UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

THE FEEDING ECOLOGY AND HABITAT USE OF THE AARDVARK *Orycteropus afer*

Peter Andrew Lindsey

Submitted in partial fulfillment of the requirements for the degree
of Master of Science

Wildlife Unit
Faculty of Veterinary Science
University of Pretoria
Onderstepoort

August 1999

The Feeding Ecology and Habitat Use of the Aardvark *(Orycteropus afer)*

Supervisor: Professor J.D Skinner
Wildlife Unit
Private Bag XO4
Faculty of Veterinary Science
Onderstepoort 0110

Abstract

The seasonal diet, feeding patterns, feeding selection and habitat selectivity of the aardvark were determined during summer and winter at Tussen die Riviere Nature Reserve in the southern Free State. Pitfall trapping, dig sampling and quadrat sampling were used to determine the resource base of three habitats in the summer and winter of 1998. A total of 44 ant species of 5 sub families and 17 genera, and two termite species of two sub families were recorded. Pitfall trapping was the most successful technique, followed by quadrat sampling (51.1%) and finally, dig sampling (48.8%). Abundance and diversity was higher during summer than winter. *Monomorium albopilosum* was the most abundant species in all habitats in winter, whilst *Anoplolepis custodiens* was the most abundant in summer. The grassland habitat yielded the highest abundance and diversity, followed by the steep slope and riverine areas.

Seasonal diet and foraging patterns were determined through faecal analysis and observation of four habituated aardvarks. The Formicidae were more important than the Isoptera in both seasons. The feeding of the aardvark was highly selective, only 28.8% of the available species having been utilised. Prey selection was found to be most highly correlated with prey size, prey abundance, prey mobility, and prey calorific value.

Aardvarks were highly selective in their habitat utilisation. The vast majority of feeds were made in the grassland areas where prey abundance was greatest, compared to negligible numbers of prey in the rocky steep slopes and no prey in the riverine areas due to periodic flooding.

ACKNOWLEDGEMENTS

I would like to thank Professor Skinner for giving me the opportunity to study aardvark at Tussen die Riviere and for his financial and intellectual support. To Free State National Parks, and Savvas Vrahimis in particular, I am very grateful for the opportunity to work at TdR, and for the provision of the aardvarks!

Martin Haupt did a great job in helping getting the project started and in organising equipment. Mark & Tracy Roods provided endless help, both with practical aspects of the project and in the provision of a social life! I would like to thank Paul Henning and Bill Townley for their help with the fieldwork and their company on the long aardvark following nights! Paul Henning and Gael La Roc also did some great work habituating aardvark and managed to increase the sample size from 2 to 4 remarkably 'tame' animals.

I would like to thank Dr Hamish Robertson for the many hours spent identifying ants from my pit fall trapping, dig sampling and quadrats. Ryan Johnson was of great help during the analysis stages and for this I am very grateful. I would also like to thank Dr Hector Dott whom provided highly professional and invaluable input into analysis stages. Dominic Moss and Mike Hoffman were very helpful throughout the project, not least for their entertainment value.

I am very grateful to Pretoria University for their provision of a foreign students bursary for the duration of my study.

Most of all, I would like to thank Andrew Taylor for getting the whole project started. He put in the long hours of habituation and developed a situation which enabled me to walk in and start research. He helped me during the protocol stages of my work and put in many hours of brain work into helping me work out analysis problems.

Contents

Ant and termite sampling

Behavioural observations

Faecal analysis

Prey selection

Habitat Utilisation

List of Figures

List of Tables

INTRODUCTION

The Aardvark *(Orycteropus afer)*

The aardvark, a semi fossorial myrmecophage, is the sole representative of the Order Tubilidentata (Skinner & Smithers, 1990), family Orycteropodidae, and genus *Orycteropus* (Kingdon, 1971). A single sub species is recognised in the southern African subregion (Skinner & Smithers, 1990). Historically, the taxonomy of the aardvark has been uncertain (Kingdon, 1971). Although initially classified with the Edentates, subsequent research has led to the isolation of the species into an order of its own (Dene, Goodman, Walz & Romero-Herrera, 1983). Recent molecular research has located the order Tubilidentata as a sister group of the Xenartha (including the armadillos) and Cetferungulata (artiodactyls, carnivores, cetaceans and perissodactyls) (Arnason, Gullberg & Janke, 1999).

The confusion surrounding the taxonomy of the aardvark has been caused to a large extent by the convergent characteristics shared by aardvarks and other myrmecophagous species (De Jong, Zweers & Goodman, 1981). Aardvarks show a variety of adaptations suited to their specialist life style. The long claws and powerful limbs provide the species with a prodigious digging ability. The long muscular tail is important in balance and in gripping the outside of termite mounds during feeding. Despite poor eyesight, the aardvark has sensory development well suited to the lifestyle. Olfaction is particularly acute and aardvarks have a greater number of olfactory lobes than any other mammal (Kingdon, 1971). In addition, the nostrils are covered by very dense, fine hair which effectively excludes detritus during feeding. The long eyelashes perform a similar function, as do the tubular ears, which are closed during feeding (Skinner & Smithers, 1999). Hearing is acute and is important in predator avoidance. Finally, the salivary glands are well developed and produce viscous saliva to which the prey readily adhere (Kingdon, 1971).

