IMPACTS OF WILDLIFE AND CATTLE GRAZING ON SPIDER (ARANEAE) BIODIVERSITY IN A HIGHLAND SAVANNA ECOSYSTEM, IN LAIKIPIA, CENTRAL KENYA

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Abstract

Spiders were sampled at Mpala Research Centre, Laikipia, Kenya by pitfall-trapping and sweep-netting from May 2001 to July 2002, at a Kenyan Long-term Exclosure Experiment. The aim was to establish species composition, checklist and examine spider responses to disturbances caused by cattle, megaherbivores (giraffe and elephants) and mesoherbivores (other ungulates) by looking at three levels of resolution, namely the overall community, guilds and individual species. This is the first controlled replicated experimental study on the effects on invertebrates (spiders) by different land uses (access by large herbivores).

A total of 10,487 individuals from 132 species belonging to 30 families were recorded. The family Salticidae had the highest number of species (24), followed by Gnaphosidae (20), Araneidae and Lycosidae (15 each), Theridiidae and Thomisidae (8 each) and Zodariidae (4). Most of the other families had fewer than 4 species. Throughout the study period, species not previously sampled emerged after rainfall peaks.

Exclosure treatments affected plant cover, spider diversity and total species mainly through the effects of cattle, whose presence significantly reduced relative vegetation cover. An increase in vegetation cover significantly increased the diversity, total species and species evenness of the overall spider community (total samples data set). Megaherbivores and mesoherbivores had no effects on overall spider diversity. Relative vegetation cover explained approximately 20-30 % of variation in community diversity, species richness and species evenness.

At the guild level of resolution, the exclosure treatments had no significant effects on diversity, species richness and species evenness of web builders, plant wanderers and ground wanderers. Plant wanderers were significantly and positively correlated with relative vegetation cover, which explained 17% of variation in their diversity. Six individual species responded strongly and in contrasting ways to the same environmental variables, indicating that this level was more sensitive to environmental changes than guilds or the overall spider community.

Spider diversity, relative vegetation cover and rainfall varied at a temporal scale of months and not at a spatial scale of hundreds of metres. Only species diversity and species richness from sweep-netting samples and total species from pitfall-trapping varied significantly at a spatial scale of hundreds of metres. Ordination analysis revealed that sweep-netting samples were a better indicator of grazing impacts than pitfall-trapping or combined samples and grouped to reflect cattle grazing, non-cattle grazing and to a small extent the control treatments. Other ordination analyses showed that only samples from sweep-netting and not from pitfall-trapping, were spatially partitioned at a scale of hundreds of metres.

This study concludes that the spider fauna of black cotton soil habitats is rich and useful for environmental monitoring and that monitoring of several individual species as indicator of grazing impacts in savanna could be useful and relatively easy.

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CHAPTER 1: GENERAL INTRODUCTION

Preface

This chapter introduces the savanna ecosystem, its uses and the existing management problems, and includes a review of past studies. It highlights the need for management activities that are compatible with the native biodiversity and introduces spiders as a taxon that may be used to help understand the ecological effects of cattle, wildlife and biodiversity. It includes a justification for the use of spiders as bio-indicators and introduces the study objectives and the rationale of the thesis.

Introduction

Savanna ecosystems are among the world's largest biomes and cover half of Africa's land surface (Scholes and Walker 1993). They form a large part of Africa's rangelands and are important to humans, wildlife and cattle. Most of their vegetation consists of woody layers dominated by *Acacia* spp. (Menault *et al.* 1985; Cole 1986). In Kenya, they cover an important portion of the country and humans use them in various ways, e.g. for fuel wood harvesting, game hunting, honey collecting, mining, other kinds of farming, pastoralism and tourism. Due to increasing human population density in sub-Saharan Africa, there is often overexploitation of these natural resources, increasing the pressure on native biodiversity, which is nevertheless poorly understood.

In Kenya the net gains of keeping livestock are reducing while those of wildlife are increasing (Young *et al*. 1998). For example, indigenous Kenyan wildlife is well adapted to live in savanna, where it is exploited for game meat and trophies, and used to promote tourism. On the other hand, cattle require higher cash and labour inputs to maintain high productivity. In order to come up with good management decisions that can enhance optimal productivity of these semi-arid ecosystems, there is need for more research work into these ecosystems. An understanding of how large mammalian herbivores, livestock and other indigenous biodiversity live and interact has therefore become more important (Young *et al*. 1998).

Substantial work has already been done on the ecology of both large and small vertebrates and the vegetation of savannas (e.g. Buss 1961; McNaughton 1983, 1994; Belsky 1984; Hatton and Smart 1984; Young and Lindsay 1988; Georgiadis and McNaughton 1990; Dublin 1995; McClanahan and Young 1996; Young *et al.* in press). However, few studies are available on the invertebrates of African savannas. Scientists have raised their concern over this lack of knowledge (e.g. Russell-Smith *et al.* 1987; Dippenaar-Schoeman *et al.* 1989; Russell-Smith 1999; Villet and van Noort 1999; Whitmore *et al.* 2001), because the invertebrates constitute the bulk of the biodiversity.

This study was part of Kenya Long-term Exclosure Experiment (KLEE), a Long-term multi-species vertebrate herbivore exclusion experiment in a semi-arid savanna ecosystem in Laikipia, Kenya (Young *et al.* 1998). KLEE is aimed at comparing the impacts of cattle and wildlife on various components of the savanna biome. The current study aimed at using a mega-diverse groups of invertebrates (spiders) as a way of better understanding these ecosystems and improving their management, and hence their productivity, while promoting the conservation of native biodiversity.

Justification

A research emphasis on spiders as a target group is justified on several grounds. First, very little is known about East African spiders and this is the first comprehensive survey on Kenyan savanna spiders. Second, systematic knowledge of this mega-diverse group of Africa although not sufficient can allow its use for inventory purposes. It is fairly easy to identify spiders at least to family using external morphological characters including that of genitalia where applicable. In addition, the availability of a world spider catalogue (Platnick 2002) and keys to the families of African spiders (Dippenaar-Schoeman and Jocqué 1997; Dippenaar-Schoeman 2002) make their identification easier. Third, spiders inhabit a large array of microhabitats ranging from the ground layer, to the tree layer. This makes them particularly suitable to integrate and evaluate activity by the different guilds of herbivores.

Fourth, since the response of spiders to the particular structure of the habitat is very fine-grained (see work by Gunnarsson 1988; Uetz 1991; Rypstra *et al.* 1999), it was expected that changes caused by different types of land use, including grazing, would be reflected in the composition of the spider fauna. Fifth, little is known about how spiders respond to land use policies. This study has undertaken to report their population and community responses to different forms of land use. The focus of the KLEE experiment (see below) is on cattle and wildlife. Sixth, little is known about the life histories of African spiders in general and Kenyan representatives of the group in particular (Russell-Smith *et al.* 1987). Finally, spider biodiversity is interesting in its own right, and worthy of protection and research.

Bio-indicators

The use of bio-indicators in land management has been well documented (e.g. Greenslade & Greenslade 1984; Cranston 1990; Noss 1990; Kremen 1992; Weaver 1995; McGeoch 1998; Kotze and Samways 1999a, b; Feinsinger 2001; Andersen *et al.* 2002; McGeoch *et al.* 2002). Samways (1994) and Feinsinger (2001) reported several factors that influence such a choice of a bio-indicator species among them including the goals in question and availability of resources.

Several groups of invertebrates have been used as bio-indicators in the past with success e.g. Villet and Capitao (1996) demonstrated the usefulness of cicadas as indicators of habitat and veld condition in South Africa; Majer (1983), Read and Andersen (2000), and Andersen *et al.* (2002) reported the importance of ants as bio-indicators in Australia land management while New (2000) reported on the limited bio-indicator value of ants; Andersen *et al.* (2001) reported the usefulness of grasshoppers as indicators of ecological disturbance related to human landuse; Armbrecht and Ulloa-Chacón (2003) wrote on fire ant *Wasmania auropunctata* (Roger) as good indicators of disturbance in tropical dry forest of Colombia; Kitching *et al.* (2000) reported that moths were useful indicators of environmental quality in Australian forests; Pollard and Yates (1993), New (1997) and Oostermeijer and Swaay (1998) demonstrated the usefulness of butterflies as bio-indicators while New (1998), Villa-Castillo and Wagner (2002) as well as Rainio and

Niemelä (2003) reported that ground beetles were important as bio-indicators but needed to be used with some degree of caution.

Spiders as bio-indicators

Spiders might also serve as good bio-indicators since they have several qualities that make them suitable for biodiversity and bio-monitoring studies (reviewed in Churchill 1997). They are abundant in nature (Wise 1993), easy to collect, found on many types of habitats. Some reproduce fairly quickly (less than one year) but although their lifecycles occur similar over time scales to the disturbance needed to be monitored, they do not track seasonal changes but do respond to sustained grazing pressure. Their webs have been used as indicators of environmental chemistry (Hose *et al.* 2002) and their growth has been used as an indicator of habitat quality (Vollrath 1988). Spiders play a role in regulation of insect and other invertebrate populations (Riechert 1974, Nyffeler & Benz 1987; Wise 1993). Spiders have been studied as indicators in Europe and America (reviewed in Coyle 1981; Clausen 1986; Churchill 1998). Other spider studies that relate to either land use or biodiversity have been reported on a worldwide basis (e.g. Jennings *et al.* 1988; Luff and Rushton 1989; Gibson *et al*. 1982, 1992; Wise 1993; Rinaldi and Forti 1997; Churchill and Arthur 1999; Downie *et al.* 1999; Nyffeler and Sunderland 2003). They have been used as bio-indicators of ecological change and land use impacts for sustainable management in tropical savannas (Churchill 1997, 1998).

Other studies related to use of spiders as indicators include that of Hatley and McMahon (1980); Clausen (1986); Rushton (1988); Wheater *et al.* 2000 and Hsieh *et al.* (2003) where their studies were conducted on habitats with differing degrees of disturbances. Maelfait and Hendrickx (1998) demonstrated the value of spiders as indicators of human related disturbances in central Belgium while Harris *et al*. (2003) demonstrated clearly that spiders are good indicators of grazing and burning above a certain intensity of grazing in Eucalypt forest in Australia. Elsewhere Vollrath (1988) reported the use of spider growth as indicator of habitat quality. A review of more studies about the usefulness of spiders as ecological indicators is reported in Skerl and Gillespie (1999).

Spiders have also been used significantly in agro-ecosystems (e.g. Carter and Rypstra (1995), reported the use of spider density as indicator of herbivore damage in soybean agro-ecosystem. Alderweireldt (1989) reported some work on ecology of spiders in maize fields in Italy while Jeanneret *et al.* (2003) reported diversity of spiders in agricultural landscapes of Switzerland. Mansour *et al.* (1983) conducted some studies on spider management in agro-ecosystems while Rypstra and Carter (1995) extensively reported communities of web spiders in soybean agro-ecosystems in America. Spiders have also been used for pest control in agro-ecosystems (see work by Nyffeler and Benz (1987), Wyss *et al.* (1995) as well as Marc and Canard (1997). Bishop and Riechert (1990) also reported how spiders colonize agro-ecosystems while Misra and Srivastava (1993) reported on spider diversity in rice fields. More work on spiders in agro-ecosystems includes spider guilds in crop farms (Uetz *et al.* 1999).

Influence of grazing on spider fauna not well known in tropical Africa except for some scarce studies e.g. Abrous-Kherbouche *et al.* 1997. Elsewhere, studies have been conducted on the impact of grazing in savanna ecosystems in Africa and some are reviewed in Skarpe (1991). A few such studies have been conducted in east Africa e.g. Woldu and Saleem (2000). There have been some studies in Africa on effects of grazing on invertebrates (e.g. Seymour (1998); Seymour & Dean (1999)). Other similar studies conducted include Rambo & Faeth (1998) on effects of mammals grazing on plant insect community structure. Abensperg-Traun *et al.* (1996) working on spiders and other invertebrates response to grazing disturbance in Australian woodland found that the abundance of Idiopidae and Lycosidae families of spiders were highest in moderately disturbed woodlands. Gibson *et al.* (1982) reported the effects of grazing on different assemblages of invertebrates. Curtis *et al.* (1990) found out that communities of spiders were negatively affected by grazing and trampling.

Compared to Europe and America, biodiversity work on African spiders is scarce and most of it is restricted to South Africa (e.g. Dippenaar-Schoeman *et al.* 1989, 1999a; van den Berg and Dippenaar-Schoeman 1991; van der Merwe *et al.* 1996; Whitmore *et al.* 2001, 2002a, b). Little studies have been conducted on savanna spiders in Africa with most of what is available being inventory oriented (see table 3.3) while only a few are based on general biology of spiders (e.g. Dippenaar-Schoeman & Leroy 1996). A few studies have been conducted in Central Africa (e.g. Blandin 1971; Blandin and Célérier 1981; Malaisse and Benoit 1979). Only few biodiversity related studies have been conducted in east Africa (e.g. Russell-Smith 1981, 1999; Russell-Smith *et al.* 1987; Scharff & Griswold 1996; Sørenson 2003, 2004). Some comprehensive studies in east Africa was by Scharff (1992), who reported on the distribution, endemism and diversity of Linyphiid spiders in east Africa. Recently, some studies were conducted in Tanzania on forest spiders (Sørenson 2003, 2004). Other work on diversity of Kenyan spiders is by Braunstein (1995) who reported some general biology of some savanna spiders. Pain (2002) and Pollard (2003) recently reported some little work on the behaviour and biology of jumping spider that feeds on blood sucking mosquitoes. The only other recent studies of Kenyan spiders are taxonomically based (e.g. by Warui and Jocqué 2002; Wesolowski and Jackson 2003). Most of other past studies in Kenya and east Africa are based on taxonomic work (reviewed in Dippenaar-Schoeman and Jocqué 1997).

Aims and Scope

The intention of this study was:

- To develop a checklist and establish the species composition of the spider fauna in the study area.
- To establish the effect of different large mammalian herbivore guilds on the spider species richness, species evenness and species diversity.
- To establish changes in relative vegetation cover and rainfall at the KLEE large mammalian herbivores plots and relate these to spider diversity, species evenness and species richness.
- To establish the variation in spider guild richness, evenness and diversity in relation to the KLEE plots.
- To explore the response of individual species' abundances to the KLEE large mammalian herbivore grazing treatments and also to relate it to changes in rainfall and relative vegetation cover.

- To establish the variation in spider fauna at a temporal scale of months and a spatial scale of hundreds of metres, and to relate this to changes in rainfall and relative vegetation cover changes.
- Establish the value of spiders as indicators of disturbance and link the study results to a feasible conservation and management strategy for the Laikipia ecosystem.

It is important to note that since the study was limited to spiders collected by sweep-netting and pitfall-trapping, the emphasis of the results is mainly on the effects of grazers and herbaceous browsers than on the effects of woody browsers such as elephants and giraffes, because no beating of vegetation was carried out.

CHAPTER 2: STUDY AREA AND SAMPLING METHODS

Preface

This chapter describes the study area and gives some geographical information. It also describes in detail the study design, and the spider and vegetation sampling methods. It highlights the advantages and limitations of the methods. In addition it also explains some statistical methods employed in the entire thesis.

Study area

The ecological study was conducted at Mpala Research Centre (MRC) adjacent to Mpala Ranch in the Laikipia District of central Kenya (Figure 2.1) from May 2001 to July 2002. Mpala Research Centre (0^o17'N, 37^o52'E) is located on 1200 ha of land and scientists have access to the 17000 ha Mpala farm. Sampling was conducted in habitats on black cotton soil, which has impeded drainage (Ahn and Geiger 1987; Taiti 1982). The altitude is 1750-1800 m above sea level and its rainfall averages 500-600 mm per year (Young *et al.* 1995, 1998). However, high precipitation (>1200 mm) was recorded in the 1997/98 seasons, while the average annual rainfall at MRC in 1999 and 2000 was about 400 mm (Paton and Ogada 2001).

Vegetation of study area

The vegetation of the black cotton soil is *Acacia drepanolobium* Sjøstedt bushed grassland (Young *et al.* 1998). The dominant tree, *A. drepanolobium*, accounts for >95% of the woody vegetation and the understorey is dominated by five species of grasses (Young *et al.* 1997, 1998). The black cotton soil ecosystem is adjacent to a different red soil ecosystem and shares wildlife and cattle with the study area. In addition, the rainfall for the two ecosystems is the same and it would be interesting to make some study comparisons between the two ecosystems. According to Young *et al.* (1998), the vegetation in red soils is dominated by relatively few species where *Cynodon plectostachyus* (K. Schum.) Pilg., *C. dactylon* (Linnaeus) Pers., and *Pennisetum* *stramineum* Peter dominate the understory, while *Acacia etbaica* Schweinf. and *A. brevispica* Harms dominates the overstory.

Study design

The detailed project study was conducted at Mpala Research Centre in exclosure plots established in 1995 (Young *et al.* 1998) that allow herbivory (grazing and browsing) in six combinations of three categories of herbivores. The first category was mesowildlife (or mesoherbivores), which comprised medium-sized wildlife from the size of a buffalo and other smaller ungulates and which were referred to as 'wildlife' in Young *et al.* (1998). The second category was megawildlife (or megaherbivores) that was comprised of only giraffes and elephants, while the last category was cattle. The details of this design are shown in Figure 2.2.

The three categories of the large mammalian herbivores were managed such that (i) only cattle (C) were allowed to graze; (ii) mesoherbivores (W) alone are allowed to graze/browse; (iii) only megaherbivores and mesoherbivores (MW) were allowed to graze/browse; (iv) megaherbivores, mesoherbivores and cattle (MWC) were allowed to graze/browse; (v) only mesoherbivores and cattle (WC) were allowed to graze; and (vi) no large mammalian herbivores (control, O) were allowed to graze/browse. These exclosures were 200m x 200m and replicated three times, once in each of three blocks (north, central and south), for a total of 18 plots. The grazing by cattle was moderate with one livestock unit per 5-8ha (Young *et al.* 1998). The suitability of the current experimental design and success of the different herbivore barriers has already been demonstrated (Young *et al*. 1998).

Materials and methods

Collecting and Sampling Spiders

The main methods of spider collection were pitfall-trapping and sweep-netting.

Pitfall traps

Ground-active spiders and other invertebrates were collected by pitfall traps (Greenslade 1964; Uetz and Unzicker 1976; Sutherland 1996). Each trap consisted of two cone-shaped plastic (polyethylene) cups 9 cm wide at the mouth and 14 cm deep, one inside the other, buried to their rims. Three pitfalls per plot for each of the 18 sampling plots were used, making a total of 54 traps. The three pitfall traps were laid on a line transect every 3 m. The inner cup of each trap was filled to a third of its volume with a 2% formaldehyde solution as a preservative. Traps were left open and emptied every second week. Where evaporation was high, refilling was done *ad hoc*. At the end of each fortnight, the contents were collected using an ordinary domestic sieve and emptied into appropriate containers for sorting in the laboratory. Since in the current study pitfall-trapping was undertaken in 6 different treatments using 9 traps/treatment for 435 days, it translated to a total trapping effort of 23,490 trap-days.

The pitfall-trapping method has been widely used for spider surveys (e.g. Uetz and Unzicker 1976; Russell-Smith, 1981; Russell-Smith *et al.* 1987; Coddington *et al.* 1991; van der Merwe *et al.* 1996; Green 1999; New 1999; Buddle and Rypstra 2003). They are employed by many surveys in agricultural ecosystems (reviewed in Green 1999). The merits of this cost-effective method include continuous sampling effort (including diurnal and nocturnal in all weather conditions) and yielding of a more accurate estimate of actual species richness in a community (Uetz and Unzicker 1976). Their use is not limited to any particular terrestrial habitat (Gist and Crossley 1973). Pitfalls are the most widely used method for sampling assemblages of ground or litter-dwelling arthropods and many scientists have continued to use them (e.g. Uetz and Unzicker 1976; Niemelä *et al.* 1986; Whicker and Tracy 1987; Halsall and Wratten 1988; Topping and Sunderland 1992; Davis 1993; Krasnov *et al.* 1996; Krasnov and Shenbrot 1996; Davis and Sutton 1998; Moseby 2001; Parr and Chown 2001; Ward *et al.* 2001; Jonas *et al.* 2002; Ranius and Jansson 2002; Pekár 2002; Magagula 2003). They allow collection in numbers suitable for statistical analyses (Spence and Niemelä 1994). They are a very popular method for coleopteran studies especially of dung beetles where they are used with a bait (e.g. Davis 1993, 1994, 1996a). The limitations of this method are that the number of individuals trapped is affected by environmental, weather and species-specific factors (Mitchell 1963; Krasnov *et al.* 1996; Krasnov and Shenbrot 1996; Parmenter *et al.* 1989; Ahearn 1971). Among the environmental factors affecting them are temperature and moisture (Ericson 1979; Honêk 1988). More precisely, degree of activity produces biases, as is shown by a high proportion of males caught in spider-related studies, and therefore does not reflect true population density. The placement of pitfalls can also influence the results (Greenslade 1964; Russell-Smith 1999; Ward *et al.* 2001) and so does the material used for their construction (Luff 1975; Wagge 1985), the preservative (Greenslade and Greenslade 1971; Luff 1975; Wagge 1985; Pekár 2002), and the size, shape and arrangement of the traps (Morrill *et al.* 1990; Spence and Niemelä 1994; Brennan *et al.* 1999; Ward 2001). In addition, habitat structure may affect the efficiency of pitfalls (Melbourne 1999). Pitfalls are also prone to damage by animals. In this study, the number of traps set was increased at the start of the study in anticipation of such damage. Despite the various limitations, pitfalls were used in this study because they could allow comparison of this study with others, are widely used, cost effective and operate on a full time basis (active during day and night).

Sweep-netting

Sweep-netting involved walking through the herb layer swinging a sweep net through the understorey vegetation for a standard number of times (Coddington *et al.* 1996). The net used for the current study was 40 cm in diameter and sweep-netting was done on a randomly selected 50 m transect in each of the 18 plots. In this study, one hundred sweeps were made along each transect. After every ten sweeps, samples were emptied on a plain sheet of cloth and all invertebrates collected with a pooter. The process was repeated every fortnight throughout the study period. A similar approach has been found effective for savanna studies (Russell-Smith pers. comm.). Since most of the early mornings were cold and late afternoons were hot and often windy, sampling for spiders was only done between 8.00am and 12.00 noon by myself and one trained assistant. Harmonisation of the sweeping span was done before the start of the study to ensure there was no variation in sample sizes. Sweep-netting was done from knee height and below with little distraction from perennial shrubs since the vegetation of the study area was dominated by *Acacia drepanolobium* bushed grassland (Young *et al*. 1998). When weather or wildlife could not permit, sampling time was adjusted accordingly.

Advantages of the method include the fact that it provides qualitative data important that might give more information about distribution (Whittaker 1952). It helps to sample arthropods fast and is not expensive. In relation to spider studies, sweep-netting is one of the best methods of capturing actively hunting spiders and small web-building species (Harris 2000).

Weather, vegetation type and age, weight of net, type of mesh, and the skills of the collection person affect sweep net collections (Marshall *et al*. 2000). It is normally difficult to use the sweep net when it is wet since the invertebrates stick together. The amount of catch is also affected by the position of an invertebrate on a plant (Delong 1932) while changes in temperature and wind velocity cause a variation in positioning of the invertebrates such that they might be found either higher on vegetation or lower near the ground surface (Romney 1945). The sweep net method could underestimate the abundance of many invertebrates. This might be more so for forest floor dwellers e.g. snails, millipedes, centipedes and those that can grasp vegetation firmly (Whittaker 1952; Hughes 1955). There is variation in the sweep net catch from one collector to another (Whittaker 1952), even when the same size of net is used. For optimal and comparable results from the sweep-netting method, it is advisable to carry out sweeping at different heights and during different weather conditions (Harper and Guynn 1998). It is important to note that although the sweep-netting method provides good qualitative data, it is not easy to calculate accurate densities since there are no accurate area changes (Whittaker 1952). It is normally a limitation when one needs to compare different studies made with this method especially when the intensities of sweeping and the sizes of nets are not the same (Harper and Guynn 1998). Another criticism of sweep-netting is that it only samples part of the grass layer and which might also vary based on the plant's stage of growth (Russell-Smith 1999).

Sweep nets have been widely used many arthropods studies (e.g. Scharff and Griswold 1996; Dippenaar-Schoeman *et al*. 1999a; Russell-Smith 1999; Frampton *et al*. 2001; Oyediran and Heinrichs 2001).

Vegetation sampling

The relative vegetation cover was sampled once every month in all the study plots using a 10-point pin frame method. Cover of a species is defined as the proportion of the ground occupied by perpendicular projection on to it of the aerial parts of individuals of the species under consideration (Greig-Smith 1983). A pin frame method with a quadrat (size $0.5m^2$) was used for this purpose. A pin frame consists of a row of 10 pins in a frame (which may be wooden or plastic), with a length of the frame equal to one side of the quadrat (Kent and Coker 1994). The pins were lowered vertically on to the ground and plant species that they touched were recorded. This procedure was repeated 8 times along each of the sweeping transects and 6 times along the pitfall transect, on the left side of each of the pitfall traps. When a pin frame and a quadrat are used together, the method is very objective and very reliable with very little personal bias. Use of a 10-point pin frame method has been made with success in studies of savanna vegetation (e.g. McNaughton 1983; Augustine 2003).

Arcsine transformation

Data on percentage relative vegetation cover were arcsine-transformed before being subjected to ANOVA. This transformation changes the binomially distributed percentages towards a normal distribution, which is recommended for ANOVA (Zar 1999), and also re-weights the contribution of common and rare species in the (non-parametric) multivariate representations (Clarke and Warwick 1994).

Rainfall measurements

The monthly rainfall was recorded using three rain gauges placed in each of the three study blocks of north, central and south (Figure 2.2). The readings were made on a daily basis but the samples were pooled together to make a monthly total. For the purpose of analysis, readings from a particular study block represented the rainfall for all six experimental treatments in that particular block. Depending on the study objective, the readings used for various analyses were either with a one-month time lag or unlagged. It was expected that response of vegetation to downpours would involve a time lag, whereas the response of spider diversity to rainfall would either be direct or indirect. The direct effects would probably not need a time lag and were thought to include changes in spider activity e.g. due to flooding. The indirect effects were thought to be through the effects of changes in vegetation cover and were thought to require a time lag. The reading used was specified before the analysis.

Determination of wet and dry seasons

The wet and dry seasons of the study period were determined by adding up monthly total rainfall through out the study period (May 2001-July 2002). A mean of these months was calculated (52.60 mm) and used to demarcate wet and dry seasons. In this case all the months with rainfall readings above this value were designated as wet months (seasons) while the other months that included the value or below it were designated as dry season.

Conversion of months to circular data

Before performing multiple regressions in chapter 9, the months were converted into a circular distribution (Batschelet 1981) that does not have a true zero. Circular distributions are finite and range from 0^o to 360^o (Batschelet 1981). The aim was to ensure that the time scale of the data set was well dispersed such that months close to one another in a calendar year were treated as so during the analysis compared to months far apart, thus reflecting the seasons of the year. The conversion involved two stages, converting the months to an angular direction using the formula:

$$a = (360^o)\ (X)/k$$

where, a = angular direction, k = 12 (months of one calendar year) and X is the month of a calendar year.

Then converting the angular reading to a circular transformation (C) using the formula

$$C = \text{Sin}\ (\pi^*(a/180),$$

where C the circular transformation, a = angular direction and $\pi = 3.14$.

Figures

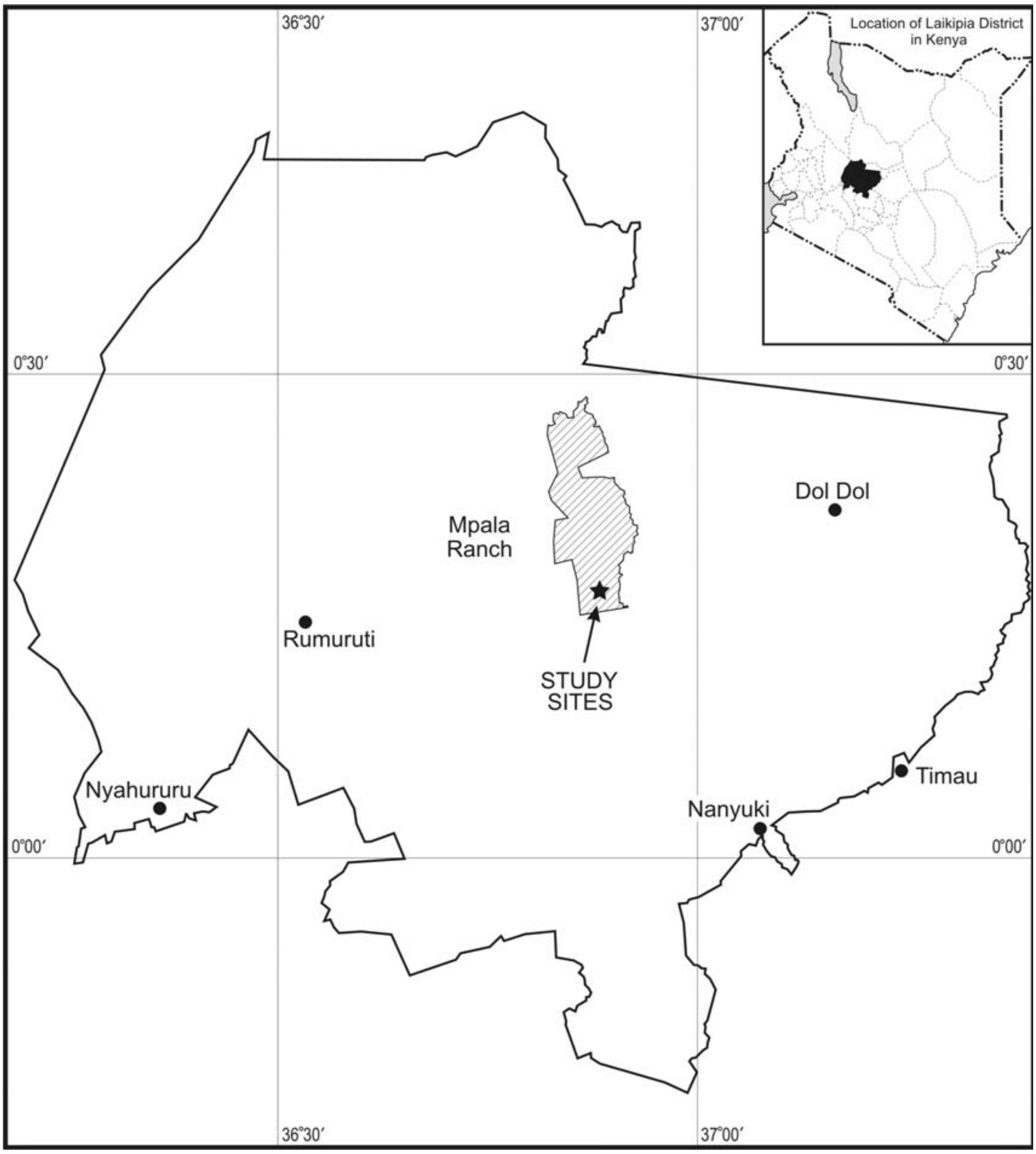

Figure 2.1. Location of Mpala Research Centre (study sites), at Mpala Ranch of Laikipia district in Central Kenya.

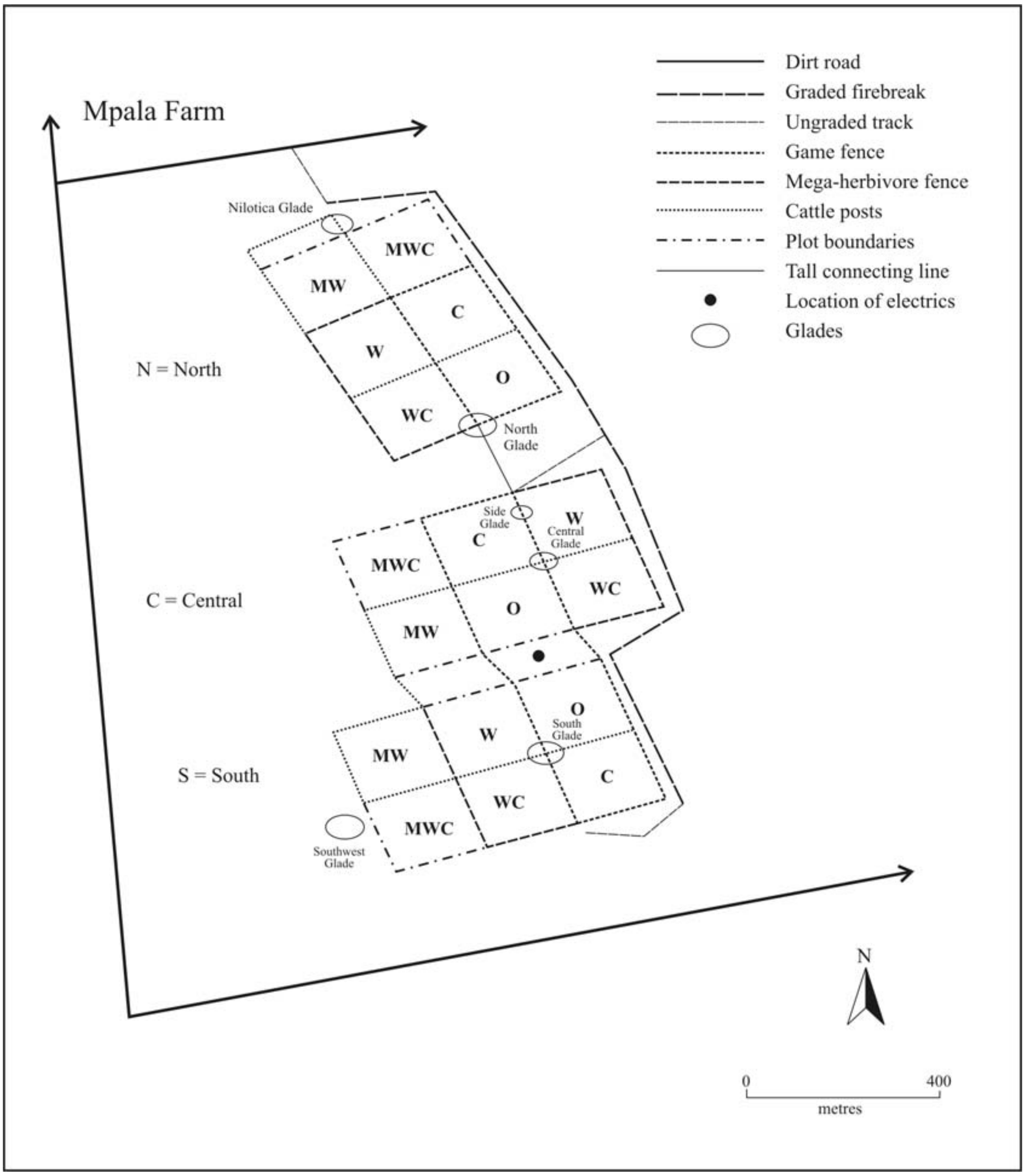

Figure 2.2. Schematic representation of the experimental design of the KLEE study plots. Letters in each plot represent the herbivores allowed in, where: C - cattle, W – Mesoherbivores, M – megaherbivores, O – control (all large mammalian herbivores excluded). N, C and S represent north, central and south blocks respectively. Each plot measures 200 X 200m. The distance between the furthest placed plots (between north and south block) was approximately 2km. Adapted fom Young *et al.* (1998).

CHAPTER 3. SPECIES COMPOSITION AND CHECKLIST OF THE SPIDERS (ARANEAE) OF THE BLACK COTTON SOIL ECOSYSTEM

Preface

This chapter describes the species composition and a checklist of spiders of the black cotton soil ecosystem. It starts by defining the systematic position of the spiders and reviewing the available taxonomic knowledge of the taxon. It also compares the current results with the past studies in Kenya, the region and the continent. This chapter has been accepted for publication in *Journal of Afrotropical Zoology* (Warui, C.M., Villet, M.H., & Young, T.P. (in press). Spiders (Araneae) from black cotton soils of a highland savanna in Laikipia, central Kenya. (*Journal of Afrotropical Zoology*).

Introduction

Spiders belong to the order Araneae, which is divided into sub-orders Opisthothelae and Mesothelae. The former is divided into two infraorders - the Araneomorphae and Mygalomorphae and is the only one found in the Afrotropical region (Dippenaar-Schoeman 2002). There are approximately 40 000 spider species that have been described worldwide belonging to 109 families (Platnick 2002). Of these, Araneomorphae is represented by 93 and Mygalomorphae by 15 families (Dippenaar-Schoeman 2002). Only 71 families, represented by 6000 species belonging to 893 genera, occur in the Afrotropical region (see work by Alderweireldt and Jocqué 1994; Dippenaar-Schoeman and Jocqué 1997). This forms a very small percentage of the known world's spider species (approximately one seventh), and suggests that the African fauna is relatively poorly known (Alderweireldt and Jocqué 1994).

Several reasons account for poor knowledge of African spiders, the main one doubtlessly being the scarcity of revisionary studies on African arachnology (Dippenaar-Schoeman and Jocqué 1997), the lack of African spider students and the fact that few institutions support taxonomic work. Most of the taxonomic work is scattered in a large number of smaller articles and is therefore difficult to compile (e.g. Dippenaar-Schoeman and

Jocqué 1997; Dippenaar-Schoeman 2002). Very little biodiversity research has been done on East African savanna spiders (e.g. Russell-Smith *et al.* 1987; Russell-Smith 1999). Ecological or inventory work on savanna spiders in other parts of Africa is equally rare and only a few scientists have contributed (e.g. Blandin 1971; Blandin and Célérier 1981; Russell-Smith 1981; Lotz *et al.* 1991; Whitmore *et al.* 2001). Although van der Merwe *et al.* (1996) and Malaisse and Benoit (1979) worked on forest and woodland respectively, they added some knowledge of savanna spiders, as they included the inventory of small spider patches of grassland in their studies. However there are many publications on the systematics of African spiders (see Dippenaar-Schoeman and Jocqué 1997; Dippenaar-Schoeman 2002; Platnick 2002). The current study provides a preliminary checklist of the savanna spiders of central Laikipia district, Kenya. It is hoped that the current checklist will add to the existing knowledge of Kenyan spiders and serve to provide a base for future research on the poorly studied East African savanna spider fauna since it might not be easy to carry out meaningful ecological/conservational based studies when the fauna is poorly known.

Objectives

i. To establish a checklist of the spider fauna of the black cotton soil ecosystem.
ii. To establish the species composition of the black cotton soil ecosystem.

Materials and methods

Specimen sorting and identification

A total of 29 fortnightly samples from each collecting technique were collected over the months. Each of these samples was replicated 18 times. Spiders were initially separated from other material and identified to the lowest possible taxonomic level (often family and sub-family initially), using the most recent keys to African spiders (Dippenaar-Schoeman and Jocqué 1997; Dippenaar-Schoeman 2002). The spiders were further sorted into morphospecies, based mainly on a combination of several morphological characters as indicated in relevant literature (see Dippenaar-Schoeman and Jocqué 1997), and a reference collection was established. Comparisons were made with voucher collections held at the National Museums of Kenya (NMK) and taxonomic manuals and photographs available there. Reference was also made to the recent world spider catalogue (Platnick 2002). Since this process was not fully satisfactory, further identification and verification of specimens was done at the Royal Museum for Central Africa, Tervuren (MRAC), Belgium, in September and October 2002. Even then, it was not possible to completely identify all the specimens, but the study identified spiders as far as the resources and availability of expert services could allow. Further identification will continue. It is likely that some of the species are new to science.

Analysis

The completeness of the checklist was assessed using species accumulation curves calculated using PRIMER statistical software (Clarke and Warwick 1994, Clarke and Gorley 2001). First the accumulation curve was calculated using the raw data in the chronological sequence in which the samples were collected. The average species accumulation curve was then calculated using the same software by iteratively resampling the raw data 999 times and averaging the results (Clarke and Gorley 2001). The calculation of diversity indices used in this chapter is explained in detail in chapter 4. Some extra tables inserted in this section (e.g. Table 3.3) referred to some studies that were not based on quantitative data but were nevertheless important in the general discussion.

Results

Overall checklist

A total of 132 species (Table 3.1) belonging to 30 families was recorded. Of all the species collected, 16.67% were identified to species, 43.94% were identified to genus and the remainder could not be identified beyond family. Salticidae, Gnaphosidae and Lycosidae were among the taxonomically problematic families. There were several immature specimens that were difficult to identify to species level.

The average species accumulation curve for the entire sample (Figure 3.1) shows a typical initial rapid increase in species with increasing number of samples, which gradually sloped down with more samples until there were few new species recorded with further sampling. This shows that the number of species continued to increase slowly right until the last sample and implies that further sampling would have continued to add species to the total for either collecting method. The overall Shannon-Wiener diversity index for the combined samples is 3.34, when calculated to base two. In most cases, the values of this diversity index range between 1.5 and 3.5 and rarely exceeds 4.5 (Magurran 1988). This implies that the diversity of the spider fauna is fairly high, especially given that only two methods were used to collect data. It is important to note that the study did not deliberately set out to sample the canopy and burrowing spiders although some were caught anyway. Pielou's evenness index was 0.671. Since the value is approximately halfway between 0 and 1, it implies that the distribution of spiders was not even and there was some dominance of some individual taxa.

Of the 10487 specimens collected in total, Araneidae was the numerically predominant family, forming 29.20% of the sample. It was followed by Salticidae (21.08%), Lycosidae (13.22%), Oxyopidae (10.85%), Thomisidae (9.82%) and Gnaphosidae (5.38%). All of the other families contributed less than 5% to the overall abundance. The most abundant species was *Cyclosa insulana* Costa, which represented 23.64% of all the specimens collected, and 80.96% of all the Araneidae collected. Other very abundant species were Salticidae sp. 19 (Salticidae) (8.21%), *Aelurillus* sp. (Salticidae) (5.01%), *Runcinia flavida* Simon (Thomisidae) (4.65%) and *Oxyopes* sp. 1 (Oxyopidae) (4.64 %).

Composition

The total number of species per family is shown in Figure 3.2. The families with the highest number of total species were the jumping spiders (Salticidae) with 24 species (19% of all species), followed by ground spiders (Gnaphosidae) (20 species; 16%). The wolf spiders (Lycosidae) and orb-web spiders (Araneidae) came third (15 species; 11% each) while crab spiders (Thomisidae) and comb-footed spiders (Theridiidae) are next (8 species; 6%). Lynx spiders (Oxyopidae), small huntsman spiders (Philodromidae) and burrowing and ant eating spiders (Zodariidae) had 4 species each (3%) while all other families had less than 4 species.

Effect of sampling methods

Pitfall trapping yielded more species (104) than sweep-netting (66), but the species accumulation curves of both sampling methods (Figures 3.3 and 3.4) suggest that neither method was exhaustive of the species present. This study also looked at the frequency of occurrence of spiders for both sweep-netting and pitfall trapping samples. In this case the individual spider presence in every sampling occasion was divided by the total sampling occasions and expressed as a percentage. The ten most frequent species for sweep-netting samples are shown in Figure 3.5, while those from pitfall trapping are shown in Figure 3.6. The overlap between species obtained by the two methods was low and only one species appeared for both methods among the first ten most frequent species.

A further comparison of the diversity indices for the two methods (Table 3.2) shows that the species composition differs according to the method used. In total, only 43 species were obtained with both methods. Only seven of these species were fairly equally abundant in both samples. These were *Thanatus* sp., *Oxyopes* sp. 1, *Oxyopes pallidecoloratus* Strand, *Oxyopes* sp. 3., *Evarcha* sp. 1, *Opopaea* sp. and *Philodromus* sp. This shows that pitfall trapping and sweep-netting are complementary methods and target different spider species. Another reason that might have contributed to variation in species collected in addition to sampling methods is the naturally occurring differences in richness and abundance between areas.

Effect of season

The species accumulation curve calculated from the sweeping samples (Fig. 3.7) showed that novel species appeared in the sample after the rainfall peaks in June and November 2001, and March to May 2002. In addition, the abundance of some species increased after rainfall set in. Species from the pitfall-trapping sample that showed remarkable increases in abundance included *Borboropactus* sp. (Thomisidae), *Diores strandi* Caporiacco (Zodariidae), *Camillina* sp. (Gnaphosidae), *Lycosa* sp., *Trochosa* sp., Lycosidae sp. 3 (Lycosidae), and Salticidae sp. 29 (Salticidae). The spider species from the sweep-netting sample that showed fairly high increases in abundance after rains included *Argiope* *trifasciata* Forskal (Araneidae), *Runcinia flavida* Simon (Thomisidae) and *Oxyopes* sp. 1 (Oxyopidae).

General discussion

Bearing in mind that the study area was not exhaustively surveyed, the overall number of species reported is fairly high compared to past work in Africa (Table 3.3). Species that had not been previously recorded emerged after rainfall peaks (Figure 3.7). Similarly, the abundance of the already recorded species continued to increase, showing that the spider community responded positively to an increase in rainfall. Although it is a well-known phenomenon that in areas with a pronounced dry season, the activity period of adult spiders starts with the onset of rainfalls, the findings from this study suggest that there are a handful of species that are largely active throughout the season e.g. *Aelurillus* sp., *Cyclosa insulana* Costa and *Oxyopes* sp. 1.

The pitfall trapping survey sample has a higher species diversity than the sweep-netting sample. This might be due to the fact that the pitfall traps were constantly in operation whereas sweep-netting was only carried out for a few hours fortnightly. It was also probable there were more species inhabiting the ground layer than the herb layer. In general however, it might not be very meaningful to compare these methods in detail, as the overall sampling effort differed and that they targeted different habitats. Similar caution was recommended by Russell-Smith *et al.* (1987) in their work on Kenyan savanna spiders. Furthermore, in pitfall trapping, male spiders show strong seasonal peaks of activity (Warui, personal observations) and therefore the numbers caught do not accurately reflect population densities. Pitfall traps have been found to be selective in the species they trap. Green (1999) and Russell-Smith (1999) have also reported that several factors, such as habitat structure (Melbourne 1999) and the positioning of traps (Russell-Smith 1999), influence pitfall trap data and this may therefore have contributed to the differences observed in this study.

Since this study was mainly based on two collecting methods, other sampling methods such as beating, fogging, visual searches and sieving, and a longer period of pitfall trapping and sweep-netting, would certainly increase the species list. Past studies have shown that different methods tend to compliment one another (e.g. Coddington *et al.* 1991; Churchill & Arthur 1999; Russell-Smith 1999). However, the presence of fierce *Crematogaster* spp. ants in *Acacia drepanolobium* (Young *et al.* 1997) and the nature of the canopy of *Balanites* sp. might make beating difficult. The study did not address some burrowing spiders (especially females which do not wander a lot) and which would also require a specialized collecting technique (Dippenaar-Schoeman 2002) but should doubtlessly increase the species list.

Some studies done in the past have reported results that are worth noting (Table 3.3). For example, pitfall traps set for 3 weeks in a lowland savanna in Kora Reserve, Kenya (200km from the current study site) collected 68 species belonging to 20 families (Russell-Smith *et al.* 1987). This is a fairly low number of species compared to that of the current study, but the difference could be attributed to the total sampling effort, and the types and number of collecting methods employed.

On the other hand, the study conducted in savanna at Mkomazi Game Reserve, Tanzania (Russell-Smith 1999) reported a much higher number of taxa: 508 species from 241 genera belonging to 52 families. Approximately 155 (30%) of these spiders were identified to species level. However, the difference in diversity can mainly be attributed to the number of habitats sampled (12) and the variation in methods used (pitfall trapping, tree fogging, hand collection, litter sorting and malaise trapping). In terms of composition, there is some similarity in the dominant families and their relative proportions. In both studies, Salticidae was the family with the highest number of species followed by Gnaphosidae. In Russell-Smith's (1999) study, Thomisidae, Theridiidae and Araneidae followed jointly, whereas in the current study, Lycosidae and Araneidae were next most species-rich. This could probably be attributed to the higher intensity of sweep-netting in the current study which produced more Araneidae compared to his (30 samples of 10 x 20 sweeps per habitat). The high number of Lycosidae in the current study is attributed to the higher intensity of pitfall trapping.

In terms of the overall abundance per family, the current study found that it was not necessarily true that the most speciose family was the most abundant. Thus Araneidae, mainly *Cyclosa insulana*, which comprised 23% of all specimens, were more abundant than Salticidae despite the later having more species. If this *Cyclosa* was removed from the list, the Salticidae would retain the top position as the richest family in terms of numbers of both species and specimens.

Most spider studies in Africa have been conducted in South Africa, where scientists have produced savanna checklists with similar results (e.g. Dippenaar-Schoeman *et al.* 1989; Whitmore *et al.* 2001; Foord *et al.* 2002; Dippenaar-Schoeman and Leroy 2003). However, they are hard to compare because of disparities in the types and number of methods employed, the duration of sampling and the numbers habitats sampled (Table 3.3). In most of these studies, it was clear that more inventory studies have been done in South Africa compared to other parts of the continent. Table 3.3 also shows that combining several methods and sampling for longer duration gives better results. That the current study came up with 132 species in just 14 months may also show that sampling intensity is important for inventory studies too.

Spider checklists from other parts of Africa include that of Russell-Smith (1981), who reported 135 species belonging to 21 families in Botswana. Blandin and Célérier (1981) and Lotz *et al.* (1991) also added to the existing knowledge on African savanna spiders. Other work is mainly a compilation of all the literature on spiders in a particular country and not an actual survey e.g. Griffin and Dippenaar-Schoeman (1991) reported an overall checklist of Namibian spiders with 578 species belonging to 238 genera and 50 families. The taxonomic impediments to identifying the majority of these spiders to species limits the scope for biogeographical comparisons of these studies. However, an improvement in identification would facilitate such comparisons and can reveal interesting faunal patterns as already shown in work on other taxa near the study area (e.g. Warui 1998; Warui *et al.* 2001).

Conclusions

This study shows that the black cotton soil ecosystem has high spider richness and abundance. It suggests that this arachnofauna is sufficiently rich that it might be useful for biological monitoring work e.g. as indicators of habitat change in these savanna ecosystems. Being among the few savanna surveys in the region, it provides baseline information for future surveys. With the increase of human activity in this biome, there is a danger of losing this fauna, yet it is not well known. Future survey work should be done using other methods such as litter sieving, visual searches, thorough beating and canopy fogging. Seasonal effects evidently affect inventories, so studies should be made over longer periods of time. There is a tremendous need for taxonomists to study and name the many undescribed species in Africa, especially since comparisons are needed between the faunas of different sites and study areas. There is also a need to extend survey work to the neighbouring red soil ecosystem as nothing is known of its arachnofauna at the moment.

Tables

Table 3.1. Provisional checklist of spiders from black cotton soil habitats of a highland savanna ecosystem in Laikipia, Kenya and the methods used for collecting. The symbol (+) shows present and (–) absent. The fourth column represents the guilds where, WB = Web builders, PW = Plant wanderers and GW = Ground wanderers.

