and a posterior part that synthesises gluey silk. The gluey silk is fibrous glycoprotein. Before being squirted, the fibres are packed in paracrystalline form in the apical part of the glandular cells. Rapid contraction of the carapace muscles squirts a mixture of venom and gluey silk from the chelicerae up to a distance of 1.5 - 2.0 cm. Their prey is glued to the substrate and the contact with the venom results in paralysis (Filmer 1991; Dippenaar-Schoeman & Jocqué 1997).

The carapace is domed in the thoracic region, sloping downwards towards the anterior aspect. They have six eyes arranged in three well-separated pairs. The colour of the different species varies from pale yellow to dark brown, with a series of dark symmetrical patterns on the dorsal side. The legs are long and delicate (Dippenaar-Schoeman & Jocqué 1997; Leroy & Leroy 2000).

Only one genus, *Scytodes*, was found in the Reserve. *Scytodes* spp. are cosmopolitan in their distribution and are very common in houses. The genus is found throughout the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Scytodids were not very abundant in the Reserve. They were found in all habitat types except type 1 and occurred at seven sites.

**Family SEGESTRIIDAE (six-eyed tunnel spiders)**

The Segestriidae occur worldwide and are represented by four genera. Two genera are known from the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Segestriids typically spin silk-lined radiating tube-webs in which they reside permanently. The webs are made in crevices in walls, rocks, fallen tree trunks, bark on trees and in the soil. The webs are closed at the bottom and consist of a tube with an open entrance from which a dozen dry silk threads, known as trip-lines, radiate outwards (Dippenaar-Schoeman & Jocqué 1997). Segestriids are nocturnal and can be observed in the entrance to their tubewebs at night.

They have six eyes closely grouped in the centre front of the chephalothorax that is longer than it is wide and generally dark brown. The abdomen is bulbous and tends to droop to one side. The third pair of legs is directed forwards and not backwards (Preston-Mafham & Preston-Mafham 1984).
One genus, *Ariadna*, was sampled from the Reserve. *Ariadna* line the opening of their tube-web with a small collar of regular white silk. The spider waits in the entrance of the tube, with six legs stretched forwards. Vibrations transmitted to the spider via trip-lines betray the presence of prey. Prey is seized and instantly pulled into the tube (Dippenaar-Schoeman & Jocqué 1997; Filmer 1991). Occurrence of segestriids was limited to habitat type 5 (mopane woodland) and one site. This genus is found throughout the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997).

**Family SELENOPIDAE (wall crab spiders or “flatties”)**

The Selenopidae are a family represented by four genera and about 200 species. The family is well represented in the Afrotropical Region where all four genera occur (Dippenaar-Schoeman & Jocqué 1997). Selenopids are free-living, agile spiders found on rocks, walls and tree trunks. They have extremely flattened bodies with legs that are spread out in a crab-like position. Their flattened bodies enable them to move into narrow crevices (Preston-Mafham & Preston-Mafham 1984; Leroy & Leroy 2000). They dart sideways for cover at an astonishing speed when disturbed. The eye pattern is 6:2 with six eyes in the anterior row and two larger eyes in the posterior row. Selenopids are among the most common spiders encountered in houses where they live on the walls. When disturbed they disappear under wall hangings or into crevices. Their round flat papery egg-sacs are attached to wooden beams stones or bark (Dippenaar-Schoeman & Jocqué 1997).

Two genera were sampled here, the *Anyphops* and *Selenops*. In *Anyphops* that anterior row of eyes is recurved. In *Selenops* the anterior eye row is straight (Filmer 1991). Interestingly, they were not found in any of the sites sampled but were collected as additional samples around the Reserve. The genera sampled from the Reserve are found in the following Afrotropical regions: *Anyphops*: Cameroon, Somalia, Central and southern Africa; *Selenops*: throughout the Afrotropical Region including Comoros, Seychelles (Dippenaar-Schoeman & Jocqué 1997).