Aardvarks are restricted to Africa, but within the continent remain widespread ranging from the tropical forests of the west, to the steppe-like savannahs of South Africa (Melton, 1976). However, within this range the distribution is patchy due to the presence of unsuitable mountainous terrain and human interference. A number of factors threaten the species in various parts of its range. The destruction of habitat through cultivation has, and will lead to the further displacement of the species. The aardvark is frequently persecuted by farmers due to damage caused to roads, fences and dams. Perhaps the most important threat however, comes from the increasing hunting pressure from burgeoning human populations, both for meat and traditional medicine (Skinner & Smithers, 1999).

Knowledge of the ecology of the aardvark is based largely upon Taylors (1998) detailed ecological study. Willis (1988) conducted research upon the feeding ecology of the aardvark, although the conclusions drawn were limited by the absence of habituated study animals. In addition, van Aarde, Willis, Skinner & Haupt (1992) looked at the home range utilisation of the species, whilst Melton (1976) summarised all that was then known about the species. Anecdotal evidence is the only information source available to fill the large gaps that remain in our understanding of the species, particularly with respect to the selection of habitat and prey.

Several studies have considered aspects of prey selection in other mammalian myrmecophages, particularly from Australia and South America e.g. the echidna *Tachyglossus aculeatus* (Abensperg-Traun, 1990), the banded ant eater *Myrmecobius f. fasciatus* (Calaby, 1960), the giant ant eater *Myrmecophaga tridactyla* (Montgomery & Lubin 1981; Redford, 1983, Redford, 1984). The vermilinguas *Cyclopes didactylus* and *Tamandua mexicana* (Montgomery, 1985). In addition, Redford (1987) wrote a comprehensive review of mammalian myrmecophagy. Reasonable coverage of the feeding of African myrmecophages such as the pangolin (Sweeney, 1956; Coulson, 1989; Jacobsen, Newberry, de Wet, Viljoen & Pietersen, 1991; and Heath & Coulson, 1997) and the aardwolf (Bothma & Nel, 1980; Richardson, 1987, Richardson & Levitan, 1994 and Anderson, 1994) has been achieved. However, Swart (1996) was the first to consider prey selection specifically in a free ranging myrmecophage. This area of study remains neglected and the factors driving prey selection in aardvark are particularly poorly understood.

This is the first study to consider in detail utilisation of prey and habitat in relation to the availability of prey and other habitat variables. In addition, for the first time, the selection of prey, and feeding patterns exhibited during foraging, are related to prey species biology and the constraints of the myrmecophagous lifestyle.

AIMS

Specifically, the study was designed to look at the following questions;

- The abundance and diversity of ant and termite species in the area
- The availability of potential prey species in three different habitats, in summer and winter, using a variety of sampling techniques.
- The availability of prey in the home ranges of the study animals
- The diet of the aardvark in both seasons
- The degree of selectivity relative to availability and various aspects of prey species biology.
- The feeding patterns exhibited during feeding on each species in summer and winter relative to various aspects of prey species biology.
- The habitat use of the aardvark relative to the availability of prey and various habitat characteristics, in summer and winter.

The research was divided up into three sections. The first, consisted of a large scale sampling of the ant and termite fauna in three different habitats within the reserve, in both summer and winter. The second involved detailed behavioural observation and faecal analysis. Finally, the third aspect of the study involved the determination of habitat use by the aardvark and its relation to various habitat characteristics.

STUDY AREA

This study was conducted on Tussen die Riviere Nature Reserve (TdR), which is located on the peninsula between the Orange and Caledon rivers, in the southern Free State. This equates to a position of 30° 30'S and 26° 15' E (Werger 1973), approximately 20 km east of the town of Bethulie. The reserve was established in 1967, with all livestock being removed and replaced with wildlife during an extensive reintroduction programme. The Reserve encompasses an area of some

22 000 Ha of Eastern Mixed Nama Karoo and as such is of enormous importance in the conservation of one of the least well preserved vegetation types (Hoffman, 1996). The climate of the area is categorised as being intermediate temperate tropical. The winter months are cold and dry, with mean temperatures between 0 - 10°C, whereas summer mean temperatures exceed 18°C. Annual rainfall averages approximately 400 mm and falls between November and March (Werger, 1973).

Three major soil types exist in the reserve, the most prevalent being solonetzic, with some lithosols (Werger, 1973). Alluvial soils of over 0.5 m in depth follow the two rivers, and are separated by a central ridge of sedimentary rock overlying highly resistant Karoo dolerite. The ridge areas have very shallow soils with a mean depth of 10 cm (Werger, 1973). The geomorphology of the area is dominated by ridges and slopes, caused by the highly resistant doleritic dykes.