FAMILY	GENUS	SPECIES	GUILD	METHODS OF COLLECTION		TOTAL
				SWEEPING	PITFALLS	(SWEEPING + PITFALLS)
Agelenidae	*Olorunia*	*Olorunia* sp.	WB	-	+	2
Araneidae	Araneidae indet.	Araneidae sp. 2	WB	+	-	2
“	“	Araneidae sp. 5	WB	+	-	1
“	“	Araneidae sp. 6	WB	+	-	64
“	“	Araneidae sp. 9	WB	+	-	12
“	*Araneus*	Araneus sp. 1	WB	+	+	5
“	*Argiope*	*Argiope trifasciata* Forskal, 1775	WB	+	+	289
“	*Caerostris*	*Caerostris* sp.	WB	+	-	10
“	*Cyclosa*	*Cyclosa insulana* (Costa, 1834)	WB	+	+	2480
“	*Cyrtophora*	*Cyrtophora* sp.	WB	+	-	1
“	*Gea*	*Gea* sp.	WB	+	-	7
“	*Hypsosinga*	*Hypsosinga* sp.	WB	+	+	125

FAMILY	GENUS	SPECIES	GUILD	METHODS OF COLLECTION		TOTAL
				SWEEPING	PITFALLS	(SWEEPING + PITFALLS)
"	*Neoscona*	*Neoscona moreli* (Vinson, 1863)	WB	+	+	37
"	"	*Neoscona* sp. 1	WB	+	-	4
"	*Poltys*	*Poltys* sp.	WB	+	-	25
"	*Pycnacantha*	*Pycnacantha* sp.	WB	+	-	1
Clubionidae	*Clubiona*	*Clubiona africana* Lessert, 1921	PW	-	+	1
Corinnidae	*Castianeira*	*Castianeira mestrali* Lessert, 1921	GW	-	+	4
"	*Merenius*	*Merenius* sp. *1*	GW	-	+	2
Cyrtaucheniidae	*Ancylotrypa*	*Ancylotrypa* sp.	GW	-	+	86
Eresidae	Eresidae indet.	*Eresidae* sp. 1	WB	-	+	1
Gallieniellidae	Gallieniellidae indet.	Gallieniellidae sp.1	GW	-	+	1
Gnaphosidae	*Asemesthes*	*Asemesthes* sp. 2	GW	-	+	5
"	*Camillina*	*Camillina* sp.	GW	-	+	52
"	*Xerophaeus*	*Xerophaeus* sp.1	GW	-	+	19
"	"	*Xerophaeus* sp. 2	GW	-	+	11
"	"	*Xerophaeus* sp. 3	GW	-	+	21
"	"	*Xerophaeus* sp. 4	GW	-	+	16

FAMILY	GENUS	SPECIES	GUILD	METHODS OF COLLECTION		TOTAL
				SWEEPING	PITFALLS	(SWEEPING + PITFALLS)
“	Gnaphosidae indet.	Gnaphosidae sp. 3	GW	-	+	15
“	“	Gnaphosidae sp. 4	GW	-	+	3
“	“	Gnaphosidae sp. 5	GW	+	+	22
“	“	Gnaphosidae sp. 7	GW	-	+	2
“	“	Gnaphosidae sp. 8	GW	-	+	12
“	“	Gnaphosidae sp. 9	GW	-	+	26
“	“	Gnaphosidae sp. 10	GW	-	+	2
“	“	Gnaphosidae sp. 11	GW	-	+	2
“	“	Gnaphosidae sp. 12	GW	-	+	11
“	“	Gnaphosidae sp. 14	GW	-	+	21
“	“	Gnaphosidae sp. 15	GW	-	+	23
“	“	Gnaphosidae sp. 16	GW	-	+	297
“	Zelotinae indet.	Zelotinae sp. 1	GW	+	+	4
“	“	Zelotinae sp. 2	GW	-	+	1
Hahniidae	*Hahnia*	*Hahnia* sp.	WB	-	+	3
Linyphiidae	*Microlinyphia*	*Microlinyphia sterilis* (Pavesi, 1883)	WB	+	-	3
“	*Tybaertiella*	*Tybaertiella convexa* (Holm, 1962)	WB	-	+	2

FAMILY	GENUS	SPECIES	GUILD	METHODS OF COLLECTION		TOTAL
				SWEEPING	PITFALLS	(SWEEPING + PITFALLS)
"	Linyphiidae indet.	Linyphiidae sp. 2	WB	+	+	2
Liocraniidae	Liocraniidae indet.	Liocraniidae sp. 1	GW	-	+	6
Lycosidae	*Evippa*	*Evippa* sp.	GW	-	+	6
"	*Geolycosa*	*Geolycosa sp. 1*	GW	-	+	226
"	"	*Geolycosa sp. 2*	GW	-	+	106
"	"	*Geolycosa sp. 3*	GW	-	+	7
"	"	*Geolycosa sp. 4*	GW	-	+	38
"	"	*Geolycosa sp. 5*	GW	-	+	32
"	"	*Geolycosa sp. 6*	GW	-	+	3
"	*Lycosa*	*Lycosa* sp.	GW	+	+	259
"	Lycosidae indet.	Lycosidae sp. 1	GW	-	+	9
"	"	Lycosidae sp. 2	GW	-	+	105
"	"	Lycosidae sp. 3	GW	-	+	478
"	"	Lycosidae sp. 4	GW	-	+	3
"	*Pardosa*	*Pardosa* sp.	GW	-	+	2
"	*Trabea*	*Trabea heteroculata* Strand, 1913	GW	-	+	35
"	*Trochosa*	*Trochosa* sp.	GW	-	+	84

FAMILY	GENUS	SPECIES	GUILD	METHODS OF COLLECTION		TOTAL
				SWEEPING	PITFALLS	(SWEEPING + PITFALLS)
Miturgidae	*Cheiracanthium*	*Cheiracanthium* sp.	PW	+	+	142
"	Miturgidae indet.	Miturgidae sp. 2	PW	-	+	1
Idiopidae	Idiopidae indet.	Idiopidae sp. 2	GW	-	+	4
Oonopidae	*Opopaea*	*Opopaea* sp. 1	GW	+	+	30
"	"	*Opopaea* sp. 2	GW	+	+	12
Oxyopidae	*Oxyopes*	*Oxyopes* sp. 1	PW	+	+	587
"	"	*Oxyopes pallidecoloratus* Strand, 1906	PW	+	+	432
"	"	*Oxyopes* sp. 3	PW	+	+	115
"	"	*Oxyopes sp. 4*	PW	-	+	4
Palpimanidae	*Boagrius*	*Boagrius incisus* Tullgren, 1910	GW	-	+	27
Philodromidae	*Philodromus*	*Philodromus montanus* Bryant, 1933	PW	-	+	2
"	"	*Philodromus* sp.	PW	+	+	47
"	*Thanatus*	*Thanatus* sp.	PW	+	+	33
"	*Tibellus*	*Tibellus minor* Lessert, 1919	PW	+	-	42
Pholcidae	Pholcidae indet.	Pholcidae sp.	WB	+	-	2
Pisauridae	*Euprosthenopsis*	*Euprosthenopsis* sp**.**	WB	-	+	66
"	Pisauridae indet.	Pisauridae sp. 1	WB	+	+	10

FAMILY	GENUS	SPECIES	GUILD	METHODS OF COLLECTION		TOTAL
				SWEEPING	PITFALLS	(SWEEPING + PITFALLS)
"	"	Pisauridae sp. 3	WB	-	+	1
Prodidomidae	*Prodidomus*	*Prodidomus* sp.	GW	-	+	8
Salticidae	*Aelurillus*	*Aelurillus* sp.	GW	-	+	526
"	*Evarcha*	*Evarcha* sp. 1	PW	+	+	65
"	"	*Evarcha* sp. 2	PW	+	+	5
"	*Harmochirus*	*Harmochirus bianoriformis* (Strand, 1907)	PW	-	+	2
"	*Heliophanus*	*Heliophanus* sp. 1	PW	+	-	13
"	*Hyllus*	*Hyllus* sp.	PW	+	-	19
"	*Myrmarachne*	*Myrmarachne naro* Wanless, 1978	PW	-	+	2
"	*Rhene*	*Rhene* sp.	PW	+	+	71
"	Salticidae indet.	Salticidae sp. 5	GW	-	+	160
"	"	Salticidae sp. 6	PW	+	+	20
"	"	Salticidae sp. 8	PW	+	+	8
"	"	Salticidae sp. 12	PW	+	+	320
"	"	Salticidae sp. 14	PW	+	-	1
"	"	Salticidae sp. 16	PW	-	+	1

FAMILY	GENUS	SPECIES	GUILD	METHODS OF COLLECTION		TOTAL
				SWEEPING	PITFALLS	(SWEEPING + PITFALLS)
“	“	Salticidae sp. 17	PW	+	-	17
“	“	Salticidae sp. 18	PW	+	-	18
“	“	Salticidae sp. 29	PW	+	-	861
“	“	Salticidae sp. 20	PW	+	+	6
“	“	Salticidae sp. 22	GW	-	+	10
“	“	Salticidae sp. 23	GW	+	+	26
“	“	Salticidae sp. 24	PW	+	+	5
“	“	Salticidae sp. 25	PW	+	-	9
“	*Thyene*	*Thyene* sp. 1	PW	+	-	41
“	“	*Thyene* sp. 2	PW	+	+	5
Scytodidae	*Scytodes*	*Scytodes* sp.	GW	+	-	1
Sparassidae	Sparassidae indet.	Sparassidae 1	PW	+	+	3
“	“	Sparassidae 2	PW	+	+	5
“	“	Sparassidae 3	PW	+	+	5
Tetragnathidae	*Leucauge*	*Leucauge* sp.	WB	+	-	7
Theridiidae	*Anelosimus*	*Anelosimus* sp.	WB	+	+	1
“	*Argyrodes*	*Argyrodes* sp.	WB	+	-	22

FAMILY	GENUS	SPECIES	GUILD	METHODS OF COLLECTION		TOTAL
				SWEEPING	PITFALLS	(SWEEPING + PITFALLS)
“	*Coscinida*	*Coscinida* sp.	WB	-	+	3
“	*Episinus*	*Episinus* sp. 1	WB	-	+	15
“	*Latrodectus*	*Latrodectus* sp.	WB	+	+	30
“	*Steatoda*	*Steatoda tristis* (Tullgren, 1910)	WB	-	+	5
“	Theridiidae indet.	Theridiidae sp.1	WB	+	+	3
“	“	Theridiidae sp. 2	WB	+	+	3
Theridiostomatidae	Theridiostomatidae indet.	Theridiostomatidae sp.	WB	+	+	1
Thomisidae	*Borboropactus* sp.	*Borboropactus* sp.	GW	-	+	234
“	*Monaeses*	*Monaeses gibbus* Dippenaar-Schoeman, 1984	PW	+	-	3
“	“	*Monaeses pustulosus* Pavesi, 1895	PW	+	+	152
“	*Runcinia*	*Runcinia flavida* Simon 1881	PW	+	+	488
“	*Stiphropus*	*Stiphropus* sp.	GW	-	+	1
“	*Synema*	*Synema* sp.	PW	+	-	33
“	*Thomisus*	*Thomisus stenningi* Pocock, 1900	PW	+	-	52
“	*Xysticus*	*Xysticus* sp.	GW	-	+	67

FAMILY	GENUS	SPECIES	GUILD	METHODS OF COLLECTION		TOTAL
				SWEEPING	PITFALLS	(SWEEPING + PITFALLS)
Uloboridae	Uloboridae indet.	Uloboridae sp. 1	WB	+	-	5
Zodariidae	*Akyttara*	*Akyttara ritchiei* Jocqué, 1987	GW	-	+	26
"	*Diores*	*Diores strandi* Caporiacco, 1949	GW	-	+	325
"	*Dusmadiores*	*Dusmadiores* sp.	GW	-	+	86
"	*Mallinella*	*Mallinella kibonotensis* (Bosmans & van Hove, 1986)	GW	-	+	1

Table 3.2. Overall diversity results for both pitfall-trapping and sweep-netting methods. S = Total species, N = abundance, d = Margalef’s richness index, J´ = Pielou’s evenness index, H´ = Shannon-Wiener diversity index.

	S	N	D	J´	H´
Pitfall-trapping	116	5201	8.65	0.54	2.33
Sweep-netting	75	5193	13.44	0.66	3.16

Table 3.3. Selected checklists of African savanna spiders, showing sampling effort, number of collecting methods employed, and the corresponding number of species and families recorded in the studies.

Locality	Country	Species	Families	Methods	Duration (years)	Source
Bloemfontein (+SA)	South Africa	-	31	1	1	Lotz *et al.* 1991)
Middelburg (SA)	"	55	21	1	3	Van den Berg and Dippenaar-Schoeman (1991)
Kora GR (Kenya)	Kenya	68	20	1	3 weeks	Russell-Smith *et al*. (1987)
Roodeplaat Dam (SA)	South Africa	98	27	2	4	Dippenaar-Schoeman *et al.* (1989)
Soutpansberg (SA)	"	127	46	4	5	Foord *et al*. (2002)
Kruger National Park (SA)	"	152	40	3	Over 16	Dippenaar-Schoeman and Leroy (2003)
Northern Province (SA)	"	268	37	6	1	Whitmore *et al.* (2001)
Mkomazi GR (Tanzania)	Tanzania	508	52	5	4	Russell-Smith (1999)

Figures

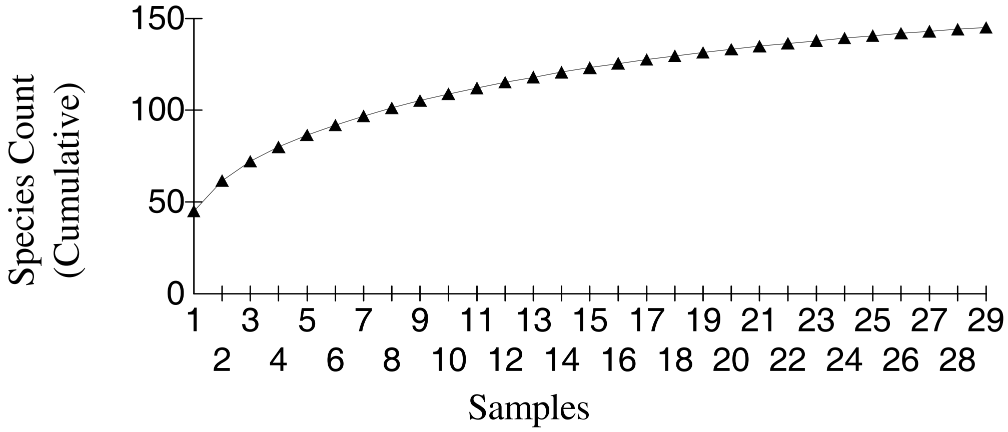

Figure 3.1. Mean species accumulation curve for spiders sampled with sweep-netting and pitfall-trapping methods combined (total data set), calculated from 999 iterations of random samples of the raw data from black cotton soil in Laikipia, Kenya.

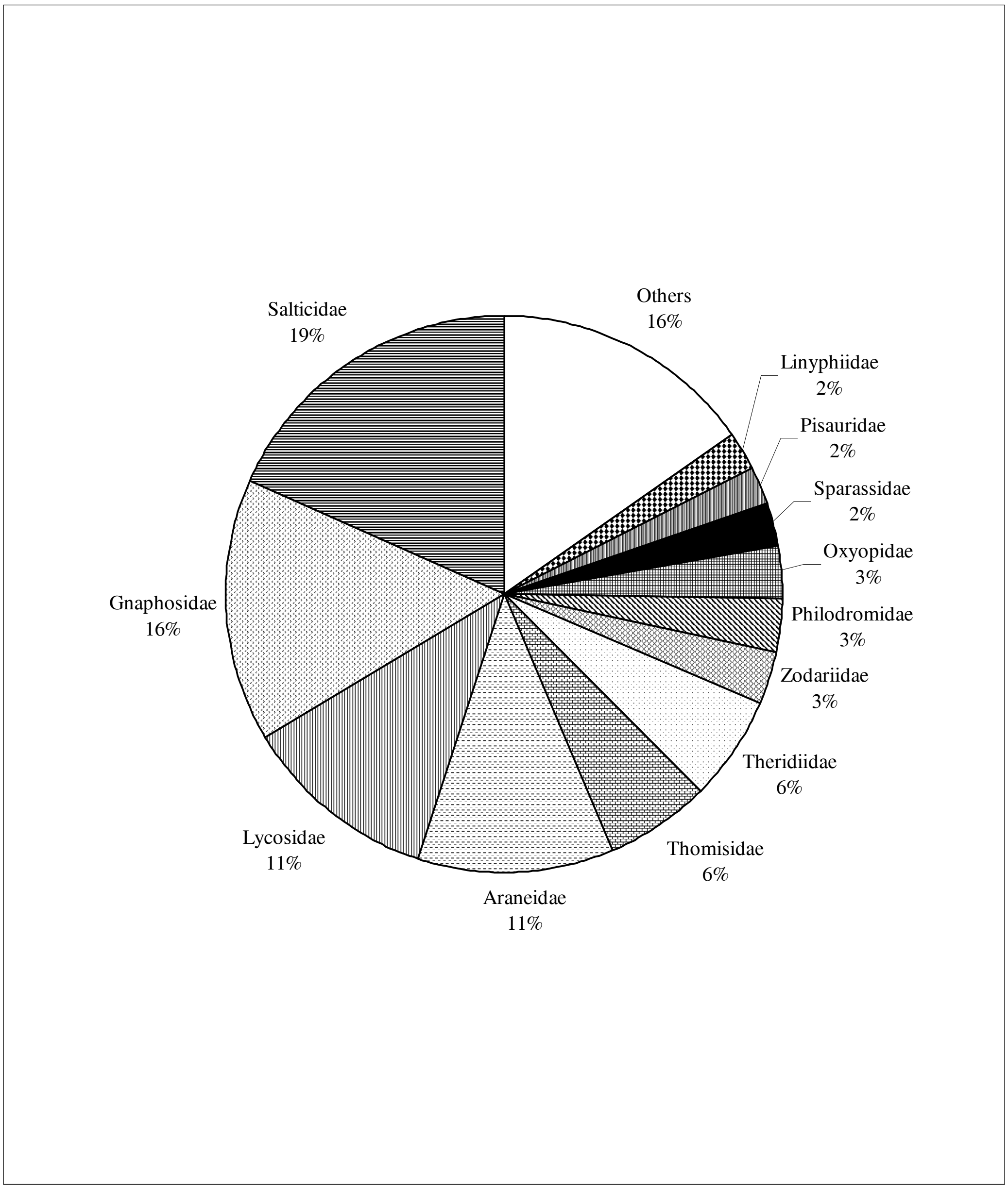

Figure 3.2. The percentage composition of family in terms total number of species per family for all spider species recorded from start of May 2001 to end of July 2002 for the black cotton soil habitat, Mpala, Laikipia. The figure was arrived at by dividing the total number of spider species per family with overall total number of species and expressed as a percentage.

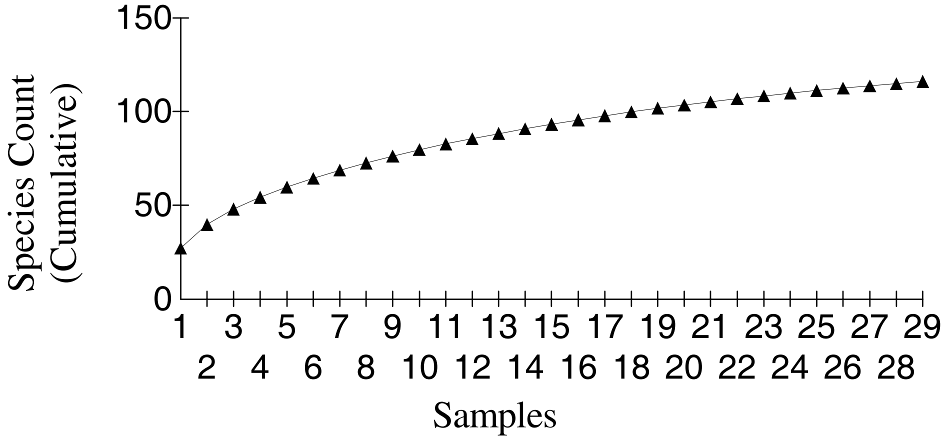

Figure 3.3. Mean species accumulation curve for spider collection by pitfall-trapping alone, calculated from 999 iterations of random samples of the raw data from black cotton soil in Laikipia, Kenya.

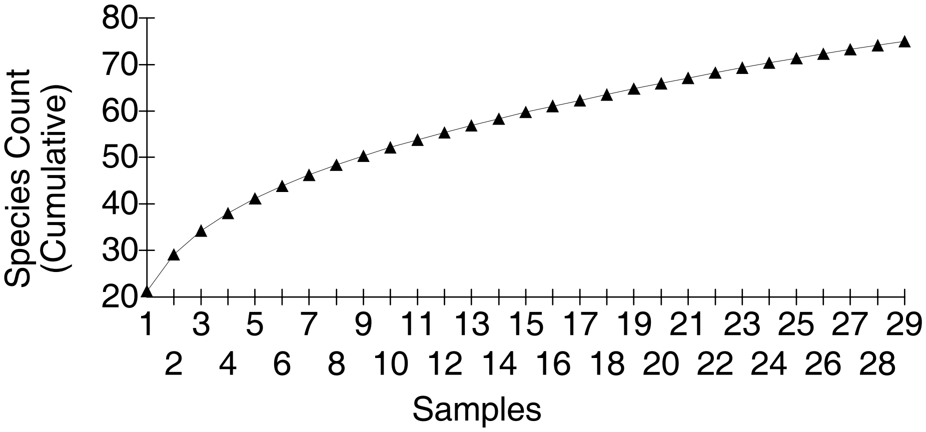

Figure 3.4. Mean species accumulation curve for spider collection by sweep-netting alone, calculated from 999 iterations of random samples of the raw data from black cotton soil in Laikipia, Kenya.

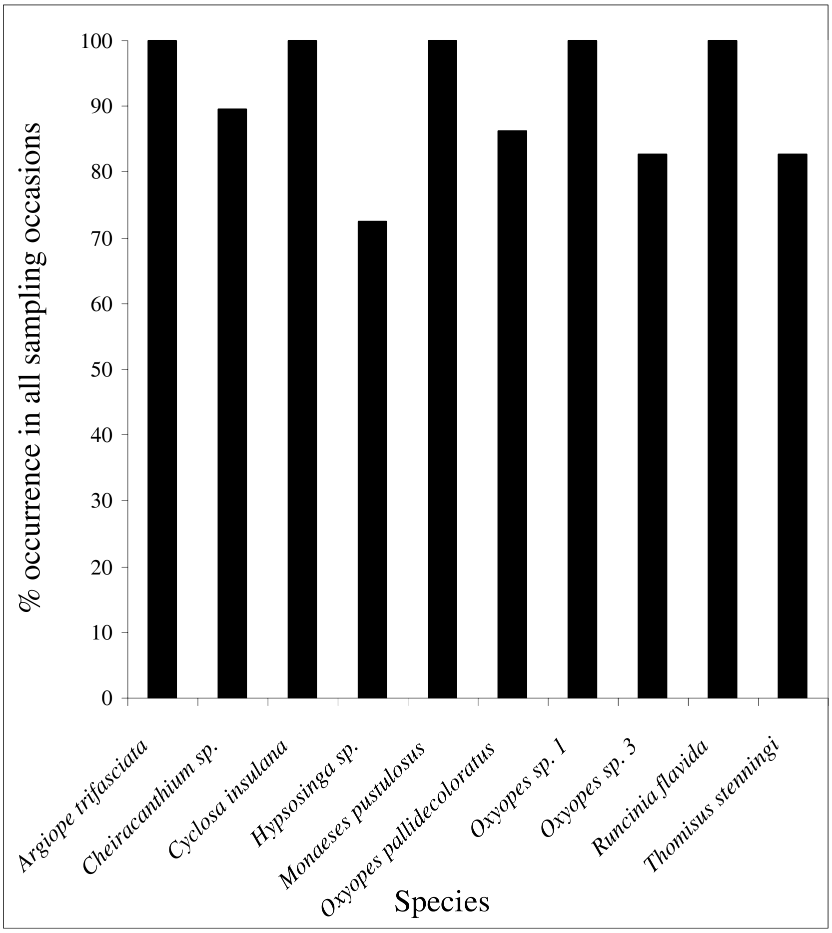

Figure 3.5. The frequency of occurrence of the ten most common spiders in the sweep-netting samples, as a percentage of the total sampling occasions during the study period.

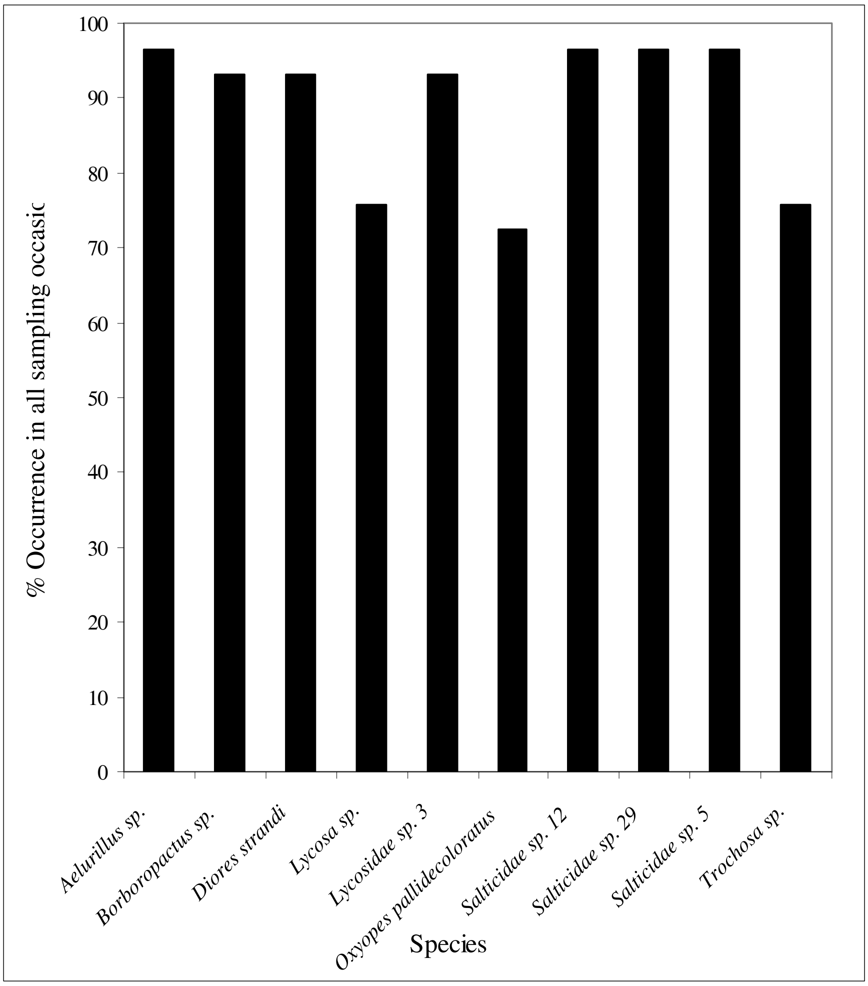

Figure 3.6. The frequency of occurrence of the ten most common spiders in the pitfall-trapping samples, as a percentage of the total sampling occasions during the study period.

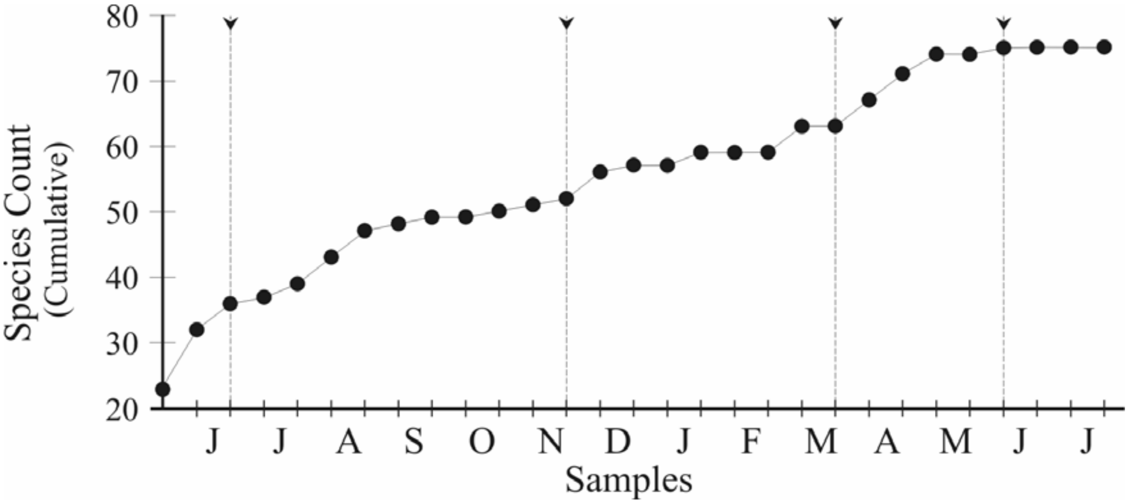

Figure 3.7. Species accumulation curve for spider collection by sweep-netting alone, showing the appearance of novel species in the samples with time of the year. The arrows indicate the timing of peaks of rainfall during the sampling period.

CHAPTER 4: BIOLOGICAL CONCEPTS OF DIVERSITY

Preface

This chapter explains in detail the concept of diversity. It reviews what is known about them and explains how the indices of the current study were chosen. It gives a justification of the choices made for the current study and also outlines their advantages and limitations.

The concept of diversity

Diversity can simply be defined as the variety of organisms. Analogous measurements appear in ecology, genetics, linguistics, information theory and economics (Lewis *et al.* 1988). Although a common concept, diversity is tricky and has many faces when one tries to make a precise quantification (Peet 1974; Southwood and Henderson 2000). Whittaker (1972), classified diversity into α, β and γ types. α diversity is that diversity of species within a community or habitat; β diversity is a measure of the rate and extent of change in species along a gradient, from one habitat to others, while γ diversity is the richness in species of a range of habitats in a geographical area.

There has been literature on measurement of species diversity and many indices have been proposed (e.g. reviews by Eberhardt 1969; Peet 1974; Magurran 1988; Krebs 1999; Southwood and Henderson 2000; Feinsinger 2001). Much debate exists about which among them are the best (Lewis *et al.* 1988; Krebs 1999), with some authors providing a critical analysis and alternative parameters (e.g. Hurlbert 1971; Peet 1974). Hurlbert (1971) believed that a single meaning of diversity does not exist. Peet (1974) believed that the species number was the oldest and most fundamental concept of diversity and suggested guidelines for application of many available diversity indices. Species richness was suggested as an alternative to species number by McIntosh (1967), because it was not easy to ascertain the total number of species in a natural community. According to Peet (1974), species richness is frequently used and is least ambiguous of all the diversity terminologies.

According to Magurran (1988) diversity measures are divided into species richness measures, species abundance models, and indices based on proportional abundance of species. Similarly according to Peet (1974), a number of concepts are lumped within the term diversity. The most important of these are species richness and equitability (evenness), with which importance is distributed among the species (Peet 1974). The third is the concept of heterogeneity, which combines richness and equitability measures. According to Peet (1974), there are two types of heterogeneity indices. Type I are the most sensitive to changes in the importance of the rare species in that sample. The most frequently encountered example is the Shannon–Wiener index. Type II are the most sensitive to changes in the most abundant/common species. The best-known example is the Simpson index. Equitability indices include Pielou's J' and Lloyd and Ghelardi's ε (Lloyd and Ghelardi 1964; Magurran 1988).

Choosing the index

There is little consensus on the best diversity measure to use and no index has received backing of even the majority of workers in the field (Magurran 1988; Feinsinger 2001; Gotelli and Colwell 2001). However, different diversity indices somehow differ in the ranking they give to communities (Hurlbert 1971) and therefore the most appropriate index will consider their theoretical properties (Southwood and Henderson 2000). There has been a lot of criticism over the use of Shannon–Wiener, Simpson, Berger-Parker, Brillouin, α and log-series indices (see Magurran 1988; Southwood 1978; Krebs 1999; Feinsinger 2001). However Southwood (1978) and Magurran (1988) provided guidelines and recommendations for the analysis of diversity data. One important point was the purpose of direct comparison of studies with one another, in which case they recommended continued use of an existing index.

Importance of diversity indices and sources of error

Diversity indices are useful in the investigation of ecological conditions because they not only illustrate intrinsic diversity patterns, but also illustrate other important information about community structure e.g. they indicate the relative contribution of both abundant and rare species to diversity, in addition to showing successional trends of a community over time as affected by abundant and rare species (Lewis *et al*. 1988). It is however important to note that diversity indices have some limitations that might adversely affect the accuracy and efficiency of a monitoring protocol (Norris 1999). These include their sensitivity to sample size, sampler bias, inclusion of juveniles, taxonomic uncertainty and stochastic sampling effects (Norris 1999).

Indices for current study and justification

This study computed a number of the above indices as measures of some attributes of community structure. Single number species richness measures computed were the total number of species (S) and Margalef's diversity index (d). These indices tend to be less informative than some measures of the way in which the total number of individuals is divided (Clarke and Warwick 1994). They are simple, easy to calculate but sensitive to sample size (Magurran 1988). It was therefore necessary to compute diversity, richness and evenness indices. Diversity indices incorporate both species richness and evenness in a single value (Magurran 1988), and allow comparisons between two habitats. However, since they are always difficult to interpret, species richness and evenness are also used in this study. In this study a number of diversity indices were computed.

Species diversity

This study adopted the Shannon-Wiener diversity index (H´) computed to base e using PRIMER statistical software (Clarke and Warwick 1994, Clarke and Gorley 2001):

$$H' = -\sum_{i=1}^{n} p_i (\log_2 p_i),$$

where n is the number of species and p_i is the proportion of the total count arising from the *i*th species (Clarke and Warwick 1994). This index is calculated on basis of what proportion of the total individuals of each species comprises. The Shannon-Wiener index has moderate discriminant ability, an intermediate ease of calculation and is widely used (Magurran 1988). It was chosen in this study because it would allow comparison with other spider studies that have widely used it (as $\log_2$). It has been used in the past African studies e.g. van der Merwe *et al.* (1996), to evaluate diversity in indigenous forests and pine plantations. It has also been used to evaluate spider guild diversity (Barrion 1999) and on other invertebrate taxa other (e.g. Rieske and Buss 2001; Tattersfield *et al.* 2001). In particular, the Shannon-Wiener index has been used in past studies dealing with pitfall-trapping of spiders (Jocqué 1973; Uetz 1975, 1976, 1979; Bultman *et al.* 1982; Green 1999). Recent research work at the same KLEE study site in Kenya has also used the same index (see Keesing 2000) and thus it would be easier to make study comparisons when the same index was used. By using H´ it was also possible to compare the current study with other studies conducted at the same site and/or elsewhere. The study also preferred H´ to the popular α (log-series) index because the later cannot discriminate situations where total species (S) and total number of individuals (N) remain constant except where there is a change in evenness (Magurran 1988). This is because it is purely based on S and N. According to Lewis *et al.* (1988), the Shannon-Wiener diversity index is very useful in describing ecological trends because it adequately includes both species count and evenness. Its weakness lies on the fact that it can be misconstrued when the base logarithm used is not reported (Feinsinger 2001). It has been criticised by some researchers e.g. Feinsinger (2001), who favours the Simpson diversity index.

Species richness

Species richness was quantified using Margalef's index (d) (Clifford and Stephenson 1975):

$$d = (S-1) / \log N$$

where S is the total number of species and N is the total number of individuals. The Margalef's index of species richness minimizes the effect of sample size bias (Odum, 1971). S and d are simple and easy to calculate, but sensitive to sample size (Magurran 1988). This index has been used with success in spider related studies e.g. Norris (1999).

Evenness

The equitability (evenness) index used was Pielou's evenness index, J′, which expresses how evenly the individuals present are distributed among the different species. The index ranges between 0 and 1, with 1 representing even distribution. Lower values on the other hand represent dominance of individual taxa. The index is computed as follows:

$$J' = H' \text{ (observed)} / H'_{\max}$$

where $H'_{\max}$ is the maximum possible diversity, which would be achieved if all species were equally abundant. It reduces dependence on the sample size and is simple to compute (Pielou 1975**;** Clarke and Warwick 1994).

In conclusion, since diversity indices are always difficult to interpret, it is important to use them together with other simpler measures such as total species, abundance and species evenness in order to give a better picture of species diversity. Feinsinger (2001), argued about importance of making use of a wide range of diversity measures since use of species diversity indices alone to evaluate indicator groups and ecological integrity could lead to grave errors in management decisions.

CHAPTER 5: COMMUNITY ANALYSIS OF DIVERSITY IN TERMS OF SAMPLING WITH REFERENCE TO VERTEBRATE HERBIVORE TREATMENTS

Preface

This chapter describes the response of individual diversity indices (univariate analyses) as well as the whole spider community (multivariate analysis of raw abundance data) to the large mammalian herbivore treatments. It examines spiders at a coarse level of resolution, in which case their diversity indices are calculated from all the individual species and their abundances to get an overall index. In addition the overall community is analysed using ordination to establish any underlying patterns reflecting the response to experimental treatments. These analyses have a fairly coarse level of resolution and the study aims to establish its sensitivity to the disturbances caused by grazing. Spider diversity is also related to the variation in vegetation cover and total rainfall. This chapter has been re-organised just about to be submitted to *Journal of Arachnology* (Warui, C. M., Villet, M. H., & Young, T. P. and Joque, R. (in press). Influence of grazing by large mammals on the spider community of a Kenyan savanna.

Introduction

Most wildlife in Kenya live outside the national parks (Mbugua 1986; Western 1989; LWF 1996), where it interacts with livestock and humans, mostly on arid and semi-arid ecosystems. Such interactions are always negative for the wildlife (MacMillan 1986; Prins 1992). However, the economic benefits of both wildlife and cattle call for a strategy that incorporates both of them into management of these ecosystems and helps to maintain native biodiversity (Hopcraft 1990, Young *et al.* 1998). Such a strategy would work well when there is adequate knowledge of livestock, wildlife and vegetation. Schulze and Mooney (1994) reported that a rapid decline in biodiversity in most ecosystems was a product of unsustainable land use that has led to an urgent need for urgent studies on the impact of land management on biodiversity.

Studies in the past have already focused on livestock effects (e.g. O'Connor, 1991; Sinclair and Fryxell 1985; Mace 1991; Dodd 1994; Fleischner 1994; Brown and McDonald 1995; Seymour 1998; Seymour and Dean 1999; Todd and Hoffman 1999).

Others were based on effects of herbivores on vegetation of protected areas (reviewed in Sinclair 1995; Gichohi *et al.* 1996) or on the effects of herbivores on vegetation of communal areas (e.g. Owen-Smith and Dankwerts 1997; Owen-Smith 1998). However, only a few studies reported work on experimental approaches to understanding the interactions among wildlife, livestock and vegetation (e.g. Loft *et al.* 1987; Brown and Heske 1990; Hobbs *et al.* 1996; Young *et al.* 1998). With time, more studies have focused on invertebrate biodiversity in differentially grazed lands (e.g. Seymour 1998; Seymour & Dean 1999; Fabricius *et al.* 2002, 2003; Mayer 2004). Others are based on the effects of cattle grazing on rodents (Jones and Longland 1999). A lot of work done on burning is reviewed in O′Connor (1985) while recent research work on communal rangelands can be found in de Bruyn and Scogings (1998).

However, a few studies have given attention to use of spider diversity in management for example Luff and Rushton (1989) on managed and unimproved upland pasture, Gibson *et al.* (1992) on succession and grazing management while Wheater *et al*. (2000) reported on their use as tools in monitoring reclaimed landforms. Others who have demonstrated use of spiders in management include Maelfait and Hendrix (1998) and Woinarski *et al.* (2002). Finally, very little work has been done on the effects of vertebrate herbivores on invertebrates and this study takes such an approach.

The current study

This study gives a report on spider diversity in relation to different herbivore communities in an East African savanna ecosystem. It hopes to show their indicator value and provide useful information that might be used to assist in sustainable management of this savanna. Very little is known about interactions among native wildlife, domestic livestock, vegetation and any other native biodiversity (Young *et al.* 1998). The central Kenyan savanna provides a great opportunity to investigate this interaction on a shared rangeland at an experimental scale. In this case, spiders are used as taxa to represent the invertebrate part of the native biodiversity and are expected to respond to the differentially grazed and browsed treatments eventually providing means to establishing a management tool for such a highly utilised and essential ecosystem. The spiders are expected to respond to vegetation changes created by different vertebrate herbivores by increasing or decreasing in diversity. According to Fabricius *et al.* (2003), a decline in species diversity is caused by degradation of land as well as the accompanying variation in landscape and plant diversity. With the exception of a few studies (e.g. Rivers-Moore & Samways 1996; Fabricius 1997), the extents to which changes in vegetation composition influence arthropod diversity remain unknown. The current study hopes to address this problem by establishing how a spider community responds to disturbances created by different guilds of large mammalian herbivores. It establishes how spider species diversity, species richness and species evenness varied in the differentially grazed plots. The study also related the resulting changes in vegetation cover to spider diversity and to some other abiotic factors such as rainfall, with a goal of finding out the best possible way of using diversity to assist in sustainable management of this savanna.

Mpala Research Centre represents these savannas and with lower ungulate densities than in the national parks. Here, indigenous wildlife grazers share much of the area with livestock, since the land is outside park protection (LWF 1996), and hence makes the area ideal for such study. There is much debate about conservation of wildlife outside national parks (e.g. McRae 1998) and the point of concern is to help mediate any conflict with humans and their livestock. Moreover, there is also a need to address the issue of populations of indigenous vertebrate herbivores since some researchers believe that they also play a role by competing with cattle for food (e.g. Prins 1992; Happold 1995; Swift *et al.* 1996). Thus by studying the response of spiders to the large mammalian herbivore treatments, it was hoped to generate knowledge that could help in future management decisions aimed at sustainable development in this ecosystem.

The increasing human population has raised pressure on the resources in the Laikipia area and research is needed to address this issue. Recent research work in Northern Kenya (e.g. de Leeuw *et al.* 2001) has reported extensively on livestock, human activities and wildlife. This study therefore hopes to provide some useful information for sustainable management by examining the spider diversity in different forms of land use (grazing regimes) in a black cotton soil savanna ecosystem with an overall aim of biomonitoring.

Objectives

The objectives of this study were:

- To establish the effect of different large mammalian herbivore guilds on the diversity, species richness and species evenness of the spider community.
- To quantify the gradient in vegetation cover in different experimental treatments and relate it to rainfall and spider diversity, species richness and species evenness.
- The null hypotheses were framed in terms of 'no differences between the treatments', where the different treatments were grazing by cattle only (C); mesoherbivores + cattle (WC); mesoherbivores + cattle + megaherbivores (MWC); megaherbivores + mesoherbivores (MW); mesoherbivores only (W) and no ungulates at all (zero or control plots).

The megaherbivores were comprised of reticulated giraffe (*Giraffa camelopardalis* (Linnaeus)), which are browsers, and elephants (*Loxodonta africana* (Blumenbach)), which are browsers but sometimes eat grass. The mesoherbivores were comprised mainly of Grevy's zebra (*Equus grevyi* Oustalet), Burchell's zebra (*E. burchelli* (Gray)), Jackson's hartebeest (*Alcelaphus buselaphus* (Pallas)), Cape buffalo (*Syncerus caffer* (Sparrman)), and Beisa oryx (*Oryx beisa* (Rüppell)), which are mainly grazers and, eland (*Taurotragus oryx* (Pallas)), which are mostly browsers, and Grant's gazelle (*Gazella granti* Brooke) which are mixed grazers and browsers. It is important to note that eland and oryx are grazers that also browse. The study did not exclude the baboons (*Papio anubis* (Lesson)), which feeds on young grass shoots, hares (*Lepus* sp.) and rodents including the common *Saccostomus mearsi* Heller (Keesing 1998, 2000). Steinbok (*Rhaphicerus campestris* (Thunberg)) moved through the fence with ease.

Hypotheses

First, since grazing, browsing and trampling cause disturbances, it was hypothesized that the habitat structure for spiders would be reduced and that there would be a resultant reduction in vegetation cover in all the experimental plots.

Second, the resultant reduction in relative vegetation cover was in turn expected to reduce spider species diversity, species richness and species evenness, since these variables have been found to be favoured by complex habitats (Robinson 1981; Gunnarsson 1988; Balfour and Rypstra 1998). It was therefore hypothesized that the spiders' Shannon-Wiener diversity, species richness, species evenness and total number of species would be significantly and positively correlated to relative vegetation cover, with sweep-netting samples showing a stronger relationship compared to pitfall-trapping samples. This was expected since there were more grazers than browsers resulting into more grazing that would interfere with the habitat of grass-active spiders (caught mainly by sweep net) more than that of ground active spiders (caught mainly by pitfall traps).

Third, overall spider diversity, species richness and species evenness was expected to be significantly different in all experimental treatments since they were subjected to varying degrees of grazing and browsing pressure.

Fourth, it was also hypothesized that the overall community distributed itself in a pattern that reflected the differences in the grazing intensity at the six experimental treatments.

Finally, it was hypothesized that rainfall, relative vegetation cover and herbivores were important predictors of species diversity, species richness, species evenness and total number of species in the experimental treatments. This was thought to be either indirect, by influencing changes in relative vegetation cover, or directly by promoting more spider activity, either due to increased food availability or in search of mates or even due to flooding.

Methods and analysis

Hypothesis 1: The relative vegetation cover varied in all the experimental treatments

Vegetation cover was measured using the pin frame and quadrat method (explained in chapter 2) on two randomly selected transects in each treatment. The first sample was on a 50 m sweeping transect with the first drop of the quadrat being made 5 m from the starting point. Other quadrats were sampled at 10 m intervals. A total of 8 quadrats were sampled on each of the 18 transects. The second transect was 21 m long, beside pitfall traps. The first quadrat was sampled 3 m away from start of the transect. The other quadrats were sampled next to pitfall traps at intervals of 3 m. A total of 6 quadrats were sampled along each transect. In total 14 quadrats (6 from pitfall transect and 8 from sweeping transect) were dropped on the same experimental treatment. For each quadrat, a total of 10 pins were dropped perpendicular to the ground making a total of 140 pin hits per treatment. A record of plant species hit and number of plant hits and bare ground hits were made. Data was collected once a month from May 2001 to end of July 2002. The percentage relative vegetation cover was calculated by deducting the total number of bare hits from 140 pin totals to give the plant cover hits, which were then expressed as a percentage of this total. For analysis of variance, the percentage vegetation cover was arcsine-transformed before being subjected to ANOVA tests as explained in chapter 2. The relative cover was subjected to the series of ANOVAs explained in the next section, to evaluate the effect of different large mammalian herbivores. All the parametric statistical analyses were computed using the program STATISTICA 6.0 (Statsoft Inc 2001).

Procedure for test of herbivory effects

The spider samples from both collecting methods' data sets were subjected to four different ANOVAs to assess six treatment effects on relative vegetation cover and spider diversity measures. These were done as follows:

- A one-way ANOVA with six treatment levels (O, C, WC, MWC, MW, W).
- A 2x3 ANOVA using all six treatments, with two levels for the factor 'cattle' (present and absent) and three levels for the factor 'herbivores' (absent, only meso-herbivores present, both mesoherbivores and megaherbivores present).
- A 2x2 ANOVA testing the effects of factors 'cattle' (with levels present vs. absent) and 'megaherbivores' (with levels present vs. absent) using all treatments containing herbivores (W, WC, MW, MWC). Two treatments (O and C) were omitted because the KLEE experimental layout was not fully crossed.

- A 2x2 ANOVA testing the effects of factors 'cattle' (with levels present vs. absent) and 'megaherbivores' (with levels present vs. absent) using all treatments containing herbivores (W, WC, MW, MWC). Two treatments (O and C) were omitted because the KLEE experimental layout was not fully crossed.

In the subsequent analyses, the two-way ANOVAs were sometimes referred to as first, second and third series ANOVAs. Levene's tests were used to assess homoscedacity of the variances. Where the variances of the data were not homogenous a Kruskal-Wallis test was performed. Tukey'smultiple comparison tests were performed where necessary and are briefly discussed below.

Tukey's multiple comparison tests

Tukey's test is among a group of popular multiple comparisons tests that include Scheffé's, Newman-Keuls' and Duncan's tests among others. It was chosen for the purpose of this study because it is the most widely accepted and commonly used when compared to others (Zar 1999). Einot and Gabriel (1975) recommend it for being simple and having lower power than other methods. More information about this method and its criticism was reviewed in Einot and Gabriel (1975), Tukey (1977) and Ramsey (1978). Tukey's scores well when compared to a number of other techniques (see Day and Quinn 1989; Zar 1999).

Hypothesis 2: species diversity, species richness, species evenness and total number of species are significantly and positively correlated to relative vegetation cover with sweep-netting samples showing a stronger relationship than the pitfall-trapping samples.

The diversity measures calculated are explained in chapter four and included the Shannon-Wiener diversity index (H′), Margalef's species richness index (d), total number of species (S) and Pielou's evenness index (J). All non-parametric multivariate and univariate analyses were computed using PRIMER (Clarke and Warwick 1994). The original abundance data matrices for sweep-netting, pitfall-trapping and total samples (combined sweep-netting and pitfall-trapping) were ran through the DIVERSE module of the PRIMER statistical package (Clark and Warwick 1994) and with reference to a recent user manual and window-based program (Clarke and Gorley 2001) to calculate the various diversity measures. The vegetation cover data were calculated as already explained in hypothesis 1 above. To test the hypothesis, a correlation analysis was done on this relative vegetation cover with the aforementioned diversity measures using the STATISTICA 6.0 program (Statsoft Inc 1999). In addition, a regression analysis was done on the arcsine-transformed relative vegetation cover with the aforementioned diversity measures using the same STATISTICA program, and the coefficient of determination (R^2-value) was used to compare the two results. R^2 value gives the fraction explained by a certain factor, e.g. 0.33 means that the particular factor explains only 33% of the observed variation. The reasons why both correlation and regression were done on the same data was meant to ensure that no information was lost or left out as I tried to establish the trend for the raw untransformed data (correlation) and that of transformed data (regression).

Hypothesis 3: There is variation in spider species diversity, species richness, species evenness and total number of species in the experimental treatments.

The diversity measures used for this analysis were calculated as explained earlier in hypothesis 2 above. The diversity matrices were then rearranged to suit the STATISTICA program, after which it was used for various analyses of variance (ANOVA). The total species, Margalef's index of species richness, Pielou's evenness and Shannon-Wiener's diversity index were all subjected to a series of ANOVAs (explained after hypothesis 1 of this chapter), to evaluate the effect of different ungulates. Levene's test for homoscedacity of data was performed before ANOVA. Tukey's multiple comparison tests were also performed to establish the sources of variation whenever ANOVA tests were significant.

Hypothesis 4: the distribution pattern of overall spider community reflected differences in the six experimental treatments.

In order to explore this hypothesis, ordination was used.

Non-Metric Multidimensional Scaling (MDS)

Unlike Principal Component Analysis (PCA), whose disadvantage is inflexibility of dissimilarity measure and poor distance-preservation (Clarke and Warwick 1994), MDS has flexibilities and has no assumptions about the form of data and is therefore a highly recommended technique (Kenkel and Orloci, 1986). According to Clarke and Warwick (1994), the advantages of MDS include giving a good link between the original data and the final picture and representing complex patterns correctly in low-dimensional space. It has a weakness in that it heavily weights large distances between samples making it important to ordinate the data found in individual clusters separately in order to distinguish their organisation pattern within large clusters (Clarke and Warwick 1994).

MDS only considers that an ordination is important representation of similarity by looking at stress values which range from 0-1 and increase with reduced dimensionality of the ordination. Low stress values (< 0.1) are the best two-dimensional presentation of data point. As the value increases to 0.2, the ordination could still provide useful data representation, but less reliance may be placed on detail of the plot as it can lead to misinterpretation. When the stress exceeds 0.3, the points on the plot are assumed to be arbitrary placed in the two-dimensional ordination space and it is not worth interpreting (Clarke and Warwick 1994).

Similarity matrix

Similarity matrices form the basis of performing most multivariate statistical tests and can be used to discriminate sites from each other, cluster sites into groups that have similar communities, or allow gradation of sites for graphical representation (Clarke and Warwick 1994).

In this study, ordinations were computed in the MDS module of the PRIMER program where the original abundance data matrix was first converted into a Bray-Curtis similarity matrix using the SIMPER module. This is the most commonly used similarity coefficient in ecological work, and in addition, it accounts well for rare species, which are very common in the current study. It naturally neutralises the effects of the rare species in a way such that the rare it is the less it contributes to the overall pattern (Clarke and Warwick 1994).

Hypothesis 5: rainfall, relative vegetation cover and herbivores were important predictors of species diversity, species richness, species evenness and total number of species in the experimental treatments.

In order to test the important predictors for spider diversity changes for the whole model, analyses of covariance (ANCOVAs) were performed. In these analyses, rainfall and relative vegetation cover were taken to be continuous predictors, while various combinations of herbivores (cattle and meso- or megaherbivores) as well as experimental treatments were the categorical predictors. The Shannon-Wiener diversity index, species evenness, and species richness and total number of species from sweep-netting, pitfall-trapping and total samples were the dependent variables. Rainfall readings were obtained and processed as explained in chapter 2. A regression analysis was also done on rainfall with the diversity measures to establish the strength of the relationship.

Terms used

The term mesoherbivores was used instead of wildlife (used by Young *et al.* 1998), to avoid confusion of terms wildlife and megawildlife (which are indeed wildlife) but exist as two different experimental groups in this study set up. The term megaherbivores was used instead of megawildlife. In all cases, the term herbivore was used instead of wildlife that was used by Young *et al.* (1998).

Results

Hypothesis 1: The relative vegetation cover varied in all the experimental treatments

Levene's test on arcsine-transformed relative vegetation cover was not significant ($F_{5, 12}$ = 1.24, p = 0.35). Similarly, the relative vegetation cover was not significantly different between the treatments ($F_{5, 12}$ = 3.07, p = 0.051, Figure 5.1), but there was a trend showing lower means for cattle + megaherbivores + mesoherbivores (MWC) and mesoherbivores + cattle (WC) treatments and high means for control (O) and mesoherbivores + megaherbivores (MW) treatments (Figure 5.1). The trend shown in the figure had the mean relative vegetation cover decreasing in the following order: 62.28 ± 2.62 % in mesoherbivores + megaherbivores, 59.76 ± 4.14 % in control, 56.35 ± 1.22 % in cattle, 55.67 ± 1.09 % in mesoherbivores, 52.94 ± 2.61 % in megaherbivores + mesoherbivores + cattle and 50.99 ± 1.07 % in mesoherbivores + cattle.

A separate 2x3 ANOVA was performed on arc-transformed relative vegetation cover using all six cattle treatments. In this case, all six treatments were used, with two levels for the factor 'cattle' (present and absent) and three levels for the factor 'herbivores' (absent, only meso-herbivores present, both mesoherbivores and megaherbivores present). Only the presence of cattle had a significant negative effect on vegetation cover (lower relative vegetation cover) (Table 5.1). In this case the mean percentage relative cover for cattle plots was 53.43 ± 1.18 while that of the control plots was 59.23 ± 1.74.

A second series of two-way ANOVA was performed on arcsine-transformed relative vegetation cover to establish the effects of the factors 'cattle' (with levels present vs. absent) and 'megaherbivores' (with levels present vs. absent), using all treatments containing herbivores (W, WC, MW, MWC). Two treatments (O and C) were omitted because the KLEE experimental layout was not fully crossed. The results showed that the presence of cattle had a significant negative effect on relative vegetation cover (Table 5.2). In this case the mean percentage relative cover for cattle plots was 51.97 ±1.96 while that of the control plots was 58.97 ± 1.33.

A third series of two-way ANOVA were performed on arcsine-transformed relative vegetation cover to determine the effects of the factors 'cattle' (with levels present vs. absent) and 'mesoherbivores' (with levels present vs. absent) in the four treatments that excluded megaherbivores (O, C, W, WC). The megaherbivore treatments (MW and MWC) were omitted because the KLEE experimental layout was not fully crossed. There was no significant effect of cattle or mesoherbivores on relative vegetation cover (Table 5.3). In both cases the means for cattle and mesoherbivores were lower than the control. The mean percentage relative covers for cattle and mesoherbivores plots were 53.67 ± 1.40 and 53.33 ± 1.24 while that of the control plots were 57.71 ± 2.12 and 58.06 ± 2.07 respectively.

Hypothesis 2: species diversity, species richness, species evenness and total number of species are significantly and positively correlated to relative vegetation cover with sweep-netting samples showing a stronger relationship than the pitfall-trapping samples.

The correlation results for diversity measures from sweep-netting and pitfall-trapping with vegetation cover are shown in Table 5.4. There was a positive significant correlation between the sweep-netting samples Pielou's evenness and Shannon-Wiener diversity index with relative vegetation cover (Figures 5.2 and 5.3 respectively). There was also a positive significant relationship between total species, Margalef's richness and Shannon-Wiener diversity index from total samples (combined sweep-netting and pitfall-trapping) with relative cover (Figures 5.4, 5.5 and 5.6 respectively). The other diversity measures were not significantly related to relative vegetation cover (Table 5.4).

A regression analysis to compare sweep-netting and pitfall-trapping samples' diversity data sets with relative vegetation cover to evaluate their relationship (R^2 or coefficient of determination) is shown in Table 5.5. In addition, regression plots showing the trend for Pielou's evenness and Shannon-Wiener diversity index from both sweep-netting and pitfall-trapping samples are shown in Figures 5.7- 5.8, respectively. Few of the relationships were statistically significant, and those that were had fairly strong predictive power (Table 5.5).

Hypothesis 3: There is variation in spider species diversity, species richness, species evenness and total number of species in the experimental treatments.

Levene's tests on the Shannon-Wiener diversity index, Margalef's species richness index, and species evenness for both sweep-netting, pitfall-trapping and total samples' data sets were not significant (last column of Table 5.6). However, Levene's test was significant for the total species and Shannon-Wiener diversity index from the total samples' data set (Table 5.6). A Kruskal-Wallis test for the total species and Shannon-Wiener diversity index from the total samples' data set were however not significant (χ^2 = 7.33, df = 5, p = 0.20 and χ^2 = 4.66, df = 5, p = 0.46, respectively).

A one-way ANOVA with six treatments levels was performed on spider diversity measures from sweep-netting and pitfall-trapping that showed homoscedacity. There were no significant differences in spider diversity measures in all six treatments for the three data sets apart from the total species and Margalef's species richness index from pitfall-trapping samples (second last column of Table 5.6). A Tukey's post-hoc test performed on total species from pitfall-trapping samples was not significant. However, a similar test on Margalef's richness index from pitfall-trapping samples was significant (Table 5.7), indicating that the plots with cattle only had a significantly higher richness than mesoherbivores + megaherbivores + cattle as well as mesoherbivores + cattle plots.