**Family SICARIIDAE (six-eyed spiders)**

This family is represented by two genera, *Loxosceles* and *Sicarius*. Both genera occur in the Afrotropical Region and are represented by about 21 species (Dippenaar-Schoeman & Jocqué 1997). Both genera are ground dwelling, wandering spiders. They are six-eyed spiders with flattened bodies and thickish legs for its size. The legs are extended sideways and held close to the substrate. The eyes are in three pairs and set on the front of the flattened carapace (Preston-Mafham & Preston-Mafham 1984; Leroy & Leroy 2000).

Only the *Loxosceles* was found here and was restricted to a single site. *Loxosceles* are generally found under rocks, logs and bark of trees, in old termite nests or rubble. Members of
this genus have cytotoxic, neurotoxic and haemotoxic venom (Preston-Mafham & Preston-Mafham 1984). Most bites to humans are inflicted when the victim is asleep and are not usually painful. After about two hours a lesion with a dusky centre develops. During the next few days a widespread, swollen often vesicular or bullous lesion develops. The oedema subsides on about the fourth day, leaving an ulcerated wound that penetrates the entire depth of the dermis. Secondary infection frequently occurs and the resulting tissue damage may result in disfiguring scars (Prins & Le Roux 1986). The genus was limited to a single site in habitat type 4. The genus sampled from the Reserve is found throughout the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997).

Family **SPARASSIDAE** (large wandering crab spiders)

The Sparassidae are a large family comprising 83 genera, 34 of which are known from the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Sparassids are free-living, nocturnal, wandering spiders with diverse life-styles. They do not build webs, only silk retreats. When disturbed they raise their front legs in warning (Filmer 1991). Most of the species are large. Most genera are covered with a fine pile of light straw-grey to brown hairs. The carapace is broader than it is long. The clypeus shows a white band (moustache) and the eye pattern is in two rows, with the anterior laterals often the largest. They have long robust legs, turned outwards in crab-like fashion (Preston-Mafham & Preston-Mafham 1984; Dippenaar-Schoeman & Jocqué 1997).

Three genera were sampled from the Reserve, *Olios*; *Panaretella*; and *Pseudomicrommata*. *Olios*, are small and yellow with black chelicerae and straw-brown legs (Filmer 1991). They build an oval retreat in the form of a finely webbed sac firmly attached to the underside of a stone or between two or three leaves fastened together with silk. All species of *Panaretella* are small in size, yellowish in colour and construct their silk retreats between two leaves held together with silk bands (Dippenaar-Schoeman & Jocqué 1997). *Pseudomicrommata* lives in the grassland and is distinguished from other members of the family by having a well-defined red or reddish-brown band down the body. Some species may be green in colour (Filmer 1991). Sparassids were widely distributed in the Reserve, occurring in all habitat types and 80% of all sites sampled.

The genera sampled from the Reserve are found in the following Afrotropical regions: *Olios*: throughout the Afrotropical region; *Panaretella*: South Africa; *Pseudomicrommata*: Ethiopia and South Africa (Dippenaar-Schoeman & Jocqué 1997).

Family **TETRAGNATHIDAE** (long-jawed spiders)

The Tetragnathidae are represented by 50 genera in several subfamilies. The Afrotropical Region has 22 genera in five subfamilies including both diurnal and nocturnal species ranging
in length from 5-30 mm (Dippenaar-Schoeman & Jocqué 1997). Tetragnathids construct orb-webs and the behaviour and construction of these orb-webs varies between subfamilies (Preston-Mafham & Preston-Mafham 1984; Leroy & Leroy 2000).

Two genera were found in the Reserve, *Leucauge* (silver marsh spiders) and *Nephila* (golden orb spiders). The *Nephila* species was widely distributed throughout the park while the *Leucauge* spp. was more restricted.

*Leucauge* spp. have a remarkable silvery abdomen with a pattern of red, green and gold markings. They spin large vertical and horizontal webs in vegetation in damp places such as marshes or rainforests (Preston-Mafham & Preston-Mafham 1984; Filmer 1991).