The vegetation of the area has been categorised by Werger (1973) in to three major types;

(1) Riverine Communities

The riverine communities occur on the levees of the Caledon and Orange rivers. The soils are alluvial with a pH of between 6.5-7.5. The *Acacia karoo-Celtis africana* community is dominant in most areas. This generally consists of three layers: A tree layer of 6-10m in height, and an average cover of 75%. A shrub layer, 2-4 m tall, with 40-50 % cover, characterised by *Rhus pyroides, Diospyros lycoides, Lycium hirsutum* and *Clematis brachiata* etc. Thirdly, there is a grass and herb layer with small shrubs and variable cover, dominated by *Atriplex semibaccata, Asparagus setaceus, Bromus willdenowii, Chenopodium murale, melica decumbens, Achyranthes aspera, and Rubia cordifolia.*

(2) Communities of the gently sloping and flat terrain.

Werger (1973) stated that these communities are generally poorer in species than the steep slopes, and structurally less complex than the riverine communities, generally only having two layers. There is typically a grass and dwarf shrub layer from 0.15-0.6 m in height, and with a maximum cover of 50 %. The second layer consists of a low lying layer of creeping and rosette plants, covering as little as 5%, with a height of only 0.05 m. Werger (1973) recognised four vegetation communities within this habitat type, based upon distinctive species combinations and in the case of (B) and (C), the presence of differential species on different soil types.

- (A) *Eragrostis lehmanniana-Chrysocoma tenuifolia* communities
- (B) *Chrysocoma tenuilfolia-Lessertia pauciflora* communities
- (C) *Chrysocoma tenuifolia-Nenax microphylla* communities
- (D) *Chrysocoma tenuifolia-Polygala leptophylla* communities.

(3) Steep Slope Communities.

Werger, (1973) describes the steep slope communities as being the most speciose in the reserve. The vegetation here has four distinct layers; An open tree layer occurs in some areas, with a ground cover of 10-30 %, and reaching up to 6m in height. A tall shrub layer with the cover varying between 10-30 % between the various steep slope communities. This layer reaches a height of between 1-4m. Thirdly, there is a grass, dwarf and small shrub layer which covers between 35-50 % and reaches 0.8m in height. Finally, there is a sparse ground layer of creeping rosette species typically covering less than 5% and reaching a height of 0.05m.

The steep slope flora has been classified into three different communities:

- (A) *Rhus erosa-Rhynchelytrum repens* communities
- (B) *Rhus erosa- Stachys burchelliana* communities
- (C) *Olea africana- Maytenus heterophylla* communities.

These communities have a large number of species in common, including: *Asparagus suaveolens, Aristida diffusa, Diospyros lycioides, Rhus erosa, Rhus undulata, Eustachys paspaloides, Sporobolus fimbriatus, Olea africana, Diospyrus austro-africana, Enneapogon scoparius, Sutera albiflora*, and *Euclea coriacea* (Werger, 1973).

A number of mammal species inhabit the reserve. Ungulate species include, buffalo *(Syncerus cafer*), eland *(Tragelaphus oryx)*, gemsbok *(Oryx gazella)*, zebra *(Equus burchellii*), black wildebeest *(Connochaetes gnou)* red hartebeest *(Alcelaphus buselaphus)*, kudu *(Tregelaphus strepsiceros)*, blesbuck *(Damiliscus pygargus)*, impala *(Aepcyeros melampus)*, springbok *(Antidorcas marsupialis)*, mountain reedbuck *(Redunca fulvorufula)*, steenbok *(Raphicerus campestris)* and grey duiker *(Sylvicapra grimmia)*. Of particular interest with regard to the aardvark, is the presence of the insectivorous aardwolf *(Proteles cristatus)* and bat eared fox *(Otocyon megalotis)*, and porcupine *(Hystrix africaeaustralis*), all three of which have been recorded inhabiting used and unused aardvark burrows (pers. obs.).

METHODS OF ESTABLISHMENT

Aardvark Capture

The establishment of the project initially required the capture of the aardvarks in order to implant radio transmitters. This was achieved by searching for individuals at night with spotlights. On finding an aardvark, it was pursued by the vehicle over a short distance until it took refuge in a hole. A steel drop door trap was then placed with the entrance over the hole. The trap was then guarded by a person lying still 30 metres down wind. Once caught, the aardvark was dosed with the tranquilising drug Ketamine hydrochloride (Anaket Centaur Labs, Isando) and the immobilising drugs Medetomidine hydrochloride (Domitor ®, Novartis AH South Africa (Pty) Ltd, Isando) and Midazolam (Dormicum ®). A comprehensive review of capture techniques and drug regimes is given elsewhere (Taylor, 1998; Nel *et al.* in prep.). The immobilised animal was then taken rapidly back to the operating table where the radio implant was inserted into the abdomen.

Following the capture period, work commenced on the habituation of the aardvark. This was achieved by locating and following the radio-tagged animal at a discrete distance for several hours a night. As the animal became habituated to the presence of the human, the distance between the researcher and the animal was gradually reduced. This continued until the aardvark ignored human observers, at which stage behavioural observation could begin. Four individuals became sufficiently habituated to permit study and these were used as the focal animals of the study, whilst the remaining radio-tagged animals were used for the collection of faeces. However, one of the four animals reverted to a non-habituated state and as a result, minimal data was collected in summer from this individual.