A separate 2x3 ANOVA was performed on each of the three data sets (sweep-netting, pitfall-trapping and total samples' data sets). In this case, all six grazing treatments were used, with two levels for the factor 'cattle' (present and absent) and three levels for the factor 'herbivores' (absent, only meso-herbivores present, both mesoherbivores and megaherbivores present). There were no significant effects of cattle and megaherbivores

+ mesoherbivores on richness, evenness, total species and diversity of sweep-netting, and total samples' data sets (Table 5.8 and 5.10) respectively. However, there were significant interactions between cattle and megaherbivores + mesoherbivores treatments for total species, Margalef's richness index and Shannon-Wiener diversity index from pitfall-trapping samples (Table 5.9). A further Tukey's post-hoc tests for the total species and Shannon-Wiener diversity index were not significant. However, a Tukey's test for Margalef's richness index revealed that the interaction between cattle plots and megaherbivores + mesoherbivores treatments was significant, with the presence of cattle resulting in a lower means for Margalef's richness index (table 5.11).

A second series of two-way ANOVAs was performed on each of the three data sets (sweep-netting and total samples' data sets) to establish the effects of the factors 'cattle' (with levels present vs. absent) and 'megaherbivores' (with levels present vs. absent), using all treatments containing herbivores (W, WC, MW, MWC). Two treatments (O and C) were omitted because the KLEE experimental layout was not fully crossed. The results showed no significant effect by cattle and megaherbivores on sweep-netting, pitfall-trapping and total samples' data sets (Table 5.12 and 5.14). However, presence of cattle had a significant negative effect on total species, and Margalef's species richness (Table 5.13) for the pitfall-trapping samples. The resulting means for total species were 40.16 ± 1.90 for the control plots and 33.67 ± 1.02 for the cattle plots. Similarly, the means for Margalef's species richness were 6.89 ± 0.28 for the control plots and 5.85 ± 0.16 for the cattle plots.

A third series of two-way ANOVAs was performed on each of the three data sets (sweep-netting, pitfall-trapping and total samples' data sets) to determine the effects of the factors 'cattle' (with levels present vs. absent) and 'mesoherbivores' (with levels present vs. absent) in the four treatments that excluded megaherbivores (O, C, W, WC). The megaherbivore treatments (MW and MWC) were omitted because the KLEE experimental layout was not fully crossed. There were no significant effects of cattle and mesoherbivores on diversity of sweep-netting and total samples' data sets in all plots that excluded megaherbivores (Table 5.15 and 5.20). Only the interaction of cattle and mesoherbivores that was significant for the total species, Margalef's richness index and Shannon-Wiener diversity index for the pitfall-trapping samples (Table 5.16). In this case the means for the significant interactions between cattle and wildlife treatments are shown (Tables 5.17, 5.18 & 5.19). Only the interaction for Margalef's richness index was significant after performing a Tukey's post-hoc test in which case the presence of cattle had a negative effect table 5.18.

Hypothesis 4: the distribution pattern of overall spider community reflected differences in the six experimental treatments.

The results of a multivariate ordination by multidimensional scaling (MDS) to establish the community pattern in grazing treatments for sweep-netting, pitfall-trapping and total (combined) data sets are shown in Figures 5.9-5.11. The stress values were 0.15, 0.01 and 0.07 respectively, which were worth interpreting (Clarke and Warwick 1994). The sweep-netting samples had a clearer separation than the other two, and were divided into two main clusters namely cattle grazing and non-cattle grazing plots with the third cluster of control not coming out clearly (Figure 5.9). Thus it appeared that with the third cluster of control plots, the southern control plot (SO), was the odd one out and seemed to be more aligned to the cattle grazing plots. If this SO was ignored, the other two control plots (NO and CO) that were more to the right hand side could be in their own "third" cluster. Overall, it thus appeared from this figure that grazing and control plots were separated by mesoherbivores (W) and Megaherbivores (M) (as one group), and therefore showing an overall picture of three clusters that reflected changes in spider diversity as a factor of grazing intensity.

A second important factor that seemed to appear in this MDS plot is a separation of the plots along the northern and southern axis with the central plots in between. This implied that there was a role of geographical positioning of plots in explaining the variation in the spider fauna.

With both pitfall-trapping and total data sets, there was almost no separation along the grazing treatments unlike the case of sweep-netting samples (Figure 5.10 and 5.11). The current convex hulls in these two figures show that the grazing treatments overlapped. However, a critical look at these two figures (Figure 5.10 and 5.11), show a faint separation with the plots aggregating to reflect two treatments of cattle- and non-cattle grazing. However some other patterns arose from the two figures. First, Figures 5.10 and 5.11 have a top left cluster of three plots from the central location indicating that pitfall spider fauna of central is slightly different from that of the northern and southern blocks. This implied that a geographical factor was responsible for this variation. A second pattern that seemed to have emerged is that of the control plots which appear as cluster to the top right hand side of Figure 5.11, implying that the overall spider samples (total samples) separated along a grazing and non grazing axis only. Finally, the pitfall fauna of NMWC and SW plots were in their own cluster (Figure 5.10) implying that they were different from the others. This separation complicated the interpretation of these results.

Hypothesis 5: rainfall, relative vegetation cover and herbivores were the important predictors of species diversity, species richness, species evenness and total number of species in the experimental treatments.

On performing analyses of covariance (ANCOVAs) for the whole model to establish the effects of rainfall, relative vegetation cover, mesoherbivores and cattle on the Shannon-Wiener diversity index from sweep-netting samples, no significant effects were observed (Table 5.21). Another similar ANCOVA on the Shannon-Wiener's index from pitfall samples was significant for vegetation cover only. However when another ANCOVA for the whole model was done to establish the effects of rainfall, relative vegetation cover and mesoherbivores and cattle on total number of species from pitfall-trapping samples, the results were significant only for the interaction between cattle and mesoherbibores. A similar analysis for sweep-netting samples showed that only rainfall was a significant factor. A series of other several ANCOVAs for the whole model showed that in all cases, only rainfall and cover and sometimes cattle that were significant predictors of Shannon-

Wiener species diversity, Margalef's species richness, Pielou's species evenness and total number of species for all sweep-netting, pitfall trapping and total samples data sets. None of the analysis was significant for megaherbivores and wildlife.

When another ANCOVA for the whole model was run to establish the effects of rain, relative vegetation cover, grazing treatments and blocks on total number of species from pitfall-trapping samples, there was a significant effect relative vegetation cover, rainfall, blocks and treatments (Table 5.22). A similar ANCOVA run to establish the effects of rain, relative vegetation cover, grazing treatments and blocks on Shannon-Wiener diversity index of spiders from pitfall-trapping samples was significant for rainfall and treatments only (Table 5.23). Other ANCOVAs performed on the effects of blocks and treatments on various diversity variables were significant only for rain and cover.

There was no significant correlation between species diversity, species richness, species evenness or total species and rainfall for total samples (Table 5.24).

Discussion

Hypothesis 1: The relative vegetation cover varied in all the experimental treatments.

The first one-way ANOVA results revealed that there was no significant difference in relative cover between all six treatments.

The results of two-way ANOVA (Tables 5.1-5.2), confirmed that presence of cattle had a significant negative effect on relative vegetation cover, unlike the presence of other large mammalian herbivores. In all cases, the means of both cattle and mesoherbivores were lower than the control. It can be suggested that these results seemed to go two ways. First, it suggests that there were insufficient replicates to give the tests good power. Secondly, the implication of significant tests was that the exclosure treatments significantly affected the vegetation cover and as such the biological hypotheses that there was a variation in relative vegetation cover within the experimental treatments was not rejected. A further conclusion was made that the reduction in relative vegetation cover was mainly an impact of cattle. It was probable that since cattle were the most frequent ungulates in the study plots, then more grazing and trampling occurred in treatments with cattle, thereby reducing the relative vegetation cover. This was in agreement with the past results of studies in the same experimental plots (e.g. Misurelli 2002) where the presence of cattle was significantly related to variation in relative vegetation cover. Research by Mwendera *et al.* (1997) also extensively demonstrated such a response of vegetation to cattle grazing.

It was also possible that factors other than cattle and large mammalian ungulate activities played a role in the variation of relative vegetation cover. For example, the presence of glades in the study area (Figure 2.2), could be speculated to influence the relative vegetation cover readings where transects were on or near them. This statement is supported by past research work near the study area by Young *et al.* (1995), who reported that understory plant species richness and species diversity in Laikipia *Acacia* bushlands were found to be lowest inside glades but increased with distance from glades.

Another factor that could influence cover results, though to a small extent, could be the activities of some animals e.g. aardvarks which threw a lot of soil on the surface (Warui pers. obs.) and could probably occur on vegetation transects and thus interfere with cover results for several months. This study noted that in the process of searching for termites, aardvarks, which were very common in the black cotton soil ecosystem, threw long piles of soil on open ground. It was feared that this could have an effect on relative cover since this study had only 140 pin hits per plot recorded once a month. A suggestion to reduce this risk by increasing vegetation survey transects or making more replicate treatments of large mammalian herbivores might allow better results. However, the logistical implications limited such a precaution during the current study.

Finally, both mesoherbivores and megaherbivores did not have any significant effect on relative vegetation cover (Tables 5.2 and 5.3). One reason might be as already suggested that lack of difference could be associated with lack of sufficient replicates to give the tests adequate power. Secondly, it was probably that both mesoherbivores and megaherbivores were not numerous or frequent enough at the experimental plots to cause any significant changes in relative vegetation cover. It was also possible that most of the common megaherbivores and mesoherbivores were browsers and therefore did not exert a lot of grazing pressure that would reduce the relative vegetation cover. The current study did not make use of beating method might have helped give a measure of some effects of browsers on spider community.

Since cattle were the most abundant mammals in the experimental plots, it was possible that the significant effect of cattle on relative vegetation cover was as a result of them being most common and frequent in the area while the other herbivores were less frequent. It was also possible that since cattle were grazers only, their effect on relative vegetation cover was easily detected through pitfall-trapping and sweep-netting.

Hypothesis 2: species diversity, species richness, species evenness and total number of species are significantly and positively correlated to relative vegetation cover with sweep-netting samples showing a stronger relationship than the pitfall-trapping samples.

Correlation of relative cover and spider diversity revealed that relative vegetation cover explained 25% ($r^2 = 0.25$) of the spider species evenness from the sweep-netting samples and 33% ($r^2 = 0.33$) of the variation in Shannon-Wiener diversity index from the sweep-netting samples. It also explained 24.1%, 21.1% and 29.1% of total species, Margalef's species richness index and Shannon-Wiener diversity index of the total samples' data set respectively. However, it did not significantly explain variation in pitfall-trapping samples, which represented ground active spiders (Table 5.4). From these results the biological hypothesis that the resultant variation in relative cover would in turn negatively affect the spiders, reducing the species richness and diversity was not rejected. However, it should be noted here that other additional factors were also probably responsible for variation in spider diversity. When the two sampling methods were compared using their coefficients of determination (Table 5.5 and Figures 5.7-5.8), it was clear that sweep-netting samples were more affected by variation in vegetation cover compared to pitfall-trapping ones. The biological hypothesis that spider species diversity, species richness and species evenness significantly and positively correlated with relative vegetation cover, with sweep-netting spider samples showing a stronger relationship was not rejected. This implied that spider samples from sweep-netting (grass-active spiders) were more sensitive to changes in vegetation cover than those from pitfall-trapping samples. An alternative explanation could be that factors other than relative vegetation cover were more important in explaining the variation in ground-active spider diversities e.g. rainfall.

Hypothesis 3: There is variation in spider species diversity, species richness, species evenness and total number of species in the experimental treatments.

Pitfall-trapping samples

The results after performing a series of tests for this hypothesis (Tables 5.9, 5.13 and 5.16) clearly showed that in all cases, the presence of cattle had a significant indirect negative effect on spider species richness. A possible explanation was that cattle trample on vegetation and also reduce cover by feeding, thus increasing disturbances. This increased disturbance then reduced spider species richness. To support this, it has been already found that a more complex habitat supports more spiders (Balfour and Rypstra 1998; Raizer and Amaral 2001), while Dean and Connell (1987) showed that increased structural habitat complexity promoted increase in species diversity. The direct effects of cattle might be through hoof action but the writer felt it probably never had major impacts on the spider diversity.

In most of the ANOVA results it was clear that a significantly lower mean in Margalef's species richness index and total species for the pitfall-trapping samples were reported from the cattle plots (i.e. C, MWC and WC plots) compared to MW and control plots. It was probable that the control plots had no disturbance at all, while megaherbivores and mesoherbivores plots had little of it, which in both cases promoted a favourable environment for spiders to thrive, hence an increased species richness. Keesing (1998), working in the same experimental plots, reported that removal of ungulates increased vegetative cover and this has again been suggested to occur in the current study. Such an increase in cover could favour an increase in spider richness as it promotes habitat complexity or structural diversity (Greenstone 1984). Further work in the same study site (Keesing 2000) reported an increased habitat quality (structural complexity) in control plots compared to ungulate plots that resulted in the rodent population becoming twice as dense when ungulates were eliminated. On the other hand, the mesoherbivores and megaherbivores plots had more disturbances that reduced plant diversity or habitat complexity and probably became less preferred by spiders. Supporting research work by Olff and Ritchie (1998) demonstrated that vertebrate herbivores might decrease plant diversity while Rambo and Faeth (1999) reported that vertebrate grazing might decrease insect abundances.

One would have expected that any plot with cattle would have lower species richness and diversity compared to control or other non-cattle plots because cattle were more frequent and were already found to significantly reduce relative vegetation cover (Tables 5.1-5.2). However since this was not so for the cattle only (C) plots, it was thought to be abnormal data behaviour and initially difficult to explain. However, following the results of chapter 8, it can now be suggested that this strange behaviour was caused by the dominant *Aelurillus sp.* whose abundance increased in cattle-grazed plots and decreased in non-cattle grazed ones (Tables 8.40-8.41) and Figure 8.6. More explanation about the behaviour of this species is done in chapter 8.

Use of pitfall trapping in the current study needs to be treated with caution. Past studies have warned about the interpretation of data from pitfall-trapping (e.g. Work *et al.* 2002) since their catches are a product of both numbers of spiders on the ground surface at any given time and of the level of activity of the spiders (Russell-Smith 1999). It is therefore important to note that although pitfall-trapping produced interesting results, it may not be the best technique for comparison of effect of different herbivores on spider diversity due to many limitations (reviewed in Uetz 1975, 1976; Work *et al.* 2002). One of the principles that need to be mentioned here is that it is now very well established that density of the field layers severely affects the efficiency of pitfall traps (Russell-Smith pers. Comm.; Bhriain *et al.* 2002). Traps placed in dense vegetation always catch a much smaller proportion of the total active fauna than those placed in short grass or bare ground. Thus, what the pitfall traps would actually "measure" in each treatment would be the proportion of different types of vegetation cover. While some of the variation in vegetation density will be related to activities of the mammal herbivores (such as grazing, trampling and, indirectly, dunging), there are a host of other factors involved. These may include burning, soil type and depth, and incidences of flooding. During the current study, there were no incidences of burning but there was flooding in November 2001.

However pitfall-trapping helped a lot in sampling species richness within treatments. In addition, since the study also had many other objectives and financial implications that limited use of other methods, it was wise to use them. It is recommended that other methods be used to get more direct measures of population densities of spiders in each of the treatments by using either hand collection from quadrats or a suction pump (if available).

Sweep-netting and the total data set (sweep-netting + pitfall-trapping)

This section indicated no significant results. This might have two implications. It could be possible that there were insufficient replicates to give the tests good power or that the impacts of different large mammalian herbivores were too mild to cause any local change in observed spider diversity. Since all megaherbivores were mainly browsers, it was probable that their browsing did not cause any significant impact on the herb layer targeted by sweep-netting and hence no impact caused on the spider communities. Since sweeping targets both grazer and browser feeding habitats (by sampling grass and low herbs), it was probable that only one of the two groups of herbivores had an indirect effect on spiders. However, it was difficult to detect the group and magnitude of this effect since the spider samples overlapped (i.e. some samples were from grazer levels and some from browser levels). Furthermore, there were a higher proportion of grazers than browsers and therefore more herbivore effects would be on spiders associated with pitfall trapping. A combination of sweep-netting and pitfall-trapping samples' data sets probably reduced the extremes of either of the data sets' sensitivity to herbivores activity. It was also probable that both megaherbivores and mesoherbivores had very little effect on relative vegetation cover and indirectly on spider diversity because they were relatively rare in the study area. It was not possible to quantify their presence during the study period.

Studies performed elsewhere on effects of grazing on diversity of other groups of invertebrates have revealed contrasting results. For example, heavy grazing by sheep reduced abundance and diversity of soil mites in semi-arid shrublands in Western Australia (Kinnear and Tongway in press). A study on effects of grazing in the succulent Karoo in South Africa on pitfall-trapping invertebrate assemblages revealed consistently high invertebrate abundance in heavily grazed areas, greater species richness on moderately grazed areas and high Shannon-Wiener diversity in moderately grazed areas (Seymour and Dean 1999). Elsewhere, research by Fabricius *et al*. (2003) comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket in South Africa, revealed that communal grazing areas are characterized by xeric-adapted reptiles and predatory type of arthropods compared to nature reserve and commercial farms that supported more mesic-adapted reptiles and herbivorous arthropods.

In conclusion, the biological hypothesis that overall spider diversity, species richness and species evenness was significantly different in all experimental treatments, since they were subjected to varying degrees of grazing and browsing pressure, was not rejected. A further conclusion was made that the exclosure treatments had only a weak effect on spider diversity. This was mainly through a direct effect of cattle on vegetation which might in turn affected the spiders. This study also found that spiders from pitfall-trapping samples were less sensitive to disturbances caused by grazing than spiders from sweep-netting samples.

Hypothesis 4: the distribution pattern of overall spider community reflected differences in the six experimental treatments.

The pattern shown by MDS analysis (Figure 5.9), seemed to correspond to the relative vegetation cover distribution pattern, which was found to be lower in grazing plots and higher in control plots i.e. it was possible that the spider community were responding to habitat complexity, which included a factor of vegetation cover. As already explained earlier in this chapter, control plots had the highest relative cover followed by mesoherbivores and megaherbivores while cattle plots had the lowest cover. The non-cattle grazing plots had an intermediate form of vegetation cover probably because they were more rare than cattle in the experimental plots. This could lead to a less complex habitat in the same order such that spiders from sweep-netting samples distributed themselves along the same gradient.

Samples from pitfall-trapping and total data sets were poorly differentiated with respect to the grazing treatments (Figure 5.10-5.11), indicating that they were not as good as sweep-netting samples as indicators of grazing. This might be due to the fact that they were not found on grass and other lower vegetation, which was mostly targeted by grazers, and especially cattle, which were more frequent than other herbivores. The results also showed that the trapping intensity of the pitfalls was higher than that of sweep-netting and had a neutralising effect on pattern of overall community and thus influenced the pattern of total samples which was similar to its samples' pattern. The overall results of the MDS analysis seemed to agree with other results of this chapter and the pattern supported the existing results that there was an effect by cattle on vegetation, which consequently affected the spider community. MDS analysis has been used with success in other biological research e.g. Mekuria *et al.* (2002).

This clustering of the spider community along control, cattle grazing and non-cattle grazing zones in an MDS analysis (although true for only part of the data), agrees with past studies that have already found that habitat complexity (a factor of relative vegetation cover), influences the distribution of grass-active spiders. For example, work by Halaj *et al*. (2000) reported that structural habitat complexity had a profound effect on canopy spiders and other arthropods. Elsewhere, studies by Rypstra (1983) and Wise (1993) found that availability of unique habitat structural features that allow more efficient prey capture may limit some spiders populations more than food itself. Ysnel and Canard (2000) demonstrated that the foliage orientation influence species composition of spider communities. More work supporting importance of habitat complexity on spiders can be found in Robinson (1981), Greenstone (1984), Balfour and Rypstra (1998), and Buddle and Rypstra (2003). Elsewhere, Downes *et al.* (1998) demonstrated the importance of habitat structure in the regulation of local species diversity in an upland stream ecosystem, while Romero-Alcaraz and Avila (2000) demonstrated the importance of landscape heterogeneity in relation to variations in epigaeic beetle diversity in a Mediterranean ecosystem.

In conclusion, the biological hypothesis that the community pattern of the spiders from the overall data set was clearly partitioned to reflect the differences of intensity of grazing and browsing in the six experimental treatments was rejected for pitfall trapping and whole community and accepted for sweep samples. It was further concluded that the spider community did not aggregate to reflect impact by all of the six experimental treatments, but did aggregated to reflect cattle grazing, non-cattle grazing and control treatments in the sweep samples. Sweep-netting samples were a better indicator of grazing effects compared to pitfall-trapping samples.

Hypothesis 5: rainfall, relative vegetation cover and herbivores were important predictors of species diversity, species richness, species evenness and total number of species in the experimental treatments.

The ANCOVAs for the whole model for both sweep-netting and pitfall trapping showed that rainfall was not a significant predictor of diversity for either collecting method when cattle and mesoherbivores were included (results include Table 5.21), but was a significant predictor for diversity of samples from the pitfall collecting method when cattle and mesoherbivores were removed and replaced with blocks and treatments (Tables 5.22 and 5.23). It might be possible that the effects of cattle and rainfall complicated the interpretation, since both cattle and rainfall have already been found to directly affect the spider community. When cattle and mesoherbivores were removed and blocks included, the system apparently became more sensitive to effects of rainfall. It might also be possible that with the inclusion of block effects, which altered the number of degrees of freedom, the power to test effects of rainfall became higher. It is also be likely that spiders from pitfall samples were more sensitive to the effects of rainfall than those from sweep-netting.

There was no significant correlation between species diversity, species richness and species evenness and rainfall as shown in the results (Table 5.24). However this is put to a further test in the next chapter, where it is hypothesized that spider diversity and species richness is strongly correlated to rainfall on a temporal scale. In conclusion the biological hypothesis that rainfall, relative vegetation cover and herbivores were important predictors of species diversity, species richness, species evenness and total number of species in the experimental treatments was rejected. Another conclusion was made that rainfall was more important for ground active spiders (pitfall-trapping samples) than grass active spiders (sweep-netting samples). The study further concluded that there was a need to investigate the effect of rainfall on spider diversity at different temporal scales in order to increase the sensitivity of the test. This is done in the next chapter.

Conclusion

The results of this chapter showed that the exclosure treatments significantly affected plant cover, with the presence of cattle significantly reducing the relative vegetation cover (Tables 5.1 and 5.2). The treatments also significantly affected spider diversity mainly, through the effects of cattle where the presence of cattle significantly reduced the diversity of spiders (Tables 5.9, 5.13 and 5.16). The study further revealed that increase in relative vegetation cover significantly increased the species diversity (Figures 5.3 and 5.6), species richness (Figures 5.4-5.5) and species evenness (Figures 5.2 and 5.7). It is therefore fair to conclude that relative vegetation cover was a fair positive predictor of spider diversity in that it explained 33% of variation in the Shannon-Wiener diversity index (Figure 5.3), 24% of variation in total species (Figure 5.4) and at least 25% of variation in Pielou's evenness index (Figure 5.2). The remaining variation was explained by factors other than relative vegetation cover. It was probable that the direct effects on vegetation mediated an indirect influence of herbivores on spider diversity. Cattle had the greatest effects on relative cover, and this was likely through both trampling and grazing.

The presence of megaherbivores (giraffe and elephants) and also mesoherbivores did not have a significant effect on spiders. It was possible that the usual effects by megaherbivores on shaping landscape through browsing and trampling savanna trees (Dublin 1995) could not be detected since this study did not employ methods such as beating and fogging that would allow such an evaluation. It was also probable that both megaherbivores and mesoherbivores had very little effect because they were relatively rare. The study therefore concluded that the exclosure treatments some effects on spider diversity, species richness and species evenness. Increase in rainfall was found to significantly increase the total number of species and Shannon-Wiener diversity index of spiders from pitfall-trapping samples.

It was also possible that a host of factors other than those investigated in this study, probably played a role in determining the species diversity, species richness and species evenness of spiders. For example the natural annual pattern of spiders that is there regardless of rain e.g. production of eggs, emerging of immatures, mating activities by adults (e.g. where number of males can shoot high within a week) etc. This can make diversity to increase during the reproductive phase and decline to low number frequently during winter. This annual pattern can vary from year to year (van den Berg and Dippenaar-Schoeman 1991). Finally, it might be possible that the effects of herbivores on vegetation and habitat for spiders are more profound in dry years.

Tables

Table 5.1. 2x3 ANOVA on effects of the factors ‘cattle’ (levels: absent [O, W and MW] vs. present [C, WC and MWC]) and ‘herbivores’ (levels: herbivores absent [O and C], only mesoherbivores present [W and CW], and both meso- and megaherbivores present [MW and MWC]) on relative vegetation cover. No treatments were omitted from the data set. * = Significant at α = 0.05.

Treatment	DF	MS	F-value	P-value
Cattle	1	151.90	8.77	0.012*
Megaherbivores + Mesoherbivores	2	40.86	2.36	0.137
Cattle*Megaherbivores + Mesoherbivores	2	14.61	0.84	0.454
Error	12	17.31		

Table 5.2. 2x2 ANOVA on the factors ‘cattle’ (levels: absent [W and MW] vs. present [WC and MWC]) and ‘megaherbivores’ (levels: absent [W and WC] vs. present [MW and MWC]) on relative vegetation cover. Two treatments (O and C) were omitted from the data set so that the analysis was fully crossed. * = Significant at α = 0.05.

Treatment	DF	MS	F-value	P-value
Cattle	1	147.35	12.31	0.008*
Megaherbivores	1	54.91	4.59	0.065
Cattle*Megaherbivores	1	16.31	1.36	0.277
Error	8	11.97		

Table 5.3. 2x2 ANOVA on the factors 'cattle' (levels: absent [O and W] vs. present [C and WC]) and 'mesoherbivores' (levels: absent [O and C] vs. present [W and WC]) on relative vegetation cover. Two treatments (MW and MWC) were omitted from the data set so that the analysis was fully crossed.

Treatment	DF	MS	F-value	P-value
Cattle	1	49.08	3.12	0.115
Mesoherbivores	1	67.07	4.26	0.073
Cattle*Mesoherbivores	1	1.19	0.08	0.790
Error	8	15.74		

Table 5.4. Correlation analysis to establish the relationship of relative vegetation cover and Shannon-Wiener diversity index (H′), Margalef's richness index (d), Pielou's evenness index (J′) and total species (S) with sweep-netting, pitfall-trapping and total samples' data sets. Df = 18. * = Significant at $\alpha = 0.05$.

Method	Diversity variable	r-value	P-value
Sweep-netting samples	S	0.35	0.160
	d	0.31	0.204
	J′	0.54	0.020*
	H′	0.61	0.007*
Pitfall-trapping samples	S	0.29	0.244
	d	0.26	0.304
	J′	0.06	0.809
	H′	0.23	0.356
Total samples (sweep-netting + pitfall-trapping)	S	0.54	0.022*
	d	0.57	0.032*
	J′	0.40	0.105
	H′	0.58	0.012*

Table 5.5. Regression analyses to establish the relationship of relative vegetation cover and Shannon-Wiener diversity index (H´), Margalef's richness index (d), Pielou's evenness index (J´) and total species (S) with sweep-netting and pitfall-trapping samples. (R^2 is the coefficient of determination). Df = 1,16. * = Significant at $\alpha = 0.05$.

Method	Diversity variable	F	R^2-value	P-value
Sweep-netting samples	S	2.19	0.12	0.158
	d	1.79	0.10	0.199
	J´	6.61	0.25	0.021*
	H´	0.37	0.33	0.007*
Pitfall-trapping samples	S	1.22	0.07	0.285
	d	0.90	0.05	0.357
	J´	0.04	0.00	0.843
	H´	0.73	0.04	0.404

Table 5.6. Results of three one-way ANOVAs to test the effects of all the six experimental treatments on Shannon-Wiener diversity index (H′), Margalef's richness index (d), Pielou's evenness index (J′) and total species (S) of samples from sweep-netting, pitfall-trapping and total sample's data sets. Df = 5, 12. * = Significant at $\alpha = 0.05$.

Method	Diversity variable	F-value	P-value	Levene's - P
Sweep-netting samples	S	0.68	0.649	0.580
	d	0.75	0.601	0.664
	J′	0.55	0.733	0.076
	H′	0.22	0.946	0.054
Pitfall-trapping samples	S	3.32	0.041*	0.32
	d	4.03	0.022*	0.606
	J′	1.17	0.379	0.246
	H′	2.41	0.098	0.583
Total samples (sweep-netting + pitfall-trapping)	S	-	-	0.050*
	d	1.04	0.439	0.075
	J′	0.71	0.629	0.078
	H′	-	-	0.017*

Table 5.7. Tukey's multiple range tests to establish the effects of all the different herbivore treatments on Margalef's richness index from the pitfall-trapping samples. Significant differences (at $p < 0.05$) are in bold. Df = 12. The codes are as follow C = cattle, MW = mesoherbivores + megaherbivores, MWC = mesoherbivores + megaherbivores + cattle, O = control, W = mesoherbivores and WC = mesoherbivores + cattle.

Treatment	C	MW	MWC	O	W
MW	0.45				
MWC	**0.04**	0.66			
O	0.10	0.90	1.00		
W	0.82	0.98	0.31	0.55	
WC	**0.03**	0.51	1.00	0.97	0.21

Table 5.8. 2x3 ANOVAs to establish the effects of the factors ‘cattle’ (levels: absent [O, W and MW] vs. present [C, WC and MWC]) and ‘herbivores’ (levels: herbivores absent [O and C], only mesoherbivores present [W and CW], and both meso- and megaherbivores present [MW and MWC]) on Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) from sweep-netting samples. No treatments were omitted from the data set.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	4.50	0.34	0.571
	Megaherbivores + Mesoherbivores	2	5.01	0.38	0.691
	Cattle*Megaherbivores + Mesoherbivores (MW)	2	15.17	1.14	0.351
	Error	12	13.28		
d	Cattle	1	0.01	0.01	0.913
	Megaherbivores + Mesoherbivores	2	0.10	0.32	0.735
	Cattle*Megaherbivores + Mesoherbivores	2	0.48	1.56	0.251
	Error	12	0.31		
J´	Cattle	1	0.00	0.01	0.913
	Megaherbivores + Mesoherbivores	2	0.10	0.32	0.735
	Cattle*Megaherbivores + Mesoherbivores	2	0.48	1.56	0.251
	Error	12	0.31		
H´	Cattle	1	0.01	0.25	0.623
	Megaherbivores + Mesoherbivores	2	0.02	0.40	0.677
	Cattle*Megaherbivores + Mesoherbivores	2	0.00	0.03	0.973
	Error	12	0.05		

Table 5.9. 2x3 ANOVAs to establish the effects of the factors ‘cattle’ (levels: absent [O, W and MW] vs. present [C, WC and MWC]) and ‘herbivores’ (levels: herbivores absent [O and C], only mesoherbivores present [W and CW], and both meso- and megaherbivores present [MW and MWC]) on Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) from pitfall-trapping samples. In this case no treatments were omitted from the data set. * = Significant at α = 0.05.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	14.22	0.91	0.359
	Megaherbivores + Mesoherbivores	2	22.06	1.41	0.282
	Cattle*Megaherbivores + Mesoherbivores	2	100.72	6.43	0.013*
	Error	12	15.67		
d	Cattle	1	0.15	0.38	0.552
	Megaherbivores + Mesoherbivores	2	0.66	1.61	0.240
	Cattle*Megaherbivores + Mesoherbivores	2	3.39	8.27	0.006*
	Error	12	0.41		
J´	Cattle	1	0.00	0.80	0.388
	Megaherbivores + Mesoherbivores	2	0.00	1.72	0.220
	Cattle*Megaherbivores + Mesoherbivores	2	0.00	0.80	0.474
	Error	12	0.00		
H´	Cattle	1	0.00	0.05	0.821
	Megaherbivores + Mesoherbivores	2	0.04	1.70	0.223
	Cattle*Megaherbivores + Mesoherbivores	2	0.10	4.30	0.039*
	Error	12	0.02		

Table 5.10. 2x3 ANOVAs to establish the effects of the factors ‘cattle’ (levels: absent [O, W and MW] vs. present [C, WC and MWC]) and ‘herbivores’ (levels: herbivores absent [O and C], only mesoherbivores present [W and CW], and both meso- and megaherbivores present [MW and MWC]) on Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) from total samples’ data set. In this case no treatments were omitted from the data set.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	40.50	1.29	0.279
	Megaherbivores + Mesoherbivores	2	10.06	0.32	0.732
	Cattle*Megaherbivores + Mesoherbivores	2	51.17	1.63	0.237
	Error	12	31.44		
d	Cattle	1	0.31	0.48	0.504
	Megaherbivores + Mesoherbivores	2	0.38	0.58	0.577
	Cattle*Megaherbivores + Mesoherbivores	2	1.16	1.78	0.210
	Error	12	0.65		
J´	Cattle	1	0.00	0.28	0.607
	Megaherbivores + Mesoherbivores	2	0.00	1.62	0.238
	Cattle*Megaherbivores + Mesoherbivores	2	0.00	0.01	0.990
	Error	12	0.00		
H´	Cattle	1	0.00	0.03	0.878
	Megaherbivores + Mesoherbivores	2	0.03	1.53	0.256
	Cattle*Megaherbivores + Mesoherbivores	2	0.01	0.46	0.637
	Error	12	0.02		

Table 5.11. Mean values for the interaction between cattle plots and megaherbivores + mesoherbivores treatments for the Margalef's richness index from the pitfall-trapping samples. The means having the same letter at the last column of the table are not significantly different using Tukey's test at $\alpha = 0.05$.

Cattle treatment	Wildlife treatment	Mean total species (S)	Standard error	Similarity of means
C	O	7.70	0.49	b
C	MW	5.92	0.22	a
C	W	5.78	0.28	a
O	O	6.17	0.30	b
O	MW	6.71	0.39	b
O	W	7.06	0.49	b

Table 5.12. 2x2 ANOVA to test the effects of factors ‘cattle’ (levels: absent [W and MW] vs. present [WC and MWC]) and ‘megaherbivores’ (levels: absent [W and WC] vs. present [MW and MWC]) on Shannon-Wiener diversity index (H′), Margalef’s richness index (d), Pielou’s evenness index (J′) and total species (S) from sweep-netting samples. In this case, two treatments (O and C) were omitted from the data set so that the analysis was fully crossed.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	10.08	1.00	0.347
	Megaherbivores	1	0.08	0.01	0.930
	Cattle*Megaherbivores	1	24.08	2.39	0.161
	Error	8	10.08		
d	Cattle	1	0.08	0.36	0.567
	Megaherbivores	1	0.02	0.08	0.785
	Cattle*Megaherbivores	1	0.81	3.79	0.088
	Error	8	0.21		
J′	Cattle treatment	1	0.00	0.00	0.949
	Megaherbivores	1	0.00	0.26	0.662
	Cattle*Megaherbivores	1	0.00	0.18	0.685
	Error	8	0.00		
H′	Cattle	1	0.01	0.29	0.608
	Megaherbivores	1	0.00	0.17	0.689
	Cattle*Megaherbivores	1	0.00	0.10	0.759
	Error	8	0.02		

Table 5.13. 2x2 ANOVA to test the effects of factors ‘cattle’ (levels: absent [W and MW] vs. present [WC and MWC]) and ‘megaherbivores’ (levels: absent [W and WC] vs. present [MW and MWC]) on Shannon-Wiener diversity index (H′), Margalef’s richness index (d), Pielou’s evenness index (J′) and total species (S) from pitfall-trapping samples. In this case, two treatments (O and C) were omitted from the data set so that the analysis was fully crossed. * = Significant at α = 0.05.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	126.75	7.84	0.023*
	Megaherbivores	1	10.08	0.62	0.452
	Cattle*Megaherbivores	1	0.75	0.05	0.834
	Error	8	16.17		
d	Cattle	1	3.25	8.96	0.017*
	Megaherbivores	1	0.03	0.09	0.768
	Cattle*Megaherbivores	1	0.18	0.50	0.499
	Error	8	0.36		
J′	Cattle	1	0.00	0.01	0.909
	Megaherbivores	1	0.00	3.51	0.979
	Cattle*Megaherbivores	1	0.00	0.51	0.494
	Error	8	0.00		
H′	Cattle	1	0.05	3.63	0.098
	Megaherbivores	1	0.03	1.85	0.207
	Cattle*Megaherbivores	1	0.01	0.63	0.448
	Error	8	0.01		

Table 5.14. 2x2 ANOVA to test the effects of factors ‘cattle’ (levels: absent [W and MW] vs. present [WC and MWC]) and ‘megaherbivores’ (levels: absent [W and WC] vs. present [MW and MWC]) on Shannon-Wiener diversity index (H′), Margalef’s richness index (d), Pielou’s evenness index (J′) and total species (S) from total samples’ data set. In this case, two treatments (O and C) were omitted from the data set so that the analysis was fully crossed.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	108.00	5.02	0.055
	Megaherbivores	1	1.33	0.06	0.810
	Cattle*Megaherbivores	1	21.33	0.99	0.348
	Error	8	21.50		
d	Cattle treatment	1	1.61	4.04	0.079
	Megaherbivores	1	0.02	0.04	0.837
	Cattle*Megaherbivores	1	0.34	0.85	0.385
	Error	8	0.40		
J′	Cattle	1	0.00	0.21	0.658
	Megaherbivores	1	0.00	0.13	0.732
	Cattle*Megaherbivores	1	0.00	0.08	0.899
	Error	8	0.00		
H′	Cattle	1	0.01	1.91	0.205
	Megaherbivores	1	0.00	0.02	0.886
	Cattle*Megaherbivores	1	0.00	0.50	0.499
	Error	8	0.00		

Table 5.15. 2x2 ANOVA to establish the effects of the factors ‘cattle’ (levels: absent [O and W] vs. present [C and WC]) and ‘mesoherbivores’ (levels: absent [O and C] vs. present [W and WC]) on Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) from sweep-netting samples. In this case two treatments (MW and MWC) were omitted from the data set so that the analysis was fully crossed.

Diversity variable	Treatment	DF	MS	F-value	P- value
S	Cattle	1	2.08	0.16	0.702
	Mesoherbivores	1	6.75	0.51	0.496
	Cattle*Mesoherbivores	1	0.08	0.01	0.939
	Error	8	13.25		
d	Cattle	1	0.26	0.81	0.394
	Mesoherbivores	1	0.09	0.28	0.611
	Cattle*Mesoherbivores	1	0.01	0.04	0.848
	Error	8	0.32		
J´	Cattle	1	0.00	0.36	0.567
	Mesoherbivores	1	0.00	1.11	0.323
	Cattle*Mesoherbivores	1	0.00	0.06	0.821
	Error	8	0.00		
H´	Cattle	1	0.01	0.10	0.760
	Mesoherbivores	1	0.02	0.32	0.588
	Cattle*Mesoherbivores	1	0.00	0.03	0.859
	Error	8	0.05		

Table 5.16. 2x2 ANOVA to establish the effects of the factors ‘cattle’ (levels: absent [O and W] vs. present [C and WC]) and ‘mesoherbivores’ (levels: absent [O and C] vs. present [W and WC]) on Shannon-Wiener diversity index (H′), Margalef’s richness index (d), Pielou’s evenness index (J′) and total species (S) from pitfall-trapping samples. In this case two treatments (MW and MWC) were omitted from the data set so that the analysis was fully crossed. * = Significant at $\alpha = 0.05$.

Diversity variable	Treatment	DF	MS	F-value	P- value
S	Cattle	1	0.33	0.02	0.897
	Mesoherbivores	1	12.00	0.65	0.444
	Cattle*Mesoherbivores	1	161.33	8.72	0.018*
	Error	8	18.50		
d	Cattle	1	0.04	0.09	0.768
	Mesoherbivores	1	0.79	1.71	0.227
	Cattle*Mesoherbivores	1	5.94	12.84	0.007*
	Error	8	0.46		
J′	Cattle	1	0.00	0.44	0.525
	Mesoherbivores	1	0.00	1.94	0.201
	Cattle*Mesoherbivores	1	0.00	1.36	0.277
	Error	8	0.00		
H′	Cattle	1	0.01	0.42	0.536
	Mesoherbivores	1	0.08	2.80	0.133
	Cattle*Mesoherbivores	1	0.18	6.43	0.035*
	Error	8	0.03		

Table 5.17. Mean values for the interaction between cattle plots and megaherbivores treatments for the total species from the pitfall-trapping samples. The means having the same letter at the last column of the table are not significantly different using Tukey's test at α = 0.05.

Cattle treatment	Wildlife treatment	Mean total species (S)	Standard error	Similarity of means
C	O	43.66	2.72	a
C	W	34.33	1.86	a
O	O	36.00	1.53	a
O	W	41.33	3.38	a

Table 5.18. Mean values for the interaction between cattle plots and megaherbivores treatments for the Margalef's richness index from the pitfall-trapping samples. The means having the same letter at the last column of the table are not significantly different using Tukey's test at α = 0.05.

Cattle treatment	Wildlife treatment	Mean total species (S)	Standard error	Similarity of means
C	O	7.70	0.49	a
C	W	5.78	0.28	b
O	O	6.17	0.30	a
O	W	7.06	0.44	a

Table 5.19. Mean values for the interaction between cattle plots and megaherbivores treatments for the Shannon-Wiener diversity index from the pitfall-trapping samples. The means having the same letter at the last column of the table are not significantly different using Tukey's test at α = 0.05.

Cattle treatment	Wildlife treatment	Mean total species (S)	Standard error	Similarity of means
C	O	3.09	0.10	a
C	W	2.68	0.07	a
O	O	2.79	0.12	a
O	W	2.87	0.06	a

Table 5.20. 2x2 ANOVA to establish the effects of the factors ‘cattle’ (levels: absent [O and W] vs. present [C and WC]) and ‘mesoherbivores’ (levels: absent [O and C] vs. present [W and WC]) on Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) from total samples’ data. . In this case two treatments (MW and MWC) were omitted from the data set so that the analysis was fully crossed.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	0.08	0.00	0.962
	Mesoherbivores	1	10.08	0.29	0.606
	Cattle*Mesoherbivores	1	30.08	0.86	0.382
	Error	8	35.08		
d	Cattle	1	0.06	0.08	0.786
	Mesoherbivores	1	0.66	0.88	0.375
	Cattle*Mesoherbivores	1	0.87	1.17	0.311
	Error	8	0.74		
J´	Cattle	1	0.00	0.14	0.718
	Mesoherbivores	1	0.00	2.43	0.157
	Cattle*Mesoherbivores	1	0.00	0.02	0.904
	Error	8	0.00		
H´	Cattle	1	0.00	0.06	0.808
	Mesoherbivores	1	0.05	1.66	0.234
	Cattle*Mesoherbivores	1	0.01	0.27	0.620
	Error	8	0.03		

Table 5.21. An analysis of covariance (ANCOVA) for the whole model to test the effects of total monthly rainfall, relative vegetation cover, mesoherbivores and cattle on the Shannon-Wiener diversity index from sweep-netting samples.

Effect	Df	MS	F-value	P-value
Arcsine-transformed relative vegetation cover	1	0.28	1.21	0.27
Total monthly rainfall	1	0.51	2.21	0.93
Cattle	1	0.00	0.06	0.14
Mesoherbivores	1	0.06	0.25	0.62
Cattle*mesoherbivores	1	0.05	0.20	0.65

Table 5.22. An analysis of covariance (ANCOVA) for the whole model to test the effects of total monthly rainfall, treatments, blocks, relative vegetation cover, mesoherbivores and cattle on the total number of species from pitfall-trapping samples. In this case the blocks represented a spatial scale of hundreds of metres represented by north, central and south sites while the treatments included all the six experimental grazing treatments. * = Significant at $\alpha = 0.05$.

Effect	Df	MS	F-value	P-value
Arcsine-transformed relative vegetation cover	1	62.33	7.78	0.005*
Total monthly rainfall	1	71.87	8.97	0.003*
Blocks	2	36.92	4.61	0.01*
Treatments	5	19.84	2.48	0.03*
Block*Treatments	10	5.01	0.63	0.793

Table 5.23. An analysis of covariance, (ANCOVA), for the whole model to test the effects of total monthly rainfall, relative cover, mesoherbivores and cattle on Shannon-Wiener species diversity from pitfall-trapping samples. In this case the blocks represented a spatial scale of hundreds of metres represented by north, central and south sites while the treatments included all the six experimental grazing treatments. * = Significant at $\alpha = 0.05$.

Effect	Df	MS	F-value	P-value
Arcsine-transformed relative vegetation cover	1	1.08	3.25	0.07
Total monthly rainfall	1	5.22	15.74	0.00*
Blocks	2	0.90	2.71	0.068
Treatments	5	0.83	2.50	0.030*
Block*Treatments	10	0.16	0.48	0.905

Table 5.24. A regression analysis of total rainfall with Shannon-Wiener diversity index, Margalef's richness index, total species and Pielou's evenness from total samples' data set. Df = 1, 85 for regression and df = 87 for correlation.

Method	Diversity variable	r-value	R^2	P-value
Total data set	Total species (S)	0.20	0.03	0.053
	Margalef's species richness index (d)	0.19	0.003	0.079
	Pielou's evenness (J´)	-0.03	0.06	0.012
	Shannon-Wiener diversity index (H´)	-0.09	0.04	0.432

Figures

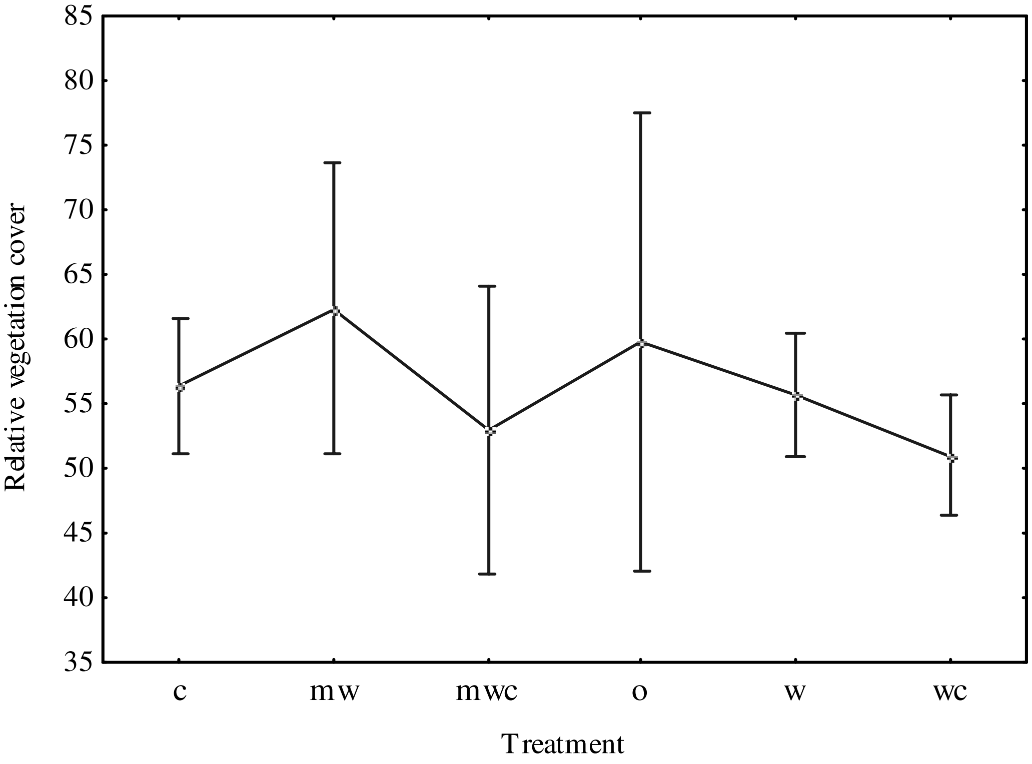

Figure 5.1. Effects of six grazing treatments on arcsine-transformed relative vegetation cover. One-way ANOVA with six treatments levels ($F_{5,\ 12} = 3.07$, $p = 0.051$). The codes are as follows: c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. The bars represent means and standard errors.

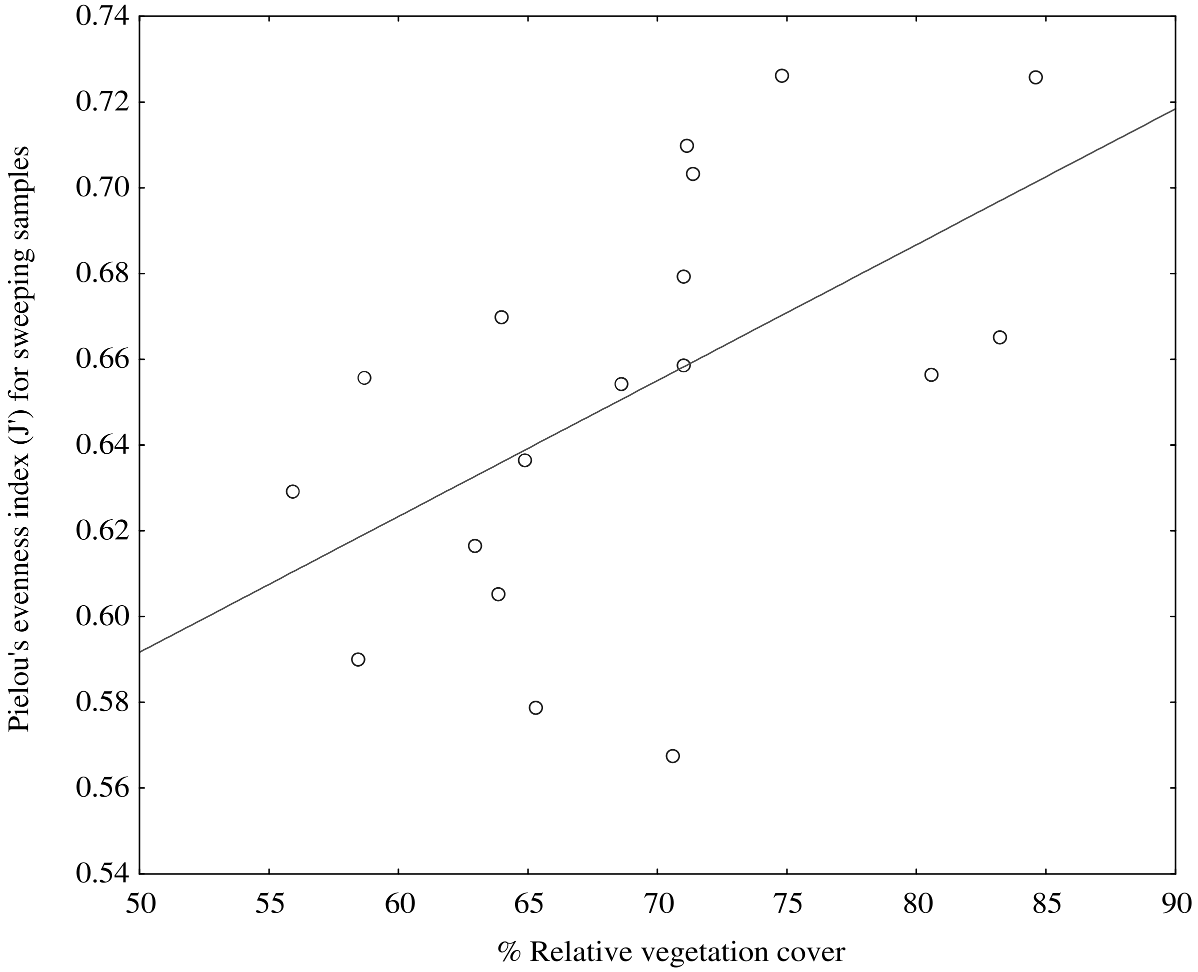

Figure 5.2. A regression of relative vegetation cover (arcsine-transformed) and Pielou's evenness index from sweep-netting samples. The equation is: J' = 0.43 + 0.003 * (relative vegetation cover); $r = 0.54$, $r^2 = 0.25$, $p = 0.02$*, where * = significant at $\alpha = 0.05$.

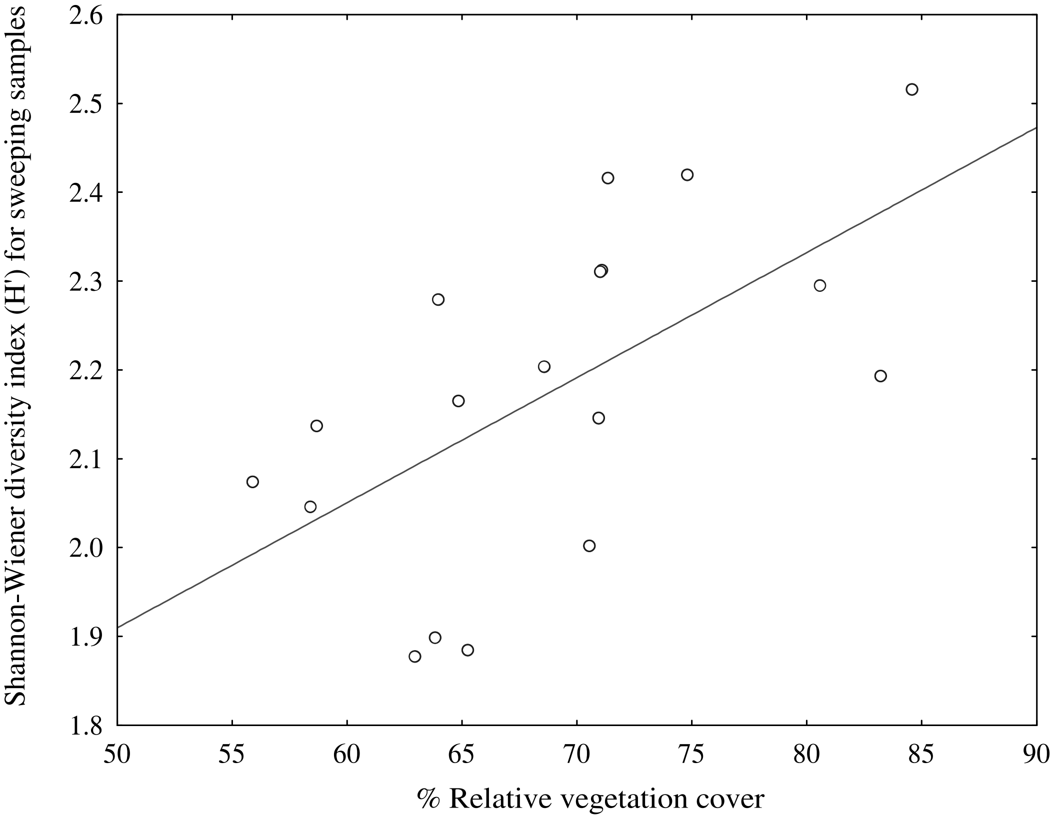

Figure 5.3. A regression of relative cover (arcsine-transformed) and Shannon-Wiener diversity index for sweep-netting samples. The equation is: H' = 1.21 + 0.014 * (relative vegetation cover); $r = 0.61$, $r^2 = 0.33$, $p = 0.007^*$, where * = significant at $\alpha = 0.05$.