The *Nephila* is large and impressive. They build large yellow orb-webs in woodlands, grasslands and gardens. The web is usually supported between two trees and can span enormous spaces, metres wide, about 1.5 metres or more from the ground. The female is almost entirely black and the first, second and fourth pairs of legs have a brush of bristles on the tibia. The abdomen is elongated (long oval) and is yellow with the posterior end black or blue with yellow speckles infusing forward into the yellow. Kleptoparasites like the dewdrop spiders of the genus *Argyrodes* (family Theridiidae) often inhabit the webs of *Nephila's* and they steal prey from the orb-webs of their hosts (Preston-Mafham & Preston-Mafham 1984; Filmer 1991; Leroy & Leroy 2000).

Tetragnathids were not very numerous (76 individuals) and were found in all habitat types and 30% of all sites surveyed. Both genera sampled from the Reserve occur throughout the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997).

Family **THERIDIIDAE** (comb-footed spiders)

Theridiids are one of the larger spider families represented by 62 genera with over 2 500 species so far described (Preston-Mafham & Preston-Mafham 1984). The Afrotropical Region has 27 genera (Dippenaar-Schoeman & Jocqué 1997). They are small to medium sized spiders with a globular abdomen and long legs of which the third pair is the shortest (Dippenaar-Schoeman & Jocqué 1997). Theridiids have diverse life-styles. Most genera construct three dimensional, untidy-looking space-webs of different shapes (Preston-Mafham & Preston-Mafham 1984). Some webs enable the spider to catch flying insects and consist of criss-cross threads or sheet platforms with viscid threads on the outside, while in other webs the viscid threads are lightly attached to the substrate. The threads break easily and prey which is glued to these threads become more entangled while being reeled in. Some theridiids build special retreats inside or outside the frame and use plant material or soil particles to camouflage the web. Other theridiids construct regular webs or the webs can be reduced or absent. Theridiids wrap their prey in viscid silk using combs on tarsi IV. This technique is unique to this group. (Dippenaar-Schoeman & Jocqué 1997).
Several species of theridiids were found in the Reserve. Genera that were sampled included: *Achaearanea*; *Argyrodes*; *Dipoena*; *Enoplognatha*; *Episinus*; *Latrodectus*; *Phoroncidia*; *Theridion*, *Steatoda* and eight unknown genera.

Members of *Argyrodes* (dew drop spider) are kleptoparasites. They are small often sliver-coloured spiders that live on the webs of other spiders, being especially common in large orb-webs (Filmer 1991, Dippenaar-Schoeman & Jocqué 1997).

Members of *Enoplognatha* are medium sized to small spiders with pale-coloured oval abdomen, and a dorsum decorated with a pattern or white spots.

In *Episinus* the webs are reduced to only a few viscid threads attached to the substrate. These webs appear to be designed to catch pedestrian prey and are frequently spun between forked branches in trees.

*Latrodectus* is a fairly well known group because it is a species of medical importance (Filmer 1991). They are commonly known as black and brown widows spiders or button spiders. They are usually black or brown with some form of orange-red marking on the dorsal or ventral side of the abdomen. The venom of *Latrodectus* has been studied extensively and the venom of *L. indistinctus* (black widow) is 3 - 4 times more harmful than *L. geometricus* (brown widow) (Prins & Le Roux 1986).

Members of *Steatoda* (false button spiders) have shiny black abdomens, frequently decorated with white markings and resemble the venomous black widows. Its venom has properties similar to *Latrodectus* but the venom is less harmful to man (Filmer 1991).

*Theridion* (false button spiders) is the largest theridiid genus. They are smaller than true button spiders, often with a shiny, globular abdomen, and occur in a wide variety of habitats. They are found in bushes, on tree trunks, in the crevices in rocks and walls and frequently also in houses (Filmer 1991).