Statistical Methods of Analysis

A variety of parametric tests were carried out using the statistical package Sigmastat ©, the most common having been one, two and three-way Anovas. Linear regression was also used. Parametric tests were preferred over non-parametric tests due to the lack of efficiency and power associated with the latter tests (Grafen, 1994). Transformations were used where necessary to make the data fit the assumptions of parametric tests, including normality and homogeneity of variance. However, in cases where no non-parametric equivalents existed, Anovas on ranks and non-parametric equivalents of the Anova tests were used. When conducting an anova, if the interaction was significant, the interaction mean sqaure was used to calculate the F ratio of the main effects.

The ant and termite sampling data, the faecal data and two aspects of behavioural observations were analysed using multivariate methods. These data sets show extreme deviation from the assumptions of parametric tests. Multivariate tests make minimal statistical assumptions (Clarke, 1993) and as a result are ideal for these types of data. In addition, the use of one test avoids the problems of multiplicity of P-values associated with multiple T-tests (Grafen, 1994). The computer package Primer was used for these analyses. Anosim, or analyses of similarity were done on the data, based upon a permutation procedure done on similarity coefficients calculated between each pair of samples (Clarke & Warwick, 1994). This method compared sample groups in terms of the extent to which species were shared at certain abundance levels. Both one-way and two-way Anosims were done. Square root transformations were applied to the data in order to reduce the importance of extreme values, whilst still emphasising the most abundant species in the analysis. Two descriptive methods were used. The first, Multi Dimensional Scaling, is based upon a similarity matrix and provides a clustering of the various groups, with between group distances based on their rank similarity (Clarke & Warwick, 1994). Here the level of 'stress' associated with the diagram is indicated on each of the plots. Stress involves the distortion associated with the imposition of a three dimensional distribution of data points onto a two dimensional diagram. Details of this phenomenon are discussed in Clark & Warwick (1994). Hierarchical Agglomerative Clustering was used as a second method of displaying mutual similarities between the groups. This method generates a dendrogram diagram by taking a similarity matrix and successively fusing samples into groups and then larger clusters (Clarke & Warwick, 1994).

Finally, Backwards Stepwise Regression analysis was used in determining the factors which predict prey selection by the aardvark. The use of this model ensured that meaningless variables were not included in the final model, thus ensuring the best prediction of utilisation (Grafen, 1994). This model starts with all variables entered into the equation. A stepwise process then follows, whereby the variable with an F-value lower than the specified value (3.900 in this case) is removed, followed by the variable with the next lowest F-value etc. After the removal of each variable, the Sigmastat © programme checks the F-value of each variable that has been removed and re enters any variable with an F-value above a specified F to enter value (4.000 in this case). The final model is reached when further addition or removal of variables ceases to significantly improve the prediction of the dependent variable.

Chapter 1

Food Resource Availability: Ant and Termite Sampling

Introduction

Knowledge of the abundance and diversity of the ant and termite population in the various habitats is vital to the understanding of habitat selection and diet of the aardvark. Ant faunas tend to vary considerably between habitat types (Room, 1975; Greenslade & Greenslade, 1977; Andersen, 1983; Samways, 1983; Majer, 1985; Koen & Breytenbach, 1988). Intra-habitat seasonal variation in ant communities has also been widely documented (Andersen, 1983, 1993; Koen & Breytenbach, 1988; Samways, 1990). In light of this, extensive sampling of the ant and termite communities was done in three habitats during summer and winter.

The only previous study done on the ant and termite fauna of TdR is that of Willis (1988). Several authors consider pitfall trapping to give a very reliable reflection of ant diversity and abundance in open habitats (Samways, 1983; Koen & Breytenbach, 1988; Andersen, 1991; Vorster, Hewitt & van der Westhuizen, 1992). However, Majer (1997) suggested that pitfall trapping alone "under-samples the complete ant community, and provides a skewed representation of the ant functional groups". The addition of alternative methods might therefore permit a more complete sampling of the ant fauna and more valid inter-habitat comparison. As a result, in this study pitfall trapping was complemented by soil sampling and quadrat sampling.

Furthermore, the abundance of mounds of *Trinervitermes trinervoides* in the three habitats was compared using line transect counts. These combined methods were designed to give an accurate picture of the relative availability of prey species in each habitat. In addition, within habitats, it would then be possible to determine the degree of spatial variation in addition to the temporal, seasonal variation in food availability of the aardvark.