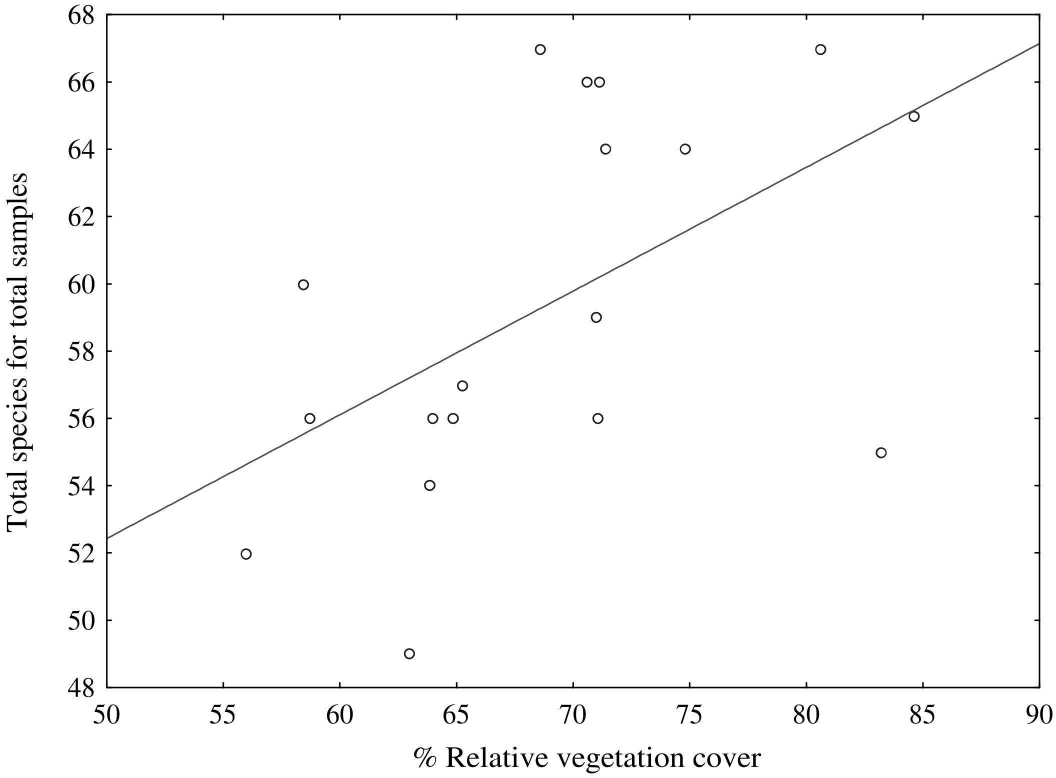

Figure 5.4. A regression of relative vegetation cover (arcsine-transformed) and total species from total samples. The equation is: S = 34.04 + 0.37 * (relative vegetation cover); $r = 0.53$, $r^2 = 0.24$, $p = 0.022^*$, where * = significant at $\alpha = 0.05$.

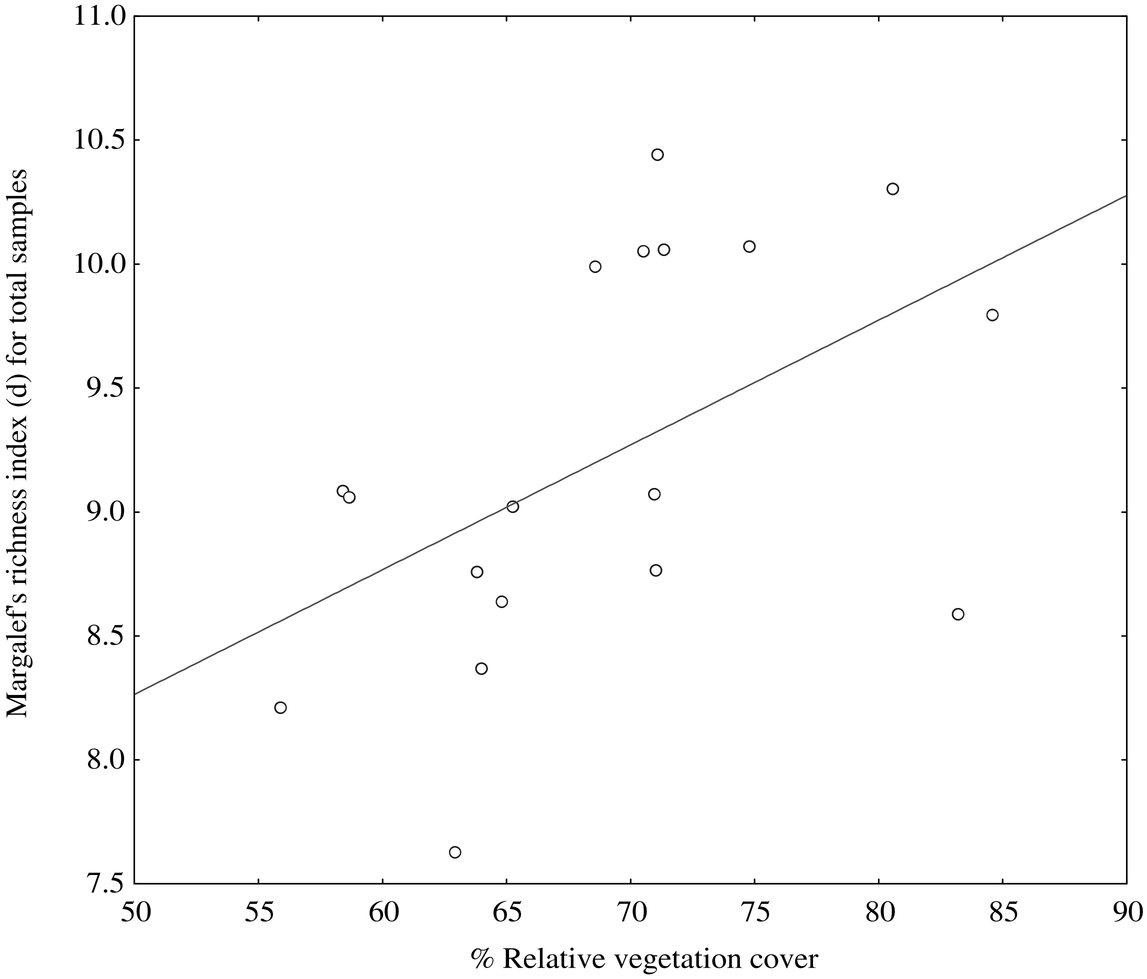

Figure 5.5. A regression of relative vegetation cover (arcsine-transformed) and Margalef's richness index from total samples. The equation is: d = 5.74 + 0 .05 * (relative vegetation cover); $r = 0.507$, $r^2 = 0.21$, $p = 0.032$*, where * = significant at $\alpha = 0.05$.

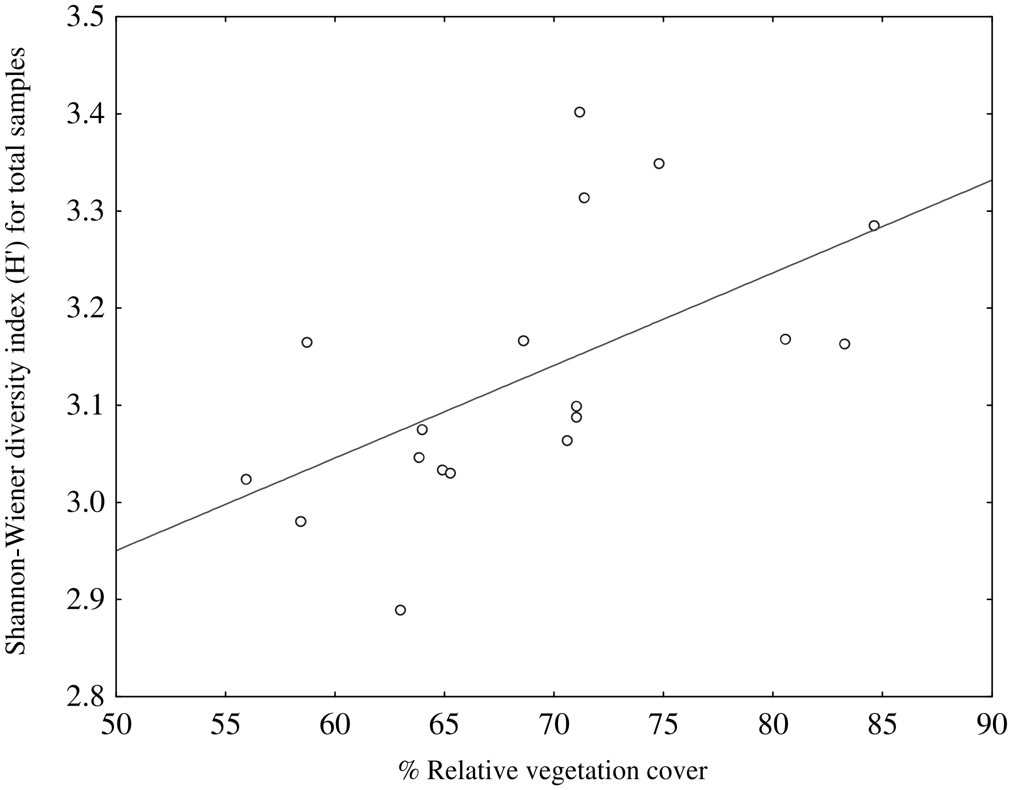

Figure 5.6. A regression of relative vegetation cover (arcsine-transformed) and Shannon-Wiener diversity index from total samples. The equation is: H' = 2.47 + 0.009 * (relative vegetation cover); $r = 0.57$, $r^2 = 0.29$, $p = 0.012$*, where * = significant at $\alpha = 0.05$.

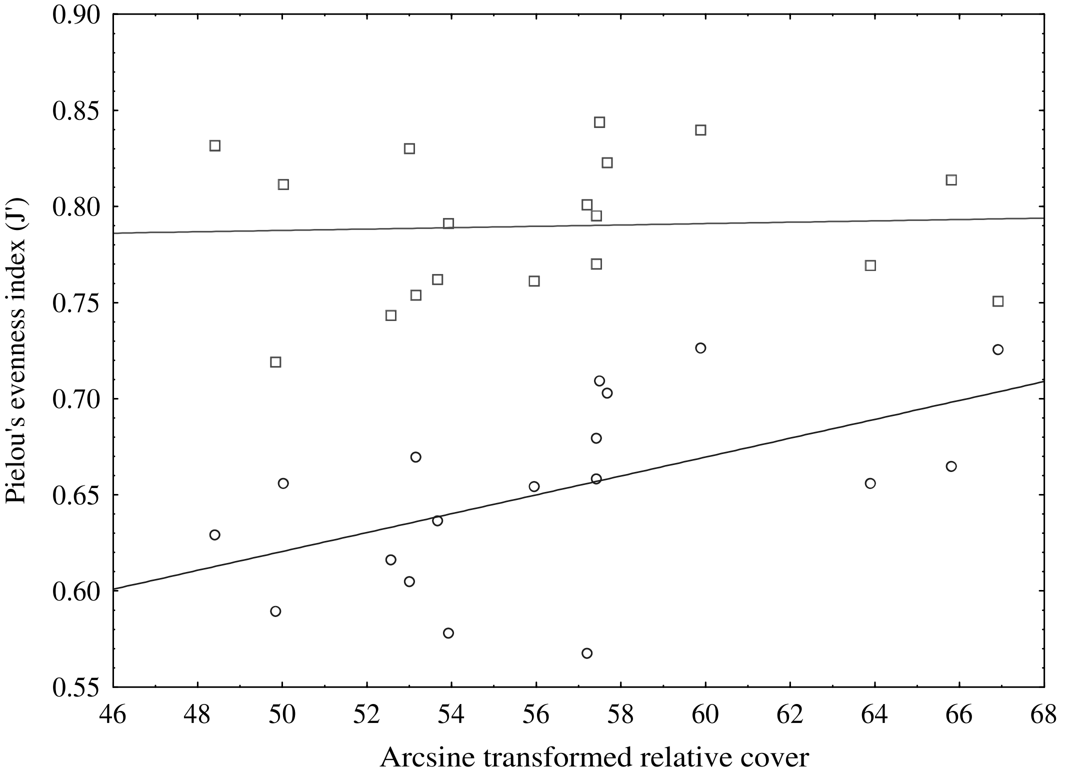

Figure 5.7. A regression of relative vegetation cover and Pielou’s evenness index from both sweep-netting and pitfall-trapping samples. The equations are (i) J´ (sweep-netting samples) = 0.375+0.004* (relative vegetation cover); $R^2 = 0.292$, $p = 0.021$*, where * = significant at $\alpha = 0.05$. (ii) J´ (pitfall-trapping samples) = 0.76+0.000* (relative vegetation cover); $R^2 = 0.003$, $p = 0.843$

Legend

○ Pielou’s evenness index from sweep-netting samples.

☐ Pielou’s evenness index from pitfall-trapping samples.

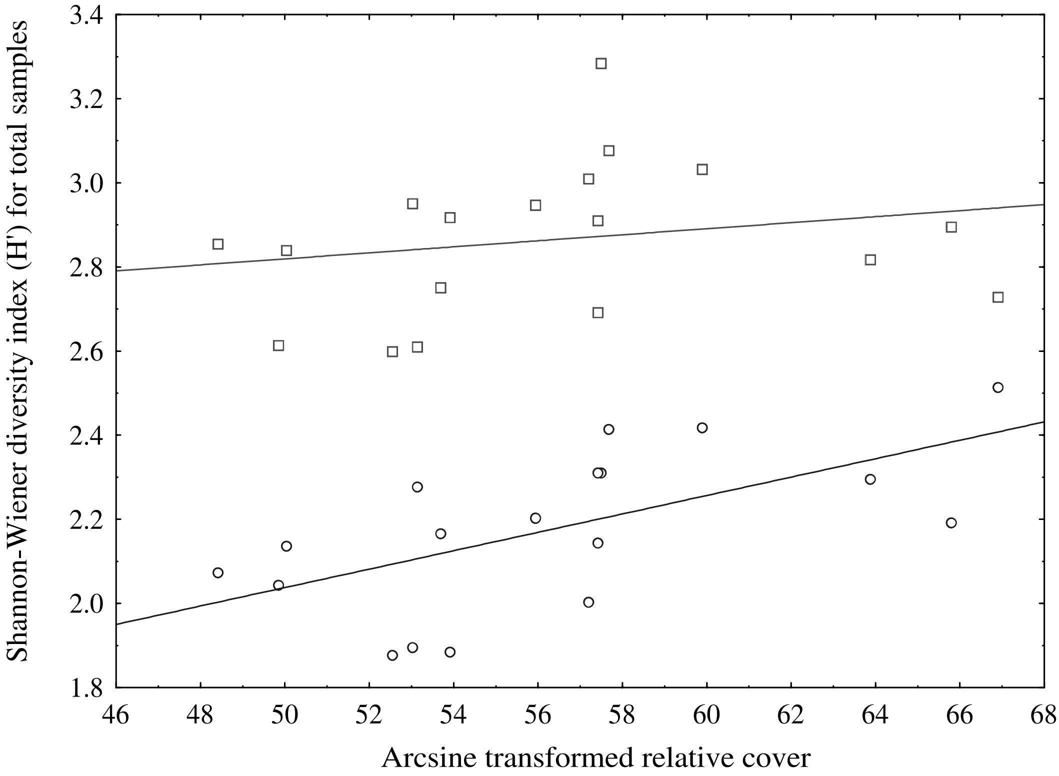

Figure 5.8. A regression of relative vegetation cover and Shannon-Wiener diversity index from both sweep-netting and pitfall-trapping samples. The equations are: (i) H' (sweep-netting samples) = 0.94+0.02 * (relative vegetation cover); $R^2 = 0.372$, p = 0.007*, where * = significant at $\alpha = 0.05$. (ii) H' (pitfall-trapping samples) = 2.46+ 0.007 * (relative vegetation cover); $R^2 = 0.044$, p = 0.404

Legend

○ Shannon-Wiener diversity (H') from sweep-netting samples.

□ Shannon-Wiener diversity (H') from pitfall-trapping samples.

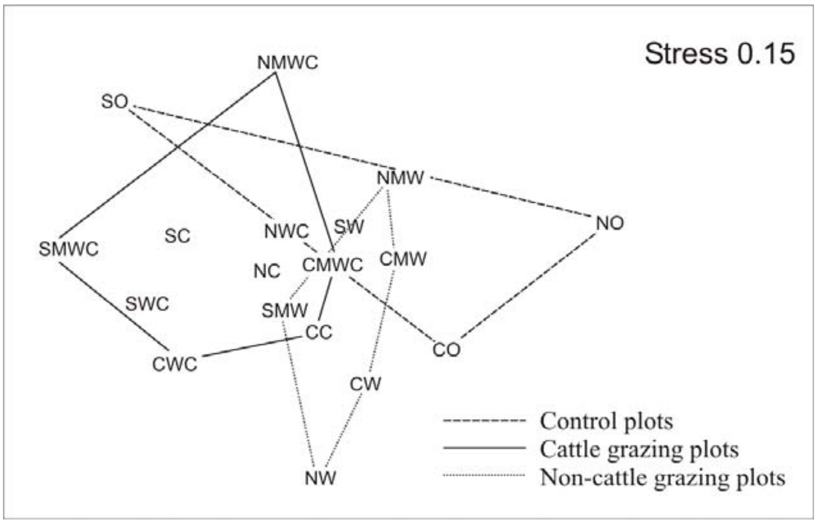

Figure 5.9. Multidimensional scaling (MDS) ordination of the spider community in the sweep-netting samples, with convex hulls superimposed to enclose regions characteristic of control, cattle and non-cattle treatments. In all cases the first letter of any code represents the three study blocks, namely north (N), central (C) and south (S). All other letters represent the animals present, where O = control, C = cattle, W = mesoherbivores, and M = megaherbivores.

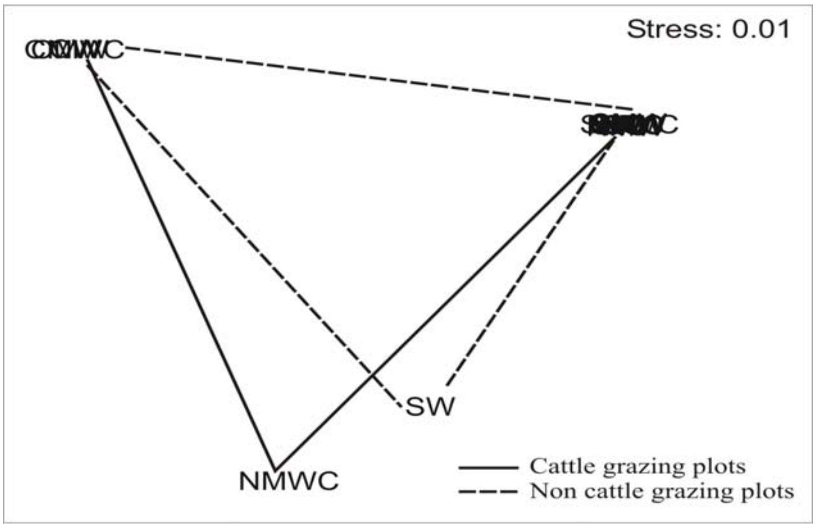

Figure 5.10. Multidimensional scaling (MDS) ordination of the spider community in the pitfall trap samples, with convex hulls superimposed to enclose regions characteristic of control, cattle and non-cattle treatments. In all cases the first letter of any code represents the three study blocks, namely north (N), central (C) and south (S). All other letters represent the animals present, where O = control, C = cattle, W = mesoherbivores, and M = megaherbivores.

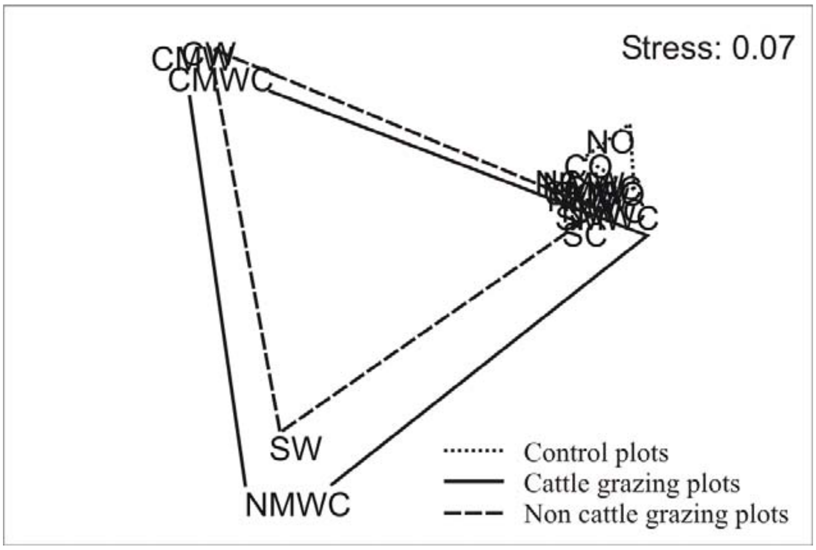

Figure 5.11. Multidimensional scaling (MDS) showing the spider community pattern in cattle grazing, non-cattle grazing and control plots for the total samples. The control plots are in the cluster on the top right hand side of the diagram. In all cases the first letter of any code represent the three study blocks namely north (N), central (C) and south (S). All other letters represent the treatments where O = control, C = cattle, W = mesoherbivores, and M = megaherbivores. Convex hulls enclosed regions characteristic of control, cattle and non-cattle treatments.

CHAPTER 6: SPATIAL AND TEMPORAL VARIATION IN SPIDER COMMUNITY, VEGETATION COVER AND RAINFALL

Preface

This chapter describes the variation in diversity of the spider community at a temporal scale of months and a spatial scale of hundreds of metres (in the form of three study blocks). It also looks at variation at an overall community level of resolution, in which case the diversity indices are calculated from all the individual spider species from all families. The spider diversity is also related to variation in relative vegetation cover and rainfall at the aforementioned scales.

Introduction

One of the important components of ecology is to study factors responsible for abundance and distribution of animals (Andrewartha and Birch 1954). Such factors include spatial and temporal effects. Understanding distribution at different spatial scales help to understand the demographic structure of a population (Kaib *et al.* 1997). Research in the past has related spider diversity to spatial heterogeneity (Uetz 1975). Temporal variation can also influence spider diversity e.g. according to Coddington *et al.* (1990) efficient sampling of spider population needs to account for day and night sampling since particular spiders may be diurnal or nocturnal. Some other examples of studies dealing with response of spiders to temporal or spatial scales are reported in Lubin (1978), Ward and Lubin (1992), Uetz (1975), Churchill and Arthur (1999), and Wagner *et al.* (2003). By understanding how these factors affect spider diversity, one can then try to incorporate such information into management decisions that are based on spider-related studies.

The aim of this chapter is to look at how spider diversity and species richness varies at a temporal scale of months and a spatial scale of hundreds of metres and then to relate it to the patterns uncovered in chapter 5. This will allow understanding of how the spider community responds to the different levels of herbivory and place one in a better position when deciding on the indicator value of the spiders in this savanna ecosystem. It is therefore important to understand how data vary at different spatial and temporal scales, and also to establish the factors that are responsible for such variation, before incorporating such data into management decisions. The short-term need here is to show how spiders respond over short time spans (months and seasons) and how they can therefore can be used as an indicator for conservation purposes. The other need is to add to the existing knowledge of savanna spiders.

Objectives

i) To establish the variation in spider community species richness, evenness and diversity in experimental plots at a spatial scale of hundreds of metres and a temporal scale of months.

ii) To establish the variation in relative vegetation cover at a spatial scale of hundreds of metres and a temporal scale of months.

iii) To establish the relationship between vegetation cover and spider species richness, evenness and diversity in the experimental plots at the aforementioned spatial and temporal scales.

Hypotheses

The first prediction was that there should be variation in relative vegetation cover at the temporal scale of months but not at the spatial scale of hundreds of metres represented by the experimental blocks within the KLEE experimental system. Since the study area has two rainfall peaks per year with some occasional monthly showers, it was expected that relative vegetation cover would respond according to variation in soil moisture caused by the rainfall.

Secondly, it was predicted that variation in relative vegetation cover should be significantly correlated to variation in monthly rainfall, with the high rainfall peaks corresponding to high relative vegetation cover peaks. This prediction was on the basis that rainfall influences the phenology of plants, for example through mineralization that promotes plant growth.

It was expected that spiders would also respond to the annual cycle and show population changes reflecting increase or decrease of food availability in the ecosystem brought by changing rainfall and vegetation cover. Thus, the third hypothesis was that there should be variation of the species diversity, species richness and species evenness of spiders from both sweep-netting and pitfall-trapping samples at the temporal scale of months but not at the spatial scale of hundreds of metres. It was also possible that individual species' timing of events in a lifecycle might change with the seasonal cycle, hence the temporal variation in diversity.

Fourth, variation in species richness, species evenness, species diversity and total number of species was related to corresponding variation in relative cover and rainfall at the temporal scale of months. Since spiders prefer more structurally complex habitats (Robinson 1981; Gunnarsson 1988; Raizer and Amaral 2001) it was expected that a positive increase in relative vegetation cover following rainfall would promote habitat complexity which would in turn favour an increase in spider diversity.

Fifth, it was also hypothesized that the spider community should be aggregated into two groups reflecting the wet and dry rainfall seasons. Since rainfall is an important ecological factor, it was expected that clear differences in vegetation community would influence the spider community. In addition, it is a well-known phenomenon that spiders found in dry habitats tend to emerge after first rains (Jocqué pers. comm.).

Lastly, it was hypothesized that the community pattern of spiders should be evenly spatially partitioned in the three experimental blocks of the KLEE system. Since the KLEE study blocks were not far apart (only a few hundreds of metres), it was expected that there would be no significant differences in soil or other factors that might promote different vegetation communities may be apart from small pockets represented by the glades.

Materials and Methods

Hypothesis 1: there is variation in relative vegetation cover at a temporal scale of months but not at the spatial scale of blocks.

The vegetation cover was sampled as explained in chapter 5. Analysis of variance was performed (on arcsine-transformed relative cover) to analyze variation in cover across months. Levene's test was performed to test homoscedacity of the data. Relative vegetation cover was only measured once a month with one transect per treatment, while pitfall sampling occurred twice a month using three pit-traps in each treatment.

Hypothesis 2: variation in relative vegetation cover is positively correlated to variation in monthly rainfall.

Rainfall measurements were taken as explained in chapter 2. An analysis of variance was performed on the total monthly rainfall (unlagged) with a Levene's test being performed to test the homoscedacity of these data. Correlation of rainfall and relative vegetation cover for each month was also performed. Since it was expected that vegetation would take some time to respond to rainfall changes, another correlation of total monthly rainfall with a one-month lag of relative vegetation cover was also performed to quantify this relationship.

Hypothesis 3: there is variation of the spider community's species diversity, species richness, species evenness and total number of species from both sweep-netting and pitfall-trapping samples, at a temporal scale of months but not at a spatial scale of hundreds of metres.

The calculation of diversity measures used in this study and their justification are explained in chapter 4. The original data matrix of individual species per replicate plot per sampling date was run through the DIVERSE program of the PRIMER software and the diversity measures re-organised. This diversity matrix was then rearranged to suit the STATISTICA 6.0 (Statsoft Inc 2001) software, after which it was used for various analyses of variance (ANOVA) for temporal and spatial variation in diversity. For spatial variation, the block effects were considered by carrying out a two-way ANOVA on the diversity variable using the blocks and treatments as factors (categorical predictors). Tukey's multiple range tests were also performed to establish the sources of variation whenever ANOVA tests were significant. Other analyses included regression and correlation, while relative vegetation cover was calculated as explained in chapter 5.

Hypothesis 4: the variation in spider species diversity, species richness, species evenness and total number of species is related to corresponding variation in relative cover and rain at the temporal scale of months.

Regressions were performed on vegetation cover with various diversity measures, namely total species, Margalef's species richness index, Pielou's evenness index and the Shannon-Wiener diversity index.

Hypothesis 5: the spider community is aggregated into two distinct groups reflecting the wet and dry rainfall seasons.

To test this hypothesis, an ordination by multi-dimensional scaling (chapter 5), was computed to evaluate the distribution of the spider community at the temporal scales of months and fortnights. The original diversity data matrix per treatment per sampling date was used for this analysis and subjected to transformation as necessary. The similarity matrix used as input to a multi-dimensional scaling (MDS) analysis is explained in chapter 5. The determination of wet and dry seasons is explained in chapter 2.

Hypothesis 6: the community pattern is evenly spatially partitioned in the three experimental blocks of north, central and south, which are spatially separated by hundreds of metres.

In order to test this hypothesis, multi-dimensional scaling (MDS) was used. Its computation is explained in chapter 5.

Results and discussion

Hypothesis 1: there is variation in relative vegetation cover at a temporal scale of months but not at the spatial scale of blocks.

The Levene's test performed on the relative vegetation cover data prior to ANOVA was not significant ($F_{12, 26} = 1.47$, $p = 0.19$). A one-way ANOVA revealed a significant difference in the monthly relative vegetation cover ($F_{12, 26} = 20.25$, $p = 0.000$, Figure 6.1). On performing a Tukey's post-hoc test (Table 6.1), the source of variation was found to be because the months of December 2001, January, March and May 2002 had a significantly higher relative cover than the months of June and November 2001. A Levene's test on the effects of study blocks on relative vegetation cover was not significant ($F_{2, 36} = 0.62$, $p = 0.53$). The one-way ANOVA was not significant ($F_{2, 36} = 0.93$, $p = 0.40$).

The results confirmed the hypothesis that relative vegetation cover varied at a temporal scale of months but not at spatial scale of hundreds of metres. Several factors might contribute to such temporal changes in vegetation communities. For example, anthropogenic disturbances or topographic changes can strongly affect vegetation through their effect on soil factors (Schimel *et al*. 1985; Collins 1992; Fisk *et al.* 1998). By influencing plant communities, such factors also affect relative plant cover and this might have happened also in the current study.

Other supporting studies include Shackleton's (1999), who reported the importance of rainfall, topography and edaphic factors in influencing the phenology of savanna woody plants community, while Scholes and Walker (1993) reported the importance of precipitation in savanna dynamics through its effect on nitrogen mineralization. In both cases these factors contribute to changes in the relative vegetation cover and hence a variation at different temporal or spatial scales. Such factors may also play a role in the current study. Bryan and Gross (1999) reported the importance of dispersal mode in controlling rate of woody plant succession and development of spatial structure in plant communities. This might not be a strong argument to explain variation in cover at short time spans, as it would require much larger time scales. However, it is more likely that the amount of rainfall dictates the vegetation community types in savanna ecosystems more than other factors.

Grazing by large mammalian herbivores could also contribute to changes in relative vegetation cover. As an example, research by Olff and Ritchie (1998) demonstrated that vertebrate herbivory occasionally decreases plant diversity, which in turn could cause cover changes. In the current study, herbivores were allowed to graze at controlled rates and this might have controlled cover changes, especially in plots grazed by cattle. Elsewhere, cattle grazing have had profound effects on physiognomy and composition of desert plants (Jones and Longland 1999). By decreasing the abundance of some plants and increasing that of others, such grazing would bring about fluctuations in relative vegetation cover. In the current study, grazing by cattle was associated with reduced relative vegetation cover.

This study found no variation on relative vegetation cover at a spatial scale of hundreds of metres. It was probable that the three blocks were not different in terms of relative vegetation cover because they were not far from one another (see Figure 2.2) and hence experienced similar rainfall, soil and other abiotic factors. The current study blocks were constructed close to one another to minimize cost effects (Young *et al.* 1998) and such a close distance might not reflect a significant change of factors that could cause significant changes in spider communities. Soil could however be an important factor that can cause variation of diversity even at small spatial scales. The biological hypothesis that there was a variation in relative vegetation cover at a temporal scale of months and not at a spatial scale of hundreds of metres in form of the study blocks was not rejected.

Hypothesis 2: variation in relative vegetation cover is positively correlated to variation in monthly rainfall.

The Levene's test performed on the total monthly rainfall data prior to ANOVA was not significant. One-way ANOVA showed a significant difference in monthly rainfall means (Figure 6.2). A Tukey's post-hoc test (Table 6.2) found very high rainfall in November and low rainfall in January and February. There was a no significant (r^2 = 0.046, p = 0.106) correlation between rainfall and relative vegetation cover for the corresponding months (Figure 6.3). When this correlation was repeated with a one-month time lag of the relative vegetation cover, no significant correlation (r^2 = 0.056, p = 0.085) was found (Figure 6.4).

Rainfall varied significantly between months and was highest in November and lowest in February. A negative correlation between rainfall and relative vegetation cover for the same months and a positive one when there was a one-month time lag indicated that vegetation cover took some time to positively respond to an increase in rainfall. Although a pattern was not very evident in this study, it was clear that a time lag existed between a downpour and an increase in vegetation cover (Figures 6.1 and 6.2) where in this case a high peak of rain (November) was followed by a lag in vegetation response to rain (December).

It might be important to note that, whereas the rain positively correlated with the vegetation, the effect is normally gradual. In conclusion, these results implied that rainfall was not a significant predictor of monthly variation in relative vegetation cover. Rain could affect plant cover directly by providing moisture necessary for growth. In summary, the hypothesis that variation in monthly rainfall brought about a variation in relative vegetation cover was rejected. It was probable that other factors played a role on the monthly variation in vegetation cover because rainfall explained only a small proportion of this variation (Figure 6.3). Recent research work by Augustine (2003) on a red soil ecosystem adjacent to the current study area has shown that the variations in herbaceous layer biomass and species composition were primarily associated with a rainfall gradient.

Hypothesis 3: there is variation of the spider community's species diversity, species richness, species evenness and total number of species from both sweep-netting and pitfall-trapping samples, at a temporal scale of months but not at a spatial scale of hundreds of metres.

a) Temporal variation (monthly)

i) Sweep-netting samples

The Levene's test performed on the data for the total species before the ANOVA test was not significant ($F_{14, 507}$ = 1.57, p = 0.082). A one-way ANOVA on total species was significant ($F_{14, 507}$ = 4.46, p = 0.000, Figure 6.5). A Tukey's test revealed a significantly higher richness in August and April compared to November, December and January, and significantly lower mean in January compared to August, June and September.

A Levene's test performed on Margalef's species richness before carrying out an ANOVA test was not significant. A one-way ANOVA of Margalef's species richness index revealed significant differences ($F_{14, 507}$ = 4.273, p = 0.000), Figure 6.6). A post-hoc test revealed high richness in April and low richness in November, January and March.

A Levene's test of Pielou's evenness index from sweep-netting samples was significant ($F_{12, 507}$ = 2.54, p = 0.001). On performing a Kruskal-Wallis test, significant results were realised (χ^2 = 147.86, df = 14, p = 0 .000).

When the Shannon-Wiener diversity indices from the sweep-netting samples were subjected to a Levene's test, the results were not significant ($F_{14, 507}$ = 1.20, p = 0.26). A one-way ANOVA on the Shannon-Wiener diversity index was significant ($F_{14, 507}$ = 3.78, p = 0.000, Figure 6.7). The corresponding Tukey's test revealed that April had a significantly higher richness than all the other months. This might reflect increased spider activity following the start of long rain season of March-May or an increase in the spider population following breeding after the onset of rains.

The spider species diversity, evenness and species richness from the sweep-netting samples varied from month to month. To some extent, the high peaks in spider diversity corresponded to peaks in relative vegetation cover, but not for all months. For example, a high diversity peak in May corresponded well to a gradual increase in rainfall from March to May and might be attributed to an increase in cover from April to May 2002. However this was not the case for some of the other months, since in some cases peaks in diversity corresponded to troughs in rainfall or vegetation cover. For example, the January-February season had very low rainfall but high vegetation cover, and low corresponding spider diversity measures. One possible explanation was that factors other than habitat complexity influenced spider diversity e.g. rainfall itself. It seemed that the relative vegetation cover of Mpala responded very well to water availability (Warui pers. obs.). This is supported by findings of Augustine (2003) that variation in biomass of the herbaceous layer was associated with a rainfall gradient. As such, when a very heavy downpour occurred in November and December, a corresponding increase in vegetation cover was realised in December and January. Cover remained high in February despite no further rain, since grass took time to disappear. However, a reduced moisture level probably made the conditions less conducive for spiders to thrive and thus it was no surprise that with no rain in January, spider species richness and diversity remained low. It was however not enough to attribute changes in cover to rainfall alone. Probably other several factors come into play, e.g. Augustine (in press) reported that factors that affect vegetation also depend on rainfall, temperature and topography (although this does not vary with month). Schimel *et al.* (1985) also reported that grasses respond directly to changes in soil properties on a monthly basis. Herbivore activity might interfere with the spider population through trampling and grazing.

Higher species richness in June 2001 was probably due to higher rainfall in April-May 2001 that brought about higher relative cover and hence a more ideal habitat for spiders. Although not very likely, it was the first month of collecting spiders in the area, so that a higher catch was gotten compared to subsequent months, because spiders were not being removed from the system prior to this month, thereby not lowering the spider diversity within the pitfall-trapping samples.

ii) Pitfall-trapping samples

On performing a Levene's test on the total species from pitfall-trapping samples, the results were not significant. The total species from pitfall-trapping samples differed significantly at a temporal scale of months ($F_{13,\ 490}$ = 9.83, p = 0.000, Figure 6.8). A similar trend was observed for Margalef's species richness index, which was also significant ($F_{13,\ 490}$ = 7.496, p = 0.000). A post-hoc test on total species (Table 6.3) revealed that the sources of variation were June 2001, which had significantly higher diversity than all the other months, and November, which was significantly lower than all the other months. Similarly, a post-hoc test on Margalef's species richness index revealed that the sources of variation were June 2001, which had significantly higher richness than all the other months, and November with a significantly lower richness then all the other months.

A Levene's test performed on species evenness from pitfall-trapping samples was significant ($F_{12,\ 490}$ = 16.19, p = 0.000). A Kruskal-Wallis test on the data was significant (χ^2 = 35.56, df = 13, p =0 .001). A Levene's test on the Shannon-Wiener diversity index from the pitfall-trapping samples was not significant and the subsequent ANOVA test was significant ($F_{12,\ 490}$ = 7.61, p = 0.000). A post-hoc test showed that June 2001 and November were the only odd months (Table 6.4).

The species diversity, species evenness and species richness from the pitfall-trapping samples also varied at the temporal scale of months. It was evident that the sources of differences in pitfall-trapping samples diversity was June 2001 with high figures and November 2001 with low figures. Just as in the case of spiders from the sweep-netting samples, the higher richness in June 2001 might be due to higher rainfall in April-May 2001 that brought about high relative cover, hence a more complex habitat ideal for spiders, with a resultant higher diversity. Another explanation could be the fact that since it was the first time of trapping for a long time, and being the first month of pitfall-trapping in the area, it might have gained higher catch of spiders than the other months (owing to the fact that no prior destructive trapping occurred), hence more richness within the pitfall traps.

The very low figures in November 2001 could be attributed to the good rainfall that was received in that month. A personal observation during this month was that there was flooding that might have affected the surface-active spiders (mostly from pitfall-trapping samples) more than the grass active spiders (mostly from the sweep-netting samples). This could thus have resulted in the big trough observed in November 2001 for the pitfall-trapping samples.

b) Spatial variation (hundreds of metres)

i) Sweep-netting samples

The results of Levene's test and one-way ANOVA showing the variation of diversity measures at a spatial scale of hundreds of metres are indicated on Table 6.5. The total species, Margalef's richness index and Shannon-Wiener diversity index showed significant differences between (Table 6.5). Tukey's post-hoc tests revealed that the source of variation was the south block, which had a significantly lower mean than the north and central blocks. The trend for the Shannon-Wiener diversity index is indicated in Figure 6.9. A Kruskal-Wallis test on Pielou's evenness index was not significant ($\chi^2 = 5.25$, df = 2, p = 0.072).

The results of a 2-way ANOVA, to test the effects of blocks and treatments on total number of species, Margalef's richness index and the Shannon-Wiener diversity index for sweeping samples are shown in appendix 1a, 2a, and 3a respectively. On performing Tukey's post-hoc test, it appeared that in all cases, the source of variation was the southern block, which had a significantly lower total number of species, Margalef's richness index and Shannon-Wiener diversity index than the north and central blocks respectively (appendix 1b, 2b, and 3b).

ii) Pitfall-trapping samples

The results of Levene's test and one-way ANOVA showing the variation of the diversity measures, relative vegetation cover and total rainfall at a spatial scale of hundreds of metres are indicated on Table 6.6. A Tukey's post-hoc test on total species revealed that the source of variation was the southern block, which had a significantly lower mean than both the north and central blocks. The results of Kruskal-Wallis tests on Pielou's evenness index and relative vegetation cover are indicated on Table 6.7.

The results of a two-way ANOVA, to test the effects of blocks and treatments on the same data i.e. total number of species for pitfall-trapping samples are shown in appendix 4a. On performing a Tukey's post-hoc test on these results, it occurred that the source of variation was the southern block, which had a significantly lower total number of species than the north and central blocks (Appendix 4b). The other sets of two-way ANOVAs for Margalef's richness index; Pielou's evenness index and the Shannon-Wiener diversity index were not significant for pitfall-trapping samples ($F_{2,\ 486} = 1.79$, $p = 0.167$ for Margalef's richness index; $F_{2, 486} = 1.09$, $p = 0.337$ for Pielou's evenness index; and $F_{2, 486} = 2.21$, $p = 0.111$ for the Shannon-Wiener diversity index).

At spatial scale of hundreds of metres represented by the three study blocks, there was a slight north-to-south gradient in diversity, which was reflected most strongly in sweep-netting samples (Table 6.5, appendix 1-3) and only by total species from the pitfall-trapping samples (Table 6.6 and appendix 4). In this gradient, the south block had a lower diversity than the central and north blocks (Figure 6.9). The north-to-south gradient was probably caused by factors other than relative vegetation cover or total rainfall. Such factors could probably be related to soil and could also have an effect on plant community and an indirect one on spiders. According to data from past research at the study area, there has been a north-south gradient at the study blocks (Young *et al.* 1998), which suggested that the blocks differ. However, the current study has no data on soil that might help establish causal relationships.

Hypothesis 4: the variation in spider species diversity, species richness, species evenness and total number of species is related to corresponding variation in relative cover and rain at the temporal scale of months.

The results of a regression analysis of diversity measures and relative cover from the sweep-netting samples is shown in Table 6.8 and the resulting patterns from significant results for Pielou's evenness index and the Shannon-Wiener diversity index are shown in Figures 6.10 and 6.11 respectively. In both cases the relationship with cover was very weak but significant.

Results of a regression analysis between diversity measures from pitfall-trapping samples and relative cover is shown in Table 6.9, with no significant relationship being found.

From the results in Tables 6.8 and 6.9, it was very clear that at a temporal scale of months, vegetation cover explained very little of the variation in spider species diversity, evenness or richness. More precisely, it explained only a small variation (0.2 - 2%) in sweep-netting samples (see r^2 in Table 6.8) and a negligible effect (less than 0.2%) in pitfall-trapping samples (see r^2 in table 6.9). These results very weakly supported the findings of chapter 5, where cover was significantly and more strongly related to variation in overall community species richness, evenness and diversity (Figures 5.2-5.7). Earlier in this chapter (Figure 6.4), rain was found to correlate positively but not significantly with relative vegetation. Although only a small fraction of the relative vegetation cover was found to explain variation at a temporal scale of months, it is important to emphasize that most studies clearly demonstrated that spiders greatly preferred structurally complex habitats (Robinson 1981; Gunnarsson 1988; Balfour and Rypstra 1998; Raizer and Amaral 2001). This is further supported by work on other invertebrates showing that structural habitat complexity affected species diversity (e.g. Pianka 1967; Dueser and Porter 1986; Dean and Connell 1987). Magagula (2003) reported very high beetle diversity in habitats with high vegetation compared to intensively managed agroecosystems. As such, a possible explanation as to why relative vegetation cover was not a strong factor at monthly scale might be that other factors came into play and more strongly influenced spider diversity at this temporal scale (e.g. the lag effect). Other such factors might include life cycles of the individual species that involve narrow breeding seasons, or weather factors such as flooding that might severely interfere with spider activities, especially in ground- or surface-active spiders. In conclusion, the null hypothesis that the variation in spider species richness, species evenness and species diversity should be related to corresponding variation in relative cover and rain at the temporal scale of months was not rejected but the relationship was weak.

Hypothesis 5: the spider community is aggregated into two distinct groups reflecting the wet and dry rainfall seasons.

The result of an MDS ordination of monthly data from sweep-netting samples is shown in Figure 6.12, while that from pitfall-trapping samples is shown in Figure 6.13. Both the sweep-netting and pitfall-trapping samples had fairly high stresses of 0.19 and 0.18 respectively. There was only a partial separation of the sweep-netting samples into wet and dry seasons, with most of the wet months clustering to one side and the dry months to the other (Figure 6.12). There was only slight separation of samples from pitfall-trapping, with the dry months clustering to the right and wet months to the left (Figure 6.13).

Although neither of the data sets seemed to aggregate completely according to wet and dry seasons, the community from sweep-netting data set had a more widespread temporal pattern. However, the high stress values for monthly sweep-netting and pitfall-trapping samples meant that less reliance could be placed on the details of these plots and that the results should not be over-interpreted (Clarke and Warwick 1994). With MDS, low stress values (< 0.1) are the best two-dimensional presentation of data points and are reliable compared to higher stress values of 0.3 or more. The spider community represented in the sweep-netting samples seemed to be slightly more evenly distributed than pitfall-trapping samples, indicating that the annual cycle might not have had a great effect on them when compared to the species from the pitfall-trapping samples. However, in both cases it was clear that the spider taxa did not aggregate completely to reflect the wet and dry seasons. There was also weak evidence of seasonally recurring patterns e.g. in Figure 6.13, June 2001 and June 2002 are in different parts of the graph and not close to one another.

The results of an MDS analysis involving complete sweep-netting samples at fortnightly interval of sampling resulted in a very high stress of 0.26 (Figure 6.14). Most samples overlay one another and it was not possible to separate them further. This could be interpreted to mean that either there was no specific temporal pattern of similarity exhibited by spiders in all treatments or that there was a highly complex pattern that was not revealed by this type of ordination. It was possible that many other factors were had a part in determining the community pattern within the treatments, hence the high stress. No reliance could be placed on the details of the plot when such levels of stress occur (Clarke and Warwick 1994). It was therefore not worth interpreting. In conclusion, the null hypothesis that the spider community is aggregated into two distinct groups reflecting the wet and dry rainfall seasons was rejected.

Hypothesis 6: the community pattern is evenly spatially partitioned in the three experimental blocks of north, central and south, which are spatially separated, by hundreds of metres.

The results of MDS analyses to establish the community pattern for data set from the sweep-netting, pitfall-trapping and total samples at a spatial scale of hundreds of metres is shown in Figures 6.15-6.17 respectively. The stress values were 0.15, 0.01 and 0.07 respectively which implied that the plots were reliable two-dimensional representations of the n-dimensional similarities of the samples and therefore worth interpreting (Clarke and Warwick 1994). The results from sweep-netting samples had the best separation compared to the other two, with no clustering of the blocks together. There was a clearer pattern in spider community for sweep-netting samples (Figure 6.15), with the south block existing as a separate unit and north and central blocks aggregating together. The separation of both pitfall-trapping and total samples was not as clear as that of sweep-netting samples (Figure 6.16 and 6.17). Out of 18 plots from the three blocks, most of them (13) clustered at one point and only a few (5) that spread to other parts of the graph, with three of the five forming a small cluster to the left side of the diagram. This cluster presented central mesoherbivore and megaherbivore plots. Thus about three quarters of the plots clustered together, implying that there was no separation for pitfall-trapping and total samples.

The results of sweep-netting samples implied that both central and north blocks were very similar in terms of community, while the south block was different from the two. However this was only based on part of the data. It was thus true that other factors other than those investigated in this study, e.g. edaphic factors, might be responsible for the observed community variation (see Augustine 2003). This study found that at a spatial scale of hundreds of metres, ground-dwelling spiders were poor indicators. The suggested changes of spatial factors such as soil changes, which might be associated with such small spatial scales, were probably not important to these spiders. The changes in soil can interfere with vegetation cover. However in the current study cover was not found to change at a spatial scale of hundreds of metres.

A likely explanation as to why samples from pitfall-trapping and total samples had a similar pattern that different from sweep-netting samples was that the trapping intensity of the pitfalls was higher than that of sweep-netting and yielded more specimens. This might have brought a swamping effect on the total sample such that the resulting pattern of total samples resembled that of pitfall-trapping (Figures 6.16 and 6.17).

In conclusion, the hypothesis that the community pattern of the spiders from the total data set was evenly spatially partitioned in the three experimental blocks of north, central and south blocks separated by hundreds of metres was rejected. However, it seemed that spiders from sweep-netting samples might support the expectation and were therefore a better indicator of spatial separation compared to pitfall-trapping samples.

General discussion and conclusions

In this study, the diversity, evenness, and richness of the spider community varied significantly between months. The same observation was made for rainfall and relative cover. A number of explanations may be put forward to explain temporal and spatial variations in spider diversity measures.

An increase in rainfall might have brought about a corresponding increase in vegetation cover since cover was found to correlate with rainfall (Figure 6.4). In addition, this study also found that relative vegetation cover directly and significantly correlated with community species richness, diversity and evenness (Chapter 5, Figures 5.2-5.6). The same trend was observed at a temporal scale of months but the relationship was not significant (Figures 6.10 and 6.11). It was expected that an increase in vegetation cover brought about a more structurally complex habitat with its own microclimate and hence promoted a more diverse spider community. This was in agreement with the views of Uetz (1991), that complex habitats support more diverse spider communities. Downie *et al*. (1999) and New (1999) further demonstrated the sensitiveness of spiders to habitat structure. Thus, a suggestion from this study was that they responded to slight disturbances caused by grazing and browsing. One of the reasons why some spiders depend on habitat structure is because they need attachment sites for their webs and which in turn their sensory organs rely on to recognize vibrations of the prey (Rovner and Barth 1981; Uetz and Stratton 1982; Arango *et al.* 2000). An environment that allows such complexity would thus enhance food acquisition and survival and was thus preferred to other, less complex habitats. However this argument might hold some truth for spiders from sweep-netting samples because a portion of them were web builders (40.9 %) and would use sensitivity of their web as compared to those from pitfall-trapping samples. The response of spiders from pitfall-trapping samples to a complex habitat may be due to greater food availability and a more secure habitat in which to live and construct their burrows or retreats.

A second possible explanation was that spider population's increase at temporal scales related to their normal life cycles. Different spider species have different life cycles and therefore might reproduce at different times, resulting in varying population peaks as observed across the months. Several different spider species have annual or biennial life cycles (Pickavance 2001). In addition some spider species within these two categories have been found to mature and breed at different times of the year, while others are intermediate between the annuals and biennials (e.g. Dondale 1977). As such it is possible that fluctuations in spider diversity at temporal or spatial scales is caused by these natural lifecycles rather than by other factors, or that these cycles complicate the temporal patterns. Draney and Crossely (1999) reported spider phenology to vary geographically and from one year to another. Such variation would strongly influence the temporal pattern of the species concerned and hence cause variation in abundance and diversity.

A third explanation might be that natural spider activity, e.g. during mating or food acquisition, following patterns of rainfall might also contribute to fluctuations in monthly abundance and also diversity and species richness measures. The arrival of rainfall might cause a change in levels of spider activity. Rain provides moisture, which in turn makes several contributions to an ecosystem. Spiders are known to increase their activity after rainfall (Jocqué pers. comm.) and such activity is mainly aimed at reproduction and parental care with a net result of an increased population. Past studies on spider activities have reported increased activity after rain and the predominance of male spiders in pitfall samples as they seek mates after rains. Diversity and abundance wolf spiders relate positively to relative soil moisture and temperature (Wenninger and Fagan 2000); moisture was a key factor in fairly specific habitat preferences of several species of the genus *Pardosa* Lowrie (1973). Apart from spiders, other invertebrates also distribute themselves along moisture gradients e.g. rainfall was a more important factor than other environmental factors in determining the faunal patterns of terrestrial mollusks (Tattersfield *et al*. 2001). Davis (1996c) reported the importance of rainfall and temperature in determining spatio-temporal variation in dung beetle (Coleoptera) activity. It is thus possible that this could be another factor that might be influencing the invertebrates and including the spiders. The importance of light intensity and temperature in determining the diel and seasonal community dynamics in assemblage of dung beetles has also been documented (Davis 1996b). However, it is unlikely that temperature may influence the activity of spiders to a big extent. It might however be possible that an increase in prey availability may affect diversity of spiders in the current study since it has been found to occur elsewhere (see work by Kronk and Riechert 1979; Henschel and Lubin 1997).

It is fair to argue that many other factors come into play and that no single factor could explain the temporal and spatial variation in spider diversity. Several factors affect species diversity, richness, abundance and evenness, including structural habitat complexity (Robinson 1981; Balfour & Rypstra 1998; Greenstone 1984); competition, productivity, predation and environmental stability (Rosenzweig 1995; Whitmore *et al.* 2002b); seasonality (Russell-Smith 1981, 1999); and habitat type (Jennings *et al.* 1988; Russell-Smith 1999). It is also important to note that even the method and time of sampling may affect the spider composition at different temporal and spatial levels (Churchill 1993; Green 1999), and therefore it is important to bring all of them into consideration. Finally it is important to take a caution when making use of species diversity data into conservation and management decisions because it can influence the comparison of data (Disney 1986). As an example, Churchill & Arthur (999) clearly demonstrated that the interval of sampling (various temporal scales) could have a profound effect on observed species diversity data at family or individual species level.

In conclusion, this study found that both relative vegetation cover and total rainfall varied at a temporal scale of months. Species diversity and species richness varied significantly at a spatial scale of hundreds of metres, with the southern blocks showing lower means. There was a north-to-south gradient, which was reflected more strongly in sweeping samples. Relative vegetation cover correlated positively and weakly to lagged total rainfall but this was not significant. The study also found that at a temporal scale of months, cover explained very little variation in spider diversity, suggesting that it was not important and other factors were also important in determining the variation of the species diversity, species richness and species evenness. Finally, the study found that the spider fauna did not aggregate into distinct groups reflecting the wet and dry seasons of the study period at a temporal scale of months. Multivariate analysis also revealed that only samples from sweep-netting (Figure 6.15) and not from pitfall-trapping and total samples (Figure 6.16 and 6.17) that were spatially partitioned at a scale of hundreds of metres (Figure 6.15).

Tables

Table 6.1. Tukey's post-hoc tests comparing relative vegetation cover changes at a temporal scale of months from June 2001 to July 2002 inclusive. The codes represent the months of the year, while numbers 1 and 2 represent years 2001 and 2002 respectively. Significant values are in bold ($p < 0.05$). Ms = 4.73, df = 26.

	Ju1	Jl1	Au	S	O	N	D	Ja	M	A	My2	Ju2
Jl1	1.00											
Au	0.96	0.95										
S	0.99	0.99	1.00									
O	0.96	0.97	0.24	0.38								
N	1.00	1.00	0.67	0.83	1.00							
D	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**						
Ja	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.97					
M	**0.00**	**0.00**	0.11	**0.06**	**0.00**	**0.00**	**0.01**	0.18				
A	0.67	0.64	1.00	1.00	0.07	0.28	**0.00**	**0.00**	0.37			
My2	**0.00**	**0.00**	**0.10**	0.05	**0.00**	**0.00**	**0.01**	0.21	1.00	0.33		
Ju2	0.57	0.53	1.00	0.99	**0.05**	0.21	**0.00**	**0.00**	0.47	1.00	0.42	
Jl2	0.95	0.94	1.00	1.00	0.23	0.65	**0.00**	**0.00**	0.12	1.00	0.10	1.00

Table 6.2. Tukey's post-hoc tests of total monthly rainfall changes from May 2001 to July 2002 inclusive. The codes represent the months of the year, while numbers 1 and 2 represent years 2001 and 2002 respectively. Significant values are in bold ($p < 0.05$). MS = 286, df = 72.