The Theridiids had a very wide distribution in the Reserve, occurring in all habitat types and 98% of all sites surveyed. The genera sampled from the Reserve are distributed in the following Afrotropical regions: *Achaearanea*: Gabon, Ivory Coast, South Africa, Comoros; *Argyrodes*: West and East Africa, Zaïre, Mozambique, South Africa, São Tomé, Reunion, St. Helena, Seychelles, Madagascar; *Dipoena*: West Africa, Kenya, Angola, South Africa, Seychelles, Madagascar; *Enoplognatha*: South Africa, St. Helena; *Episinus*: Cameroon, Equatorial Guinea, Ethiopia, Kenya, Zaïre, Angola, South Africa, Seychelles; *Latrodectus*: throughout the Afrotropical region; *Phoroncidia*: West Africa, Kenya, Tansania, South Africa, Madagascar; *Theridion*: throughout the Afrotropical Region including the islands; *Steatoda*: West and Central Africa, Ethiopia, Tanzania, South Africa, St. Helena, Bioko, Cape Verde (Dippenaar-Schoeman & Jocqué 1997).
Family **THERAPHOSIDAE** (baboon spiders)

The Theraphosidae are a large family that comprise 86 genera and about 612 species. Of the eight subfamilies, three, represented by 26 genera, occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). The theraphosids are known as baboon spiders in South Africa and occur in a variety of habitats. Most species live on the ground in silk-lined burrows. Baboon spiders are large and hairy, with heavy legs that retain the basal diameter throughout the length of the leg. They have large, hairy pedipalps that look like another pair of legs (Filmer 1991). They are similar to barychelids but have a distinct lobe on the anterior aspect of the maxillae. They have a wide clypeus and their eight eyes are arranged on an ocular protuberance on the front portion of the carapace, behind the clypeus. Some species have a horn on the carapace (Dippenaar-Schoeman & Jocqué 1997; Leroy & Leroy 2000).

Four genera, *Brachionopus*; *Ceratogyrus* (horned baboon spider); *Harpactirella* (lesser baboon spider) and *Pterinochilus* (golden-brown baboon spider), were found in the Reserve. *Ceratogyrus* is distinguished from *Harpactirella* and *Pterinochilus* by having a large horn in the centre of its carapace, sloping either forwards or backwards, depending on the species (Filmer 1991). Some members of *Ceratogyrus* are considered endangered. They are currently listed as Commercially Threatened in terms of the IUCN system (De Wet & Schoonbee 1991). *Harpactirella* are dark in colour and are slightly smaller than other genera in this family (Filmer 1991). Species of the subfamily harpactirinae are commonly found in dry acacia scrubland, grassland and savanna woodland (Dippenaar-Schoeman & Jocqué 1997). *Pterinochilus* may vary in colour from grey-yellow to bright orange (Filmer 1991).

The theraphosids were fairly widely distributed, occurring in all habitat types and 38% of all sites sampled. The genera sampled from the reserve occur in the following Afrotropical regions: *Brachionopus*: South Africa; *Ceratogyrus*: Southern Africa; *Harpactirella*: Southern Africa; *Pterinochilus*: East, Central and southern Africa (Dippenaar-Schoeman & Jocqué 1997).

Family **THOMISIDAE** (crab spiders)

Thomisids are represented by 160 genera and about 2000 species in seven subfamilies (Dippenaar-Schoeman & Jocqué 1997). Thomisids are wandering spiders found mainly on foliage (Preston-Mafham & Preston-Mafham 1984; & Leroy & Leroy 2000). They do not usually produce webs. They have lots their agility and have become semi-sedentary, excelling as ambushers ("sit-and-wait" predators; Leroy & Leroy 2000). Thomisids are commonly abundant in the field layer and they are mainly active during the day. They have strong bodies and robust front legs, enabling them to attack prey much larger than themselves. With their cryptic colouration, most species await their prey, usually on plants. They are able to see prey 20 cm away. They seize their prey, frequently from the air, when 0.5 - 1 cm away. Although
they have weak chelicerae they have extremely potent venom that enables them to attack prey
3 - 4 times bigger their own size (Dippenaar-Schoeman & Jocqué 1997).

The thomisids were abundant in this study and 15 genera were collected. Genera
included Diaea, Felsina, Heriaeus, Misumenops, Monaeses, Oxytate, Pherecydes† (including
a potentially new species), Runcinia, Simorcus, Smodicinus, Synema, Thomisops, Thomisus,
Tmarus and Xysticus.