Materials and Methods

1.Pitfall trapping

The ant and termite communities of TdR were sampled using three different techniques. The first, and most intensive method used was pitfall trapping. This was done in nine randomly selected sites within each habitat. Large sample sizes are required in sampling surveys in order to account for the patchiness in ant distribution and to increase efficiency of the capture of rare species (Adis, 1979; Abensperg-Traun & Steven, 1995; Miller & New, 1997; Hinkley & New, 1997) For this reason, the sample size employed was considerably greater than that of Willis (1988). The use of nine sites provided a statistically valid sample size, and enabled the convenient break up of trapping into groups of three areas per time. At each site, five traps were placed in a line, ten metres apart. The direction of the line was chosen randomly. Numerous small traps are more efficient than fewer larger traps (Abensperg-Traun & Steven, 1995), and each habitat was sampled with 45 traps. Three areas of each habitat were sampled simultaneously. A second set of three areas in each habitat was trapped a fortnight later and a third set a fortnight later still. This method reduced the potential effect of unusual weather conditions in the short term. Using the techniques explained above, each habitat was sampled to an equal intensity.

The pitfall traps were based upon those of Majer (1978). Rimmed Pyrex tubes of 16 mm diameter and 160 mm in length were inserted into sunken plastic piping, so that the lip of the tube was level with the surface. The depth of the trap reduces the chances of flooding, and escape of ants (Luff, 1975; Majer, 1978). The hole in which the traps were placed was made by hammering a steel stake of 16 mm diameter into the ground. Prior to the commencement of trapping, the pitfall traps were left for one week to reduce 'digging in' effects (Greenslade, 1973).

No problems of attraction are caused by the use of alcoholic preservatives (Greenslade & Greenslade, 1973; Robertson, pers. comm [1].) and consequently, 20 mm of three parts glycerol, and seven parts 80% ethanol solution was added to each trap, following the method used by Willis (1988). The traps were set between 16h00-18h00 and left for a total of five days, as suggested by Robertson (pers. comm.), before being emptied in the reverse order to which they were set. Sampling was done in both the summer and winter to enable a seasonal comparison.

1. H.G. Robertson, S.A. Museum, PO Box 61, Cape Town 8000.

2. Dig Sampling

A second method used was that of soil sampling. This was achieved by taking soil samples from digs in the rough proportions of an aardvark dig and collecting all ants and termites found within the soil for further identification. Again, sampling was done to the same intensity in nine randomly selected sites in each habitat. At each site four digs were made in a line 10 m apart, in a randomly chosen direction. Each dig was of the same proportions (10 cm deep X 10 cm wide X 15 cm long). The method was used to complement the pitfall trapping to ensure as complete a survey as possible, not as a comparison. As a result, ants or termites that walked into the dig during the extraction of the soil were also counted. Once extracted, the soil was sorted carefully on a white tray, using a fine paint brush and a teaser. Ants and termites where then collected using a pair of tweezers and stored in 80% alcohol in a plastic film case prior to identification. As with the pitfall trapping, sampling was done in both summer and winter to enable seasonal comparison. Note that the pitfall trapping and dig sampling were done over relatively wide areas, so as to permit comparison with faeces from a large sample of aardvark.

3 Quadrat Sampling

Quadrat sampling was done in the home range of each of the habituated animals in order to enable a specific comparison of the ants and termites available with the observed diets of these animals. This would help determine whether the study animals were selecting their food in proportion to its availability, or if they were being more selective. Quadrat sampling was the chosen technique because of its relatively quick and efficient application, and the use of a third sampling technique complemented the other methods used. This sampling was done in ten randomly chosen sites within each animals' home range. At each of the ten sites, three 1 m^2 quadrats were sampled in a line of random direction. This was done between 16h30-18h00 in the afternoon and again between 23h30-00h30 at night. This temporal separation ensured that both diurnal and nocturnal species were sampled and provided an invaluable description of the activity patterns of the aardvark prey species. Each quadrat was sampled for a period of five minutes. This standardisation was important because the number of species recorded is likely to increase with time as individuals walked inside the quadrat from outside. During the five minutes sampling time, the surface of the soil was overturned with a small trowel to aid in the search for ants and termites. As with pitfall trapping, quadrat sampling was undertaken in a staggered fashion so as to minimise the potential influence of weather conditions on the results. One quadrat was done at each of the 10 sites in an afternoon. The next day ten quadrats were done during the night session. The home range of the same aardvark was never sampled on consecutive days.

This method was used solely to record the presence of species, with no record being made of abundance. Ant and termite species were recorded as being present or absent. Unfamiliar species were collected and stored in a plastic film case in 80% ethanol for future identification.

4. Line Transect Sampling

Line transect sampling provides a very useful method for sampling immotile populations (Anderson, Laake, Crain, & Burnham, 1979). In this instance, the method was used specifically to provide a comparative quantification of the density of *T. trinervoides* mounds between habitats. As with pitfall trapping, the use of the same technique as Willis (1988) enables comparison of results obtained. The methods used in the line transect sampling are described in detail in Chapter Three. Nine transects, each 100 m long and 2.5 m wide were done in each habitat in summer and winter. The location and direction of the lines was random. The number of mounds and the proportion that were alive and that had been affected by aardvark activity, were recorded. The mounds were counted if over 50% of their base lay within the transect area.

Using these four methods, several specific questions were addressed:

1) Do the habitats vary in ant and termite species composition and abundance?

2) Do the three habitats differ significantly in the availability of species utilised by the aardvark?