	My1	Ju1	Jl1	Au	S	O	N	D	Ja	F	M	A	My2	Ju2
Ju1	0.66													
Jl1	1.00	0.99												
Au	1.00	0.61	1.00											
S	0.99	**0.00**	0.17	0.75										
O	1.00	0.16	0.92	1.00	0.99									
N	**0.00**	**0.03**	**0.00**	**0.00**	**0.00**	**0.00**								
D	1.00	0.66	1.00	1.00	0.69	1.00	**0.00**							
Ja	0.06	**0.00**	**0.00**	**0.00**	0.41	**0.02**	**0.00**	**0.00**						
F	**0.00**	**0.00**	**0.00**	**0.00**	**0.02**	**0.00**	**0.00**	**0.00**	0.99					
M	0.95	**0.00**	0.07	0.51	1.00	0.94	**0.00**	0.45	0.65	**0.04**				
A	1.00	0.92	1.00	1.00	0.36	0.99	**0.00**	1.00	**0.00**	**0.00**	0.18			
My2	0.94	1.00	1.00	0.96	**0.03**	0.56	**0.00**	0.97	**0.00**	**0.00**	**0.01**	1.00		
Ju2	1.00	**0.02**	0.49	0.97	1.00	1.00	**0.00**	0.96	0.13	**0.00**	1.00	0.75	0.15	
Jl2	0.98	**0.00**	0.12	0.63	1.00	0.98	**0.00**	0.58	0.53	**0.03**	1.00	0.26	**0.02**	1.00

Table 6.3. Tukey's post-hoc tests of monthly total species from the pitfall-trapping samples from June 2001 to July 2002 inclusive. The codes represent the months of the year, while numbers 1 and 2 represent years 2001 and 2002 respectively. Significant values are in bold ($p < 0.05$). MS = 6.70, df = 490.

	Ju1	Jl1	Au	S	O	N	D	Ja	F	M	A	My2	Ju2
Jl1	**0.00**												
Au	**0.02**	1.00											
S	**0.00**	1.00	0.74										
O	**0.03**	1.00	1.00	0.61									
N	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**								
D	**0.00**	0.32	**0.04**	0.98	**0.02**	0.09							
Ja	**0.00**	1.00	1.00	1.00	0.99	**0.00**	0.54						
F	**0.00**	1.00	0.98	1.00	0.94	**0.00**	0.77	1.00					
M	**0.00**	0.98	0.61	1.00	0.47	**0.00**	1.00	1.00	1.00				
A	**0.00**	0.99	0.64	1.00	0.51	**0.00**	0.99	1.00	1.00	1.00			
My2	**0.00**	1.00	0.85	1.00	0.74	**0.00**	0.95	1.00	1.00	1.00	1.00		
Ju2	**0.00**	1.00	0.96	1.00	0.91	**0.00**	0.82	1.00	1.00	1.00	1.00	1.00	
Jl2	**0.00**	1.00	1.00	1.00	0.98	**0.00**	0.61	1.00	1.00	1.00	1.00	1.00	1.00

Table 6.4. Tukey's post-hoc tests of monthly Shannon-Wiener diversity index from the pitfall-trapping samples from June 2001 to July 2002 inclusive. All the codes represent the months of the year, while numbers 1 and 2 represent years 2001 and 2002 respectively. Significant values are in bold ($p < 0.05$). MS = 0.283, df = 490.

	Ju1	Jl1	Au	S	O	N	D	Ja	F	M	A	My2	Ju2
Jl1	0.41												
Au	0.63	1.00											
S	**0.00**	0.87	0.69										
O	0.08	1.00	1.00	1.00									
N	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**								
D	**0.00**	0.19	0.09	1.00	0.67	**0.00**							
Ja	0.15	1.00	1.00	0.99	1.00	**0.00**	0.47						
F	0.06	1.00	1.00	1.00	1.00	**0.00**	0.73	1.00					
M	**0.01**	0.99	0.93	1.00	1.00	**0.00**	0.96	1.00	1.00				
A	**0.00**	0.95	0.83	1.00	1.00	**0.00**	0.99	1.00	1.00	1.00			
My2	0.20	1.00	1.00	0.97	1.00	**0.00**	0.39	1.00	1.00	1.00	0.99		
Ju2	0.07	1.00	1.00	1.00	1.00	**0.00**	0.69	1.00	1.00	1.00	1.00	1.00	
Jl2	**0.01**	0.99	0.94	1.00	1.00	**0.00**	0.96	1.00	1.00	1.00	1.00	1.00	1.00

Table 6.5. Levene's tests and one-way ANOVAs comparing the variation of the Shannon-Wiener diversity index (H′), Margalef's richness index (d), Pielou's evenness index (J′) and total species (S) from sweep-netting samples at a spatial scale of hundreds of metres, in form of three study blocks of north, central and south. Df = 2, 519. * = Significant at α = 0.05.

Diversity variable	Levene's p-value	F	P-value
S	0.223	14.20	0.000*
d	0.600	9.048	0.000*
J′	0.008*	-	-
H′	0.45	14.20	0.000*

Table 6.6. The results of a Levene's test and one-way ANOVA comparing the variation of Shannon-Wiener diversity index (H′), Margalef's richness index (d), Pielou's evenness index (J′) and total species (S) from pitfall-trapping samples at a spatial scale of hundreds of metres in the form of three study blocks of north, central and south. Df = 2, 519. * = Significant at α = 0.05.

Variables	Levene's p-value	F	p-value
S	0.235	3.18	0.042*
d	0.613	1.80	0.166
J′	0.017*	-	-
H′	0.595	2.21	0.111
Relative vegetation cover	0.001*	-	-
Total monthly rainfall	0.430	0.19	0.825

Table 6.7. Kruskal-Wallis tests to establish the variation of Pielou’s evenness index (J′) from pitfall-trapping samples and relative vegetation cover at a spatial scale of hundreds of metres in the form of three study blocks of north, central and south. Df = 2, 519.

Variables	χ^2	p-value
Pielou’s evenness	0.761	0.683
Relative vegetation cover	1.334	0.513

Table 6.8. Regression analysis showing the relationship between relative vegetation cover and monthly Shannon-Wiener diversity index (H′), Margalef’s richness index (d), Pielou’s evenness index (J′) and total species (S) from sweep-netting samples. Df = 1, 502. * = Significant at $\alpha = 0.05$.

Diversity variable	Multiple r^2	R-value	P-value
S	0.002	0.004	0.929
d	0.005	0.083	0.062
J′	0.022	0.155	0.000*
H′	0.007	0.092	0.038*

Table 6.9. Regression analysis showing the relationship between relative vegetation cover and monthly Shannon-Wiener diversity index (H′), Margalef’s richness index (d), Pielou’s evenness index (J′) and total species (S) from pitfall-trapping samples. Df = 1, 502.

Diversity variable	Multiple r^2	R value	P value
Total species - S	0.000	0.043	0.366
Margalef’s species richness - d	0.002	0.016	0.721
Pielou’s evenness - J′	0.002	0.062	0.166
Shannon index - H′	0.002	0.016	0.715

Figures

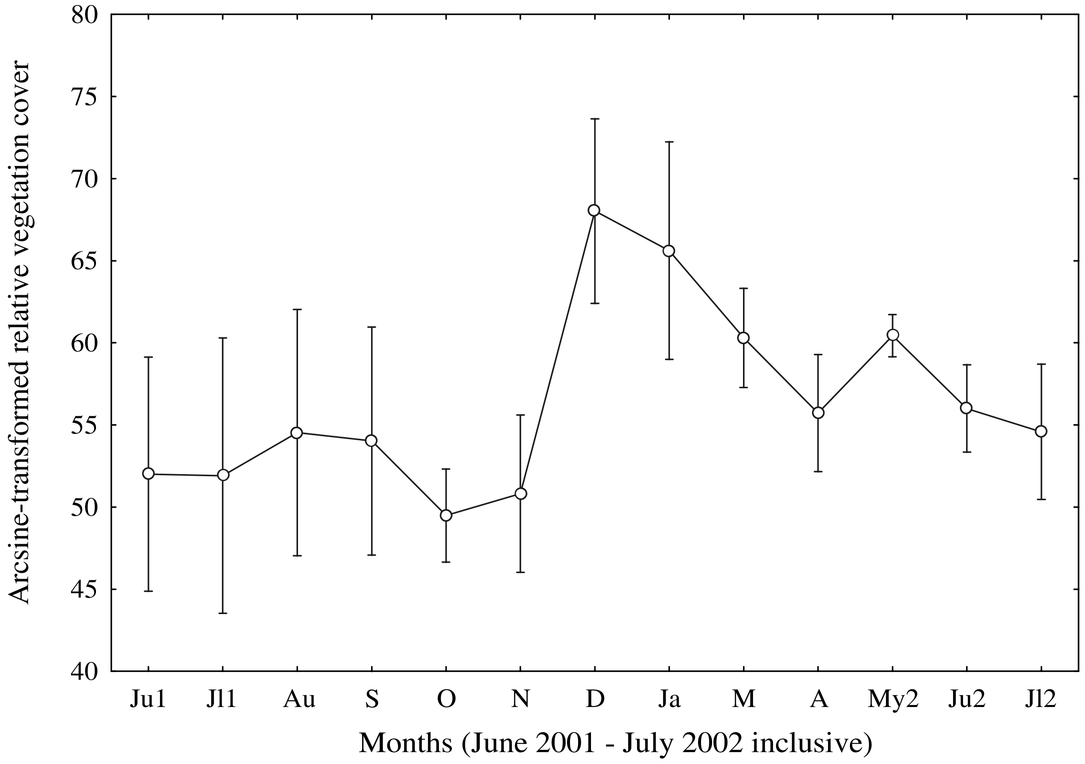

Figure 6.1. Variation in the relative vegetation cover at a temporal scale of months. The codes on the x-axis represent the months of the year, with the numbers 1 and 2 representing years 2001 and 2002 respectively. The bars represent the mean and standard error.

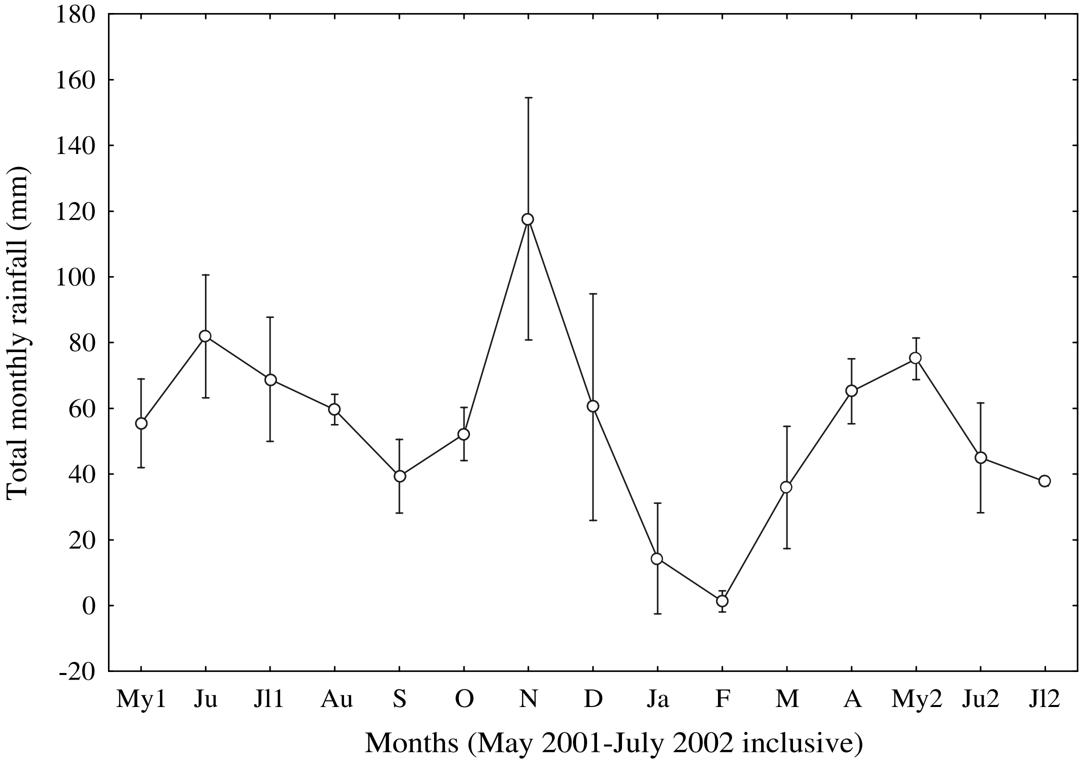

Figure 6.2. Variation of the total rainfall at the study sites at a temporal scale of months. The codes on x-axis represent the months of the year, with the numbers 1 and 2 representing years 2001 and 2002 respectively. The bars represent the means and standard errors.

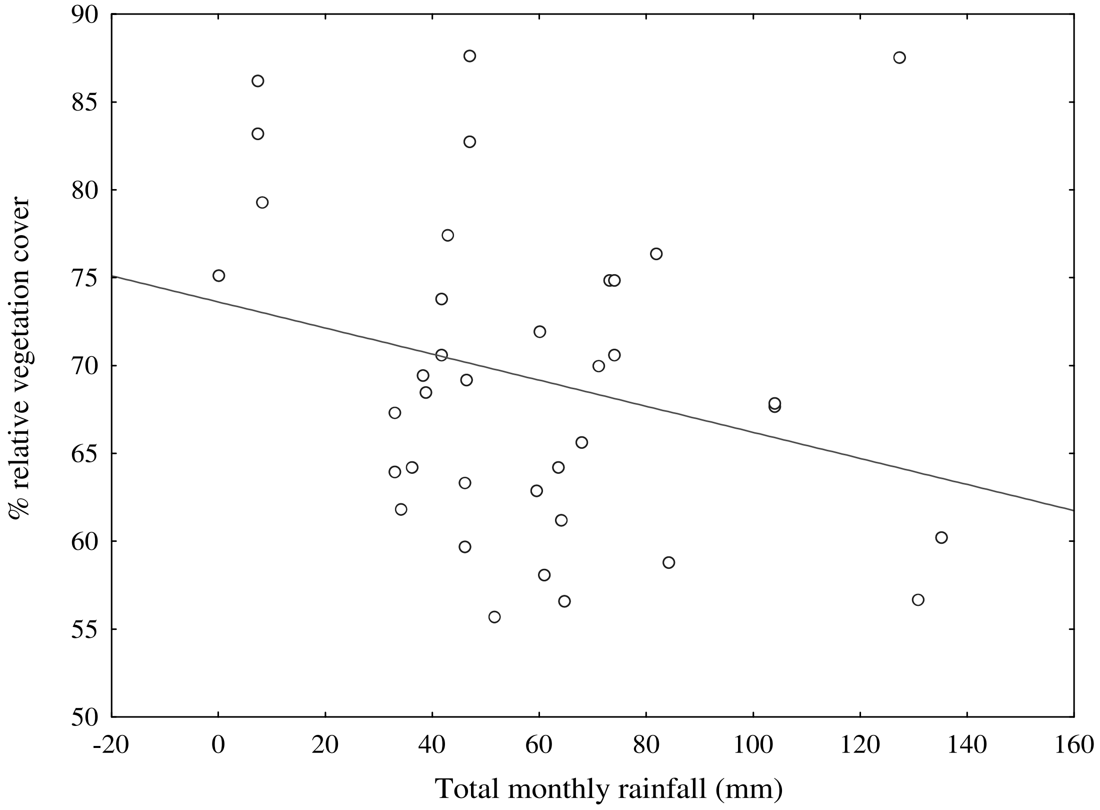

Figure 6.3. The results of a regression of monthly relative vegetation cover and total monthly rainfall (unlagged). The equation is: relative vegetation cover = 73.62 - 0.0742 * (monthly total rainfall); $r^2 = 0.046$, F = 2.76, df = 1, 37, p = 0.106.

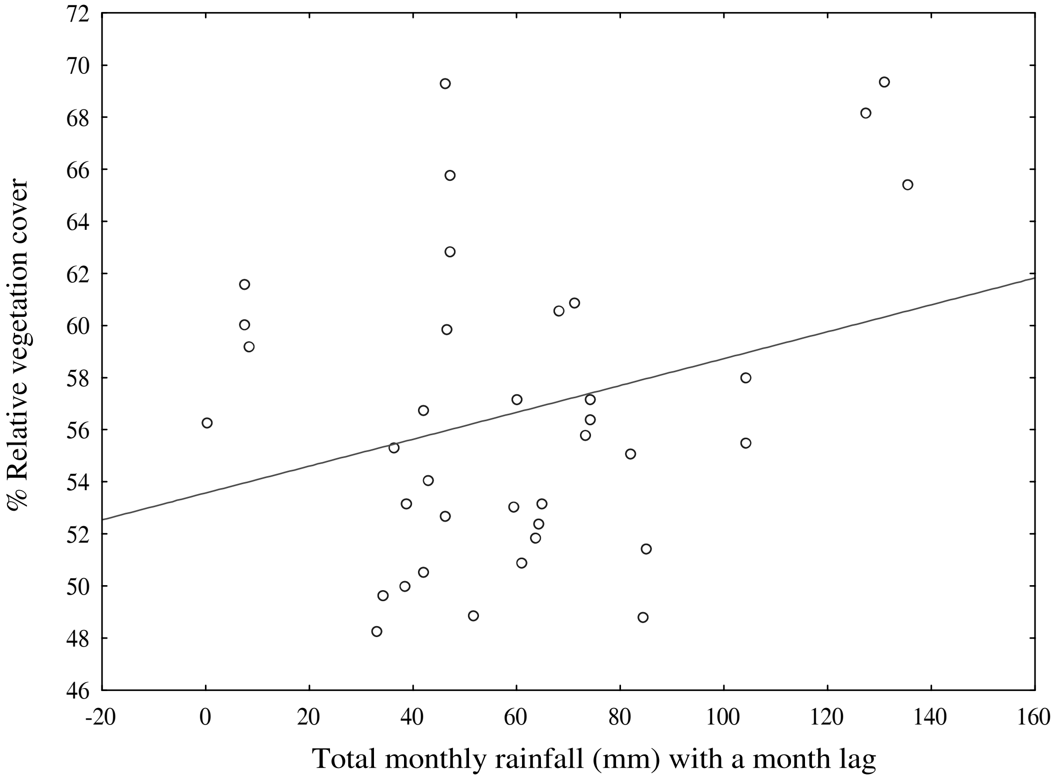

Figure 6.4. The results of a regression of total rainfall and relative vegetation cover on a monthly basis when there was a one-month time lag of rainfall. The equation was: relative vegetation cover (lagging one month behind) = 53.57 + 0.051 * (total monthly rainfall); $r^2 = 0.056$, F = 3.15, df = 1, 35, p = 0.085.

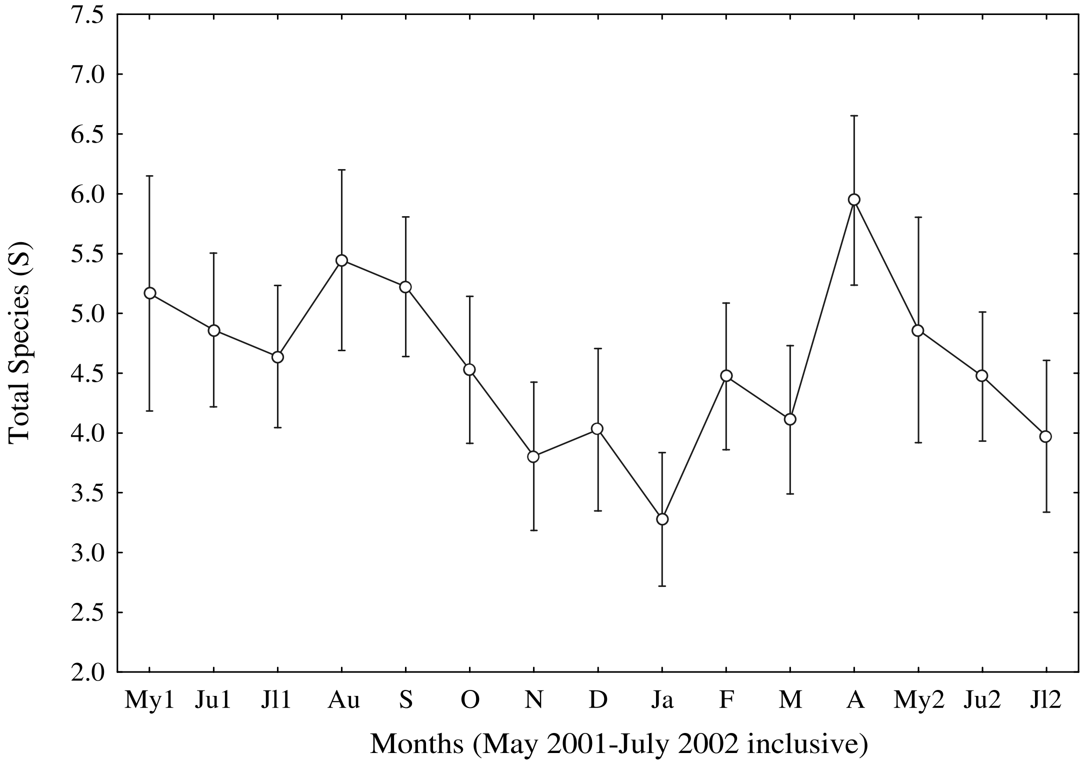

Figure 6.5. Variation of total species (S) from sweep-netting samples at a temporal scale of months. The codes on x-axis represent the months of the year, with the numbers 1 and 2 representing years 2001 and 2002 respectively. The bars represent the means and standard errors.

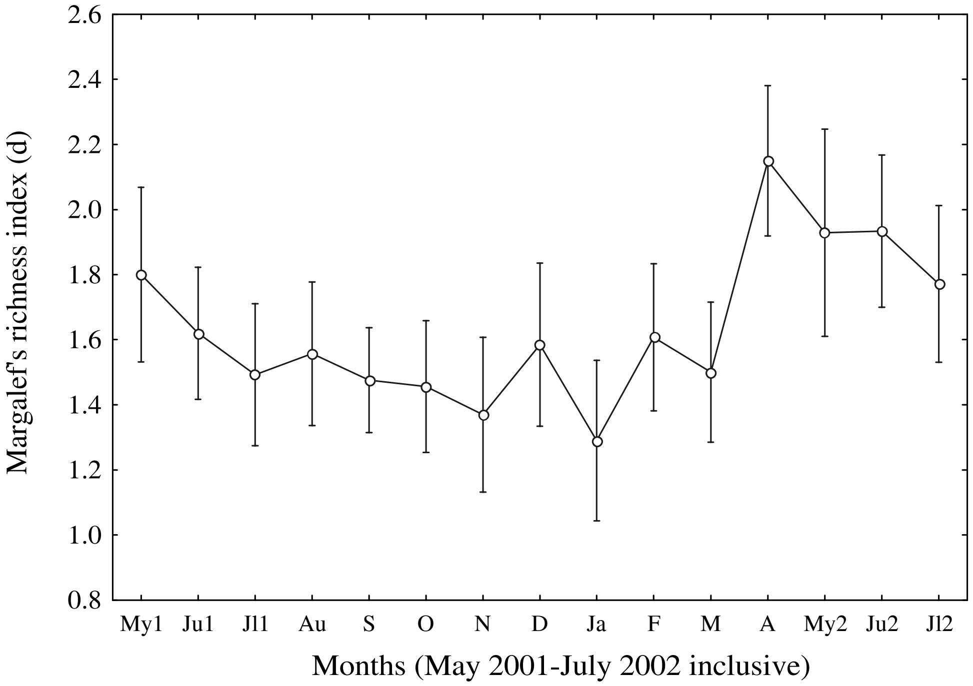

Figure 6.6. Variation in Margalef's richness index from sweeping samples' data set at a temporal scale of months. The codes on x-axis represent the months of the year, with the numbers 1 and 2 representing years 2001 and 2002 respectively. The bars represent the means and standard errors.

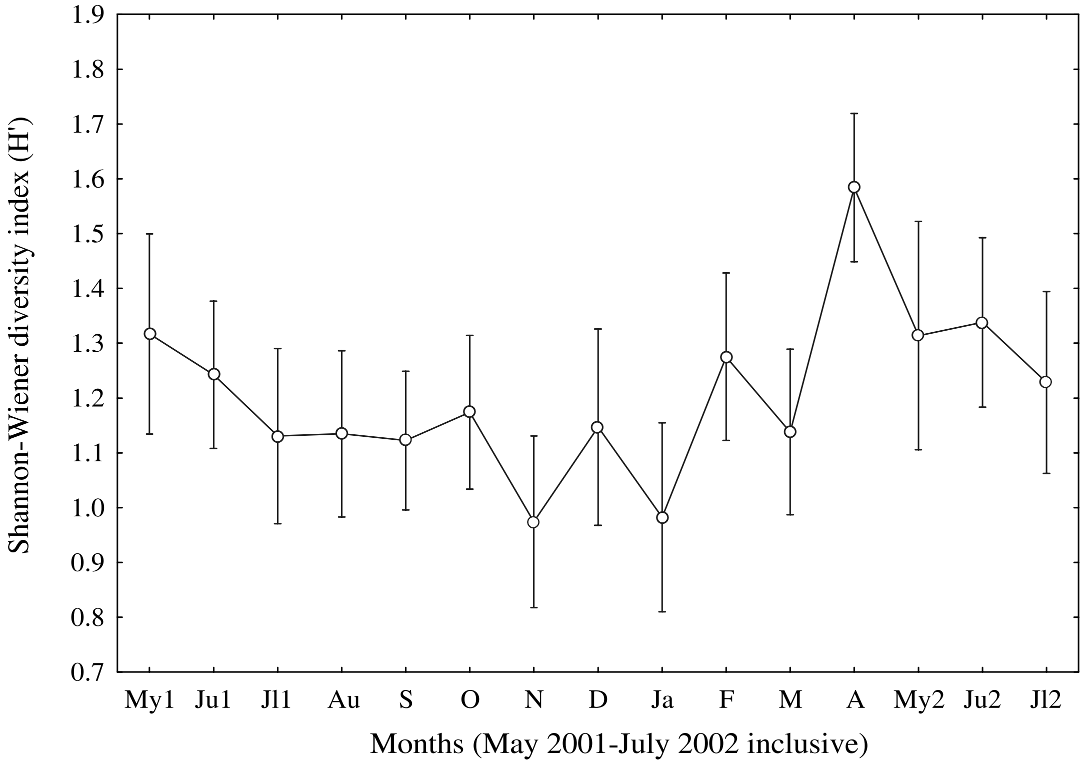

Figure 6.7. Variation in the Shannon-Wiener diversity index from sweep-netting samples at a temporal scale of months. The codes on x-axis represent the months of the year, with the numbers 1 and 2 representing years 2001 and 2002 respectively. The bars represent the means and standard errors.

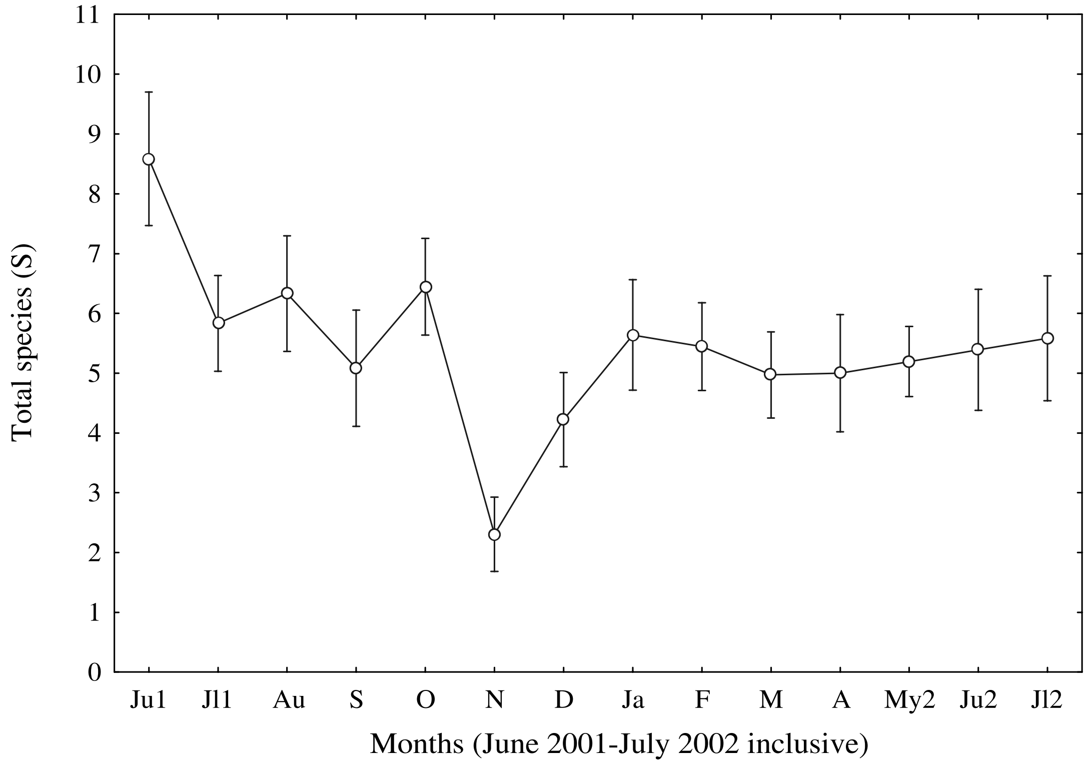

Figure 6.8. Variation in total species (S) from pitfall-trapping samples at a temporal scale of months. The codes on x-axis represent the months of the year, with the numbers 1 and 2 representing years 2001 and 2002 respectively. The bars represent the means and standard errors.

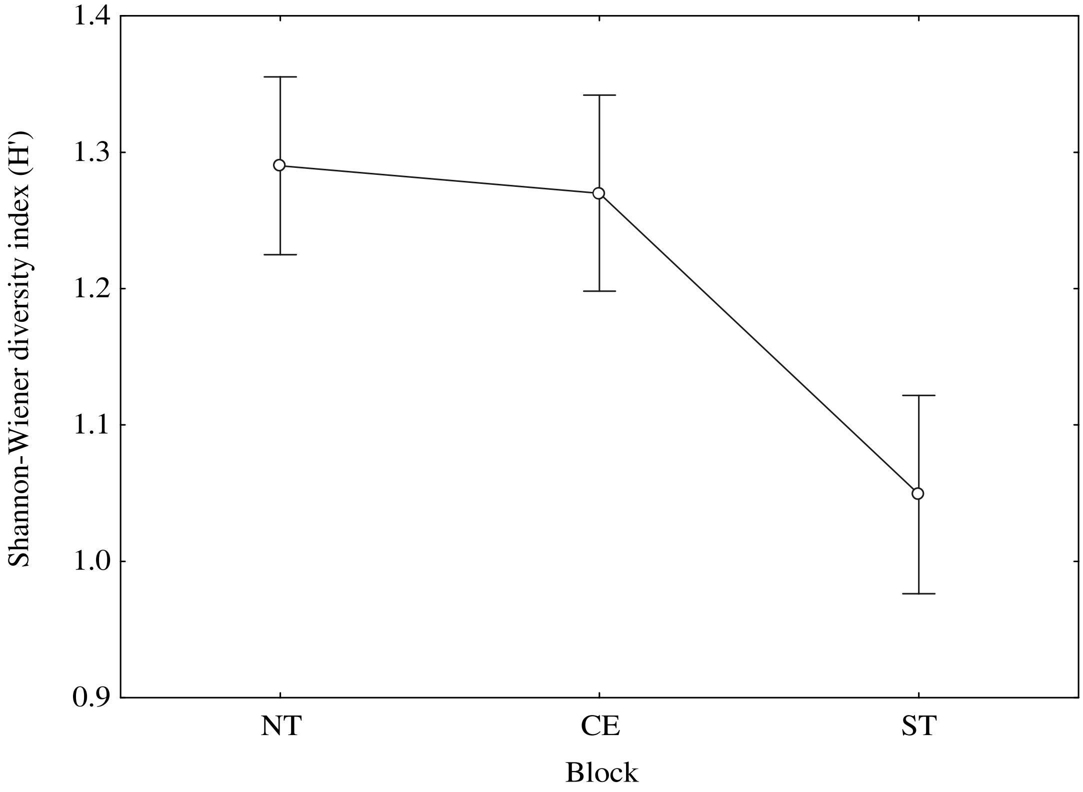

Figure 6.9. Variation of the Shannon-Wiener diversity index from sweep-netting samples at a spatial scale of hundreds of metres between the three KLEE experimental study blocks (Figure 2.2). The codes NT, CE and ST represent north, central and south study blocks respectively. The bars represent the means and standard errors.

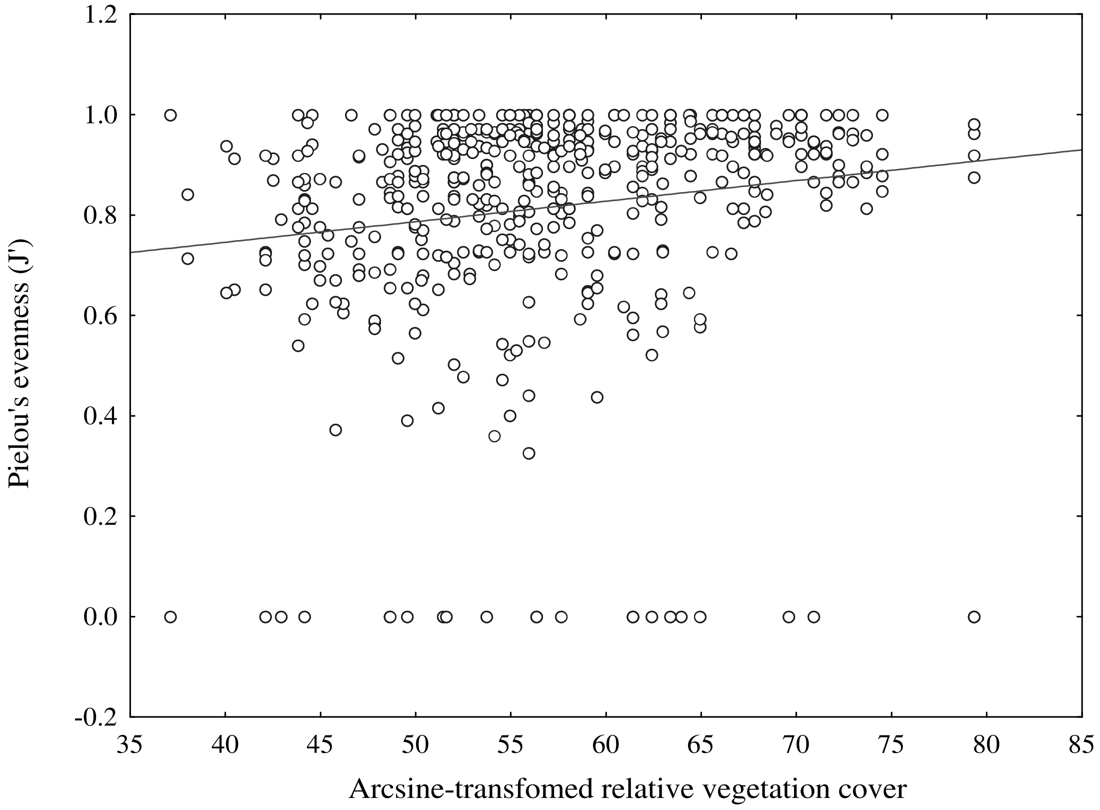

Figure 6.10. The relationship between Pielou's evenness index (J′) from sweep-netting samples and relative vegetation cover at a temporal scale of months. The equation is: J′ = 0.58 + 0.004 * (arcsine-transformed relative vegetation cover); $r^2 = 0.022$, F = 12.44, df = 1, 502, p = 0.001*. * = Significant at $\alpha = 0.05$.

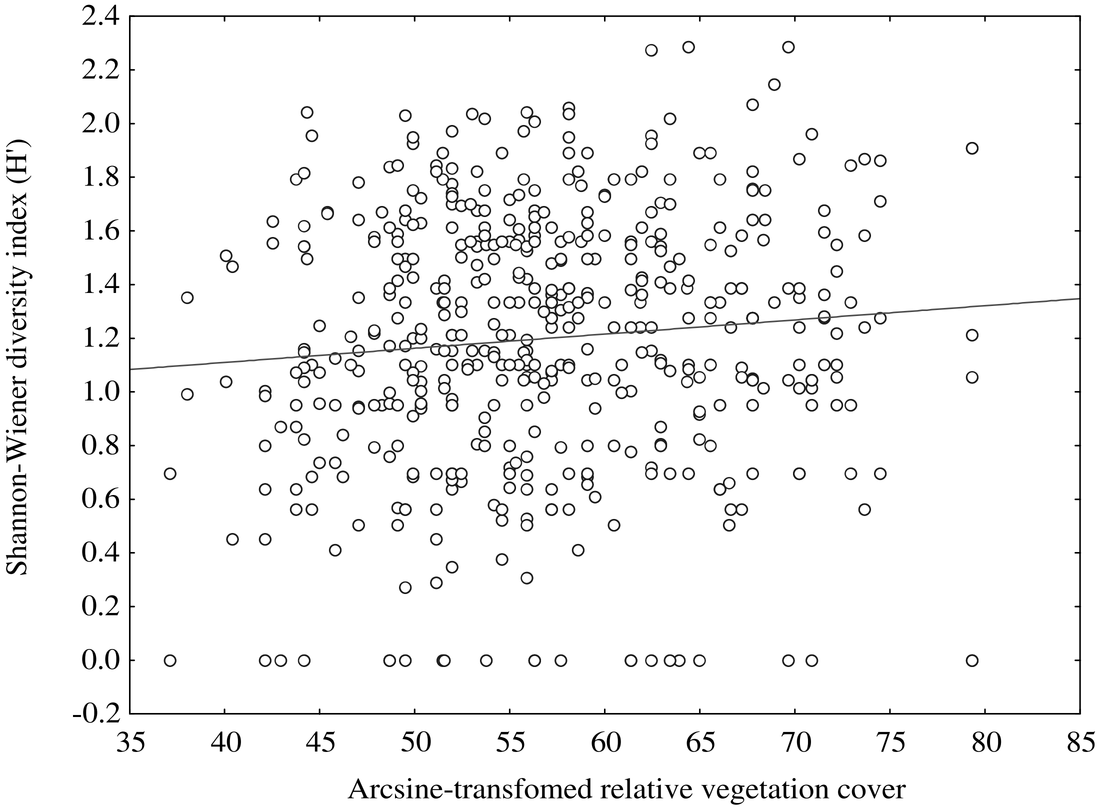

Figure 6.11. Relationship between the Shannon-Wiener diversity index from sweep-netting samples and relative vegetation cover at a temporal scale of months. The equation is: H' = 0.898 + 0.005 * (arcsine-transformed relative vegetation cover); $r^2 = 0.007$, F = 4.33, df = 1, 502, p = 0.038*. * = Significant at $\alpha = 0.05$.

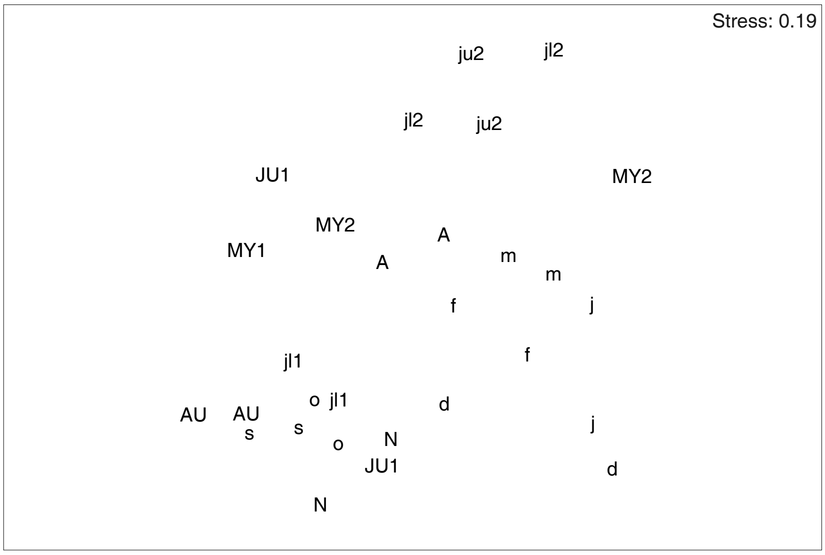

Figure 6.12. A multidimensional scaling plot for sweep-netting samples showing the spider community pattern at a temporal scale of fortnightly. The codes inside the plot represent the months of the calendar year (with two readings per month), while numbers 1 and 2 represent years 2001 and 2002 respectively. In all cases, the wet seasons are represented by upper case codes and dry season by the lower case codes. The raw data were condensed to just the average of 29 bi-monthly samples (except May 2001 which was sampled only once) from the three study blocks between May 2001 and July 2002.

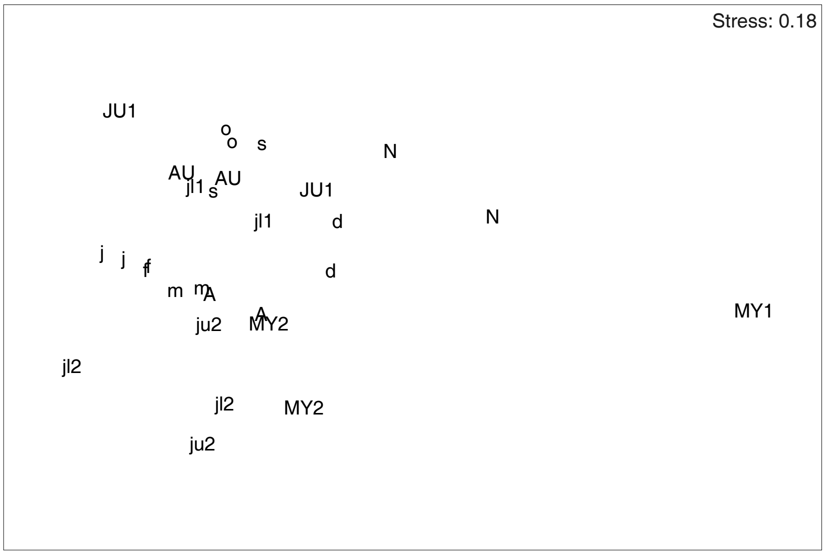

Figure 6.13. A multidimensional scaling plot for pitfall-trapping samples showing the spider community pattern at temporal scale of fortnights. The codes inside the plot represent the months of the calendar year (with two readings per month), while numbers 1 and 2 represent years 2001 and 2002 respectively. In all cases, the wet seasons are represented by upper case codes and dry season by the lower case codes. The raw data were condensed to just the average of 29 bi-monthly samples (except May 2001 which was sampled only once) from the three study blocks between May 2001 and July 2002.

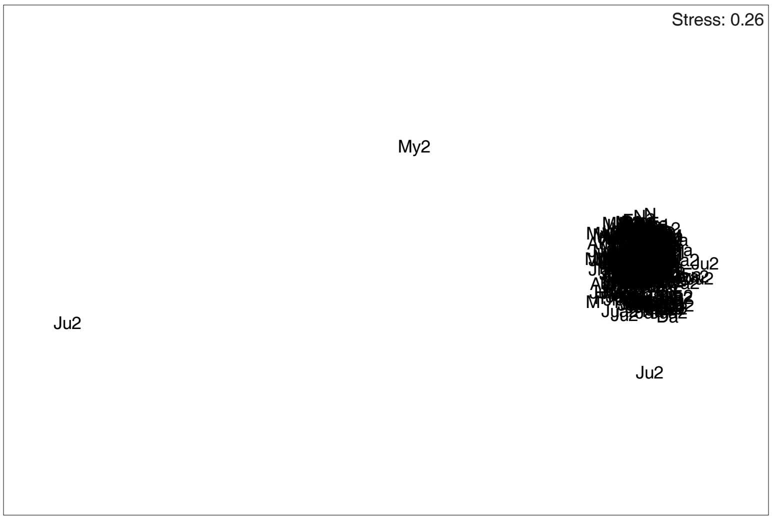

Figure 6.14. A multidimensional scaling plot for sweep-netting samples showing the spider community pattern at temporal scale of fortnights. The codes inside the plot represent the months of the year (with two readings per month), while numbers 1 and 2 represent years 2001 and 2002 respectively. The raw data was taken from the original matrix of bi-monthly samples from the three study blocks replicated 6 times to make a total of 513 data samples. This was for the period between May 2001 and July 2002.

Figure 6.15. A multidimensional scaling plot for sweep-netting samples showing the distribution pattern of the spider community at a spatial scale of hundreds of metres. The letters N, C and S represent North, Central and South blocks, while M = megaherbivores, W = mesoherbivores, C = cattle, O = control treatments. Convex hulls enclosed regions characteristic of a spatial scale of hundreds of metres in the form of three study blocks of north, central and south.

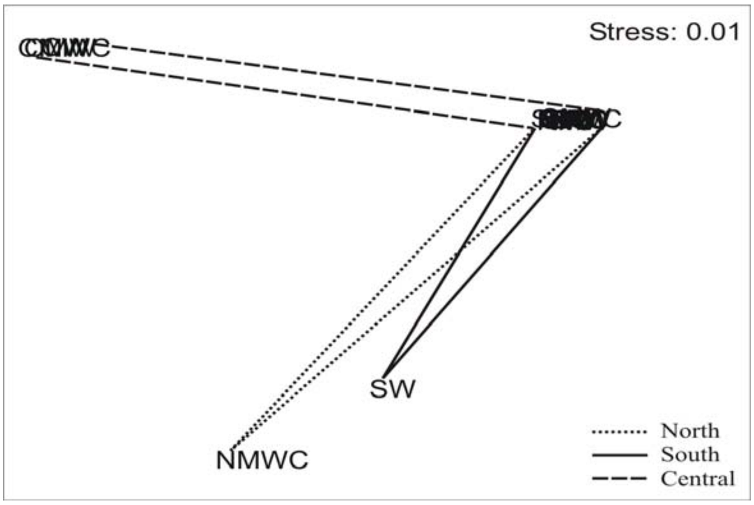

Figure 6.16. A multidimensional scaling plot for pitfall-trapping samples showing the distribution pattern of the spider community at a spatial scale of hundreds of metres. The letters N, C and S represent North, Central and South blocks, while M = megaherbivores, W = mesoherbivores, C = cattle, O = control treatments. Convex hulls enclosed regions characteristic of a spatial scale of hundreds of metres in the form of three study blocks of north, central and south. There was a cluster of central mesoherbivores and megaherbivores plots to the top left side of the figure.

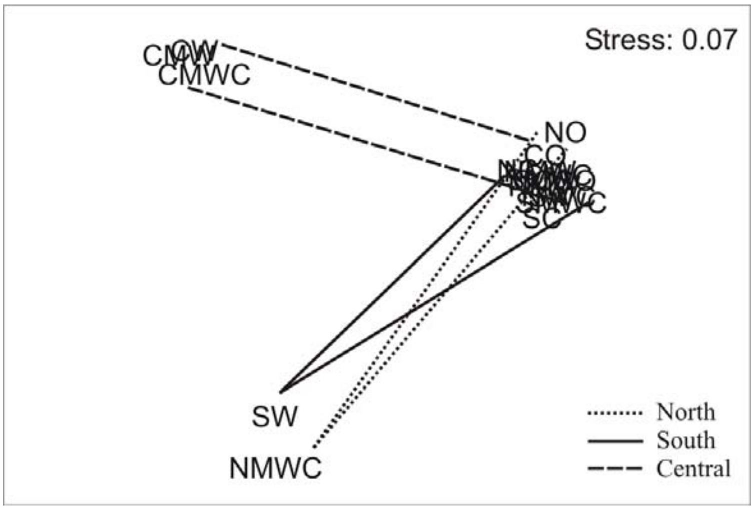

Figure 6.17. A multidimensional scaling plot for total samples showing the distribution pattern of the spider community at a spatial scale of hundreds of metres. The letters N, C and S represent North, Central and South blocks, while M = megaherbivores, W = mesoherbivores, C = cattle, O = control treatments. Convex hulls enclosed regions characteristic of a spatial scale of hundreds of metres in the form of three study blocks of north, central and south. There was a cluster of central mesoherbivores and megaherbivores plots to the top left side of the figure.

CHAPTER 7: SPIDER GUILD DIVERSITY AND ITS RESPONSE TO LARGE MAMMALIAN HERBIVORES GRAZING IMPACTS

Preface

This chapter starts with explanation of the guild concept and then describes the response of spiders to the large mammalian herbivore treatments at such a guild level of resolution. In this case their diversity indices were calculated from individual spiders belonging to a particular guild. This resolution was finer than that of chapter 5 and the aim was to establish whether analysis at such increased resolution was more sensitive to disturbances caused by grazing. The relationship of spider guild diversity to the variation in vegetation cover and rainfall was also explored.

The guild concept

A guild is a group of species that exploit the same class of environmental resources in a similar way (Root, 1967; Uetz *et al.* 1999). The concept of guilds is useful in community ecology as it allows investigation of the functional structure of a system without reference to a specific species' behaviour and thus gives a better understanding of a community (Root 1973; Terbough and Robinson 1986). As such, it simply gives an immediate level of analysis between a whole community and its individual species' responses at which to search for patterns and causal factors (Ross 1994). Since the taxonomic knowledge limits the use of individual species in ecological or monitoring studies, it is still helpful to use guilds or functional groups in order to continue providing vital information for conservation purpose and management of the environment. Such studies are supported by work of several scientists who demonstrated this approach to conservation with success (e.g. Andersen (1995, 1997a, b) on ants; Barrion (1999) and Uetz *et al.* (1999) on spiders; O'Connell *et al.* (1998) on birds; and Ribeiro *et al.* (1998) and Cagnolo *et al.* (2002) on a range of insect guilds).

The idea behind guilds is simply that organisms are grouped by how similarly they use environmental resources. It differs greatly from a functional group (see Blondel 2003). The use of the guild concept is popular among biologists and has been widely employed in ecological studies especially in relation to birds (e.g. Root 1967; Eckhardt 1979; Szaro 1986; Poulin *et al.* 1994; Corcuera 2001; Pearman 2002; Waldenström *et al.* 2002), and insects (e.g. Price 1971; Root 1973; Stork 1987; Ross 1994). The concept of the guild has been of importance to arachnologists in the context of the different ways in which spiders forage, and has been the subject of differing approach in terms of classification (Uetz *et al.* 1999).

There have been numerous views over how the guild units of study are assigned and the situation under which the guild concept can be used (e.g. Johnson 1981; Verner 1984; Szaro 1986; Uetz *et al.* 1999). Critics of the guild concept include Adams (1985) and Hawkins and MacMahon (1989). As such, it is not a surprise that there have been several efforts to classify spiders into as few as two guilds and as many as eleven (Uetz *et al.* 1999). Further details of such classifications are extensively discussed in Uetz *et al.* (1999). A list of past classifications includes eleven guilds by Post and Riechert (1977), two by Uetz (1977), eight by Riechert and Lockely (1984), five by Young and Edwards (1990), and eight by Uetz *et al.* (1999).

Uses of guilds

Guilds are widely used in environmental assessment and management (Hawkins and MacMahon 1989). From an impact assessment point of view, the assumption of the guild concept is that factors that affect a certain resource in the environment will also affect the guild in more or less the same way (Severinghaus 1981). In other words, once the impact of any one species in a guild is determined, the impact on every other species in the guild is assumed to be the same (Simberloff and Dayan 1991).

Hawkins and MacMahon (1989) argue that guilds are most useful when they include a variety of interacting taxa and when species co-occur in space and time. According to Severinghaus (1981) and Simberloff and Dayan (1991), it is possible to predict the effect of environmental management on a guild in one region from its effect on a similar guild in another region. The guild concept has been used to compare spider communities in agro-ecosystems (e.g. Uetz *et al.* 1999). Such use can help to identify their value in crops so that they can be incorporated into integrated pest management (Whitehouse and Lawrence 2002).

Other research on guilds includes that of Severinghaus (1981), Verner (1984), Adams (1985), Foelix (1996), Polis and McCormick (1986), Szaro (1986), Hawkins and MacMahon (1989) and Simberloff and Dayan (1991). Specific work on spider guilds has been reported (e.g. Uetz 1977; Bultman *et al.* 1982; Riechert and Lockely 1984; Barrion 1999; Dippenaar-Schoeman *et al.* 1999a, b; Uetz *et al.* 1999)

Limitations of the guild concept

Some limitations of using the guild concept include (i) that there are too many connotations (multiple viewpoints about designation of guilds) (ii) with no formal or testable definitions and (iii) ambiguities in partitioning a community into guilds (Hawkins and MacMahon 1989; Adams 1985; Simberloff and Dayan 1991). Such problems have been reported in bird-related studies, with a lot of inconsistency when assigning bird species to guilds (Verner 1984; Szaro 1986). Other problems include taxonomy- and knowledge-related issues e.g. in spiders, taxonomic knowledge and information on foraging behaviour and microhabitat utilization patterns are limiting, and most of the designated guilds are based on information about some and not all spider species. Whenever new information in such fields comes up, there are good chances that the basic delimitations of guild membership may change (Uetz *et al.* 1999). As such, this study would favour use of many guilds, as they would give a high level of resolution, and hence room for more sensitivity to the environmental factors. However the actual number of guilds chosen for the current study was influenced by available knowledge of individual species' biology and taxonomy.

Choosing guilds

Description of a guild depends on the vision of the user and has no guidelines, with the purpose of a scientist playing a major role on the usefulness of the concept (Hawkins and MacMahon 1989). It is therefore important that a clear account is always given of the criteria and reasoning that lead to designating a particular guild, in order to enable other investigators to consider the validity of a designation (Simberloff and Dayan 1991). Such criteria, used for the current study are explained in details in the methods section below, while the actual guilds assigned to the spiders for the current study are shown in table 3.1.

The Current Study

In the current study, it was expected that a particular guild would respond in a fine way to changes in their natural habitat. Disturbances caused by herbivores grazing, browsing and trampling would interfere with the habitat structure of spiders with a resultant "stress" by reducing habitat heterogeneity. The "stress" was then expected to manifest itself accordingly in the form of variation in vegetation cover in the different treatments. It was expected that the different combinations of mammalian herbivores in treatments would cause varying degrees of disturbance to the vegetation. This was in turn expected to negatively affect the spiders, reducing their species richness and diversity, and that of their prey. As such, it was expected that all the guilds would respond to these experimental treatments in unique ways, based on the pressure from large mammalian herbivores.

Since there were more individual grazers than browsers, and since both contribute to trampling, it was expected that the ground-active spiders would be the most affected. The most variation in spider richness, evenness and diversity was expected in samples from pitfall-trapping compared to the sweeping-netting method. In addition, since there were more wild grazers than wild browsers (see chapter 5), and since most of the ecosystem was dominated by grass, it was expected that dividing the spiders into different guilds would give a higher level of resolution that would be sensitive enough to reflect these disturbances.