Thomisids display an interesting range of adaptations to their habitats. Genera such as
Tmarus and Pherecydes, with their mottled brown and grey bodies decorated with tubercles,
are primarily found on bark, whereas Monaeses and Runcinia, with their elongated bodies,
occur on grass. Heriaeus spp. with their spiny appearance inhabit inflorescences. Xysticus
spp. With their predominantly brown colouration are soil dwellers whereas Thomisus spp. live
on flowers. Some species of Thomisus have the ability to change their colour to conform with
their background (Dippenaar-Schoeman & Jocqué 1997). Thomisids are very common on
plants and could play an important role in the natural control of pests (Dippenaar-Schoeman
& Jocqué 1997). Thomisids were very widely distributed in the Reserve, occurring in all
habitats types and 98% of all sites sampled.

The genera sampled from the Reserve occur in the following Afrotropical regions:
Diaea: throughout the Afrotropical Region including Yemen; Felsina: West Africa, Ruanda,
South Africa; Heriaeus: East Africa, Equatorial Guinea, Malawi, South Africa; Misumenops:
West Africa, Sudan, Zaïre, southern Africa, São Tomé, Cape Verde; Monaeses: throughout
the Afrotropical region; Oxytate: East, Central and southern Africa; Pherecydes: West Africa,
Tanzania, Zaïre, Namibia, South Africa; Runcinia: throughout the Afrotropical Region
including Madagascar and St. Helena; Simorcus: Ivory Coast, Guinea-Bissau, Malawi,
Mozambique, South Africa; Smodicinus: Sierra Leone, Ivory Coast, Zaïre, South Africa;
Synema: throughout the Afrotropical Region including Madagascar and Yemen; Thomisops:
throughout the Afrotropical region; Thomisus: throughout the Afrotropical Region including
Madagascar and Yemen; Tmarus: throughout the Afrotropical Region including the Comoros
and Yemen; Xysticus: throughout the Afrotropical Region including Madagascar and Yemen
(Dippenaar-Schoeman & Jocqué 1997).

Family ULOBORIDAE (lace orb-web spiders)
The Uloboridae are cosmopolitan in their distribution, attaining great diversities in tropical
and subtropical regions. The family comprises 19 genera in four subfamilies. Five of the
genera occur in the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Uloborids
characteristically spin orb-webs of cribellate silk, ranging from a section of an orb to a single
line.

Two genera, Miagrammopes and Uloborus, were sampled from the Reserve.
Miagrammopes (single-line web spiders) have a long and narrow carapace and a cylindrical abdomen which is truncated above the spinnerets. The eyes are arranged in two rows. The anterior eye row is reduced while the posterior eye row is recurved and widely spaced on the carapace. Uloborus (lace orb-web spiders) are characterised by its long front legs, rather humped abdomen and almost horizontal orb-web. It has a brush of coarse hairs on the tibiae of the first leg and hence its common name "feather-legged spider". They build webs in low bushes, between objects near the ground and are frequently found in and around buildings (Filmer 1991; Leroy & Leroy 2000).

The uloborids were found in all habitat types except type 5 (mopane woodland) and occurred at eight of the site sampled. They were absent from the mopane woodland habitat type. The genera sampled from the Reserve occur in the following Afrotropical regions: Miagrammopes: Ethiopia, Somalia, South Africa, Zanzibar, Mozambique, Rodriguez; Uloborus: throughout the Afrotropical Region including some cosmopolitan species (Dippenaar-Schoeman & Jocqué 1997).

Family ZODARIIDAE (armoured spiders)
The Zodariidae are a family represented by 54 genera in five subfamilies, four of which, represented by 24 genera, are known to the Afrotropical Region (Dippenaar-Schoeman & Jocqué 1997). Zodariids are characteristic of semi-arid habitats in Africa where they are active nocturnal hunters. Some species of zodariids specialise in ants and termites as prey. They are eight-eyed hunting spiders very diverse in general appearance. In some genera the epidermis of the carapace is thick and looks like armour (Filmer 1991). The legs are usually similar in length and thickness. The anterior spinnerets are usually the longest and are situated close together (Dippenaar-Schoeman & Jocqué 1997).