3) What is the degree of spatial variation in ant and termite distribution within each habitat?

4) What is the temporal, seasonal variation in ant and termite abundance and diversity?

5) What are the activity patterns of the ant and termite species utilised by the aardvark?

In the following chapters, these parameters are related to various aspects of aardvark behaviour pertaining to feeding patterns and habitat choice.

RESULTS

Sampling Of Epigaeic Ant and Termite Species

A total of 44 ant species representing 17 genera, and six subfamilies, and two termite species were caught using all three methods.

1 Pitfall Trapping

A total of 6346 individuals were caught using pitfall trapping, comprising 38 ant species and two termite species. Table 1 lists the species caught and the numbers of each trapped in the three habitats. A total of 3872 individuals of 36 species were trapped in summer, whilst 2474 individuals of 24 species were caught in winter. The two termite species were caught in both summer and winter. The number of species caught in the various habitats in summer and winter is illustrated in Figure 1. More species were caught in summer than winter in each habitat. In addition, more species were caught in the grassland than the steep slopes, which in turn had a higher species count than the riverine habitat. This pattern held in both summer and winter. The steep slope and grassland habitats were very similar in terms of the number of species caught, whereas considerably fewer species were caught in the riverine habitat.

Figure 2 shows the numbers of individual ants and termites caught in the three different habitats in summer and winter. The habitats differ more in terms of abundance of individuals than in numbers of species. A far greater number of individuals were caught in the grassland habitat in both summer and winter than in the steep slopes, or in the riverine habitats. As with species numbers, fewest individuals were caught in the riverine areas. Over all three habitats more individuals were caught in summer than in winter.

The pitfall trap results were analysed in terms of Relative Importance (RI), or adjusted abundance. Adjusted abundance (AA) represents an adjustment of the total abundance of a species relative to its percentage occurrence, whilst the RI represents the % of the total AA made up by each species.

$$\text{Adjusted abundance (AA)} = A*(O/100)$$

$$\text{Relative Importance} = AA/\Sigma AA*(100)$$

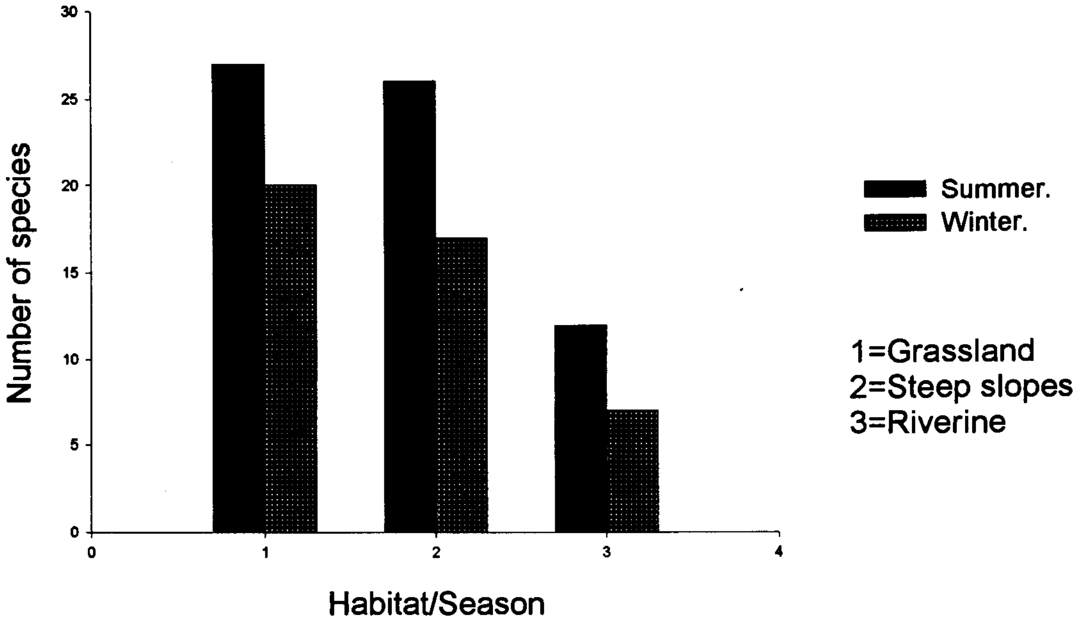


Figure 1. The number of species caught in pitfall traps in each of the study habitats in summer and winter