Thus the current analysis provided a further assessment of species richness, evenness and diversity to establish the effect of different grazing treatments on spiders and hence throw light onto the impact of different large herbivores and ungulates on spider guilds. It was hoped that this approach would reveal patterns that could be masked by the effect of combining spider diversity at the community level.

Objectives

The objectives of this study were:

- To explore spider guild composition.
- To establish the variation in various spider guilds' Shannon-Weaner diversity index, Margalef's richness index and Pielou's evenness in the experimental treatments.
- To relate the gradient in vegetation cover under different experimental grazing treatments and to spider guild species richness, evenness and diversity.

Hypotheses

The null hypotheses were framed in terms of 'no differences between the treatments', where the different treatments were plots with cattle only (C), mesoherbivores + cattle (WC), megaherbivores + mesoherbivores + cattle (MWC), megaherbivores + mesoherbivores (MW), mesoherbivores (W) and no large herbivores at all (control or O).

The biological hypotheses were thus:

i. The Shannon-Weaner diversity index, Margalef's richness index and Pielou's evenness of each of the spider guilds varied in all the six-herbivore treatments. It was expected that grazing, browsing and trampling by different herbivores would cause disturbances of varying intensity and would interfere with diversity of spider guilds, with each guild responding to these experimental treatments in a unique way.

ii. The Shannon-Weaner diversity index, Margalef's richness index and Pielou's evenness of each spider guild should be positively correlated with relative vegetation cover. It was expected that increase in relative vegetation cover would create a more complex habitat that would attract more spiders. Spiders have been found to prefer more structurally complex habitats that provide unique habitat structural features that allow more efficient prey capture (Rypstra 1983; Wise 1993).

Materials and methods

The current study initially used Uetz's (1977) classification of spiders into two guilds, namely web builders (WB) and wanderers (W). However, after considering species collected in this study, the available taxonomic knowledge, data on spiders' biology and behaviour, habitat data recorded with the spider species collected, study objectives and the methods used, the wanderers were further subdivided into two guilds, namely plant wanderers (PW) and ground wanderers (GW). The details showing the guilds assigned to each of the current study species for the analysis of this chapter are shown in shown in column four of Table 3.1 (chapter 3). Such an approach was used in past work on African spiders (Dippenaar-Schoemann *et al.* 1999a, b; Whitmore *et al.* 2002b) and gives much weight to microhabitat and hunting behaviour. A list of the characteristics used in defining guilds was the same as those used by Dippenaar-Schoeman *et al.* (1999a). It was not possible to go beyond three guilds because of limitations of knowledge of the biology and taxonomy of some species. For the analysis, data from sweep-netting and pitfall-trapping was combined to make one data set (total data set).

One limitation to the current choice of guilds was that some species were only identified to family level and there was a chance that members of the same family belonging to different guilds might be erroneously placed in the same or erroneous guilds in the current study. This was attributed to limitations in taxonomic knowledge especially where species were thought to be new and could not be identified further with the help and time available. However the study consulted relevant literature (e.g. Uetz's 1977; Dippenaar-Schoeman and Jocqué 1997; Dippenaar-Schoemann *et al.* 1999 a, b).

Justification of choice of guilds

As already explained at the beginning of this chapter, there are no fixed guidelines as to how a guild should be designated and in most cases it is based on the user's definition (Hawkins and MacMahon 1989). The reasons for the current choice of guilds were based on the data available on spider biology and behaviour, the collecting methods used, the habitat sampled, and the objectives of the study. Most past researchers sampled one habitat e.g. Dippenaar-Schoeman *et al.* (1999a), and in addition used the same three guilds. This research sampled two habitats, namely the ground and the herbaceous layer, which meant that there were different guilds in the two habitats i.e. both plant wanderers (collected mainly by sweep-netting) and ground wanderers (collected mainly by pitfall-trapping). Since one of the objectives of the study was to establish the effect of large mammalian herbivores on spiders, it was important that the two habitats were treated separately to allow more sensitivity to ungulate activity.

In addition, the current study yielded 30 spider families, six more than the study by Uetz (1977), which classified spiders into two guilds. More families meant more species and an increase in guilds was hence a possibility. Finally, recent work on savanna spiders in Africa has adopted the same three-guild classification for their diversity analysis (e.g. Dippenaar-Schoeman *et al.* 1999a; Whitmore *et al.* 2002b). As such, assigning the three guilds makes the current study comparable with other related spider work in the region. It was important to note that such comparisons are made relevant when sampling methods are standardised or at least understood (Southwood 1994; Spence and Niemelä 1994).

Statistical analysis

Four different ANOVAs were performed to look at effects of treatment. These are explained in details in the methods and analysis section of chapter 5. Levene's tests were used to assess homoscedacity. Where the variances of the data were not homogenous (significant Levene's test), a Kruskal-Wallis was performed. Tukey's multiple comparison tests were performed where necessary.

Results and discussion

The overall guild structure, including total abundance of all specimens and species richness for each individual guild, is shown in Table 7.1. The data for this table were extracted from Table 3.1. These results show that there was no much variation in abundance of the three guilds. However it is important to note that in the absence of a few numerically dominant species corrected from pitfall traps only (e.g. *Aelurillus* sp. with 526 specimens and Salticidae sp. 5 with 160 specimens), there would be a greater difference in the relative abundance of the guilds e.g. the ground wanderers would be the least abundant. Meanwhile the results on the species richness indicated in Table 7.1 also showed that ground wanderers were more common when compared to the other two guilds.

Hypothesis 1: The mean diversity, species richness and species evenness of guilds differed between the experimental treatments.

The results of Levine's tests on Shannon-Weaner diversity index, Margalef's richness index and Pielou's evenness for the web builders, plant wanderers and ground wanders are shown in Table 7.2. Similarly the results for one-way ANOVA on the effects of different treatments on the Shannon-Wiener diversity index, Margalef's richness index and Pielou's evenness for the web builders, plant wanderers and ground wanders are shown in Table 7.2. There were no significant differences in any of the diversity measures in all six experimental treatments. Following a significant Levene's test on the Shannon-Wiener diversity index for plant wanderers (Table 7.2), the resultant Kruskal-Wallis tests was not significant ($\chi^2 = 2.00$, df = 5, p = 0.85).

A first two-way ANOVA was performed on spider guild Shannon-Weaner diversity index, Margalef's richness index and Pielou's evenness from the combined (total) sweep-netting and pitfall-trapping samples for all six grazing treatments. In this case, all six cattle treatments had two levels for the factor 'cattle' (present and absent), and three levels for the factor 'herbivores' (absent, only mesoherbivores present, both meso- and megaherbivores present). No treatments were omitted from the data set. There were no significant effects of cattle or game (megaherbivores + mesoherbivores) on the species diversity, species richness and species evenness of each of the three spider guilds (Tables 7.3-7.5).

A second analysis on the species diversity, species richness and species evenness of guilds from the combined data set tested the effects of the factors 'cattle' (with levels present vs. absent) and ‘megaherbivores’ (with levels present vs. absent), using all treatments containing herbivores (W, WC, MW, MWC). Two treatments (O and C) were omitted because the KLEE experimental layout was not fully crossed. The results showed no significant effect of cattle and megaherbivores on diversity index, species richness and species evenness of each guild (Tables 7.6-7.8).

A third analysis on guild diversity tested the effects of the factors ‘cattle’ (with levels present vs. absent) and ‘mesoherbivores’ (with levels present vs. absent) in the four treatments that excluded megaherbivores (O, C, W, WC). The megaherbivore treatments (MW and MWC) were omitted because the KLEE experimental layout was not fully crossed. Again there were no significant effects of cattle or mesoherbivores on diversity of each guild in all plots that excluded megaherbivores (Tables 7.9-7.11).

It was clear that the Shannon-Weiner diversity index, Margalev’s species richness index and Pielou’s evenness index of the three spider guilds, namely the web-builders, plant wanderers and ground wanderers, were not significantly affected by the six treatments of large mammalian herbivores. In addition, none of the individual herbivore interactions significantly influenced spider diversity. Such lack of significant effects by the large mammalian grazing treatments on guilds in this study compares differently with findings from other spider guild studies. Some studies e.g. Whitmore *et al.* (2002b) on spider diversity in different savanna habitats found a significant effect of habitat type on diversity of web builders and species evenness of plant wanderers. On the contrary, a study by Barrion (1999) on spider guild structure and diversity in four different habitats (three selected non-rice and one irrigated rice habitat) with very different dominant cover values revealed no differences in spider guilds. One of the likely reasons was that the guild level of resolution was not sensitive enough to habitat difference. Since a guild comprised of species from different families, it was possible in the current study that individual behaviour and niche of some family members differed such that members of same family were categorised into the three different guilds and probably neutralised the ‘sensitivity’ of a particular guild at the expense of another. Another possible explanation was that probably both mesoherbivores and megaherbivores were not sufficienty numerous or frequent at the experimental plots to cause significant changes in relative vegetation cover that would consequently cause variation in the diversity and species richness of spider guilds. It was also possible that most of the common megaherbivores and mesoherbivores were browsers and therefore did not exert or cause a lot of grazing pressure that would affect grass cover and consequently pitfall-trapping and sweep-netting spider samples.

Hypothesis 2: The species diversity, richness and evenness of each of the spider guilds is positively correlated with relative vegetation cover.

Of all of the diversity measures (Table 7.12), only the total species (S) for the plant wanderers was significantly and positively correlated with relative vegetation cover ($r = 0.47$, $r^2 = 0.17$, $p = 0.048$, Figure 7.1).

The results in chapter 5 (Tables 5.1 and 5.2) revealed that relative vegetation cover was significantly affected by large mammalian herbivores only through the effects of cattle. It was expected that this effect on vegetation would also affect the different spider guilds. However, the results of the study indicate that spider guilds' species diversity, species richness and species evenness did not significantly respond to vegetation cover apart from plant wanderers, which were positively correlated to it. However, positive response by plant wanderers was in line with predictions. One possible explanation was that since the plant wanderers were found on plants, they utilised them as living habitat and as a place to acquire food. It was expected that when the plant cover was high, the habitat was more complex and hence provided more optimal conditions that supported more spiders. Similarly, when the cover was low, the habitat was less complex and provided less optimal conditions with a net result of lower spider diversity. This could be further supported by the fact that spiders prefer a more complex habitat to a less complex one (Gunnarsson 1988; Uetz 1991; Rypstra *et al.* 1999). In addition, other research has shown that more complex vegetation provides arthropods with sites for shelter, foraging, oviposition, and mating (Lawton 1983, Halaj *et al.* 2000). Such conditions ideally support an increase in spider diversity.

It is important to mention that the significant positive correlation between plant wandering spiders and relative vegetation cover was weak ($r = 0.47$; $r^2 = 0.17$), and meant that other factors were playing a part (83%) in the variation too. Such factors might include habitat complexity (e.g. Greenstone 1984; Balfour and Rypstra 1998; Downes *et al.* 1998); landscape heterogeneity (Romero-Alcaraz and Avila 2000); and spatial heterogeneity (Brown 2003). Studies on spiders and other arthropods reflecting similar responses include that of Uetz *et al*. (1999) and Ross *et al.* (2000).

The response by ground wanderers (cursorial spiders) was contrary to the expectation that the diversity of the ground wandering guild (mainly collected by pitfall-trapping) would be negatively correlated to vegetation cover, whereby a decrease in cover would lead to an increase in their activity and hence their abundance in pitfall traps. A high activity and abundance would positively influence the diversity of the spiders in pitfall traps. According to Russell-Smith (1999), spider catches from such pitfall traps are a product of both the numbers of spiders on the ground surface at any given time and the level of activity of the spiders, and there is need for caution whenever interpreting such data.

Recent work has shown interesting patterns of diversity of spiders collected in pitfall traps (e.g. Gasnier and Höfer 2001; Work *et al*. 2002). Russell-Smith (1999) reported that the density of vegetation affects activity of spiders and other soil surface arthropods. The higher the density of vegetation, the higher the relative vegetation cover. Spiders roamed about more (higher activity) when the ground was bare and hence there was a greater chance of being caught in pitfalls. Based on this argument, it was expected that there would be more ground wanderers caught in plots with cattle present, namely C, WC and MWC, as these had less cover and therefore more space for spider activity. However, this did not happen. The reality was that the intensity of grazing/browsing in the treatments was moderate and had been calculated to imitate the stocking rate of ranches in the region as explained in Young *et al.* (1998). Russell-Smith (1999) reported that a much larger proportion of active ground hunters were vulnerable to trapping in open ground than in densely vegetated areas.

The implication of the above findings was that the proportion of the vegetation cover present in the most densely stocked of the ungulates treatments (megaherbivores + mesoherbivores + cattle) had not reached very low relative cover levels that would promote a significant increase in spider activity (e.g. in search for food or shelter) and hence increased pitfall sample abundance and consequently altered diversity. In other words, despite lower relative cover in cattle treatments, the low level of cover was still not sufficient to cause a significant effect within the large mammalian herbivore treatments. This also implied that the spider guilds are poor biomonitoring agents that respond slowly to changes in disturbance created by the different groups of ungulates.

Moreover, since the research plots were erected 8 years ago (about 4-8 spider generations assuming a maximum annual cycle of 1-2 years), it was probable that no further big differences were expected in the spider community over time suggesting that the spider guilds would be poor indicators. On the contrary, the plots with no ungulates (O plots) showed increased abundance of small mammals (Keesing 2000). This was attributed to the reduced competition for food between the ungulates and small mammals, which are mostly herbivorous, unlike spiders. It might also be possible that the mice were eating ground wandering spiders. Keesing (1998) also reported increased weight of males of common pouched mouse, *Saccostomus mearnsii,* in the absence of ungulates and associated this with increase quality of the habitat. A study on the effects of the same treatments on bird populations (Misurelli 2002) revealed that the presence of megaherbivores (elephants and giraffes) had a significantly effect on lowering bird diversity whereas control plots reported the highest diversity of birds. This was attributed to the effect of megaherbivores on woody vegetation that reduced the canopy area, a significant predictor of bird diversity (Misurelli 2002). In the current study, there was no beating that could have helped to better assess the effects of browsing by megaherbivores.

General discussion and conclusions

It is also possible that the use of only three guilds did not give the best sensitivity to detect changes in the herbivore treatments. There might be a need to subdivide the guilds further based on recent classifications e.g. Young & Edwards (1990) and Uetz *et al.* (1999). Lists of past classifications are already provided in chapter 4 and despite the fact that most of them are based on agricultural ecosystems, it is helpful to use their knowledge to understand natural savanna ecosystems. This could give a finer resolution that was more sensitive to the changes caused by large mammalian herbivores. However this was not possible at this stage owing to the taxonomic limitations that this study faced. Furthermore, taxonomic knowledge on African spiders is still relatively poor (Dippenaar-Schoeman and Jocqué 1997; Dippenaar-Schoeman 2002). According to Uetz *et al*. (1999), problems do occur when one is assigning an individual species to particular guild since it is not possible generalize when it comes to all members of a higher taxon. As an example, not all web builders are restricted to webs; some may also wander around plants (Uetz *et al*. 1999).

In conclusion, diversity and richness of spider guilds collected by both sweep-netting and pitfall-trapping was not a good predictor of large mammalian herbivores effects. Plant wanderers were the only guild sensitive to the effect of ungulates on vegetation cover, but explained only a small amount of variation (17%; $r^2 = 0.17$). Overall, it emerged that there was a weak indirect influence of cattle on spider guild diversity, which was mediated by their effect on relative vegetation cover.

The use of guilds in this study therefore did not reveal much but would be important for such future studies to consider their limits. This is clearly also stressed in the views of Uetz *et al*. (1999): “ideally, a guild should reflect the natural history and behaviour of a single species, but such precision is not realistic as such data are presently not available for most families”. Other workers have criticized use of guilds as indicators of disturbance e.g. according to Caro and O'Doherty (1999), their use is problematic in that only one species needs to be tolerant of a perturbation and respond positively for abundance to be maintained, even though the others respond negatively. This might be an important point to consider because in the current study *Cyclosa insulana* (a web builder) comprised 23.64% of all the spiders collected. Finally, it is true that this study has not exhausted all that needs to be done on spider guilds in the KLEE experiments as it used only two sampling methods. Many spiders were left out when other methods such as beating, sieving and visual searches were not used. These could probably give more sensitive results to the herbivore treatments, and so would analysis at the species level.

Tables

Table 7.1. The guild structure of all the spiders collected from the study area in the black cotton soil. The data were extracted from Table 3.1.

	Total specimens (Abundance)	% Guild composition (Abundance)	Species richness	% Species richness
Ground wanderers	3601	34.34	57	43.18
Plant wanderers	3636	34.67	39	29.54
Web builders	3250	30.99	36	27.27
Total	10487	100	132	100

Table 7.2. One-way ANOVAs on the effects of all six-herbivore treatments on the Shannon-Wiener diversity index (H´), Margalef's richness index (d), Pielou's evenness index (J´) and total species (S) of web builders, plant wanderers and ground wanderers from the total data set. DF = 5, 12. * = Significant at $\alpha = 0.05$.

Guild	Diversity variable	F-value	P-value	Levene's P-value
Web builders	S	0.91	0.509	0.420
	d	0.92	0.506	0.191
	J´	0.13	0.983	0.204
	H´	2.49	0.932	0.062
Plant wanderers	S	0.75	0.599	0.625
	d	0.48	0.785	0.798
	J´	0.99	0.459	0.239
	H´	-	-	0.017*
Ground wanderers	S	1.68	0.212	0.454
	d	1.75	0.197	0.559
	J´	0.602	0.700	0.200
	H´	1.24	0.350	0.270

Table 7.3. 2x3 ANOVAs on effects of the factors ‘cattle’ (levels: absent [O, W and MW] vs. present [C, WC and MWC]) and ‘herbivores’ (levels: herbivores absent [O and C], only mesoherbivores present [W and CW], and both meso- and megaherbivores present [MW and MWC]) on the Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) of web builders from the total data set. No treatments were omitted from the data set.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	0.06	0.02	0.895
	Mesoherbivores + Megaherbivores	2	6.17	2.02	0.176
	Cattle*Mesoherbivores + Megaherbivores	2	0.72	0.24	0.793
	Error	12	3.06		
d	Cattle	1	0.02	0.20	0.660
	Mesoherbivores + Megaherbivores	2	0.17	1.86	0.199
	Cattle*Mesoherbivores + Megaherbivores	2	0.03	0.32	0.733
	Error	12	0.09		
J´	Cattle	1	0.00	0.04	0.849
	Mesoherbivores + Megaherbivores	2	0.00	0.12	0.886
	Cattle*Mesoherbivores + Megaherbivores	2	0.00	0.18	0.835
	Error	12	0.01		
H´	Cattle	1	0.00	0.01	0.914
	Mesoherbivores + Megaherbivores	2	0.03	0.53	0.604
	Cattle*Mesoherbivores + Megaherbivores	2	0.01	0.09	0.913
	Error	12	0.06		

Table 7.4. 2x3 ANOVAs on effects of the factors ‘cattle’ (levels: absent [O, W and MW] vs. present [C, WC and MWC]) and ‘herbivores’ (levels: herbivores absent [O and C], only mesoherbivores present [W and CW], and both meso- and megaherbivores present [MW and MWC]) on the Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) of plant wanderers from the total samples’ data set. No treatments were omitted from the data set.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	20.06	1.94	0.188
	Megaherbivores + Mesoherbivores	2	4.67	0.55	0.588
	Cattle*Megaherbivores + Mesoherbivores	2	4.22	0.36	0.705
	Error	12	9.89		
d	Cattle	1	0.31	0.53	0.479
	Megaherbivores + Mesoherbivores	2	0.11	0.42	0.667
	Cattle*Megaherbivores + Mesoherbivores	2	0.16	0.51	0.611
	Error	12	0.32		
J´	Cattle	1	0.00	0.27	0.612
	Megaherbivores + Mesoherbivores	2	0.00	0.45	0.651
	Cattle*Megaherbivores + Mesoherbivores	2	0.00	1.19	0.189
	Error	12	0.00		
H´	Cattle	1	0.01	0.10	0.757
	Megaherbivores + Mesoherbivores	2	0.00	0.12	0.884
	Cattle*Megaherbivores + Mesoherbivores	2	0.06	1.88	0.194
	Error	12	0.03		

Table 7.5. 2x3 ANOVAs on the effects of the factors ‘cattle’ (levels: absent [O, W and MW] vs. present [C, WC and MWC]) and ‘herbivores’ (levels: herbivores absent [O and C], only mesoherbivores present [W and CW], and both meso- and megaherbivores present [MW and MWC]) on the Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) of ground wanderers from total data set. All the six treatments were used. No treatments were omitted from the data set.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	4.50	0.38	0.547
	Megaherbivores + Mesoherbivores	2	49.56	2.85	0.096
	Cattle*Megaherbivores + Mesoherbivores	2	20.67	1.16	0.346
	Error	12	16.72		
d	Cattle	1	0.31	0.18	0.675
	Megaherbivores + Mesoherbivores	2	0.11	2.77	0.102
	Cattle*Megaherbivores + Mesoherbivores	2	0.16	1.51	0.260
	Error	12	0.32		
J´	Cattle	1	0.00	0.37	0.554
	Megaherbivores + Mesoherbivores	2	0.01	0.87	0.443
	Cattle*Megaherbivores + Mesoherbivores	2	0.00	0.446	0.650
	Error	12	0.01		
H´	Cattle	1	0.01	0.04	0.948
	Megaherbivores + Mesoherbivores	2	0.22	2.32	0.141
	Cattle*Megaherbivores + Mesoherbivores	2	0.06	0.78	0.480
	Error	12	0.07		

Table 7.6. 2x2 ANOVAs on the effects of the factors ‘cattle’ (levels: absent [W and MW] vs. present [WC and MWC]) and ‘megaherbivores’ (levels: absent [W and WC] vs. present [MW and MWC]) on the Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) of web builders. Two treatments (O and C) were omitted from the data set so that the analysis was fully crossed.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	0.00	0.00	1.000
	Megaherbivores	1	8.33	3.03	0.119
	Cattle*Megaherbivores	1	1.33	0.48	0.505
	Error	8	2.75		
d	Cattle	1	0.02	0.37	0.561
	Megaherbivores	1	0.31	5.19	0.052
	Cattle*Megaherbivores	1	0.05	0.91	0.367
	Error	8	0.06		
J´	Cattle	1	0.00	0.09	0.770
	Megaherbivores	1	0.00	0.13	0.724
	Cattle*Megaherbivores	1	0.00	0.23	0.641
	Error	8	0.01		
H´	Cattle	1	0.00	0.05	0.833
	Megaherbivores	1	0.04	0.52	0.491
	Cattle*Megaherbivores	1	0.01	0.09	0.778
	Error	8	0.08		

Table 7.7. 2x2 ANOVAs on the effects of the factors ‘cattle’ (levels: absent [W and MW] vs. present [WC and MWC]) and ‘megaherbivores’ (levels: absent [W and WC] vs. present [MW and MWC]) on the Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) of plant wanderers. Two treatments (O and C) were omitted from the data set so that the analysis was fully crossed.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	27.00	3.31	0.107
	Megaherbivores	1	0.33	0.04	0.844
	Cattle*Megaherbivores	1	1.33	0.04	0.845
	Error	8	8.17		
d	Cattle	1	0.59	157	0.245
	Megaherbivores	1	0.04	0.11	0.750
	Cattle*Megaherbivores	1	0.03	0.09	0.895
	Error	8	0.31		
J´	Cattle	1	0.00	0.28	0.612
	Megaherbivores	1	0.00	0.74	0.415
	Cattle*Megaherbivores	1	0.00	167	0.237
	Error	8	0.00		
H´	Cattle	1	0.07	3.13	0.114
	Megaherbivores	1	0.01	0.47	0.511
	Cattle*Megaherbivores	1	0.01	0.145	0.263
	Error	8	0.02		

Table 7.8. 2x2 ANOVAs on the effects of the factors ‘cattle’ (levels: absent [W and MW] vs. present [WC and MWC]) and ‘megaherbivores’ (levels: absent [W and WC] vs. present [MW and MWC]) on the Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) of ground wanderers. Two treatments (O and C) were omitted from the data set so that the analysis was fully crossed.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	27.00	1.71	0.226
	Megaherbivores	1	12.00	0.58	0.470
	Cattle*Megaherbivores	1	5.33	0.39	0.552
	Error	8	17.50		
d	Cattle	1	0.88	1.73	0.224
	Megaherbivores	1	0.34	0.48	0.508
	Cattle*Megaherbivores	1	0.05	0.22	0.65
	Error	8	0.54		
J´	Cattle	1	0.00	0.27	0.617
	Megaherbivores	1	0.00	0.01	0.908
	Cattle*Megaherbivores	1	0.00	0.71	0.424
	Error	8	0.00		
H´	Cattle	1	0.00	0.10	0.764
	Megaherbivores	1	0.01	0.13	0.732
	Cattle*Megaherbivores	1	0.08	0.87	0.378
	Error	8	0.09		

Table 7.9. 2x2 ANOVA on the factors ‘cattle’ (levels: absent [O and W] vs. present [C and WC]) and ‘mesoherbivores’ (levels: absent [O and C] vs. present [W and WC]) on the Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) of web builders. Two treatments (MW and MWC) were omitted from the data set so that the analysis was fully crossed.

Diversity variable	Treatment	DF	MS	F-value	P- value
S	Cattle	1	0.75	0.281	0.610
	Mesoherbivores	1	0.08	0.031	0.864
	Cattle*Mesoherbivores	1	0.08	0.031	0.864
	Error	8	2.67		
d	Cattle	1	0.04	0.467	0.514
	Mesoherbivores	1	0.02	0.165	0.695
	Cattle*Mesoherbivores	1	0.03	0.312	0.591
	Error	8	0.09		
J´	Cattle	1	0.00	0.263	0.622
	Mesoherbivores	1	0.00	0.006	0.938
	Cattle*Mesoherbivores	1	0.00	0.621	0.453
	Error	8	0.00		
H´	Cattle	1	0.00	0.098	0.763
	Mesoherbivores	1	0.00	0.045	0.838
	Cattle*Mesoherbivores	1	0.01	0.504	0.498
	Error	8	0.02		

Table 7.10. 2x2 ANOVA on the factors ‘cattle’ (levels: absent [O and W] vs. present [C and WC]) and ‘mesoherbivores’ (levels: absent [O and C] vs. present [W and WC]) on Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) of plant wanderers. Two treatments (MW and MWC) were omitted from the data set so that the analysis was fully crossed.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	6.75	0.69	0.427
	Mesoherbivores	1	10.08	1.04	0.336
	Cattle*Mesoherbivores	1	4.08	0.42	0.533
	Error	8	9.66		
d	Cattle	1	0.02	0.05	0.816
	Mesoherbivores	1	0.12	0.34	0.574
	Cattle*Mesoherbivores	1	0.22	0.63	0.447
	Error	8	0.35		
J´	Cattle	1	0.00	0.06	0.801
	Mesoherbivores	1	0.00	0.55	0.477
	Cattle*Mesoherbivores	1	0.01	2.93	0.125
	Error	8	0.00		
H´	Cattle	1	0.00	0.02	0.881
	Mesoherbivores	1	0.00	0.02	0.885
	Cattle*Mesoherbivores	1	0.15	2.59	0.145
	Error	8	0.05		

Table 7.11. 2x2 ANOVA on the factors ‘cattle’ (levels: absent [O and W] vs. present [C and WC]) and ‘mesoherbivores’ (levels: absent [O and C] vs. present [W and WC]) on the Shannon-Wiener diversity index (H´), Margalef’s richness index (d), Pielou’s evenness index (J´) and total species (S) of ground wanderers. Two treatments (MW and MWC) were omitted from the data set so that the analysis was fully crossed.

Diversity variable	Treatment	DF	MS	F-value	P-value
S	Cattle	1	0.75	0.04	0.846
	Mesoherbivores	1	44.08	2.36	0.162
	Cattle*Mesoherbivores	1	14.08	0.75	0.410
	Error	8	18.66		
d	Cattle	1	0.07	0.12	0.727
	Mesoherbivores	1	1.38	2.48	0.153
	Cattle*Mesoherbivores	1	0.79	1.42	0.267
	Error	8	0.55		
J´	Cattle	1	0.00	1.28	0.289
	Mesoherbivores	1	0.00	2.18	0.178
	Cattle*Mesoherbivores	1	0.00	0.51	0.493
	Error	8	0.00		
H´	Cattle	1	0.04	0.69	0.427
	Mesoherbivores	1	0.19	3.12	0.115
	Cattle*Mesoherbivores	1	0.00	0.00	0.933
	Error	8	0.06		

Table 7.12. Regression to establish the relationship between relative vegetation cover and the Shannon-Wiener diversity index (H´), Margalef's richness index (d), Pielou's evenness index (J´) and total species (S) of web builders, plant wanderers and ground wanderers. Df = 1, 16. * = Significant at $\alpha = 0.05$.

Guild	Diversity variable	r	r^2	P-value
Web builders	S	0.03	0.06	0.903
	d	0.01	0.06	0.967
	J´	0.38	0.09	0.117
	H´	0.33	0.06	0.183
Plant wanderers	S	0.47	0.17	0.048*
	d	0.43	0.10	0.100
	J´	0.05	0.05	0.750
	H´	0.31	0.04	0.217
Ground wanderers	S	0.36	0.06	0.160
	d	0.30	0.03	0.248
	J´	0.06	0.06	0.742
	H´	0.16	0.04	0.559

Figures

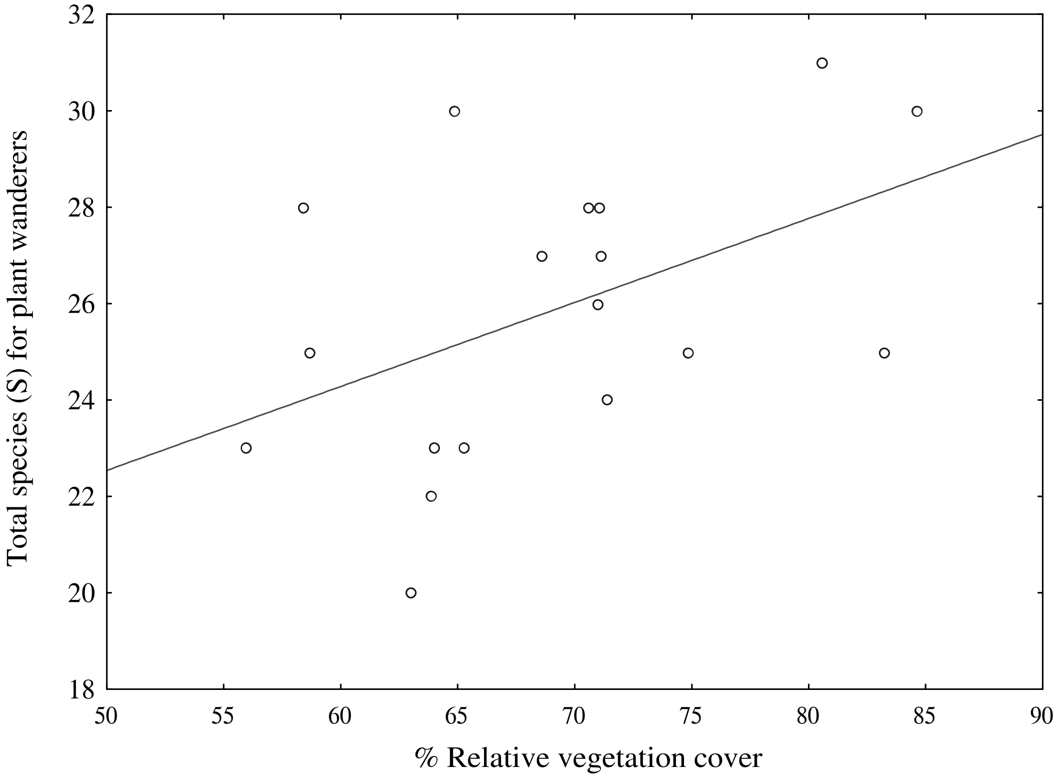

Figure 7.1. The relationship between relative vegetation cover and total species (S) for plant wanderers. The equation is: S = 13.82 + 0.17 * (relative vegetation cover); r = 0.47; r^2 = 0.17, p = 0.048*. * = Significant at α = 0.05.

CHAPTER 8: INDIVIDUAL SPECIES' ABUNDANCE AND THEIR RESPONSE TO LARGE MAMMALIAN HERBIVORES' ACTIVITY

Preface

This chapter describes the response of abundance of six individual spider species to the large mammalian herbivore treatments. It is a finer level of resolution than is used in chapters 5 and 7 and establishes whether such a resolution is more sensitive to disturbances caused by grazing. Three of the species under investigation were from sweep-netting samples and the other three from pitfall-trapping samples. The relationship of abundances to relative vegetation cover and rainfall was also explored.

Introduction

Results from the previous chapters revealed that at the overall community and guild levels of resolutions, diversity, richness and evenness of spiders were not very sensitive to disturbances caused by herbivore activity in the experimental plots. Only cattle were found to have a significant effect on spiders, while mesoherbivores and megaherbivores (game) had no significant effects. This might mean that the disturbances caused by mesoherbivores and megaherbivores were too mild to cause any significant effects on spiders, or that the taxonomic resolution at the two levels was not sensitive enough to reflect disturbances of mesoherbivores and megaherbivores, or both. This would agree with work that noted that higher taxa (surrogate taxa) are not sufficient for use as indicators of overall biodiversity (e.g. Noss 1990; Kremen *et al*. 1994; Alonso 2000). This chapter therefore proposes to analyse individual species' responses to establish whether abundances at this taxonomic level are more sensitive to disturbances. It was hoped that at this level, the individual behavioural responses would be clearer i.e. the resolution would be higher than when all species are treated collectively as a community (chapter 5) or aggregated into three guilds (chapter 7). The study therefore analysed the three most abundant species from each of the two collecting methods, namely sweep-netting and pitfall-trapping.

Since individual species could also vary across time depending on lifecycle, it was hoped that better results would be realised by analysing more than one species. In addition, both methods of data collection were considered before choosing the individual species so that each method was represented by three common species. This choice was justified by the fact that different methods target ecologically different groups of spiders. In turn these different groups of species behave differently and their potential as indicators could also be different. For example, ground–dwelling spiders can be good predictors for overall invertebrate biodiversity (Duelli and Obrist 1998). In the current study, the pitfall-trapping method targeted the ground active spiders. As such, taking into consideration spiders from the two collecting methods was a better approach that might give a clearer and more precise picture of individual species' responses to grazing.

According to Churchill (1997), spiders need to have a number of qualities in order to qualify as good bio-indicators, e.g. they should be diverse, abundant and readily sampled. It was therefore hoped that by analysing the common, abundant and readily sampled spider species, a clear picture or pattern would be portrayed about the impacts of large mammalian herbivores, thus providing useful information that can help develop a management tool for conservation.

Objectives

1. To establish the effect of different large mammalian herbivores on abundance of *Cyclosa insulana* (Costa 1834), *Runcinia flavida* (Simon 1881), *Argiope trifasciata* Forskal 1775, *Aelurillus* sp*., Diores strandi* Caporiacco 1949 and *Borboropactus* sp.
2. To establish the effect of rain and relative vegetation cover on the abundance of the same selected species of spiders.

Hypothesis

The large mammalian herbivore treatments, time, rainfall and relative vegetation cover significantly influenced the abundance of *C. insulana, R. flavida*, *A. trifasciata*, *D. strandi*, *Borboropactus* sp. and *Aelurillus* sp.

Methods

Spiders were selected from the KLEE spider survey based on their abundance and distribution, with each method of spider collection being represented by three common and well-sampled species. These selected species had the following abundances: *C. insulana* - 2480, *R. flavida* - 488, *A. trifasciata* - 289, *Aelurillus sp.* - 526, *D. strandi* - 325, and *Borboropactus sp.* - 234. The square root transformation was performed on all spider abundance data in order to make the underlying distribution normal, since most counts per sampling occasion were less than twenty (Fry 1993). In this study, the formula $X' = \sqrt{(x + 0.5)}$ was used instead of $X' = \sqrt{x}$, where X' was the square root-transformed value when some observations are found to be zero (Bartlett 1936; Zar 1999).

Statistical analyses

The evaluation of part of the hypothesis on how the abundance of each of the six species varied with time and with all the large mammalian herbivore treatments was carried out using repeated measures ANOVA, and one-way and two-way ANOVA. Since the effects of the experimental treatments was not fully crossed, it was not possible to do just a single ANOVA and the study was obliged to do several such tests in order to satisfactorily answer the research questions. Two-way ANOVAs were performed on the square root-transformed abundance of spiders to evaluate the effects of blocks and treatments. The data matrix for the repeated measures ANOVA was organised according to sampling occasions such that there were 14 repeated measures representing monthly intervals of data collection.

The evaluation of the other part of the hypothesis on the effect of rainfall and relative vegetation cover on the abundance of the six species under different grazing treatments were established with analysis of covariance (ANCOVA). Here, rainfall and relative vegetation cover were the continuous predictors or covariates, while various combinations of herbivores (cattle and meso- or megaherbivores) were the categorical predictors or experimental treatments. In this analysis, there was a repetition of part of the previous analysis by including herbivore treatment. The intention was to get the best results out of this analysis by making sure that rainfall, relative vegetation cover and herbivore effects were all included, since they could be interrelated. In other words both cattle and rainfall had an effect on relative vegetation cover and it was thus interesting to evaluate how they all interacted to affect the abundance of the species in question.

Levene's test was used to test the homoscedacity of the data. Where this test was significant but close to $\alpha = 0.05$, I assumed no serious violation of the ANOVA rule of homoscedacity of data and I proceeded with ANOVA tests. This was also the case when there was a need to perform a two-way ANOVA, since there was no test to perform a non-parametric analysis equivalent to two-way ANOVA. In some cases, non-significant Levene's tests prior to ANOVA were not reported to avoid redundancy, but the significant ones were stated and the non-parametric analysis that followed explained. Tukey's multiple comparison tests were performed where ANOVA results were significant.

Results and discussion

Cyclosa insulana

The results of a Levene's test performed on the square root-transformed abundance of *C. insulana* indicated that most figures were not significant (Table 8.1). Since only one month that was significant, with this level being fairly close to $\alpha = 0.05$, there was no serious violation of the assumptions of ANOVA and I therefore proceeded with ANOVA tests. Repeated measures ANOVA on the effects of cattle and mesoherbivores on the abundance of *C. insulana* revealed that time was the only significant factor affecting the species' abundance (Table 8.2). Similarly, only time had a significant effect on the abundance of *C. insulana* when a repeated measures ANOVA was performed to establish the effects of cattle and mesoherbivores + megaherbivores. Another repeated measures ANOVA to establish the effects of cattle and megaherbivores showed that only time had a significant effect on the abundance of *C. insulana*.

A Levene's test performed on data re-organised to test the effect of treatments on the abundance of *C. insulana* was significant ($F_{5,\,498} = 3.27$, $p = 0.006$), while the following Kruskal-Wallis test was not significant ($\chi^2 = 5.13$, df = 5, $p = 0.40$). A two-way ANOVA performed on the same square root-transformed abundance data to evaluate the effects of block and treatment revealed a significant result (Table 8.3), with the resultant pattern shown in Figure 8.1. A further post-hoc test (Table 8.4) revealed that the source of variation was the NO plot, which had a significantly lower mean abundance than the CWC, CMWC, CW, NMW, SC, SO and SW plots. Another two-way ANOVA on the effects of cattle and mesoherbivores on the abundance of *C. insulana* was not significant. Similarly, a two-way ANOVA on the effects of cattle and mesoherbivores + megaherbivores on the abundance of *C. insulana* and another on the effects of cattle and megaherbivores on the abundance of the same species were not significant.

An analysis of covariance to establish the effects of vegetation, total rainfall, mesoherbivores and cattle on the abundance of *C. insulana* revealed that the relative vegetation cover and cattle significantly affected the abundance of this species with cattle plots returning a significantly lower species abundance than control plots (Table 8.5). In this case rainfall and relative vegetation cover were used as covariates. The results of a correlation and regression of this abundance with relative vegetation cover were significant ($r = 0.32$, $r^2 = 0.10$, $F_{1, 502} = 57.98$, $p = 0.00$), and implied that cover explained 10% of variation in this abundance.

The fact that time was significant after a repeated measure ANOVA implied that the events that go with it were important in influencing the abundance of *C. insulana.* Such events may include changes in rainfall and temperature that may cause a variation in spiders' surrounding environment. Other time changes may include the lifecycles of individual species that are marked with reproduction. In all such cases, there is bound to be a variation of the abundance of species with time.

It was not clear why the northern control plot returned a significantly lower mean abundance than most of other plots since most past studies of the KLEE system (Keesing 1998, 2000; Misurelli 2002; Young *et al.* 2003) had not found any anomalous results with the northern control plot, but rather in southern plots. Results of the previous chapters of this study, pitched at the community and guild levels, similarly indicate that the southern plots were the odd ones. It was thus difficult to interpret given that the results of an MDS analysis (Figure 5.11) indicated that the spider community of the southern control plot differed from that of others.

Although the results of a regression indicate that relative vegetation cover explains only 10% of the variation in the abundance of this species, it cannot be concluded that any effects of cattle on this species were mediated through relative vegetation cover.

In general, *C. insulana* was the most abundant (comprising 23.64% of all the specimens collected) and a very common spider throughout the sampling occasions. Some work has been published about the biology of this species and especially about the web's stabilimenta and their functions (Neet 1990; McClintock and Dodson 1999). The members of the genus *Cyclosa* build their webs on shrubs in open woodlands (Dippenaar-Schoeman and Jocqué 1997). *C. insulana* places its egg sacs and debris from prey remains in the stabilimentum of its web. It is a cosmopolitan, introduced species and not endemic to Africa (Dippenaar-Schoeman and Jocqué 1997; McClintock and Dodson 1999). It was probably a very hardy species that could tolerate high levels of disturbances and was found therefore in all habitats, thus reducing its sensitivity to disturbances. It was probably a poor monitor of disturbances. Andersen (1990), Noss (1990) and New (1995) showed that for any invertebrate taxon to be considered as a good indicator of ecological change, it needs to display sensitivity to changes in environmental variables that are associated with stress and disturbance. Several workers have shown that other different groups of invertebrates possess such qualities e.g. Collembola (Greenslade 1997); ground beetles (New 1998; Rainio and Niemelä 2003); dragonflies (Hawking and New 2002; Clausnitzer 2003) and butterflies (Oostermeijer & van Swaay 1998; Pollard & Yates 1993).

In conclusion, there was not sufficient evidence to reject the null hypothesis that the large mammalian herbivore treatments, time, rainfall and relative vegetation cover significantly influenced the abundance of *C. insulana.* However it became clear that time, relative vegetation cover and cattle were important factors for the current study. In this case, its abundance varied with time, significantly decreased with the presence of cattle, and increased significantly with increase on relative vegetation cover.

Argiope trifasciata

A Levene's test performed on the square root-transformed abundance of *A. trifasciata* is indicated in Table 8.6. Since only one month that was significantly different, with this level being fairly close to $\alpha = 0.05$, there was no serious violation of the assumptions of ANOVA and I therefore proceeded with ANOVA tests. Repeated measures ANOVA on the effects of cattle and mesoherbivores on the abundance of *A. trifasciata* revealed that only time had a significant effect on this species (Table 8.7). Another repeated measures ANOVA on the effects of cattle and mesoherbivores + megaherbivores on abundance also revealed that only time was a significant factor. Similarly, repeated measures ANOVA on the effects of cattle and megaherbivores on abundance was not significant except for the factor of time. In all the above cases, there were no statistically significant interactions.

A Levene's test performed on data re-organised to test the effects of treatments on the abundance of *A. trifasciata* was significant ($F_{5, 498} = 11.49$, $p = 0.00$). The Kruskal-Wallis test that followed was significant ($\chi^2 = 13.52$, df = 5, $p = 0.02$).

A two-way ANOVA performed on the square root-transformed abundance data to evaluate the effects of block and treatment revealed a significant result (Table 8.8) with the pattern shown in Figure 8.2. A further post-hoc test (Table 8.9) revealed that the source of variation was the north control (NO) plot, which had a significantly higher mean abundance than all the other plots. In addition, the central mesoherbivores + megaherbivores plot (CMW) had a significantly higher abundance than the south cattle (SC), south mesoherbivores + cattle (SWC) and south control (SO) plots.

Another two-way ANOVA on the effects of cattle and mesoherbivores on the abundance of *A. trifasciata* was significant for cattle (Table 8.10), with the cattle plots returning a significantly lower abundance than the control plots after performing a post-hoc test.

There was no interaction between cattle and mesoherbivore treatments. Similarly, two-way ANOVA on the effects of cattle and mesoherbivores + megaherbivores on the abundance of *A. trifasciata* was only significant for cattle (Table 8.11), and a resultant post-hoc test revealed that only the cattle plots returned a significantly lower abundance than the control plots. There was no interaction between cattle and mesoherbivores + megaherbivores (game). Finally, a two-way ANOVA on the effect of cattle and megaherbivores on the abundance of the same species was also significant for cattle (Table 8.12). A resultant post-hoc test revealed that it was only the cattle plots that had a significantly lower abundance than the control plots. There was no interaction between the cattle and megaherbivore effects.

An analysis of covariance to establish the effects of vegetation, total rainfall, mesoherbivores and cattle on the abundance of *A. trifasciata* revealed that only the presence of cattle significantly decreased the abundance of this species, with cattle plots returning a significantly lower abundance than control plots (Table 8.13). Similarly, an analysis of covariance on the effect of vegetation, total rainfall, mesoherbivores + megaherbivores (game) and cattle on the abundance of *A. trifasciata* revealed that only cattle significantly decreased the abundance of this species. However, when the same analysis of covariance was done to test the effects of megaherbivores and cattle on the abundance of the same species, rainfall and cattle were found to significantly affect the species, with the presence of cattle reducing the abundance.

The results revealed that time, rain and cattle were important factors. This spider's abundance was significantly higher in control plots (higher relative vegetation cover) than cattle plots (lower relative vegetation cover). In order to explain its response to herbivore treatments, it is wise to review its biology.

This species is a member of the subfamily Argiopinae, which are orbweb-weaving, diurnal sit-and-wait predators (Dippenaar and Jocqué 1997). *Argiope trifasciata* makes its webs exclusively in tall grass (Edmunds 1982). Its web is considered the spider's home territory. The results of Table 8.8 suggest that this species preferred least disturbed places (e.g. control plots where the grass was tall and the spider could build its webs) to disturbed ones (e.g. cattle plots) where the grass was short. The taller grasses would provide better sites for attachments for their large webs, which would enhance more efficient prey capture. Thus, it makes sense that cattle plots had low abundance compared to controls. There was higher abundance in control plot and mesoherbivores + megaherbivores (MW) plots, which had more vegetation cover and less disturbance. As indicated in the post-hoc test, most of the cattle plots had significantly lower abundances of this species, which could imply that the presence of cattle had an indirect effect on *A. trifasciata*, probably through their effect on relative vegetation cover. This supports findings that the availability of unique habitat structural features that allow more efficient prey capture could limit some spiders' populations more than food itself (Rypstra 1983, Wise 1993).

The effect of rain to this species was probably through effects on relative vegetation cover and increased food abundance after rainfall. Most spiders are expected to respond to changes in rainfall because rain is linked with changes in habitat complexity and food availability. The effect of time on this species can be explained in the same way for *C. insulana* in the previous section.

In conclusion, the hypothesis that the large mammalian herbivore treatments, time, rainfall and relative vegetation cover significantly altered the abundance of *A. trifasciata,* was not rejected as there was no sufficient evidence. Time, rainfall and cattle were found to be important factors. As such, an increase in rainfall increased the abundance of *A. trifasciata* while the presence of cattle reduced it. This study found that *A. trifasciata* was sensitive to grazing impacts.

Runcinia flavida

Levene's tests performed on the square root-transformed abundance of *R. flavida* is shown in Table 8.14. Since less than half of the values were significant and also close to $\alpha = 0.05$, there was no serious violation of assumptions of ANOVA and I therefore proceeded with ANOVA tests. Repeated measures ANOVA on the effects of cattle and mesoherbivores on the abundance of *R. flavida* revealed that time had a significant effect, while cattle had an almost significant effect on the abundance of *R. flavida* (Table 8.15). However, mesoherbivores had no effects on the same species and there were no interactions between cattle and mesoherbivores.

In the next repeated measures ANOVA to test the effects of cattle and mesoherbivores + megaherbivores on the abundance of *R. flavida*, only time had a significant effect and there were no significant interactions. Lastly, a repeated measures ANOVA on the effect of cattle and megaherbivores on the abundance of *R. flavida* revealed that both cattle and time had a significant effect on abundance, with no interactions between cattle and megaherbivores.

A Levene's test performed on data re-organised to test the effect of treatments on the abundance of *R. flavida* was significant ($F_{5,\ 498} = 2.73$, $p = 0.029$), while the subsequent Kruskal-Wallis test was significant ($\chi^2 = 13.52$, df = 5, $p = 0.02$).

A two-way ANOVA performed on the same square root-transformed abundance data to evaluate the effects of block and treatment revealed a significant result (Table 8.16) with a resultant pattern shown in Figure 8.3. A post-hoc test revealed that the source of variation was CO, which had significantly higher abundance than SMWC, SWC and SO, and in addition CMW had significantly higher abundance than SMWC and SWC.

Another two-way ANOVA on the effects of cattle and mesoherbivores on the abundance of *R. flavida* was significant (Table 8.17), with the cattle plots returning a significantly lower abundance than the control plots. There was no interaction between cattle and mesoherbivores. Similarly, a two-way ANOVA on the effects of cattle and megaherbivores on the abundance of *R. flavida* was only significant for the cattle plots which returned a significantly lower abundance than the control plots. There were no interactions between cattle and megaherbivores.

Lastly, two-way ANOVA on the effects of cattle and mesoherbivores + megaherbivores on the abundance of *R. flavida* showed that only cattle had a significant effect on the abundance of this species, in which case the mean abundance was low for cattle plots compared to the other plots. There were no interactions between cattle and mesoherbivores + megaherbivores. An analysis of covariance to establish the effects of vegetation, total rainfall, mesoherbivores and cattle on the abundance of *R. flavida* revealed that the total monthly rainfall and cattle significantly affected the abundance of this species with cattle plots returning a significantly lower species abundance than control plots (Table 8.18). Another analysis of covariance to establish the effects of vegetation, total rainfall, mesoherbivores + megaherbivores and cattle on the abundance of *R. flavida* revealed that the total monthly rainfall and cattle again significantly affected the abundance of this species. The same results were revealed when the same analysis was conducted when megaherbivores and cattle were chosen as categorical factors.

In summary, time, rainfall and cattle had significant effect on the abundance of *R. flavida.* The effect of time probably implied that the annual life cycle of the species or the effects of monthly changes (such as rainfall and temperature) on relative vegetation cover altered the habitat complexity and thus affected the spider's abundance accordingly. The fact that cattle had a significant negative effect on the abundance of this species also meant that its negative effect on relative vegetation cover consequently affected the species. It was probable that the presence of cattle caused more trampling and reduced the relative vegetation cover by grazing, hence its negative effect on the abundance of this species. It was expected that rainfall might exert its influence through relative vegetation cover, consequently promoting habitat complexity as already mentioned. The following biology of the species might probably explain better its habitat preferences.

Runcinia flavida (a member of the family Thomisidae or crab spiders) is mainly diurnal. It has an elongated body and occurs mainly on grass (Dippenaar and Jocqué 1997). Members of this family have lost their agility and have become semi-sedentary, excelling as ambushers. They do not hunt actively like wolf spiders and instead remain stationary and wait in ambush for unsuspecting insects (Dippenaar and Jocqué 1997). This therefore might suggest that they would prefer a heterogeneous habitat (structurally complex one) where they would hide and maximise food acquisition through ambushing. Since they are slow movers, it was probable that a complex habitat compensated for their slowness by providing abundant food resources.

The hypothesis that rainfall, relative vegetation cover and large mammalian herbivores treatments significantly affected the abundance of *R. flavida* was not rejected, as there was no sufficient evidence. Time, rainfall and cattle were found to be important factors in determining the abundance of this species. Increased rainfall significantly increased the abundance of *R. flavida*, while the presence of cattle decreased its abundance. This study found this species sensitive to grazing impacts.

Diores strandi

A Levene's test performed on the square root-transformed abundance of *D. strandi* is shown in Table 8.19. Since only two values were significant and close to $\alpha = 0.05$, there was no serious violation of the assumptions of ANOVA and I therefore proceeded with ANOVA test. Repeated measures ANOVA on the effects of cattle and mesoherbivores on the abundance of *D. strandi* revealed that time was the only significant factor affecting the species' abundance (Table 8.20). A repeated measures ANOVA on the effects of cattle and mesoherbivores + megaherbivores as well as that of cattle and megaherbivores on the abundance of *D. strandi* showed that time significantly affected the abundance of this species and that there was a resultant interaction between cattle and mesoherbivores + megaherbivores. Lastly, another repeated measures ANOVA on the effects of cattle and megaherbivores on the abundance of *D. strandi* showed that only time significantly affected the abundance of this species. There were no interactions.

A Levene's test performed on data re-organised to test the effect of treatments on the abundance of *D. strandi* was significant ($F_{5,\,498} = 3.27$, $p = 0.006$), while the subsequent Kruskal-Wallis test was not significant, ($\chi^2 = 5.13$, df = 5, $p = 0.40$). A two-way ANOVA performed on the same square root-transformed abundance data of *D. strandi* to evaluate the effects of block and treatment revealed a significant result (Table 8.21) with a resultant pattern shown in Figure 8.4. A further post-hoc test (Table 8.22) revealed that the source of variation was mainly due to CWC, which was significantly higher than CW, NMWC, NW, SC, and SMWC plots, and NMW, which had significantly higher abundance than SC.

Another two-way ANOVA on the effects of cattle and mesoherbivores on the abundance of *D. strandi* was significant for cattle (Table 8.23). A post-hoc test revealed that cattle plots had significantly lower means than the control. A third two-way ANOVA on the effects of cattle and mesoherbivores + megaherbivores on the abundance of *D. strandi* revealed that only the interaction between cattle and mesoherbivores + megaherbivores was significant (Table 8.24). A Tukey's post-hoc test revealed that cattle plots had a significantly lower abundance than mesoherbivores + megaherbivores.

A last two-way ANOVA to establish the effects of cattle and megaherbivores on the abundance of the same species was significant (Table 8.25). A Tukey's post-hoc test on effects of cattle revealed that the cattle plots had significantly lower abundance than the control plots. There was an interaction between cattle and megaherbivores with a Tukey's post-hoc test revealing that cattle plots had significantly lower abundance than megaherbivores.

An analysis of covariance to establish the effects of vegetation, total rainfall, mesoherbivores and cattle on the abundance of *D. strandi* revealed that increased relative vegetation cover and total monthly rainfall significantly increased the abundance of the species while the presence of cattle significantly reduced the abundance of this (Table 8.26). The cattle plots had significantly lower abundance than control plots and there was no interaction between cattle and mesoherbivores.