Five genera were found these included Caesetius*; Capheris; Cydrela; Diores and Ranops. Diores is diurnal and are specialist ant eaters. They live in ant colonies where they have easy access to their prey (Filmer 1991). They do not dig burrows but use silk and sand grains to build small retreats which resemble inverted igloos on the underside of stones. Some species of Cydrela make a tube-like burrow with a lid, like those of a trapdoor spider (Filmer 1991). Caesetius are adapted to living in the sand and if threatened can rapidly burrow head-first into the sand (Filmer 1991). Zodariids were found in all habitat types and 25% of all sites sampled.

The genera sampled at the Reserve occur in the following Afrotropical regions: Caesetius: is endemic to South Africa; Capheris: throughout the Afrotropical region; Cydrela: Tanzania, Zaire, Kenya, Southern Africa; Diores: Cameroon, East Africa, Zaire, southern Africa, Comoros, Madagascar; Ranops: Tanzania, southern Africa (Dippenaar-Schoeman & Jocqué 1997).
REFERENCES


### Appendix 3.3a: Jaccard’s similarity coefficient between different sites based on families shared between them. All values have been multiplied by 100 for ease of interpretation.

| Site | 1.1 | 1.2 | 1.3 | 1.4 | 1.5 | 1.6 | 1.7 | 1.8 | 1.9 | 2.0 | 2.1 | 2.2 | 2.3 | 2.4 | 2.5 | 2.6 | 2.7 | 2.8 | 3.1 | 3.2 | 3.3 | 3.4 | 3.5 | 3.6 | 3.7 | 3.8 | 4.1 | 4.2 | 4.3 | 4.4 | 4.5 | 4.6 | 4.7 | 4.8 | 5.1 | 5.2 | 5.3 | 5.4 | 5.5 | 5.6 | 5.7 | 5.8 |
|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1    | 61  | 62  | 63  | 64  | 65  | 66  | 67  | 68  | 69  | 70  | 71  | 72  | 73  | 74  | 75  | 76  | 77  | 78  | 79  | 80  | 81  | 82  | 83  | 84  | 85  | 86  | 87  | 88  | 89  | 90  | 91  | 92  | 93  | 94  | 95  | 96  | 97  | 98  | 99  | 100 |
| 2    | 62  | 63  | 64  | 65  | 66  | 67  | 68  | 69  | 70  | 71  | 72  | 73  | 74  | 75  | 76  | 77  | 78  | 79  | 80  | 81  | 82  | 83  | 84  | 85  | 86  | 87  | 88  | 89  | 90  | 91  | 92  | 93  | 94  | 95  | 96  | 97  | 98  | 99  | 100 |
| 3    | 63  | 64  | 65  | 66  | 67  | 68  | 69  | 70  | 71  | 72  | 73  | 74  | 75  | 76  | 77  | 78  | 79  | 80  | 81  | 82  | 83  | 84  | 85  | 86  | 87  | 88  | 89  | 90  | 91  | 92  | 93  | 94  | 95  | 96  | 97  | 98  | 99  | 100 |
### Appendix 3.3b: Jaccard’s similarity coefficient for the number of species shared between the sites. All values have been multiplied by 100 for ease of interpretation.

|   | 1.1 | 1.2 | 1.3 | 1.4 | 1.5 | 1.6 | 1.7 | 1.8 | 2.1 | 2.2 | 2.3 | 2.4 | 2.5 | 2.6 | 2.7 | 3.1 | 3.2 | 3.3 | 3.4 | 3.5 | 3.6 | 3.7 | 3.8 | 4.1 | 4.2 | 4.3 | 4.4 | 4.5 | 4.6 | 4.7 | 4.8 | 5.1 | 5.2 | 5.3 | 5.4 | 5.5 | 5.6 | 5.7 | 5.8 |
|---|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
Appendix 5.1: Plant community classification

Prior to this study (December 1998 to February 1999) students, under the supervision of David Druce of the University of Natal, Durban, undertook a vegetation analysis of the Reserve.