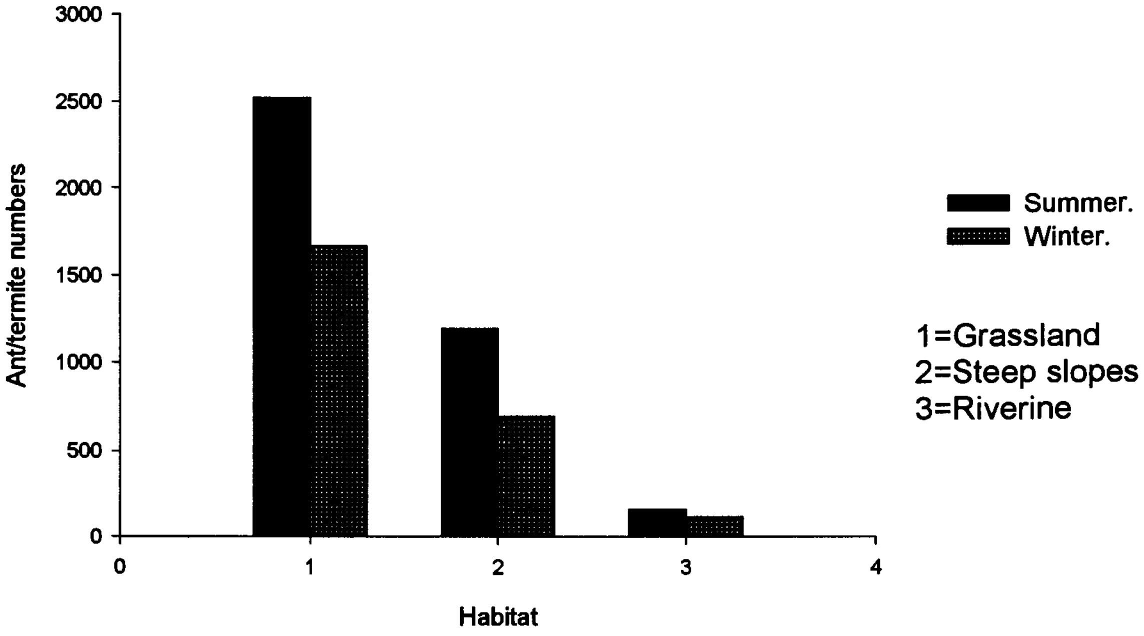


Figure 2. The numbers of ants and termites recorded in each habitat in summer and winter

Where A=abundance, and O=% occurrence. This removes some of the problems associated with analysing either of these two parameters separately. The use of % occurrence figures alone can be a problem because if two species occurred in all samples, they would have the same importance even if they occurred at greatly different abundances. In contrast, if abundance figures were used alone, then problems would arise when species occurred in very high numbers in very few pitfall traps. Such a species would then be seen as being a more important component of the community than a species that occurred in consistently high numbers across all traps.

Table 1. The AA of each of the species caught in pit fall traps in summer and winter.

ANT/TERMITE SPECIES	Gw	Gs	Sw	Ss	Rw	Rs	**Total**
Dolinchoderinae							
Linepthema humile	1.2	0	2	0	0.2	0	**3.4**
Techonomyrmex albipes	0	0	0	2.0	0	0	**2.0**
Formicinae							
Anoplolepis sp. 1	0	17	0	7	0	0.4	**24.4**
Anoplolepis custodiens	31	1111	0.4	255	0	7	**1404**
Anoplolepis steingroeveri	2	331	0	2	0	0	**335**
Camponotus fulvopilosus	0	0.2	0	0	0	0	**0.2**
Camponotus maculatus group	0.2	10	0	4	2	0	**16.2**
Camponotus nasutus	0	0.4	0	1	0	0	**1.2**
Camponotus simulans	0	0.2	0	0	0	0	**0.2**
Camponotus species.2 emarginatus	0	1	0	0	0	0	**1**
Lepisiota capensis	0	0.2	2	1	1	0	**4.2**
Lepisiota sp1	0.2	0	0.4	0	0	0	**0.6**
Lepisiota sp2	0	0	0	0	0	0.2	**0.2**
Myrmicinae							
Crematogaster melanogaster	0	0	3	26	0	0	**29**
Crematogaster sp1	0	0	2	1	1	0	**4**
Messor capensis	48	13	5	6	0	14	**86**
Monomorium albopilosum	958	217	485	225	48	12	**1945**
Monomorium havilandi	6	225	1	219	0	7	**458**
Monomorium notulum	2	12	2	7	0	0	**23**
Monomorium sp1	0.2	0	0	0	0	0	**0.2**
Monomorium sp2	1	0	1	0	0	0	**2**
Monomorium sp.1 salomonis gp	0	7	0	0.2	0	7	**14.2**
Monomorium willomorense	0	3	0.4	2	0.2	2	**7.6**
Ocymyrmex weilzecher	0	36	0.2	10	0	4	**50.2**
Pheidole sp .1	350	110	59	70	0.8	4	**593.8**
Pheidole sp. 2	0	0.2	0	0	0	3	**3.2**
Pheidole sp. 3	0	0.2	0	0	0	0	**0.2**
Tetramorium clunem	7	0	0	0.6	0	0	**7.6**
Tetramorium dichroum r	0	0	0	20	0	0	**20**
Tetramorium erectum	0.4	0.8	0.2	0.7	0	0	**2.1**
Tetramorium nr amaurum	0	0.2	0	0	0	0	**0.2**
Tetramorium sericeiventre	0.2	15	0.4	33	0	8	**56.6**
Tetramorium setigerum	1	2	2	3	0	0	**7**
Tetramorium sp. 1	0.2	0.2	0	0.3	0	0	**0.7**
Tetramorium sp. nr frigidum	0	0.4	0	8	0	0	**8.4**
Tetramorium sp. 2 simillum gp	0	8	0	0	0	0	**8**
Ponerinae							
Anochetus levaillanti	0	0.2	0	0.2	0	0	**0.4**
Pachycondyla ambigua	0	0	0	0.8	0	0	**0.8**
TERMITIDAE							
Hodotermitidae							
Hodotermes mossambicus	6	20	0	5	0	5	**36**
Nasutitermitinae							
Trinervitermes trinervoides	0	0	0	3	0	0	**3**