Another analysis of covariance to establish the effect of vegetation, total rainfall, mesoherbivores + megaherbivores and cattle on the abundance of *D. strandi* revealed that increased relative vegetation cover significantly increased abundance of the species while the presence of cattle significantly reduced the abundance of this species. There was a significant interaction between mesoherbivores + megaherbivores and cattle, with the cattle plots returning a significantly lower mean than mesoherbivores + megaherbivores (game) plots. Similarly, when the same analysis was conducted when megaherbivores and cattle were chosen as categorical factors or effects, increase relative vegetation cover significantly increased the abundance of this species, while the presence of cattle significantly reduced its abundance. In this case, there was a significant interaction between mesoherbivores + megaherbivores and cattle. A post-hoc test again revealed that the cattle plots returned a significantly lower mean than mesoherbivores.

It was found that time, cattle, relative vegetation cover and rainfall were important factors in determining the abundance of *D. strandi.* The effects of time can be proposed to be indirectly through annual changes in rainfall and temperature, which in turn would cause changes in the spider living environment, thereby influencing its abundance.

In terms of biology, *D. strandi* belongs to the family Zodariidae, whose members are found in arid and semi-arid areas and are among the most abundant families in pitfall-trapping samples in most parts of Africa (Russell-Smith *et al.* 1987). Most of the zodariids are specialised ant or termite predators (Jocqué 1990; Jocqué and Dippenaar-Schoeman 1992). Some zodariids build igloo-shaped retreats while other are burrowers. They are small, and quick-moving spiders (Dippennaar and Jocqué 1997) and this may contribute to the fact that they are quite common in pitfall traps.

The results of repeated measures ANOVA on *D. strandi* revealed that only time was important in the variation of the abundance of this species. When the first two-way ANOVA was performed, the resultant pattern was contradictory and not easy to explain. The abundance of *D. strandi* was found to be high in some cattle plots and low in others, while in other cases it was high in less disturbed mesoherbivores + megaherbivores plots and low in cattle plots. One suggestion might be that the species was not limited by the factors under investigation and probably not sensitive to disturbances. Being an ant and/or termite eater (Jocqué 1990) the spider species was probably not affected by changes in relative vegetation cover due to weak indirect link between spiders, ants, termites and relative vegetation cover. However, when a further series of ANOVAs were performed, the results clearly showed that the cattle plots had significantly lower abundance than the control plots, and that there were interactions between cattle and megaherbivores and also between cattle and mesoherbivores + megaherbivores. A suggestion to explain this behaviour might be that vegetation cover might indirectly affect the many ant species found in the black soil ecosystem and thus influence the distribution of this spider species. There are nine ant species that co-exist with two swollen-thorn *Acacia* species on the black cotton soil ecosystem (Young *et al.* 1997, Stanton and Young 1999, Palmer *et al* 2000). Four of these species are obligate *Acacia*-ants that compete for possession of the *Acacia drepanolobium* host trees but still co-exist at fine spatial scales (Stanton *et al.* 1999, 2002; Palmer *et al* 2000). Since some of these ants were always crawling on the ground (personal observation), it was possible that they formed part of the diet of this spider species (although not proved) and hence their distribution influenced that of the spider. Otherwise, the diet of most spiders varies and most of them are generalists feeding on insects and other invertebrates. Large spiders may eat small vertebrates such as frogs or birds (Dippenaar and Jocqué 1997).

Rainfall may increase the abundance of this species through its increase of food resources but this might not be very likely if the species feeds on ants. It might also have promoted their activity since spiders from dry land are known to emerge with the start of rains and their activity increases as they seek mates and food and might also promote reproduction and hence increased abundance. Rain also promotes growth of vegetation and thus promotes a more complex habitat that might favour increase in species abundance. As already explained earlier, cattle reduced relative vegetation cover thus reducing the habitat complexity that in turn caused a reduction in spider abundance.

In conclusion, there was no sufficient evidence to reject the hypothesis that rainfall, relative vegetation cover and large mammalian herbivores treatments significantly affected the abundance of *Diores strandi.* Time, rainfall, relative vegetation cover and cattle were important factors in determining the abundance of this species. As such, increased rainfall and relative vegetation cover significantly increased the abundance of

Diores strandi while the presence of cattle decreased its abundance. This study found that this species was sensitive to grazing impacts.

Borboropactus sp.

Levene's test performed on the square root-transformed abundance of *Borboropactus* sp. before performing a repeated measures ANOVA on effects of cattle and mesoherbivores on the abundance of *Borboropactus* sp. is shown in Table 8.27. Since there was no serious violation of the assumptions of ANOVA, I therefore proceeded with ANOVA tests. Other Levene's tests on the subsequent analysis on this species were not significant, and tables of their results are not included to avoid redundancy.

Repeated measures ANOVA on the effects of cattle and mesoherbivores on the abundance of *Borboropactus* sp. revealed that time was the only significant factor affecting the species (Table 8.28). Similarly, repeated measures ANOVA on the effects of cattle and mesoherbivores + megaherbivores on the abundance of *Borboropactus* sp. revealed that time was the only significant factor affecting the species. However, another repeated measures ANOVA on the effects of cattle and megaherbivores on the abundance of the same species showed that both time and cattle had a significant effect on the abundance of *Borboropactus* sp. (Table 8.29). There were no resulting interactions in this analysis.

A Levene's test performed on data re-organised to test the effect of treatments on the abundance of *Borboropactus* sp. was significant ($F_{5,\ 498} = 6.07$, $p = 0.000$), while the resultant Kruskal-Wallis test was not significant, ($\chi^2 = 7.62$, df = 5, $p = 0.18$). A two-way ANOVA performed on the same square root-transformed abundance data of *Borboropactus* sp. to evaluate the effects of block and treatment revealed a significant result (Table 8.30) with the resultant pattern shown in Figure 8.5. A further post-hoc test revealed that the source of variation was mainly due to NW and NWC, which were significantly higher than most of the other plots (Table 8.31).

Another two-way ANOVA on the effects of cattle and mesoherbivores on the abundance of *Borboropactus* sp. was not significant (Table 8.32). Similarly, a third two-way ANOVA on the effects of cattle and mesoherbivores + megaherbivores on the abundance of *Borboropactus* sp. was not significant and there was no resultant interactions between cattle and mesoherbivores + megaherbivores. The last two-way ANOVA to establish the effects of cattle and megaherbivores on the abundance of the same species was significant (Table 8.33). A Tukey's post-hoc test revealed that the cattle plots had a significantly lower abundance compared to control plots. There was no interaction between cattle and megaherbivores.

An analysis of covariance to establish the effect of vegetation, total rainfall, mesoherbivores and cattle on the abundance of *Borboropactus* sp. revealed that only increase in the relative vegetation cover and total monthly rainfall significantly increased the abundance of this species (Table 8.34). There were no interactions between cattle and mesoherbivores.

Another an analysis of covariance to establish the effect of vegetation, total rainfall, mesoherbivores + megaherbivores (game) and cattle on the abundance of *Borboropactus* sp. again revealed that only increases in the relative vegetation cover and total monthly rainfall significantly increased the abundance of this species. There was no significant interaction between mesoherbivores + megaherbivores and cattle. A last analysis of covariance conducted when megaherbivores and cattle were chosen as categorical factors, showed that only an increase in total monthly rainfall significantly increased abundance of this species

In summary the results showed that time, rainfall, relative vegetation cover and cattle were important factors affecting the abundance of this species. However, cattle, mesoherbivores and megaherbivores were not important factors. It was probable that time affected the species indirectly in a number of ways that might include monthly changes in rainfall and temperature, which in turn may affect relative vegetation cover influencing a variation in spider habitat complexity and thus the spider abundance. It was expected that increase in rainfall increased relative vegetation cover influencing a variation in spider habitat complexity and thus the spider abundance. The negative effect by cattle meant that resulting low relative vegetation cover interfered with habitat complexity and hence the spiders, in a similar version to the effects of rainfall. However the fact that the effects of cattle were not highly significant might mean that the species was not very sensitive to the disturbances caused by grazing. In terms of biology of this species, members of the genus *Borboropactus* are mostly found in the litter layer (Dippenaar and Jocqué 1997). They are slow-moving spiders that do not actively hunt but wait to ambush the prey (Koh 2000). They might therefore prefer a complex habitat where they would be able to hide properly and ambush the prey. At the same time, such a habitat might provide more food resources.

In conclusion, the hypothesis that rainfall, relative vegetation cover and large mammalian herbivores treatments significantly affected the abundance of *Borboropactus* sp. was not rejected, as there was insufficient evidence. Time, rainfall, relative vegetation cover and cattle were found to be important factors in determining the abundance of this species. Increased rainfall and relative vegetation cover significantly increased the abundance of *Borboropactus* sp. while the presence of cattle decreased its abundance. This study found that this species was sensitive to grazing impacts.

Aelurillus sp.

Levene's test performed on the square root-transformed abundance of *Aelurillus* sp. is shown in Table 8.35. Only one value was significant hence there was no serious violation of the assumptions of ANOVA and I therefore proceeded with ANOVA test. Repeated measures ANOVA on the effects of cattle and mesoherbivores on the abundance of *Aelurillus* sp. revealed that both time and cattle were significant factors affecting the species (Table 8.36). A repeated measures ANOVA on the effects of cattle and mesoherbivores + megaherbivores on the abundance of *Aelurillus* sp. revealed that both time and cattle were significant factors affecting the species (Table 8.37). A Levene's test prior to this analysis was not significant. A last repeated measures ANOVA on the effect of cattle and megaherbivores on the abundance of the same species showed that only time significantly affected the abundance of this species (Table 8.38). A Levene's test performed prior to this analysis was also not significant.

A Levene's test performed on the re-organised matrix to test the effect of treatments on the abundance of *Aelurillus* sp. was not significant ($F_{5, 498} = 1.98$, $p = 0.08$). The results of one-way ANOVA on the same data revealed a significant result, ($F_{5, 498} = 4.24$, df = 5, $p = 0.01$), with MWC, WC and C plots reporting significantly higher abundance than other plots. A two-way ANOVA performed on the same square root-transformed abundance data of *Aelurillus* sp. to evaluate the effects of block and treatment revealed a significant result (Table 8.39) with a resultant pattern shown in Figure 8.6. A further post-hoc test revealed that the source of variation was mainly due to CWC and NMWC, which had a significantly higher abundance than CMW and CO plots (Table 8.40).

A two-way ANOVA on the effects of cattle and mesoherbivores on the abundance of *Aelurillus* sp. was significant for cattle (Table 8.41). A post-hoc test revealed that cattle plots had higher means than the control plots. A third two-way ANOVA on the effects of cattle and mesoherbivores + megaherbivores on the abundance of *Aelurillus* sp. revealed that both cattle and also mesoherbivores + megaherbivores had a significant effect on the abundance of *Aelurillus* sp. (Table 8.42). A post-hoc test on the results indicated on this table revealed that where the results were significant, the plots with cattle had a significantly higher abundance than the control and mesoherbivore + megaherbivore plots.

A last two-way ANOVA to establish the effects of cattle and megaherbivores on the abundance of the same species was significant with the cattle plots returning a significantly higher abundance than the control plots. There were no interactions between cattle and megaherbivores.

An analysis of covariance to establish the effect of vegetation, total rainfall, mesoherbivores and cattle on the abundance of *Aelurillus* sp. revealed that increase in total monthly rainfall significantly increased the abundance of this species, as did the presence of cattle (Table 8.43). There were no interactions between cattle and mesoherbivores.

Another analysis of covariance to establish the effect of vegetation, total rainfall, mesoherbivores + megaherbivores and cattle on the square root-transformed abundance of *Aelurillus* sp. revealed that only cattle and mesoherbivores + megaherbivores significantly increased the abundance of this species. In these results, the cattle plots had significantly higher *Aelurillus* sp. abundance than control plots, while mesoherbivore plots had significantly higher *Aelurillus* sp. abundance than both megaherbivore and control plots. A last analysis of covariance conducted when megaherbivores and cattle were chosen as categorical factors, showed that only increase in total monthly rainfall and presence of cattle that significantly increased the abundance of this species.

The results show that time, rainfall, cattle and mesoherbivores + megaherbivores affected the abundance of this species. The effect of time was expected to be a complex one involving annual cycles of a year as already explained with the other species above. However the most striking results of this species is that unlike other species, the presence of cattle and mesoherbivores + megaherbivores were found to significantly increase the abundance of the species with control plots returning a significantly lower abundance of the same species. It seems this species thrived well where there was a lot of grazing and simply preferred open places and not complex habitats. A brief mention of its biology might help understand and explain this behaviour.

The species is a member of the family Salticidae, which are diurnal, cursorial, hunting spiders with well-developed vision (Dippenaar and Jocqué 1997). Their eyes are such that the anterior median eyes discriminate between objects while smaller anterior lateral eyes detect movement and help spider orientate towards objects (Hallas and Jackson 1986). Being a member of genus *Aelurillus*, the current study species does not spin capture webs or use silk to catch prey. According to Jackson and Pollard (1996), salticids detect and pursue prey by a combination of stalking, chasing and leaping or lunging.

Being a salticid, it was therefore expected that the study species would also behave in a similar way.

This study suggests that the behaviour of this species could be responsible for its observed distribution. Since it was a jumping spider and a hunter, it is possible that the species preferred more open places in order to allow room for food acquisition. Since it is also not a web builder, a more complex habitat was not necessary, but a rather more open habitat where it could spot prey from afar and pursue it efficiently. Meanwhile, with such a hunting behaviour, it might mean that its presence in pitfall samples might not be of the same magnitude as that of other species from pitfall-trapping samples e.g. *Borboropactus* sp., since the later are slow-moving, sit-and-wait predators. It is therefore not surprising that with such contrasting qualities, the two species of spiders preferred different habitats to live in.

In conclusion, the hypothesis that rainfall, relative vegetation cover and large mammalian herbivores treatments significantly affected the abundance of *Aelurillus* sp. was not rejected since there was no sufficient evidence. Time, rainfall, cattle and mesoherbivores + megaherbivores were important factors in determining the abundance of this species. Increased rainfall and the presence of cattle and mesoherbivores + megaherbivores increased the abundance of *Aelurillus* sp. This meant that the presence of cattle and mesoherbivores + megaherbivores decreased the relative vegetation cover, which in turn *Aelurillus* sp., a behaviour that was different from the other five species.

General discussion and conclusions

This study found that the most important factors affecting the abundance of the six spider species were time, cattle, rainfall and relative vegetation cover. Though not tested in this study, it could be speculated that the numerous events that correlate with time such as rainfall, temperature, humidity, phenology etc. affected the abundance of the six spider species, causing a population fluctuation during the study period. Since the lifecycle of most spiders is not more than two years (Jocqué pers. comm.), it was expected that their abundance and activities varied as they responded to seasonal changes that influenced their food acquisition and reproduction. It was expected that all six species would have a variation in their seasonal abundances. As an example, *C. insulana* reproduced in the months of August and September 2001 (Warui pers. obs.), which were just after rains. Many males and several juveniles were also caught in sweep nets in September 2001 (Warui pers. obs.).

Rain is an important ecological factor in an ecosystem and was expected to influence the spiders both directly and indirectly. In areas with a pronounced dry season, adult spider activity periods start with the first rains (Jocqué pers. comm.). The trend indicated by Figure 3.7 clearly showed that new species emerged after rainfall peaks and such an increase in activity has many implications. For example, the spiders might be searching for mates or food. In the current study, presence of more males than females in pitfall-trapping compared to the sweep-netting samples reflected more mate seeking activity .

Another way in which rainfall might influence abundance of spiders in the current study was through occasional flooding which might interfere with the activity of ground-active spiders, either killing them by flooding or forcing them to seek alternative shelter, thereby interfering with consistent traps efficiency. Such flooding was experienced in November 2001 and consequently influenced the pitfall catch for that particular month of study. In general the study found that only four of the six species (*Runcinia flavida, Argiope trifasciata, D. strandi* and *Borboropactus sp.*) were significantly affected by rainfall. This also suggested that both grass- and ground-active spiders were affected by rainfall.

Indirect effects of rainfall included that on vegetation, which was thought to influence the abundance of spiders. Recent work by Shackleton (1999) showed the importance of rainfall in influencing the growth of plants community of an African savanna. Knowledge of the effects of vegetation on spider abundance was mainly based of the fact that spiders prefer complex habitats to less heterogenous ones (Balfour and Rypstra 1998; Uetz *et al.* 1999; Ross *et al.* 2000). One explanation to this preference might be that spiders (mostly web-builders) need more places for their webs attachment, in the process assisting their food acquisition and sensing of the environment. The species *A. trifasciata* from the current study portrayed such tendencies. Furthermore, invertebrates prefer more complex habitats in order to get better oportunities for shelter, reproduction and foraging (Lawton 1983; Halaj *et al.* 2000). For non-web-building spiders, it was also expected that a more heterogeneous habitat would provide more opportunity for food acquisition and therefore less interspecific competition. In this study, three species (*C. insulana*, *D. strandi* and *Borboropactus* sp.), significantly responded to the increase in relative plant cover by an increase in their abundance, while *Aelurillus sp.* decreased in abundance.

The effects of cattle on spiders were mostly indirect and were probably mediated by changes in relative vegetation cover although the study might not rule out direct effects through trampling (hoof action that include physical damage to spiders, loosening of soil and making burrowing more difficult to build or maintain). However since the stocking rate was still moderate, it was probable that there were some negative effects on the abundance by the later. On the other hand the indirect effects might be through two mechanisms. First, reduced vegetation cover might increase open space and hence suitable habitat for ground-dwellers, thus increasing their abundance. Second, reduced relative vegetation cover might reduce the habitat complexity, which might then have a negative effect on most spiders. In this study, the presence of cattle significantly affected all of the selected spider species in two ways. It promoted the increase in abundance of one species, *Aelurillus* sp., but not the other five species. The results of chapter 5 (Tables 5.1 and 5.2) clearly support the fact that the presence of cattle significantly reduced the relative vegetation cover, while other results (Figures 5.2-5.6 and 7.1) demonstrated that diversity, species richness and species evenness were correlated to relative vegetation cover. In all cases, it was expected that the presence of cattle reduced the relative vegetation cover by trampling and grazing, thereby reducing the habitat complexity. This in turn affected different spider species differently. The results discussed in this paragraph further suggest that the biology of individual species is also a very important factor to consider when assigning the spiders indicator values.

In general, four of the six spider species tested (*D. strandi, R. flavida, A. trifasciata* and *Borboropactus sp.*) were sensitive to disturbance and could be used as indicators of habitat health. Despite being the most common species, *C. insulana* was not very sensitive to disturbances and occasionally showed high abundances in more grazed plots and low abundances in control plots and vice versa. *Aelurillus* sp. was more abundant in more disturbed places (cattle plots) and less abundant in less disturbed places (control plots). It was therefore thought to be a good indicator but not in the usual sense. Its presence was a sign of disturbance just like the presence of certain weeds. Despite the fact that one of the qualities of a good indicator is a quick response over short timespans, it might not be wise to conclude about the indicator value of these six species just by comparing them without trying to test their sensitivity to more environmental variables and over longer durations. This statement is supported further by research work by Goldstein (1999) and Alonso (2000), which showed that every species has a unique life history that influences its ecological distribution. As such it is important to note that diversity of a selected indicator taxon need not necessarily show a relationship with that of another taxa (Goldstein 1999).

The ways to choose an indicator species or taxon is reviewed by Gaston (1996, 2000), Caro and O'Doherty (1999), and Grelle (2002). Caro and O'Doherty (1999) warn that taxa that are used as indicators for a particular purpose might be unreliable for another. Other similar views include by Noss (1990), Prendergast *et al.* (1993), Kremen *et al.* (1994), Lawton *et al.* (1998), Niemelä and Baur (1998), Oliver *et al.* (1998), Reid (1998) and Alonso (2000), who all argued against use of individual or limited number of taxa since it might not provide an correct picture of overall change. Lambeck (1997) recommend use of a multi-species approach for use as indicators of overall biodiversity, arguing that it yields good results for optimal management decisions.

Similar work to the current study has been performed on grasshoppers in an Australian savanna ecosystem (Andersen *et al.* 2001). In this study, they clearly demonstrated that grasshoppers responded well to disturbances associated with human land use and were able to identify six indicator species within this taxon. This is fairly similar to the current spider study that also found that some species might be better indicators than others. More studies have shown that ants are good indicators and posses several desirable qualities (see Majer 1983; Andersen 1995, 1997a, b; Andersen *et al.* 2002; Kaspari and Majer 2000; Read and Andersen 2000; Watt *et al.* 2002). However it is important to note that even for such a group that appear to score well as good indicators, there are some small limitations that need to be thoroughly considered. As an example, several reasons as to why ants are good indicators are reviewed in Alonso (2000) and Kaspari and Majer (2000), but New (2000) has singled out the problem of high small-scale spatial heterogeneity as a limit to their value as indicator species at certain spatial scales. It is likely that such a scenario can also occur in the spiders.

In conclusion, this study has found out that at the species level, some spiders can serve as good indicators of disturbances caused by grazing. A number of factors make the selected spiders fairly good indicators. They were fairly sensitive to changes in environmental variables such as disturbances caused by grazing and rainfall. This agrees with views of Noss (1990), New (1995) and Churchill (1998), which emphasizes the need for a species to display sensitivity to changes in environmental variables in order to count as a good indicator. Other factors that made them good indicators were that some of them were quite abundant and hence readily sampled and thus not costly to sample. Lastly, they had fairly short lifecycles, in most cases less than one year (Jocqué pers. comm.).

Some factors that made them poor indicators included inconsistency, whereby some species were not available through out the sampling time. Most of the species were poorly understood i.e. their natural history and taxonomy is not well known. In conclusion, this study illustrated the potential of spiders to serve as bio-indicators, and pointed some areas for further studies. Finally, this chapter has shown that at the species level of analysis, spiders were more sensitive indicators of environmental changes as compared to guilds and the overall community.

Tables

Table 8.1. Levene's tests on the square root-transformed abundance of *Cyclosa insulana.* The significant values (at $p < 0.05$) are in bold. The letter codes represent the months of the calendar year and the accompanying numbers 1 and 2 referring to either the first or second year of sampling. Df = 1, 16.

Year	Sampling time (Once a month)	MS Effects	MS Error	F-value	P-value
2002	Ju1	0.01	0.10	0.07	0.80
"	Jl1	0.00	0.14	0.02	0.88
"	Au1	3.11	0.40	7.86	**0.01**
"	S1	0.13	0.30	0.42	0.52
"	O1	0.16	0.13	1.17	0.30
"	N1	0.43	0.22	1.99	0.18
"	D1	0.06	0.07	0.81	0.38
2003	Ja1	0.01	0.06	0.09	0.76
"	F1	0.10	0.09	1.17	0.30
"	M1	0.00	0.12	0.01	0.94
"	A1	0.13	0.04	3.08	0.10
"	My1	0.15	0.09	1.77	0.20
"	Ju2	0.35	0.19	1.89	0.19
"	Jl2	0.01	0.03	0.19	0.67

Table 8.2. A repeated measures ANOVA on the effects of cattle and mesoherbivores on the square root-transformed abundance of *Cyclosa insulana.* * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1.00	830.12	937.25	0.00*
Cattle	1.00	0.01	0.01	0.92
Mesoherbivores	1.00	3.31	3.74	0.07
Cattle*Mesoherbivores	1.00	0.42	0.47	0.50
Error	14.00	0.89		
Time	13.00	8.80	20.53	0.00*
Time*Cattle	13.00	0.23	0.55	0.89
Time*Mesoherbivores	13.00	0.53	1.24	0.25
Time*Cattle*Mesoherbivores	13.00	0.47	1.10	0.36
Error	182.00	0.43		

Table 8.3. Two-way ANOVA on the effects of blocks and experimental grazing treatments on the square root-transformed abundance of *Cyclosa insulana*. In this case the blocks represented a spatial scale of hundreds of metres in the form of north, central and south sites. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Blocks	2	0.17	0.18	0.83
Treatments	5	0.97	1.04	0.39
Blocks*Treatments	10	1.79	1.91	0.04*
Error	486	0.94		

Table 8.4. Tukey’s post-hoc tests on the effects of blocks and experimental grazing treatments on the square root-transformed abundance of *Cyclosa insulana.* The blocks represented a spatial scale of hundreds of metres in the form of north (NT), central (CT) and south sites (ST). The other codes represented the grazing treatments as follows: c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Significant values (at α = 0.05) are in bold. Df = 486.

Block		CT	CT	CT	CT	CT	CT	NT	NT	NT	NT	NT	NT	ST	ST	ST	ST	ST
		c	mw	mwc	o	w	wc	c	mw	mwc	o	w	wc	c	mw	mwc	o	w
CT	mw	0.91																
CT	mwc	0.31	0.35															
CT	o	0.84	0.92	0.39														
CT	w	0.26	0.30	0.90	0.34													
CT	wc	0.10	0.12	0.51	0.14	0.53												
NT	c	0.72	0.79	0.47	0.85	0.42	0.19											
NT	mw	0.07	0.09	0.41	0.10	0.44	0.84	0.14										
NT	mwc	0.80	0.87	0.42	0.94	0.37	0.16	0.90	0.11									
NT	o	0.21	0.19	**0.03**	0.18	**0.02**	**0.00**	0.14	**0.00**	0.16								
NT	w	0.31	0.35	0.99	0.39	0.89	0.51	0.47	0.41	0.42	**0.03**							
NT	wc	0.44	0.50	0.76	0.54	0.69	0.36	0.65	0.28	0.58	0.06	0.76						
ST	c	0.28	0.32	0.94	0.36	0.95	0.52	0.45	0.43	0.39	**0.03**	0.93	0.72					
ST	mw	0.69	0.76	0.50	0.82	0.44	0.20	0.95	0.15	0.86	0.13	0.50	0.67	0.47				
ST	mwc	0.55	0.61	0.64	0.66	0.57	0.28	0.78	0.21	0.70	0.09	0.63	0.84	0.60	0.81			
ST	o	0.28	0.32	0.94	0.36	0.95	0.54	0.44	0.44	0.39	**0.03**	0.93	0.72	1.00	0.47	0.60		
ST	w	0.32	0.36	0.97	0.40	0.87	0.50	0.48	0.40	0.43	**0.03**	0.97	0.77	0.91	0.50	0.64	0.91	
ST	wc	0.98	0.89	0.30	0.83	0.26	0.10	0.71	0.07	0.79	0.19	0.30	0.44	0.28	0.68	0.54	0.27	0.31

Table 8.5. An analysis of covariance (ANCOVA) to establish the effects of relative vegetation cover, total rainfall, mesoherbivores and cattle on the square root-transformed abundance of *Cyclosa insulana.* * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1	107.23	128.15	0.00*
Arcsine-transformed relative cover	1	41.46	49.55	0.00*
Total monthly rainfall	1	2.39	2.86	0.09
Cattle	1	3.52	4.21	0.04*
Mesoherbivores	1	0.42	0.51	0.48
Cattle*Mesoherbivores	1	2.82	3.36	0.07
Error	498	0.84		

Table 8.6. Levene’s tests on the square root-transformed abundance of *Argiope trifasciata*. The significant values (at α = 0.05) are in bold. The letter codes represent the months of the calendar year and the accompanying numbers 1 and 2 referring to either the first or second year of sampling. Df = 1, 16.

Year	Sampling time (Once a month)	MS Effects	MS Error	F-value	P-value
2002	Ju1	0.23	0.15	1.47	0.24
"	Jl1	0.58	0.69	0.84	0.37
"	Au1	0.07	0.25	0.26	0.61
"	S1	0.12	0.10	1.19	0.29
"	O1	0.10	0.09	1.13	0.30
"	N1	0.07	0.07	0.96	0.34
"	D1	0.13	0.07	1.81	0.20
2003	Ja1	0.02	0.03	0.64	0.43
"	F1	0.01	0.05	0.21	0.66
"	M1	0.02	0.03	0.68	0.42
"	A1	0.02	0.07	0.23	0.64
"	My1	0.01	0.02	0.29	0.60
"	Ju2	0.05	0.05	0.99	0.34
"	Jl2	0.38	0.05	7.56	**0.01**

Table 8.7. A repeated measures ANOVA on the effects of cattle and mesoherbivores on the square root-transformed abundance of *Argiope trifasciata*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1.00	821.25	585.41	0.00*
Cattle	1.00	3.41	2.43	0.14
Mesoherbivores	1.00	1.03	0.74	0.41
Cattle*Mesoherbivores	1.00	0.09	0.06	0.80
Error	14.00	1.40		
Time	13.00	1.98	7.73	0.00*
Time*Cattle	13.00	0.19	0.73	0.73
Time* Mesoherbivores	13.00	0.40	1.57	0.10
TIME*Cattle*Mesoherbivores	13.00	0.16	0.64	0.82
Error	182.00	0.26		

Table 8.8. A two-way ANOVA on the variation of *Argiope trifasciata* square root-transformed abundance between block and experimental grazing treatments. In this case the blocks represented a spatial scale of hundreds of metres in the form north, central and south sites. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Blocks	2	2.120	15.07	0.000*
Treatments	5	0.563	4.00	0.001*
Block*Treatments	10	0.546	3.88	0.000*
Error	486	0.14		

Table 8.9. Tukey’s post-hoc tests on the effects of blocks and experimental grazing treatments on the square root-transformed abundance of *A. trifasciata.* The blocks represented a spatial scale of hundreds of metres in the form of north (NT), central (CT) and south sites (ST). The other codes represented the grazing treatments as follows: c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Significant values (at α = 0.05) are in bold. Df = 486.

Block		CT	CT	CT	CT	CT	CT	NT	NT	NT	NT	NT	NT	ST	ST	ST	ST	ST
		c	mw	mwc	o	w	wc	c	mw	mwc	o	w	wc	c	mw	mwc	o	w
CT	mw	0.83																
CT	mwc	0.94	0.78															
CT	o	0.85	0.80	0.89														
CT	w	0.97	0.71	0.95	0.97													
CT	wc	0.82	0.25	0.86	0.86	0.83												
NT	c	0.91	0.73	0.89	0.90	0.86	0.44											
NT	mw	0.96	0.76	0.96	0.96	0.95	0.65	0.72										
NT	mwc	0.80	0.26	0.82	0.83	0.71	0.94	0.45	0.65									
NT	o	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**								
NT	w	0.92	0.80	0.97	0.96	0.98	0.82	0.87	0.91	0.80	**0.00**							
NT	wc	0.96	0.74	0.87	0.95	0.90	0.86	0.87	0.95	0.80	**0.00**	0.98						
ST	c	0.45	**0.04**	0.56	0.52	0.60	0.74	0.11	0.24	0.85	**0.00**	0.42	0.60					
ST	mw	0.96	0.60	0.95	0.96	0.82	0.81	0.78	0.91	0.58	**0.00**	0.96	0.93	0.65				
ST	mwc	0.77	0.19	0.84	0.82	0.84	0.85	0.35	0.57	0.97	**0.00**	0.76	0.85	0.58	0.85			
ST	o	0.37	**0.03**	0.49	0.45	0.57	0.79	0.07	0.17	0.86	**0.00**	0.34	0.55	0.85	0.64	0.74		
ST	w	0.96	0.78	0.97	0.97	0.97	0.77	0.82	0.81	0.76	**0.00**	0.86	0.97	0.35	0.95	0.69	0.27	
ST	wc	0.29	**0.02**	0.42	0.37	0.51	0.80	0.05	0.12	0.85	**0.00**	0.26	0.48	0.93	0.60	0.79	0.85	0.20

Table 8.10. Two-way ANOVA to establish the effects of cattle and mesoherbivores on square root-transformed abundance of *Argiope trifasciata*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Cattle	1	1.71	10.90	0.001*
Mesoherbivores	1	0.52	3.30	0.07
Cattle*Mesoherbivores	1	0.05	0.29	0.59
Error	500	0.16		

Table 8.11. Two-way ANOVA to establish the effects of cattle and megaherbivores on the square root-transformed abundance of *Argiope trifasciata*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Cattle	1	1.99	12.64	0.000*
Megaherbivores	1	0.00	0.02	0.89
Cattle*Megaherbivores	1	0.01	0.07	0.80
Error	500	0.16		

Table 8.12. Two-way ANOVA to establish the effects of cattle and megaherbivores on the square root-transformed abundance of *Argiope trifasciata*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Cattle	1	2.13	13.60	0.00*
Mesoherbivores + Megaherbivores	2	0.32	2.04	0.13
Cattle*Mesoherbivores + Megaherbivores	2	0.02	0.14	0.87
Error	498	0.16		

Table 8.13. An analysis of covariance (ANCOVA) to establish the effects of relative vegetation cover, total rainfall, mesoherbivores and cattle on the square root-transformed abundance of *Argiope trifasciata*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1	5.09	32.64	0.00*
Arcsine-transformed relative cover	1	0.00	0.01	0.92
Total monthly rainfall	1	0.54	3.46	0.06
Cattle	1	1.47	9.44	0.02*
Mesoherbivores	1	0.49	3.15	0.08
Cattle*Mesoherbivores	1	0.04	0.28	0.60
Error	498	0.16		

Table 8.14. Levene's tests on the square root-transformed abundance of *Runcinia flavida.* The significant values (at $\alpha = 0.05$) are in bold. The letter codes represent the months of the calendar year and the accompanying numbers 1 and 2 referring to either the first or second year of sampling. Df = 1, 16.

Year	Sampling time (Once a month)	MS Effects	MS Error	F-value	P-value
2002	Ju1	0.67	0.11	6.07	**0.03**
"	Jl1	0.16	0.03	5.64	**0.03**
"	Au1	0.00	0.04	0.03	0.87
"	S1	0.45	0.08	5.76	**0.03**
"	O1	0.56	0.20	2.88	0.11
"	N1	0.11	0.01	11.18	**0.00**
"	D1	0.11	0.24	0.46	0.51
2003	Ja1	0.01	0.15	0.05	0.83
"	F1	2.48	0.28	8.81	**0.01**
"	M1	0.52	0.40	1.29	0.27
"	A1	0.13	0.22	0.60	0.45
"	My1	0.33	0.04	7.37	**0.02**
"	Ju2	0.01	0.05	0.17	0.68
"	Jl2	0.07	0.08	0.95	0.34

Table 8.15. Repeated measures ANOVA to establish the effects of cattle and mesoherbivores on the square root-transformed abundance of *Runcinia flavida*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1.00	1045.34	866.75	**0.00**
Cattle	1.00	4.36	3.61	0.08
Mesoherbivores	1.00	0.06	0.05	0.83
Cattle*Mesoherbivores	1.00	0.67	0.55	0.47
Error	14.00	1.21		
Time	13.00	4.44	10.45	**0.00**
Time*Cattle	13.00	0.34	0.81	0.65
Time*Mesoherbivores	13.00	0.46	1.07	0.39
Time*Cattle*Mesoherbivores	13.00	0.37	0.86	0.59
Error	182.00	0.43		

Table 8.16. Two-way ANOVA to establish the effects of blocks and experimental grazing treatments on square root-transformed abundance of *Runcinia flavida.* In this case the blocks represented a spatial scale of hundreds of metres in the form of north, central and south sites. * = Significant at α = 0.05.

Effect	DF	Ms	F-value	P-value
Blocks	2	1.90	7.86	0.000*
Treatments	5	0.72	2.97	0.012*
Block*Treatments	10	0.46	1.90	0.044*
Error	486	0.24		

Table 8.17. A two-way ANOVA to establish the effects of cattle and mesoherbivores on the abundance of *Runcinia flavida*. * = Significant at α = 0.05.

Effect	DF	Ms	F-value	P-value
Cattle	1	2.18	8.68	0.003*
Mesoherbivores	1	0.03	0.117	0.73
Cattle*Mesoherbivores	1	0.33	1.33	0.25
Error	500	0.25		

Table 8.18. An analysis of covariance (ANCOVA) to establish the effects of relative vegetation cover, total rainfall, mesoherbivores and cattle on variation square root-transformed abundance of *Runcinia flavida*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1	6.06	25.29	0.00*
Arcsine-transformed relative cover	1	0.58	2.43	0.12
Total monthly rainfall	1	3.75	15.64	0.00*
Cattle	1	1.27	5.28	0.02*
Mesoherbivores	1	0.09	0.38	0.54
Cattle* Mesoherbivores	1	0.25	1.04	0.31
Error	498	0.23		

Table 8.19. Levene's tests on the square root-transformed abundance of *Diores strandi*. The significant values (at α = 0.05) are in bold. The letter codes represent the months of the calendar year and the accompanying numbers 1 and 2 referring to either the first or second year of sampling. Df = 1, 16.

Year	Sampling time (Once a month)	MS Effects	MS Error	F-value	P-value
2002	Ju1	0.01	0.09	0.08	0.78
"	Jl1	0.03	0.16	0.20	0.66
"	Au1	0.44	0.08	5.47	**0.03**
"	S1	0.02	0.32	0.07	0.80
"	O1	0.01	0.02	0.36	0.56
"	N1	0.14	0.08	1.89	0.19
"	D1	0.02	0.10	0.21	0.65
2003	Ja1	0.05	0.01	5.22	**0.04**
"	F1	0.05	0.06	0.81	0.38
"	M1	0.04	0.04	1.04	0.32
"	A1	0.03	0.02	1.55	0.23
"	My1	0.05	0.02	2.75	0.12
"	Ju2	0.00	0.03	0.07	0.79
"	Jl2	0.01	0.09	0.08	0.78

Table 8.20. Repeated measures ANOVA to establish the effects of cattle and mesoherbivores on the square root-transformed abundance of *Diores strandi*. * = Significant at $\alpha = 0.05$.

Effect	DF	MS	F-value	P-value
Intercept	1.00	809.42	1083.00	0.00*
Cattle	1.00	2.64	3.54	0.08
Mesoherbivores	1.00	1.04	1.39	0.26
Cattle * Mesoherbivores	1.00	0.76	1.02	0.33
Error	14.00	0.75		
Time	13.00	2.62	8.94	0.00*
Time*Cattle	13.00	0.22	0.73	0.73
Time*Mesoherbivores	13.00	0.29	1.00	0.45
Time*Cattle*Mesoherbivores	13.00	0.18	0.62	0.84
Error	182.00	0.29		

Table 8.21. Two-way ANOVA on the effects of blocks and experimental grazing treatments on the abundance of *Diores strandi*. In this case the blocks represented a spatial scale of hundreds of metres in the form of north, central and south sites. * = Significant at $\alpha = 0.05$.

Effect	DF	MS	F-value	P-value
Blocks	2	0.04	0.20	0.82
Treatments	5	0.85	4.31	0.00*
Blocks*Treatments	10	0.43	2.17	0.02*
Error	486	0.20		

Table 8.22. Tukey's post-hoc tests on the effects of blocks and experimental grazing treatments on the square root-transformed abundance of *Diores strandi*. The blocks represented a spatial scale of hundreds of metres in the form of north (NT), central (CT) and south sites (ST). The other codes represented the grazing treatments as follows: c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Significant values (at $\alpha = 0.05$) are in bold. Df = 486.

Block		CT	CT	CT	CT	CT	CT	NT	NT	NT	NT	NT	**NT**	ST	ST	ST	ST	ST
		c	mw	mwc	o	w	wc	c	mw	mwc	o	w	wc	c	mw	mwc	o	w
CT	mw	0.56																
CT	mwc	0.89	0.95															
CT	o	0.95	0.91	0.91														
CT	w	0.75	0.92	0.99	1.00													
CT	wc	**0.00**	0.23	0.12	0.06	**0.04**												
NT	c	0.86	0.97	0.97	0.71	0.99	0.13											
NT	mw	0.06	0.52	0.50	0.34	0.30	0.42	0.54										
NT	mwc	0.63	0.85	0.98	1.00	0.81	**0.02**	0.97	0.19									
NT	o	0.76	0.97	0.91	0.92	0.97	0.22	0.97	0.63	0.94								
NT	w	0.88	0.90	0.98	0.99	1.00	**0.04**	0.97	0.27	0.97	0.96							
NT	wc	0.76	0.98	0.74	0.88	0.97	0.22	0.93	0.66	0.94	0.94	0.95						
ST	c	0.85	0.45	0.84	0.93	0.79	**0.00**	0.82	**0.03**	0.77	0.67	0.89	0.68					
ST	mw	0.64	0.97	0.91	0.89	0.94	0.28	0.96	0.68	0.89	0.81	0.92	0.94	0.54				
ST	mwc	0.93	0.89	0.97	0.97	1.00	**0.04**	0.94	0.28	0.99	0.95	0.95	0.93	0.92	0.91			
ST	o	0.39	0.79	0.91	0.83	0.83	0.23	0.94	0.41	0.72	0.95	0.80	0.97	0.29	0.96	0.80		
ST	w	0.67	0.84	0.96	0.93	0.96	0.22	0.98	0.56	0.91	0.97	0.94	0.99	0.57	0.99	0.93	0.88	
ST	wc	0.93	0.92	0.97	0.95	1.00	0.05	0.90	0.34	0.99	0.95	0.97	0.93	0.91	0.92	0.88	0.84	0.95

Table 8.23. Two-way ANOVA to establish the effects of cattle and mesoherbivores on the square root-transformed abundance of *Diores strandi*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Cattle	1	1.13	5.52	0.02*
Mesoherbivores	1	0.65	3.18	0.08
Cattle*Mesoherbivores	1	0.50	2.42	0.12
Error	500	0.21		

Table 8.24. Two-way ANOVA to establish the effects of cattle and mesoherbivores + megaherbivores on the square root-transformed abundance of *Diores strandi*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Cattle	1	0.77	3.84	0.05
Mesoherbivores + Megaherbivores	2	0.33	1.62	0.20
Cattle*Mesoherbivores + Megaherbivores	2	1.41	7.02	0.00*
Error	498	0.20		

Table 8.25. A two-way ANOVA to establish the effects of cattle and megaherbivores on the square root-transformed abundance of *Diores strandi*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Cattle	1	1.33	6.47	0.01*
Megaherbivores	1	0.17	0.81	0.37
Cattle*Megaherbivores	1	0.94	4.58	0.03*
Error	500	0.21		

Table 8.26. An analysis of covariance (ANCOVA) to establish the effects of relative vegetation cover, total rainfall, mesoherbivores and cattle on variation square root-transformed abundance of *Diores strandi*. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1	10.16	50.77	0.00*
Arcsine-transformed relative cover	1	1.08	5.40	0.02*
Total monthly rainfall	1	0.80	3.98	0.04*
Cattle	1	1.84	9.18	0.00*
Mesoherbivores	1	0.37	1.87	0.17
Cattle* Mesoherbivores	1	0.36	1.79	0.18
Error	498			

Table 8.27. Levene's tests on the square root-transformed abundance of *Borboropactus* sp. The significant values (at α = 0.05) are in bold. The letter codes represent the months of the calendar year and the accompanying numbers 1 and 2 referring to either the first or second year of sampling. Df = 1, 16.

Year	Sampling time (Once a month)	MS Effects	MS Error	F-value	P-value
2002	Ju1	0.04	0.03	1.27	0.28
"	Jl1	0.01	0.08	0.16	0.70
"	Au1	0.07	0.09	0.83	0.38
"	S1	0.10	0.06	1.75	0.20
"	O1	0.01	0.03	0.48	0.50
"	N1	0.05	0.07	0.82	0.38
"	D1	0.77	0.17	4.45	0.05
2003	Ja1	0.00	0.06	0.07	0.80
"	F1	0.18	0.03	7.03	**0.02**
"	M1	0.00	0.06	0.02	0.90
"	A1	0.01	0.34	0.03	0.86
"	My1	0.01	0.57	0.02	0.88
"	Ju2	0.18	0.23	0.80	0.38
"	Jl2	0.13	0.03	5.22	**0.04**

Table 8.28. A repeated measures ANOVA establishing the effects of cattle and mesoherbivores on the abundance of *Borboropactus* sp. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1.00	747.19	512.20	0.00*
Cattle	1.00	1.00	0.69	0.42
Mesoherbivores	1.00	0.28	0.19	0.67
Cattle * Mesoherbivores	1.00	0.01	0.01	0.92
Error	14.00	1.46		
Time	13.00	2.34	8.75	0.00*
Time*Cattle	13.00	0.38	1.42	0.16
Time*Mesoherbivores	13.00	0.12	0.46	0.94
Time*Cattle * Mesoherbivores	13.00	0.11	0.43	0.96
Error	182.00	0.27		

Table 8.29. A repeated measures ANOVA to establish the effects of cattle and megaherbivores on the square root-transformed abundance of *Borboropactus* sp. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1.00	748.01	528.78	0.00*
Cattle	1.00	1.53	1.08	0.32
Megaherbivores	1.00	0.24	0.17	0.69
Cattle *Megaherbivores	1.00	0.68	0.48	0.50
Error	14.00	1.41		
Time	13.00	2.34	9.54	0.00*
Time*Cattle	13.00	0.58	2.38	0.01*
Time*Megaherbivores	13.00	0.14	0.59	0.86
Time*Cattle*Megaherbivores	13.00	0.40	1.65	0.08
Error	182.00	0.25		

Table 8.30. Two-way ANOVA on the effects of blocks and experimental grazing treatments on the square root-transformed abundance of *Borboropactus* sp. In this case the blocks represented a spatial scale of hundreds of metres in the form of north, central and south sites. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Blocks	2	0.62	4.24	0.01*
Treatments	5	0.31	2.15	0.06
Blocks*Treatments	10	0.81	5.54	0.00*
Error	486	0.15		

Table 8.31. Tukey’s post-hoc tests on the effects of blocks and experimental grazing treatments on the square root-transformed abundance of *Borboropactus* sp. The blocks represented a spatial scale of hundreds of metres in the form of north (NT), central (CT) and south sites (ST). The other codes represented the grazing treatments as follows: c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Significant values (at α = 0.05) are in bold. Df = 486.

Block		CT	CT	CT	CT	CT	CT	NT	NT	NT	NT	NT	**NT**	ST	ST	ST	ST	ST
		c	mw	mwc	o	w	wc	c	mw	mwc	o	w	wc	c	mw	mwc	o	w
CT	mw	0.95																
CT	mwc	0.93	0.98															
CT	o	0.85	0.71	0.92														
CT	w	0.96	0.97	0.97	0.92													
CT	wc	0.90	0.96	0.82	0.87	0.96												
NT	c	0.95	0.98	0.86	0.94	0.97	0.91											
NT	mw	0.97	0.98	0.97	0.94	0.88	0.96	0.96										
NT	mwc	0.94	0.96	0.97	0.91	0.84	0.94	0.97	0.93									
NT	o	1.00	0.97	0.98	0.89	0.98	0.99	0.98	0.98	0.96								
NT	w	**0.00**	**0.04**	**0.01**	**0.08**	**0.03**	**0.00**	**0.01**	**0.03**	0.05	**0.00**							
NT	wc	**0.00**	**0.01**	**0.00**	**0.02**	**0.01**	**0.00**	**0.00**	**0.00**	**0.01**	**0.00**	0.55						
ST	c	0.85	0.89	0.93	0.93	0.96	0.87	0.95	0.96	0.96	0.88	0.07	**0.02**					
ST	mw	**0.04**	0.20	0.09	0.29	0.20	0.06	0.13	0.18	0.24	0.05	0.45	0.36	0.21				
ST	mwc	1.00	0.96	0.99	0.87	0.98	1.00	0.99	0.99	0.96	0.98	**0.00**	**0.00**	0.85	**0.03**			
ST	o	0.17	0.38	0.29	0.44	0.43	0.20	0.35	0.41	0.46	0.19	0.39	0.23	0.25	0.59	0.15		
ST	w	1.00	0.98	0.99	0.90	0.99	1.00	0.99	0.99	0.97	0.97	**0.00**	**0.00**	0.89	0.05	0.89	0.19	
ST	wc	0.93	0.99	0.90	0.97	0.98	0.91	0.80	0.98	0.98	0.97	**0.03**	**0.00**	0.97	0.20	0.98	0.46	0.98

Table 8.32. Two-way ANOVA to establish the effects of cattle and mesoherbivores on the square root-transformed abundance of *Borboropactus* sp.

Effect	DF	MS	F-value	P-value
Cattle	1	0.50	3.09	0.08
Mesoherbivores	1	0.14	0.88	0.35
Cattle*Mesoherbivores	1	0.01	0.05	0.83
Error	500	0.16		

Table 8.33. Two-way ANOVA on the effects of cattle and megaherbivores on the square root-transformed abundance of *Borboropactus* sp. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Cattle	1	0.76	4.73	0.03*
Megaherbivores	1	0.19	0.74	0.39
Cattle*Megaherbivores	1	0.34	2.10	0.14
Error	500	0.16		

Table 8.34. An analysis of covariance (ANCOVA) to establish the effects of relative vegetation cover, total rainfall, mesoherbivores and cattle the square root-transformed abundance of *Borboropactus* sp. * = Significant at α = 0.05.

Effect	DF	Ms	F-value	P-value
Intercept	1	1.21	8.06	0.000*
Arcsine-transformed relative cover	1	0.64	4.23	0.040*
Total monthly rainfall	1	6.16	40.97	0.000*
Cattle	1	0.15	1.02	0.31
Mesoherbivores	1	0.26	1.74	0.19
Cattle*Mesoherbivores	1	0.03	0.18	0.67
Error	498	0.15		

Table 8.35. Levene's tests on the square root-transformed abundance of *Aelurillus* sp. The significant values (at $\alpha = 0.05$) are in bold. The letter codes represent the months of the calendar year and the accompanying numbers 1 and 2 referring to either the first or second year of sampling. Df = 1, 16.

Year	Sampling time (Once a month)	MS Effects	MS Error	F-value	P-value
2002	Ju1	0.98	0.24	4.09	0.06
"	Jl1	0.00	0.08	0.02	0.88
"	Au1	0.08	0.12	0.64	0.44
"	S1	0.00	0.29	0.00	0.98
"	O1	0.22	0.17	1.31	0.27
"	N1	0.14	0.04	3.75	0.07
"	D1	0.12	0.12	0.94	0.35
2003	Ja1	0.16	0.18	0.88	0.36
"	F1	0.01	0.06	0.23	0.64
"	M1	0.69	0.16	4.30	0.05
"	A1	0.38	0.18	2.16	0.16
"	My1	0.29	0.04	7.28	**0.02**
"	Ju2	0.00	0.02	0.07	0.79
"	Jl2	0.00	0.10	0.00	0.96

Table 8.36. Repeated measures ANOVA to establish the effects of cattle and mesoherbivores on the square root-transformed abundance of *Aelurillus* sp. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1.00	1126.33	1031.85	0.00*
Cattle	1.00	6.08	5.57	0.03*
Mesoherbivores	1.00	1.21	1.11	0.31
Cattle*Mesoherbivores	1.00	0.25	0.23	0.64
Error	14.00	1.09		
Time	13.00	1.07	2.83	0.00*
Time*Cattle	13.00	0.31	0.81	0.65
Time*Mesoherbivores	13.00	0.59	1.57	0.10
Time*Cattle*Mesoherbivores	13.00	0.44	1.16	0.31
Error	182.00	0.38		

Table 8.37. A repeated measures ANOVA to establish the effects of cattle and mesoherbivores + megaherbivores on the square root-transformed abundance of *Aelurillus* sp. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1.00	1294.99	1193.50	0.00*
Cattle	1.00	5.95	5.48	0.04*
Mesoherbivores + Megaherbivores	2.00	1.70	1.57	0.25
Cattle*Mesoherbivores + Megaherbivores	2.00	0.16	0.15	0.86
Error	12.00	1.09		
Time	13.00	1.25	3.16	0.00*
Time*Cattle	13.00	0.42	1.06	0.40
Time*Mesoherbivores + Megaherbivores	26.00	0.41	1.03	0.43
Time*Cattle*Mesoherbivores + Megaherbivores	26.00	0.38	0.98	0.50
Error	156.00	0.39		

Table 8.38. A repeated measures ANOVA to establish the effects of cattle and megaherbivores on the square root-transformed abundance of *Aelurillus* sp. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Intercept	1.00	1134.66	994.64	0.00*
Cattle	1.00	4.57	4.00	0.07
Megaherbivores	1.00	0.53	0.47	0.51
Cattle *Megaherbivores	1.00	0.24	0.21	0.66
Error	14.00	1.14		
Time	13.00	1.11	2.79	0.00*
Time*Cattle	13.00	0.61	1.53	0.11
Time*Megaherbivores	13.00	0.25	0.63	0.83
TIME*Cattle*Megaherbivores	13.00	0.49	1.23	0.26
Error	182.00	0.40		

Table 8.39. A two-way ANOVA to establish the effects of blocks and experimental grazing treatments on the abundance *Aelurillus* sp. In this case the blocks represented a spatial scale of hundreds of metres in the form of north, central and south sites. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Blocks	2	0.27	1.23	0.29
Treatments	5	0.97	4.39	0.00*
Blocks*Treatments	10	0.60	2.71	0.00*
Error	486	0.22		

Table 8.40. Tukey’s post-hoc tests on the effects of blocks and experimental grazing treatments on the square root-transformed abundance of *Aelurillus* sp. The blocks represented a spatial scale of hundreds of metres in the form of north (NT), central (CT) and south sites (ST). The other codes represented the grazing treatments as follows: c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Significant values (at α = 0.05) are in bold. Df = 486.

Block		CT	CT	CT	CT	CT	CT	NT	NT	NT	NT	NT	**NT**	ST	ST	ST	ST	ST
		c	mw	mwc	o	w	wc	c	mw	mwc	o	w	wc	c	mw	mwc	o	w
CT	mw	**0.04**																
CT	mwc	0.10	0.64															
CT	o	**0.00**	0.39	0.23														
CT	w	0.08	0.71	0.89	0.26													
CT	wc	0.27	**0.00**	**0.01**	**0.00**	**0.00**												
NT	c	0.07	0.74	0.86	0.26	0.95	**0.00**											
NT	mw	0.11	0.59	0.92	0.20	0.83	**0.01**	0.79										
NT	mwc	0.51	**0.01**	**0.02**	**0.00**	0.02	0.60	**0.02**	0.03									
NT	o	0.15	0.49	0.79	0.16	0.70	**0.01**	0.67	0.85	**0.04**								
NT	w	0.92	**0.03**	0.08	**0.00**	0.07	0.29	0.06	0.10	0.55	0.13							
NT	wc	0.95	**0.04**	0.11	**0.00**	0.09	0.26	0.08	0.12	0.50	0.16	0.88						
ST	c	0.89	**0.05**	0.12	**0.01**	0.10	0.24	0.09	0.14	0.46	0.18	0.82	0.93					
ST	mw	0.29	0.29	0.51	0.07	0.45	**0.04**	0.43	0.56	0.10	0.67	0.26	0.30	0.32				
ST	mwc	0.15	0.49	0.80	0.16	0.71	**0.01**	0.68	0.86	0.04	0.98	0.13	0.16	0.18	0.66			
ST	o	0.10	0.64	0.99	0.22	0.89	**0.01**	0.86	0.92	**0.02**	0.78	0.08	0.11	0.12	0.51	0.80		
ST	w	0.24	0.35	0.60	0.09	0.53	0.03	0.50	0.65	0.08	0.76	0.21	0.25	0.27	0.87	0.76	0.60	
ST	wc	0.41	0.19	0.37	0.04	0.32	0.07	0.30	0.41	0.16	0.49	0.38	0.43	0.45	0.76	0.49	0.37	0.67

Table 8.41. A two-way ANOVA on the effects of cattle and mesoherbivores on the square root-transformed abundance of *Aelurillus* sp. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Cattle	1	3.04	13.23	0.00*
Mesoherbivores	1	0.61	2.64	0.10
Cattle*Mesoherbivores	1	0.12	0.54	0.46
Error	500	0.23		

Table 8.42. Two-way ANOVA to establish the effects of cattle and mesoherbivores + megaherbivores on the square root-transformed abundance of *Aelurillus* sp. * = Significant at α = 0.05.