In addition to the ground survey of vegetation, 1:60 000 aerial photographs of the area surrounding and including the Greater Makalali Conservancy were used to distinguish habitat boundaries, roads and fences. These landmarks were traced and then scanned into the computer and saved as bitmap images. The images were imported into Idrisi separately using the import function for bitmap images. These images were then georeferenced to degrees using the resample function in Idrisi and a correctly referenced road map. This road map had been created by the Makalali research staff and students from the University of Natal, Durban, using a GPS (Garmin 12XL) and a mapping program called Cartalinx. These corrected maps were then joined to each other using the concat function in Idrisi. This produced a final image for the entire Reserve showing the boundaries of the vegetation types. The image was then exported to Cartalinx as a backdrop and the edges of the vegetation types digitised using the on-screen-digitising function in Cartalinx. Polygons were then built using these boundaries and classed into different habitat types based on visual characteristics of the aerial photographs.

The resulting habitat type map was ground-truthed by to determine the exact position of certain habitat boundaries. The ground-truthing also involved determining the areas where habitat types had changed since the aerial photographs had been taken in 1997. This included areas that had undergone bush-clearing and those areas which contained an abundance of *Colophospermum mopane* trees. These areas were included on the vegetation map by on-screen digitising.

The data collected from the transects was used to classify the vegetation types. The density of each tree species in each transect and the density of each species per hectare vegetation was determined using a computer program written by Mr B. Page of the University of Natal, Durban. This density calculations were then run through the CANOCO and TWINSPLAN analysis programmes.

TWINSPLAN (Two-way indicator species analysis) is a divisive method of classification that proceeds iteratively to divide existing groupings into two. In the current context it was used to classify tree species, producing an ordered two-way table of their occurrence. The program first constructs a classification of the sites, then uses this classification to obtain a classification of species according to their ecological preferences. Divisions in the classification are based on indicator and preferential species. Indicator or diagnostic species are those which occur in more than 80% of the sites of one group and less
than 20% of the sites of the other at that level of division (Hill 1979). Preferential species are those that occur in more than 20% of the sites and are twice as likely to occur in one group than the other at that level of division. The species and site classifications are then used together to produce an ordered two-way table that expresses the species synecological relations (Hill 1979).

The TWINSPAN program produces an extensive output consisting of the ordered two-way table of species and sites and associated information on the divisions that it performs. The output also highlights the indicator and preferential species for the two groups formed at each division, and provides eigen values for each division. The eigen values allows the researcher to assess how similar or dissimilar the two groups formed by the divisions are to each other. Eigen values range between 0 and 1, where low eigen values indicate a high degrees of similarity between groups and values close to 1 indicate a low degree of similarity between groups at that division.

Once the density data had been run through TWINSPAN, the habitat types were reclassified according to the results of this analysis. This allowed one to determine which of the polygons occurred within the same vegetation type. All transects occurring within the same vegetation type were grouped together and run through a population structure computer program designed by Mr B. Page. The results from this analysis determined the exact species composition, density and structure of each vegetation type. The results from all the programs were used to classify vegetation patch types according to the dominant and diagnostic species for that patch. The methods followed were recommended by Edwards (1983). The final vegetation map was compiled by D Druce, a MSc. student (6th year) of the University of Natal, Durban, who was also completing a study on millipede diversity in the Reserve.
Appendix 5.2: The vegetation types at Makalali Private Game Reserve.
Appendix 5.3: The vegetation density of (a) trees < 1 m and (b) trees > 2 m at Makalali Private Game Reserve.
Appendix 5.4: The (a) soil Zn content (range = 0.20 to 2.10), (b) pH (range = 3.99 to 7.35), (c) soil cation (range = 2.01 to 24.48), (d) soil moisture (range = 0.09 to 10.53), (e) soil temperature (range = 28.5 to 36.5) and (f) slope (range = 1.00 to 40.0) at Makalali Private Game Reserve.
Appendix 5.5: The (a) rock size (range = 0.00 to 50.00), (b) insect biomass (range = 0.02 to 100.36) from sweep samples, (c) leaf litter thickness (range = 0.63 to 3.00) and (d) aspect at Makalali Private Game Reserve.
Appendix 2.1: The species accumulation for (a) late summer, (b) autumn, (c) early summer and (d) mid summer.
Appendix 2.2: The species accumulation for (a) sweeping, (b) beating, (c) active searching and (d) pitfall traps.