Effect	DF	MS	F-value	P-value
Cattle	1	2.97	13.03	0.00*
Mesoherbivores + Megaherbivores	2	0.85	3.72	0.02*
Cattle*Mesoherbivores + Megaherbivores	2	0.08	0.35	0.70
Error	498	0.23		

Table 8.43. An analysis of covariance (ANCOVA) to establish the effects of relative vegetation, total rainfall, mesoherbivores and cattle on the square root-transformed abundance of *Aelurillus* sp. * = Significant at α = 0.05.

Effect	**DF**	Ms	F-value	P-value
Intercept	1	8.54	37.44	0.00*
Arcsine-transformed relative cover	1	0.02	0.09	0.77
Total monthly rainfall	1	0.89	3.89	0.04*
Cattle	1	2.84	12.46	0.00*
Mesoherbivores	1	0.63	2.75	0.09
Cattle*Mesoherbivores	1	0.11	0.49	0.48
Error	498	0.23		

Figures

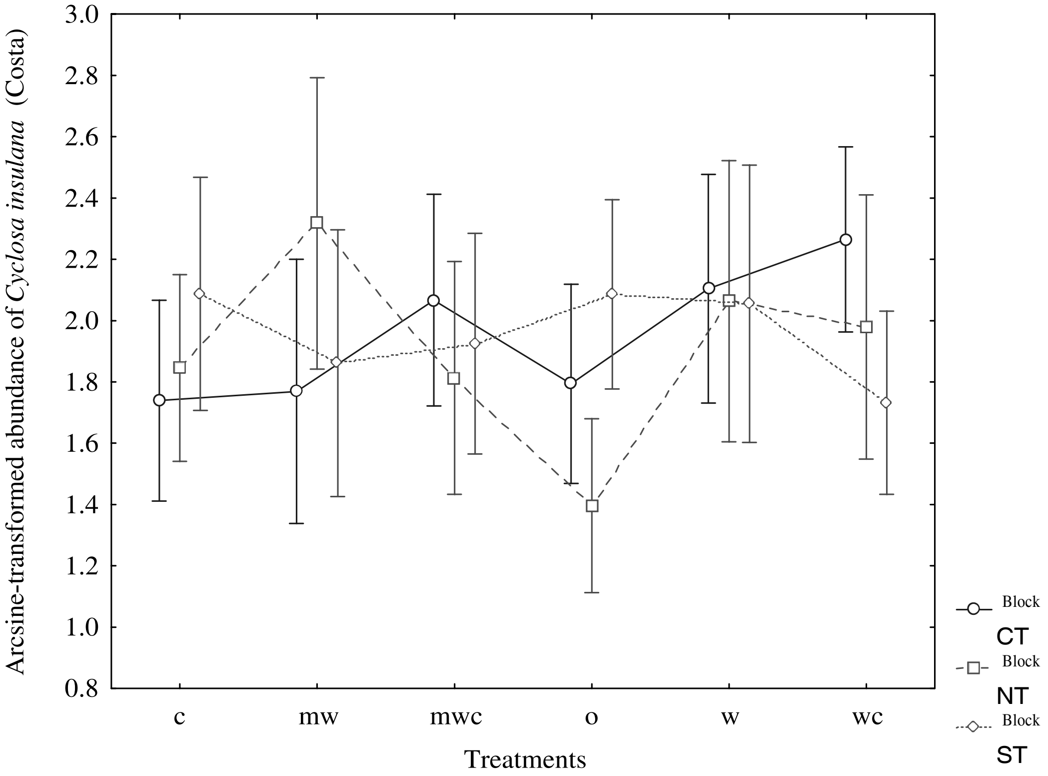

Figure 8.1. Two-way ANOVA to establish the effects of large mammalian herbivore experimental treatments and blocks on square root-transformed abundance of *Cyclosa insulana.* ($F_{10\ 486} = 1.91$, $p = 0.042$). The codes represent the grazing treatments where, c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Bars represent means and standard errors.

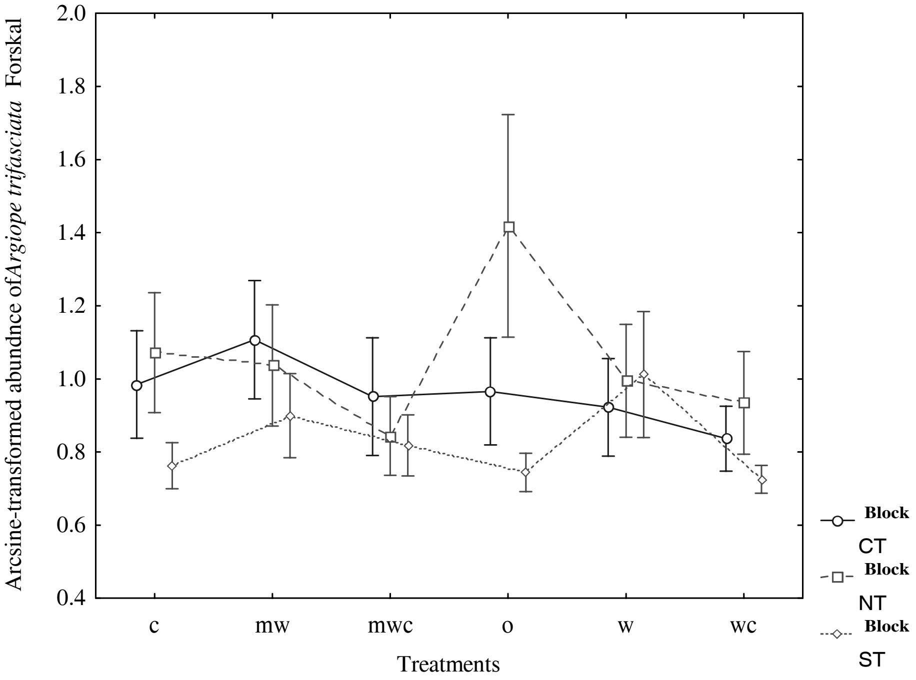

Figure 8.2. Two-way ANOVA to establish the effects of large mammalian herbivore experimental treatments and blocks on square root-transformed abundance of *Argiope trifasciata.* ($F_{10\ 486} = 3.87$, $p = 0.000$). The codes represent the grazing treatments where, c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Bars represent means and standard errors.

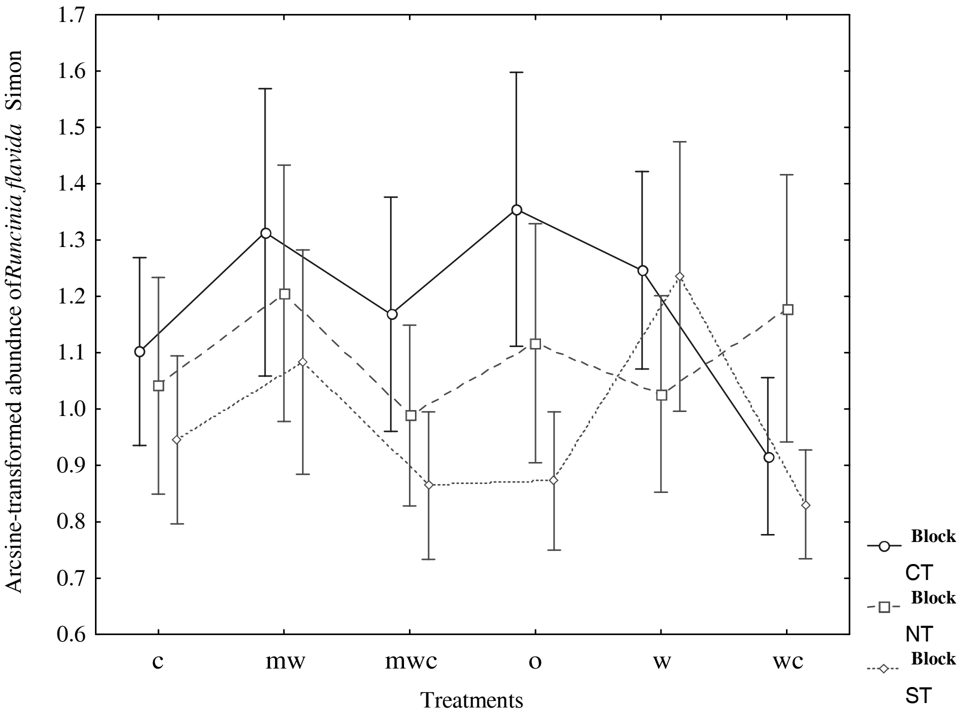

Figure 8.3. Two-way ANOVA to establish the effects of large mammalian herbivore experimental treatments and blocks on square root-transformed abundance of *Runcinia flavida.* ($F_{10, 486} = 1.89$, $p = 0.043$). The codes represent the grazing treatments where, c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Bars represent means and standard errors.

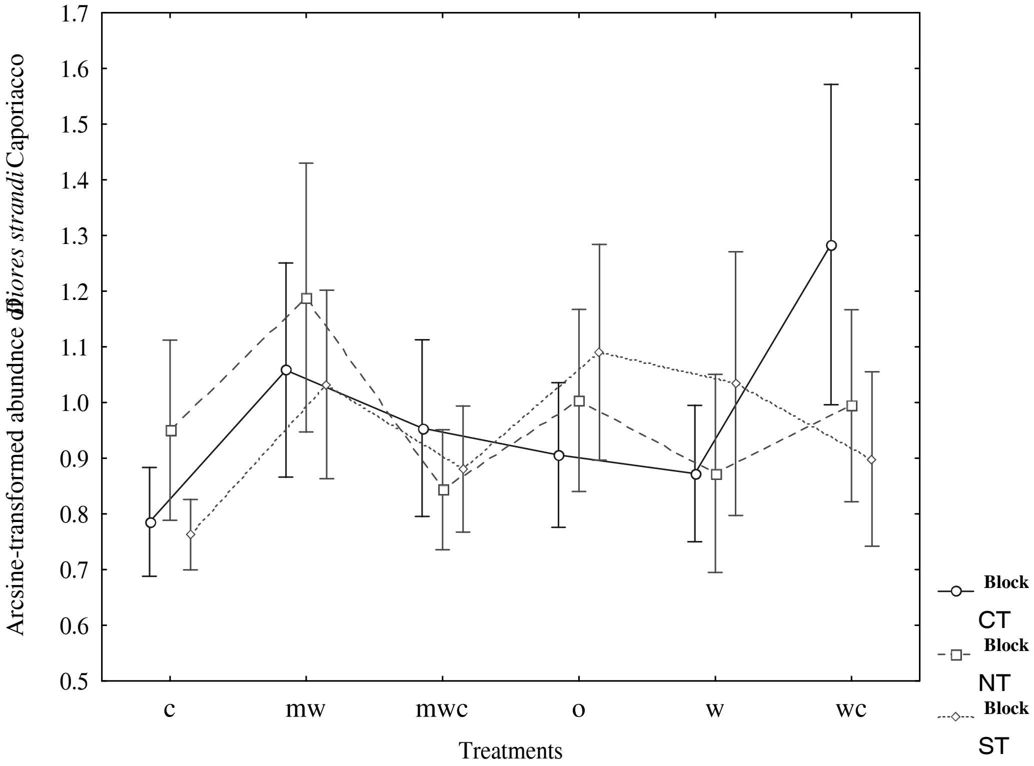

Figure 8.4. Two-way ANOVA to establish the effects of large mammalian herbivore experimental treatments and blocks on square root-transformed abundance of *Diores strandi*. ($F_{10, 486} = 2.17$, $p = 0.018$). The codes represent the grazing treatments where, c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Bars represent means and standard errors.

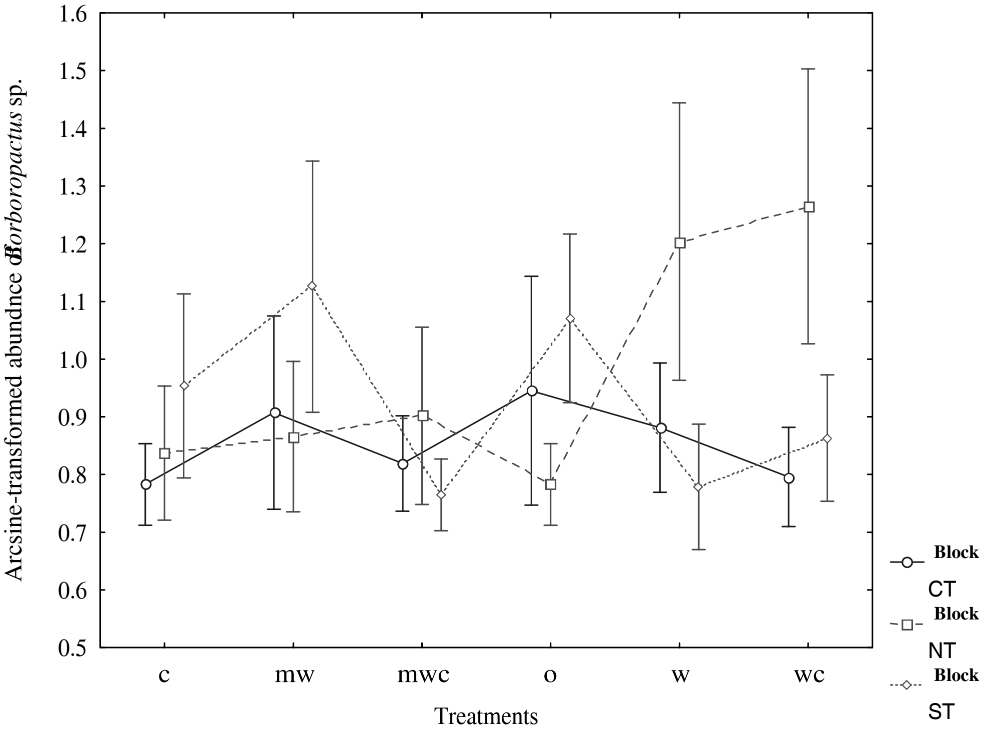

Figure 8.5. Two-way ANOVA to establish the effects of large mammalian herbivore experimental treatments and blocks on square root-transformed abundance of *Borboropactus* sp. ($F_{10, 486} = 5.54$, p = 0.000). The codes represent the grazing treatments where, c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Bars represent means and standard errors.

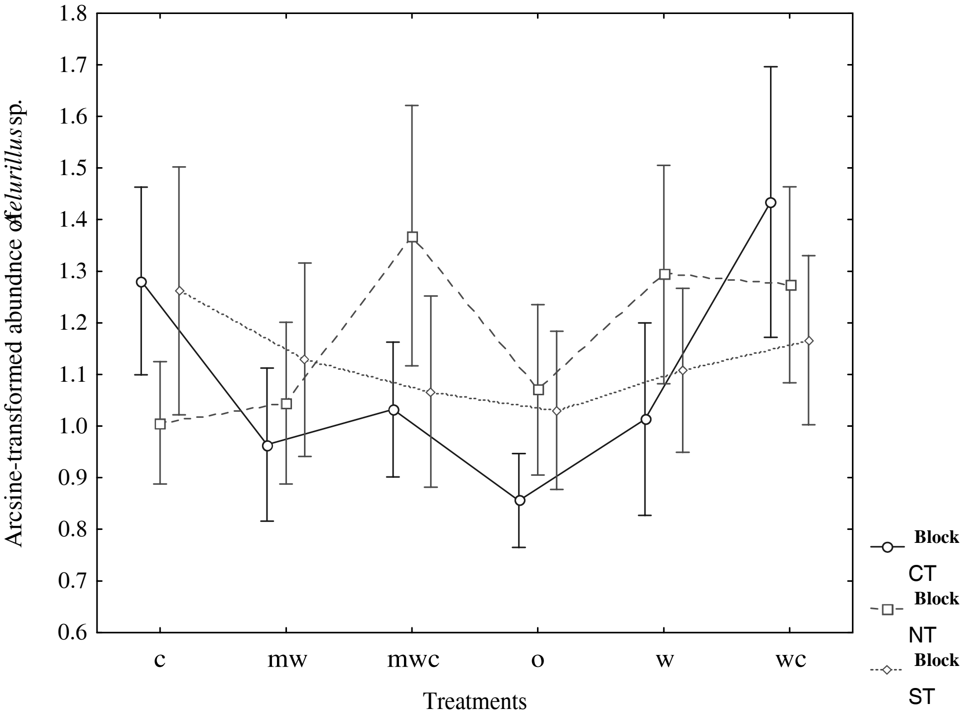

Figure 8.6. Two-way ANOVA to establish the effects of large mammalian herbivore experimental treatments and blocks on square root-transformed abundance of *Aelurillus* sp. ($F_{10,\ 486}$ = 2.71, p = 0.003). The codes represent the grazing treatments where, c = cattle, mw = mesoherbivores + megaherbivores, mwc = mesoherbivores + megaherbivores + cattle, o = control, w = mesoherbivores and wc = mesoherbivores + cattle. Bars represent means and standard errors.

CHAPTER 9: GENERAL DISCUSSION AND CONCLUSION

Preface

This chapter is a synthesis of the whole study, the objective of which was to establish a checklist of spiders in an African savanna habitat and to evaluate their use as indicators of grazing impacts by cattle and an ecological community of large mammalian herbivores. It highlights the major findings of the study and gives an overview of the usefulness of spiders as indicators of grazing impacts in this system. It suggests some ways in which the results might be incorporated into conservation and management decisions, and also gives some recommendations for future studies.

Checklist and species composition

Chapter 3 presents a checklist of 132 species of spiders from the black cotton soil ecosystem, based on two methods of data collection, namely pitfall-trapping and sweep-netting. This was a good contribution to our knowledge of spiders in Kenya and East Africa in general since this taxon is not well known or studied. When compared to the few past studies on Kenyan spiders e.g. Russell-Smith (1981) and Russell-Smith *et al.* (1987), the current study was a success in that it reported more specimens and possibly new species. It was the first of its kind in Kenyan savanna, the longest of all studies of spiders in Kenya, and probably among the most intensive pitfall-trapping study of savanna spiders in Africa. When compared to some regional studies e.g. work by Russell-Smith (1999); Foord *et al.* (2002); Dippenaar-Schoeman and Leroy (2003) and Whitmore *et al.* (2003), the current study had either a smaller total number of families or species. This was attributed to being restricted to only one type of habitat and two sampling methods, as opposed to the five methods and twelve habitats in the Tanzanian study. When compared to some South African studies (Table 3.3), the study had fairly similar results in terms of checklist sizes but differed in terms of sampling methods employed. In general, it can be argued that this black cotton soil checklist was not exhaustive when compared to the regional studies. There was a likelihood that at least a quarter of the species were new to science, reflecting that the Kenyan fauna is not well known. However, it is still difficult to interpret such biodiversity comparisons between studies because there is no standard procedure that exists for sampling spiders for ecological monitoring (Brennan *et al.* 1999). Scientists have continued to urge for standardisation of sampling methods to help comparisons between studies (e.g. Coddington *et al.* 1991; Churchill 1993; Brennan *et al.* 1999). However, such standardisation of spider collection methods is still at its infancy (Brennan *et al.* 1999), which therefore limits detailed comparison of different geographical locations.

Taxonomic resolution for statistical analysis

Three levels of taxonomic resolution were used to assess the response of spiders to the experimental treatments. The first case involved treating all collected spiders from all families as one taxonomic unit of Araneae (overall community resolution) and then calculating the diversity indices and analysing for significant differences in various experimental treatments. The second case was based on aggregating the spiders into three guilds based on past studies (see Dippenaar-Schoeman *et al.* 1999a, b; Uetz *et al.* 1999) and re-analysing the data to assess the spiders' sensitivity to experimental treatments. The last level of resolution was using selected individual species and establishing the response of their abundance to the experimental treatments. It is important to note that although the indices of diversity are made up of abundance values for individual species, there are differences between cases 1 and 3 above in that the first was a product of condensing all individuals present into an index, while the third was a sole species' abundance.

Effects of herbivores

On spider diversity

The results in chapter 5 clearly indicated that large mammalian herbivore treatments affected the diversity of spider (e.g. Tables 5.9, 5.13 and 5.16). This might have been through an indirect effect, where the presence of cattle significantly reduced the relative vegetation cover (Tables 5.1 and 5.2) that in turn significantly increased the spider richness, evenness and diversity indices (e.g. Figures 5.4, 5.5 and 5.6 respectively). Thus it may be concluded that plant cover was a fair but not a very strong predictor of spider diversity, especially because it accounted for 33% of variation in the Shannon-Wiener diversity index and 29% of variation in Pielou's evenness index from sweep-netting samples (Figures 5.3 and 5.8 respectively). This was further supported by results of Table 5.22 for samples from pitfall-trapping.

In particular, spiders were significantly affected by the presence of cattle but not by that of other large mammalian herbivores, thus showing that at an overall community level of resolution, it was possible to detect the effects of cattle. As already explained in chapter 5, this study suggested that the direct effects on vegetation partly mediated an indirect influence of cattle on the spider diversity. This implied that at this level of resolution, spiders were not very fine-tuned indicators of disturbance. Already research from the study area has shown that removal of ungulates in the control plots resulted in a 60% increase in total number of small mammals (Keesing 2000), thereby showing that these small mammals were good indicators although it was not wise to compare them with spiders. In general however, some reasons might be put forward to explain this.

First, it was probable that this level of taxonomic and ecological resolution was not fine enough to detect disturbances, proposing that spiders were poor indicators. Second, it was also likely that both megaherbivores and mesoherbivores had very little effect because they were relatively rare or at low natural densities and this may be supported by the fact that most wildlife in Laikipia live outside national parks (LWF 1996). In this case, most wildlife might have left because of the presence of cattle. Similarly, the presence of researchers at the experimental plots for long durations probably limited utilisation of the plots by wildlife, and hence they probably left the area for more favourable sites.

On overall community

Multivariate analysis of the whole spider community (Figure 5.9-5.11) found that the community from sweep-netting samples responded well to habitat complexity by aggregating into three clusters that were associated with the control, cattle grazing and non-cattle grazing (Figure 5.9). The three clusters reflected a gradient in relative vegetation cover such that the control plots had the highest relative vegetation cover followed by wildlife plots, while the cattle plots had the lowest relative vegetation cover. This variation in relative cover might have led to a corresponding variation in complexity of the habitat in the same order such that spiders distributed themselves along the same gradient, indicating the impacts of the large mammalian herbivores on the spider community through their grazing or browsing and trampling action. Research by Halaj *et al*. (2000) reported that structural habitat complexity had a profound effect on canopy spiders and other arthropods. Similarly, according to the habitat heterogeneity hypothesis (Hart and Horowitz 1991), arthropod community richness should be greater where there is higher structural heterogeneity in the form and species of vegetation present (Evans 1988, Tscharntke and Greiler 1995; Dennis *et al.* 1998). In summary therefore, sweep-netting samples (Figure 5.9), were a better indicator of grazing effects compared to pitfall-trapping samples (Figure 5.10) in that separation was possible along a grazing gradient.

On guilds

At this level of resolution, exclosure treatments had no significant effect on species diversity, richness, or evenness of any guild (Chapter 7). Plant wanderers were the only guild sensitive to the effects of large mammalian herbivore treatments in that they were significantly correlated to relative vegetation cover, which explained 17% of the variation in the diversity of this guild. This was still a low proportion of the factors affecting the diversity and meant that the remaining 83% of variation in diversity of plant wandering spiders was not explained (Table 7.12). The other guilds were not sensitive to the effects of large mammalian ungulates. The resolution at this level was still not sufficiently sensitive to changes caused by grazing, possibly because most individual species responded differently to effects of large mammalian herbivores and thus complicated the responses. For example, the abundance of *Aelurillus* sp. increased with presence of cattle, unlike that of *Borboropactus* sp. that decreased with the presence of cattle, yet both were from the guild of ground wanderers (chapter 8). Such a scenario would complicate the sensitivity of the guild and affect the guild as a unit of resolution.

It is also possible that at resolution at the level of three guilds was still course and not sensitive enough to disturbances. The fact that field observations of biology of most live spiders from the study is not known may imply that the current guilds used might be wrong i.e. some individuals have been placed in their current guild based on knowledge of their family and not individual species behaviour since such information was not available. As an example, members of the family Pisauridae belong to many different guilds e.g. genus *Cispius* is a plant wanderer while *Euprosthenops* is a web-builder (Dippenaar-Schoemann *et al.* 1999b). The current study collected three different species of this family but only one was clearly identified to genus while the others (suspected to be new species), were assigned guild with difficulties as their natural history was lacking and information on their morphology could not help assign guilds.

Finally, it was probable that factors other than those investigated in the current study (e.g. soil factors, amount of surface leaf litter and prey abundance) were important in determining the variation in spider diversity.

Overall, it was clear from the current study that spiders were not useful indicators at a guild level of resolution. Past studies have shown that this level of resolution has a limitation when used for analysis since a single species tolerant of a perturbation might strongly influence the results (Caro and O'Doherty 1999). This was also noted in the current study, where *C. insulana* was found to be very dominant.

On individual species

This study found that the most important factors affecting the abundance of the six focal study species were time, cattle, rainfall and relative vegetation cover. Among all these variables, the abundance of all six species (namely *A. trifasciata, R. flavida, C. insulana, Aelurillus* sp. *Borboropactus* sp. and *D. strandi* significantly varied with change in time, which probably represents a response to a spectrum of factors that are integrated by change of season.

Increase in amount of rainfall increased the abundance of all species except *C. insulana.* The direct effects of rain on these species were probably through drowning, higher humidity, effects on relative vegetation cover and altered food abundance that might stimulate reproduction. It was not clear why *C. insulana* was not sensitive to rainfall but the species which is introduced and widely distributed through out the region (Dippenaar-Schoeman and Jocqué 1997; McClintock and Dodson 1999) seemed to be hardy and therefore probably not limited by local climatic factors.

An increase in relative vegetation cover significantly increased the abundance of *C. insulana, D. strandi* and *Borboropactus* sp., decreased that of *Aelurillus* sp., and had no effect on *A. trifasciata* and *R. flavida.* Such an increase in cover was thought to promote increased habitat complexity that favoured the survival of three of the concerned species e.g. by enhancing a habitat to hide against predator and presence of more food in form of available invertebrates. The two that did not respond to this factor probably meant other factors (e.g. mode of food acquisition, species behaviour) were important in determining their responses. In other words factors that go with increased relative cover such as increased habitat for attachment of webs, hiding sites against predators or more food availability were not important for the two species. It was probable that *Aelurillus* sp. preferred open habitats, which are less complex because of its mode of feeding which ivolves hunting, and this could become hindered by a complex habitat.

The presence of cattle significantly reduced the abundance of all the species except *Aelurillus* sp.*,* which significantly increased in abundance. This, combined with the previous finding and the fact that the presence of cattle was correlated with lower vegetation cover, implied that the effect of cattle on *Aelurillus* sp. was mediated through decreased vegetation cover. The species might be more adapted to thriving in such an open habitat by having special adaptations or unique behaviour to suit the environment. The same argument would account for the effect of cattle on *C. insulana, D. strandi* and *Borboropactus* sp., even though the trend was opposite to that of *Aelurillus* sp.

In conclusion, at the species level of analysis, spiders were more sensitive indicators to environmental changes as compared to guilds and overall community diversity. The six species discussed in chapter 8 responded in contrasting ways to the same environmental variables. This indicated that this level of resolution was more sensitive to changes and thus gave more room to understanding of the value of spiders as indicators of landuse.

Individual species were thus better indicators than guild and overall community. It would be important to know the biology of individual species since it would help in understanding and interpretation of their responses to environmental parameters. It was possible that contrasting responses were averaged out, or that unique responses were swamped, at guild and community levels of resolution so that the signal was lost.

Temporal effects

Relative vegetation cover (Table 6.1 and Figure 6.1), rainfall (Table 6.2 and Figure 6.2) and total species, species richness and species diversity (Figures 6.5-6.8) varied at a temporal scale of months. Although plant cover and rainfall were only weakly correlated at the temporal scale of months (Figures 6.3 and 6.4), their variation explained little of the variation in spider diversity (Tables 6.8 and 6.9). It was probable that at this temporal scale, so many factors came into play that it was not easy to represent a strong pattern in community structure in a single explanatory variable. Such explanatory factors might include the various lifecycles of the different spider species, in which breeding season varied from one species to another; the effect of large mammalian herbivores; the weather e.g. changes in temperature and rainfall; or relative vegetation cover, among others. Hidden variables, like the abundance of predatory small mammals (e.g. Keesing 1998), obviously could not be taken into account. Essentially, this study suggests that the short-term temporal changes in rainfall, cover and hidden variables complicated the effects of the large mammalian herbivores on the community of spiders.

Spatial effects

Species richness and species diversity varied significantly at a spatial scale of hundreds of metres (Tables 6.5-6.6), with the southern blocks reporting lower means. There was a north-to-south gradient, which was reflected more strongly in sweeping samples. Multivariate analysis also revealed that samples from sweep-netting were spatially partitioned at a scale of hundreds of metres (Figure 6.15). It was clear that the separation of both pitfall-trapping and total samples was not as clear as that of sweep-netting samples (Figure 6.16 and 6.17). About three quarters of the plots from these samples clustered together, implying that there was no separation for pitfall-trapping and total samples. In conclusion, spiders from sweep-netting samples might support the expectation and were therefore a better indicator of spatial separation compared to pitfall-trapping samples.

The study model

A flow chart summarizing the whole model on interactions between the spiders, larger mammalian herbivores and other biotic and abiotic factors is presented in Figure 9.1. In this figure, biotic and abiotic factors affect spiders directly and indirectly. The indirect effects involve the mediation by relative vegetation cover where disturbances caused by grazing or the effects of abiotic factors such as rainfall directly influence changes in relative vegetation cover. This in turn brought about a variation in habitat complexity, which affected the spider community. Spiders have been found to prefer more structurally complex habitats (Balfour and Rypstra 1998; Rypstra *et al.* 1999).

In order to test this whole study model, multiple regressions were carried to establish the relationship between each of the spider diversity variables (Shannon-Wiener diversity index, total species, Margalef's richness index and Pielou's evenness index) from both sweep-netting and pitfall-trapping samples with the abiotic and biotic factors (namely cattle, mesoherbivores, megaherbivores, relative vegetation cover, rainfall, time, and the study blocks). In this analysis, the blocks represented unspecified spatial factors such as soil. The time was in months and was converted to circular data (as explained in chapter 2).

The analysis of sweep-netting samples revealed that the total species varied significantly with the presence of cattle and at a spatial scale of hundreds of metres in the form of the study blocks, with all the factors explaining only 9% of the variation in diversity (Table 9.1). The results of a multiple regression on Margalef's richness index revealed that rainfall and the study blocks were the only significant factors affecting the spider community, and all the factors explained only 11% of the variation in species richness (Table 9.2). However, the results of a multiple regression on Pielou's evenness index revealed that cattle, rainfall, relative vegetation cover, time and blocks were all significantly important with all the factors accounting for 27% of variation in evenness (Table 9.3). Meanwhile the Shannon–Wiener diversity index was significantly affected by only rainfall, relative vegetation cover, time and blocks, with all the factors explaining only 13% of the total variation in diversity (Table 9.4).

The results from pitfall-trapping samples revealed that rainfall, time and blocks were the only significant factors affecting total species, explaining 8% of the variation (Table 9.5). Only rainfall and time significantly influenced Margalef's richness index and the Shannon–Wiener diversity index and all the factors explained only 5% and 4% of the variation in richness and diversity (Tables 9.6 and 9.8 respectively. Pielou's evenness index from this collecting method was not significantly affected by any of the factors (Table 9.7).

The above multiple regression models show that the abiotic and biotic factors under investigation were more important for sweep-netting samples than were for pitfall-trapping samples. However, in both cases, the correlations between spider community structure and vegetation cover were always very weak (Tables 9.1-9.8). This therefore implied that the factors under investigation explained only a very small percentage (about 10%) of the spider community's structure. It means that sweep-netting is a better monitoring method and also explains why spider communities are not ideal indicators although individual species are. It also implied that most of the effects on spider communities were not mediated through cover. However, this was contrary the results of direct correlation between the spider diversity and relative vegetation i.e. there were some disparity between the results of chapters 5 and 9 about the overall pattern of spider community structure.

In chapter 5, the results of direct correlation (Figures 5.2-5.8) were very clear that changes in relative cover explained approximately 25-30% of variation in spider diversity, while that of chapter 9 (Tables 9.1-9.8) on overall multiple regression revealed that only about 10% of spider variation was explained by several factors (namely relative vegetation cover, months, rainfall, cattle, mesoherbivores, megaherbivores and study blocks) put together. It was only Pielou's evenness index that was close to results of chapter 5 with 27% of its variation being explained by the same factors (Table 9.3). The implication here was that there were problems of interpreting the community data and a conclusion was made that the species level of analysis (chapter 8), was far more effective in explaining the response of spiders to disturbances and environmental factors.

Conclusion

In conclusion, this study suggests that individual spider species were fairly good indicators of habitat quality and change. They were sensitive to changes caused by cattle and helped to separate the effects of cattle from those of mesoherbivores and megaherbivores. Spiders were even more sensitive to disturbances caused by grazing when dealt with at individual species level rather than at the overall community level, or at the guild level. In most cases the spiders responded to effects of cattle, relative vegetation cover, rainfall and season, making them a useful taxon for monitoring. According to Kremen *et al.* (1994) such a goal of monitoring is to select indicators that respond to human impacts long before changes ramify through complex network of ecological interactions to affect higher trophic levels and more long-lived organisms.

However one of the problems when looking at spider diversity at a coarse level of resolution e.g. at the guild level, is the fact that it is not possible to detect the sensitivity of individual species to disturbances and rather assumes that all the species grouped together will respond in a similar way to changes. Lawton *et al.* (1998) argued that different species vary in their requirements within a natural ecosystem. This was further supported by Goldstein (1999) and Alonso (2000) who emphasized that individual species always had their unique history that dictated their distribution. Such arguments are against analysis at a course level of resolution to detect disturbances caused by grazing and would instead tend to support the species-level approach.

However there are strong views that individual higher taxa, let alone individual species, are not sufficient as indicators (Noss 1990; Kremen *et al.* 1994; Lawton *et al.* 1998). Reasons for such views might include the taxonomic limitation reflected by many morphospecies in this study and the many undescribed species that remain in arachnological studies, as emphasized in Dippenaar and Jocqué (1997). This is also supported by the views of New (1997), who pointed out clearly the overwhelming abundance and diversity of arthropods, and the taxonomic instability of some groups that limit the development of assessment programs that include invertebrate communities for monitoring purposes. Another serious limitation is that the biology and or ecology of the described species are still not well documented, which makes understanding of many individual species difficult. Fortunately they are common and thus easy to study. Goldstein (1999) and by Alonso (2000) emphasized the need for conservation and management plans that not only incorporate the number of species but also the identity and biology of species present. Such knowledge is still lacking among many African savanna species.

When compared to other invertebrates groups, spiders were fairly good but not excellent indicators, despite having several qualities listed in chapter 1, and other invertebrates are useful too. For example, research has shown that ants have many good qualities that make them better indicators than spiders. Such qualities include narrow tolerance to disturbances and reliance on relatively high temperatures that make them sensitive to microhabitat changes (Kaspari and Majer 2000). Ants have stationary and perennial nests with fairly restricted foraging ranges that make them more frequent in the habitat, easily sampled and reliably monitored (Alonso 2000). They also function at many levels in an ecosystem e.g. as detritivores, mutualists and as herbivores (Alonso 2000).

This study has used the levels of single species, guilds and overall community to show the value of spiders as indicators of disturbances. In most cases, the spiders were sensitive to disturbances caused by cattle but not other large mammalian herbivores (e.g. Tables 5.7, 5.9, 5.13). The spider community was seen to be sensitive to large mammalian herbivore treatments (Figure 5.9), while individual species responded well to a range of factors (e.g. Tables 8.5, 8.11, 8.18, 8.21, 8.31 and 8.43 among others). However, the guild level of resolution was not very sensitive to the disturbances caused by cattle or large mammalian herbivores (Tables 7.3-7.11) except for the plant wanderers, which significantly correlated with increase in relative vegetation cover (Figure 7.1). This study thus concludes that monitoring of individual species, as indicators of grazing impacts in savanna could be useful and relatively easy. This conclusion agrees with the work of some scientists (e.g. Samways 1994; Churchill 1997; Feinsinger 2001), who preferred use of abundant species to rare ones for use as indicators.

Meanwhile, the overall results of this study have shown that the response of spiders to environmental variables or disturbances caused by large herbivores is always not the same e.g. guilds were not very sensitive to changes while individual species and the plant-inhabiting spider community did respond well. At times the method of analysis also determined the outcome of results.

Application of results to management

This might be useful information for future management planning. For example, it could now be used in future experimental manipulations to establish the optimal cattle density/stocking rate that would not cause significant effects on cover, and hence be compatible with high spider diversity and the other native large mammalian herbivores. In other words, the results of the current study can now be used to help manipulate cattle density such that it meets a desirable cattle-stocking rate, compatible with large mammalian herbivores and other native biodiversity. Similarly, the same results could be used in ranches where wildlife cropping and livestock keeping are practised e.g. neighbouring Segera Ranch, which is on black cotton soil like Mpala. In such a place, a similar experimental approach could be employed to help detect the optimal stocking rates of wildlife by evaluating the direct changes on vegetation cover (when their densities are known) and then projecting the spiders diversity as already done in the current study. However, this might not project well with spiders since the coefficient of determination was low in the current study, but may be applied to other more sensitive taxa. This would fulfil a Long-term goal in semi-arid ecosystems for sustainable management activities that are compatible with native biodiversity. It is however important to note that such an experimental approach might need utilisation of more spider collecting methods and more resources to give better results. The study would already point out that spiders are not very good indicators especially when analysed at coarse levels of resolution.

Recommendations

Since this study was based mainly on two methods of data collection and only for a period of 14 months, it certainly does not represent all the species present in the study area (Figures 3.1, 3.3 and 3.4). A more diversified array of sampling methods such as beating, fogging, visual searches and sieving (where applicable), and a longer sampling period, would certainly increase the species list. Past studies have reported that the number of species counted in a community increases with the length of time over which sampling occurs, the numbers of study sites sampled and the number of specimens collected in the sample (Preston 1960; Hansen 1980; Rosenzweig 1995; Gaston 1996; McKinney and Frederick 1999; Hadly and Maurer 2001). It might be wise to extend this survey to other ranches within the Laikipia district that have slightly different rainfall but the same type of soil e.g. Segera ranch, since it might increase the number of the known species in this ecosystem.

The study recommends that the black cotton soil spider fauna is rich and useful for monitoring work, and that support for the conservation of this ecosystem should be continued. More individual spider species need to be studied in order to evaluate their indicator values that would help in establishment of a longer list of indicator species for landuse management. It further highlights the urgent need for taxonomic studies on Kenyan spiders and other invertebrates to enhance future studies for monitoring work.

Tables

Table 9.1. Results of a multiple regression to establish the relationship of total species (S) from sweep-netting samples with cattle, mesoherbivores, megaherbivores, relative vegetation cover, total (lagged) monthly rainfall, months and blocks. The blocks represented a spatial scale of hundreds of metres. The results of the summary regression are: R = 0.30, $R^2 = 0.09$, $F_{7,\,242} = 3.51$, p = 0.0002.

	Beta	Std.Err.	B	Std.Err.	$t_{(242)}$	p-value
Intercept			80.04	20.91	3.83	0.00*
Blocks	-0.20	0.06	-0.66	0.20	-3.25	0.00*
Cattle	-0.16	0.07	-0.88	0.36	-2.44	0.02*
Mesoherbivores	0.02	0.07	0.10	0.43	0.24	0.81
Megaherbivores	-0.12	0.07	-0.70	0.42	-1.68	0.09
Months (circular-sine)	-0.08	0.07	-0.59	0.58	-1.01	0.31
Relative vegetation cover	-0.05	0.07	-0.01	0.02	-0.75	0.45
Total monthly rainfall (Lagged)	-0.13	0.08	-0.01	0.01	-1.77	0.08

Table 9.2. Results of a multiple regression to establish relationship of Margalef's richness index (d) from sweep-netting samples with cattle, mesoherbivores, megaherbivores, relative vegetation cover, total (lagged) monthly rainfall, months and blocks. The blocks represented a spatial scale of hundreds of metres. The results of the summary regression are: $R = 0.32$, $R^2 = 0.11$, $F_{7, 242} = 4.19$ $p = 0.0001$.

	Beta	Std.Err.	B	Std.Err.	t(242)	p-value
Intercept			19.61	5.04	3.89	0.00*
Blocks	-0.20	0.06	-0.16	0.05	-3.25	0.00*
Cattle	-0.07	0.07	-0.10	0.09	-1.12	0.27
Mesoherbivores	-0.02	0.07	-0.03	0.10	-0.25	0.80
Megaherbivores	-0.11	0.07	-0.15	0.10	-1.48	0.14
Months (circular-sine)	-0.22	0.07	-0.42	0.14	-3.01	0.00*
% Relative vegetation cover	0.09	0.07	0.00	0.00	1.25	0.21
Total monthly rainfall (Lagged)	-0.19	0.07	0.00	0.00	-2.54	0.01*

Table 9.3. Results of a multiple regression to establish the relationship of Pielou's evenness index from sweep-netting samples with cattle, mesoherbivores, megaherbivores, relative vegetation cover, total (lagged) monthly rainfall, months and blocks. The blocks represented a spatial scale of hundreds of metres. The results of the summary regression are: R = 0.52, R² = 0.27, $F_{7, 242}$ = 13.00, p = 0.0002.

	Beta	Std.Err.	B	Std.Err.	t(242)	p-value
Intercept			1.93	0.51	3.77	0.00*
Blocks	-0.12	0.05	-0.01	0.01	-2.19	0.03*
Cattle	0.20	0.06	0.03	0.01	3.42	0.00*
Mesoherbivores	-0.09	0.07	-0.01	0.01	-1.38	0.17
Megaherbivores	0.05	0.07	0.01	0.01	0.79	0.43
Months (circular)	-0.39	0.07	-0.08	0.01	-5.82	0.00*
% Relative vegetation cover	0.37	0.06	0.00	0.00	5.84	0.00*
Total monthly rainfall (Lagged)	-0.30	0.07	0.00	0.00	-4.50	0.00*

Table 9.4. Results of a multiple regression to establish the relationship of Shannon-Wiener diversity index (H´) from sweep-netting samples with cattle, mesoherbivores, megaherbivores, relative vegetation cover, total (lagged) monthly rainfall, months and blocks. The blocks represented a spatial scale of hundreds of metres. The results of the summary regression are: $R = 0.37$, $R^2 = 0.13$, $F_{7, 242} = 5.38$, $p = 0.000$.

	Beta	Std.Err.	B	Std.Err.	t(242)	p-value
Intercept			11.05	2.39	4.62	0.00*
Blocks	-0.23	0.06	-0.09	0.02	-3.81	0.00*
Cattle	0.00	0.06	0.00	0.04	-0.03	0.97
Mesoherbivores	-0.03	0.07	-0.02	0.05	-0.46	0.65
Megaherbivores	-0.08	0.07	-0.06	0.05	-1.18	0.24
Months (circular)	-0.22	0.07	-0.20	0.07	-2.99	0.00*
% Relative vegetation cover	0.17	0.07	0.00	0.00	2.43	0.02*
Total monthly rainfall (Lagged)	-0.25	0.07	0.00	0.00	-3.33	0.00*

Table 9.5. Results of a multiple regression to establish relationship of total species from pitfall-trapping samples with cattle, mesoherbivores, megaherbivores, relative vegetation cover, total (lagged) monthly rainfall, months and blocks. The blocks represented a spatial scale of hundreds of metres. The results of the summary regression are: $R = 0.30$, $R^2 = 0.08$, $F_{7, 243} = 3.35$, $p = 0.012$.

	Beta	Std.Err.	B	Std.Err.	t(243)	p-value
Intercept			43.12	17.22	2.50	0.01*
Blocks	-0.12	0.06	-0.34	0.17	-2.01	0.04*
Cattle	-0.08	0.07	-0.33	0.29	-1.13	0.26
Mesoherbivores	0.01	0.07	0.04	0.34	0.11	0.91
Megaherbivores	-0.10	0.07	-0.44	0.34	-1.31	0.19
Month (circular)	-0.24	0.08	-1.52	0.47	-3.21	0.00*
% Relative vegetation cover	-0.09	0.07	-0.02	0.01	-1.25	0.21
Total monthly rainfall (lagged)	-0.27	0.08	-0.02	0.01	-3.49	0.00*

Table 9.6. Results of a multiple regression to establish relationship of Margalef’s richness index from pitfall-trapping samples with cattle, mesoherbivores, megaherbivores, relative vegetation cover, total (lagged) monthly rainfall, months and blocks. The blocks represented a spatial scale of hundreds of metres. The results of the summary regression are: R = 0.23, $R^2 = 0.05$, $F_{7, 243} = 1.90$, p = 0.041.

	Beta	Std.Err.	B	Std.Err.	t(243)	p-value
Intercept			11.17	5.46	2.05	0.04*
Blocks	-0.10	0.06	-0.09	0.05	-1.62	0.11
Cattle	-0.01	0.07	-0.01	0.09	-0.13	0.90
Mesoherbivores	-0.03	0.07	-0.04	0.11	-0.39	0.70
Megaherbivores	-0.09	0.07	-0.13	0.11	-1.18	0.24
Month (circular)	-0.19	0.08	-0.37	0.15	-2.49	0.01*
% Relative vegetation cover	0.02	0.07	0.00	0.00	0.21	0.83
Total monthly rainfall (lagged)	-0.19	0.08	0.00	0.00	-2.45	0.02*

Table 9.7. Results of a multiple regression to establish relationship of Pielou’s evenness index from pitfall-trapping samples with cattle, mesoherbivores, megaherbivores, relative vegetation cover, total (lagged) monthly rainfall, months and blocks. The blocks represented a spatial scale of hundreds of metres. The results of the summary regression are: R = 0.16, R² = 0.03, $F_{7,\,243}$ = 0.98, p = 0.23.

	Beta	Std.Err.	B	Std.Err.	t(243)	p-value
Intercept			1.95	1.62	1.21	0.23
Blocks	-0.05	0.06	-0.01	0.02	-0.77	0.44
Cattle	0.09	0.07	0.03	0.03	1.27	0.20
Mesoherbivores	-0.06	0.08	-0.02	0.03	-0.75	0.45
Megaherbivores	-0.04	0.08	-0.02	0.03	-0.59	0.55
Month (circular)	0.00	0.08	0.00	0.04	0.03	0.97
% Relative vegetation cover	0.13	0.07	0.00	0.00	1.69	0.09
Total monthly rainfall (lagged)	-0.02	0.08	0.00	0.00	-0.29	0.77

Table 9.8. Results of a multiple regression to establish relationship of the Shannon-Wiener diversity index from pitfall-trapping samples with cattle, mesoherbivores, megaherbivores, relative vegetation cover, total (lagged) monthly rainfall, months and blocks. The blocks represented a spatial scale of hundreds of metres. The results of the summary regression are: R = 0.22, R² = 0.04, $F_{7, 243}$ = 1.80, p = 0.035.

	Beta	Std.Err.	B	Std.Err.	t(243)	p-value
Intercept			7.51	3.54	2.12	0.04*
Blocks	-0.11	0.06	-0.06	0.03	-1.69	0.09
Cattle	0.01	0.07	0.01	0.06	0.18	0.85
Mesoherbivores	-0.01	0.08	-0.01	0.07	-0.18	0.85
Megaherbivores	-0.09	0.07	-0.08	0.07	-1.20	0.23
Month (circular)	-0.16	0.08	-0.20	0.10	-2.02	0.04*
% Relative vegetation cover	0.04	0.07	0.00	0.00	0.56	0.58
Total monthly rainfall (lagged)	-0.20	0.08	0.00	0.00	-2.58	0.01*

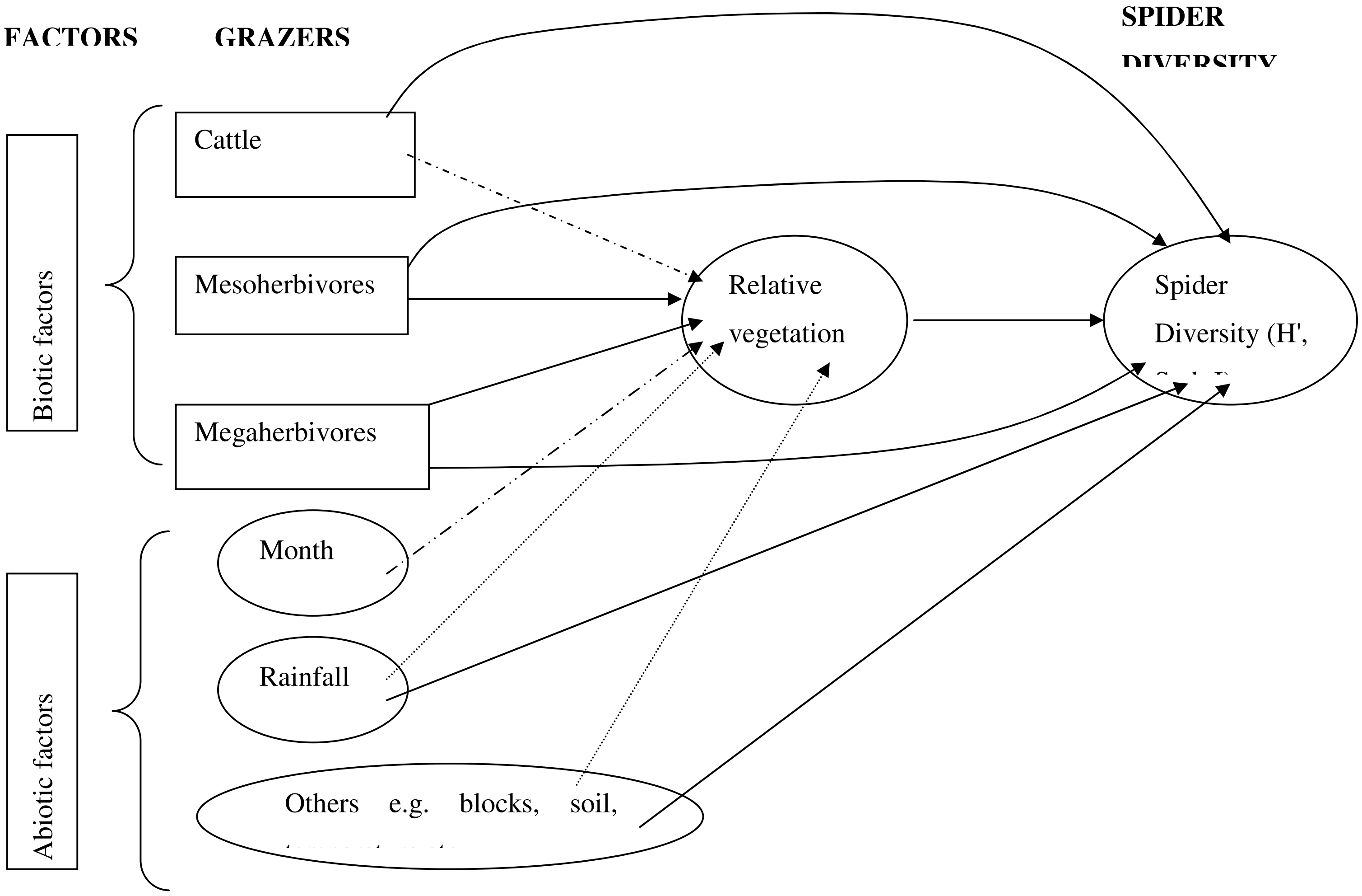

Figure 9.1. A summary flow chart for the whole study model, showing the interaction between spiders, large mammalian herbivores, relative vegetation cover, rainfall and other abiotic factors. The strength of the relationships, estimated by multiple regressions, for this model for each of the total species (S), Margalef’s richness index, Pielou’s evenness index (J') and the Shannon-Wiener diversity index (H’) for sweep-netting samples are shown in Tables 9.1-9.4 respectively. Similarly, the relationships for the pitfall-trapping samples are shown Tables 9.5-9.8 respectively.

Appendices

Appendix 1a. A 2x2 ANOVA, to test the effects of blocks and treatments (spatial scale of hundreds of metres) on the total number of species for sweeping-netting samples. * = Significant at $p < 0.05$.

	DF	F	P
Block	2	14.36	0.00*
Treatment	5	2.12	0.06
Block*Treatment	10	1.01	0.43
Error	504		

Appendix 1b. The means and standard errors for a 2x2 ANOVA, to test the effects of blocks and treatments on the total number of species for sweeping-netting samples. The means having the same letter at the last column of the table are not significantly different using Tukey's test at $p < 0.05$.

	Mean	SE	Similarity
North	4.93	0.15	a
Central	4.86	0.16	a
South	3.91	0.14	b

Appendix 2a. A 2x2 ANOVA, to test the effects of blocks and treatments (spatial scale of hundreds of metres) on Margalef's richness index for sweeping-netting samples. * = Significant at $p < 0.05$.

	DF	F	P
Block	2	9.11	0.00*
Treatment	5	1.27	0.28
Block*Treatment	10	1.20	0.29
Error	504		

Appendix 2b. The means and standard errors for a 2x2 ANOVA, to test the effects of blocks and treatments on the Margalef's richness index for sweeping-netting samples. The means having the same letter at the last column of the table are not significantly different using Tukey's test at p < 0.05.

	Mean	SE	Similarity
North	1.72	0.05	a
Central	1.72	0.05	a
South	1.45	0.05	b

Appendix 3a. A 2x2 ANOVA, to test the effects of blocks and treatments (spatial scale of hundreds of metres) Shannon Wiener' diversity index for sweeping-netting samples. * = Significant at p < 0.05.

	DF	F	P
Block	2	14.38	0.00*
Treatment	5	1.51	0.19
Block*Treatment	10	1.37	0.19
Error	504		

Appendix 3b. The means and standard errors for a 2x2 ANOVA, to test the effects of blocks and treatments on the Shannon Wiener' diversity index for sweeping-netting samples. The means having the same letter at the last column of the table are not significantly different using Tukey's test at p < 0.05.

	Mean	SE	Similarity
North	1.29	0.03	A
Central	1.27	0.04	A
South	1.05	0.04	B

Appendix 4a. A 2x2 ANOVA, to test the effects of blocks and treatments (spatial scale of hundreds of metres) total number of species for pitfall-trapping samples. * = Significant at $p < 0.05$.

	DF	F	P
Block	2	3.18	0.04*
Treatment	5	1.67	0.14
Block*Treatment	10	0.62	0.80
Error	486		

Appendix 4b. The means and standard errors for a 2x2 ANOVA, to test the effects of blocks and treatments on the total number of species for pitfall-trapping samples. The means having the same letter at the last column of the table are not significantly different using Tukey's test at $p < 0.05$.

	Mean	SE	Similarity
North	5.81	0.24	a
Central	5.45	0.20	a
South	5.03	0.21	b

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