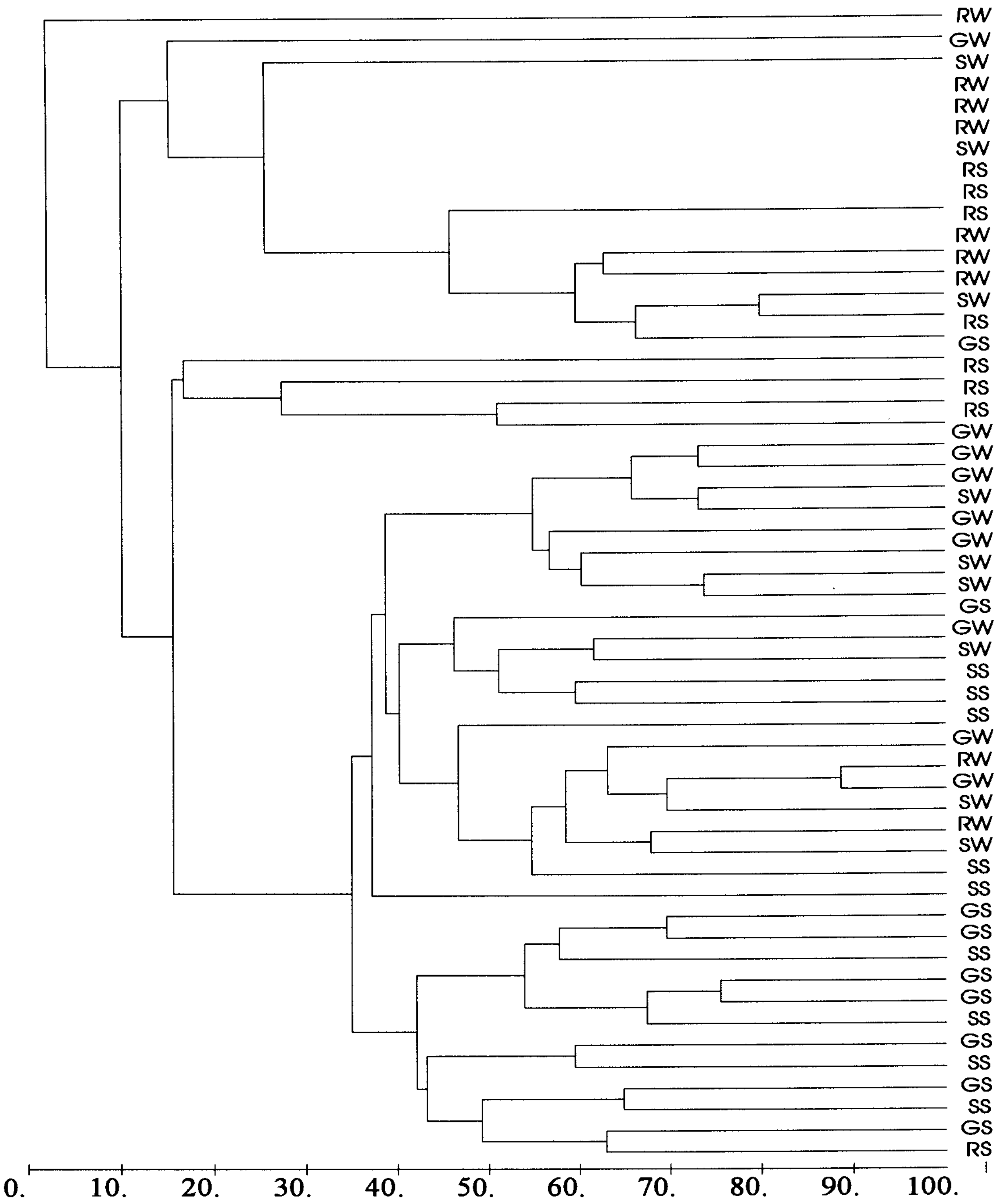
It can be seen from Table 1 that the Isoptera are outnumbered both in terms of species numbers and in abundance by the Formicidae. Of the Formicidae, the Myrmicinae is the dominant subfamily in terms of species numbers and abundance, followed by the Formicinae. These two subfamilies represent the vast majority of ant species present in the area. The most abundant species recorded were *M. albopilosum* with an AA of 1945 followed by *A. custodiens* at 1404, and finally *Pheidole* sp. 1 at 593.8. The ant and termite communities of the three habitats in the two seasons were compared in terms of the AA's of the various species, using a two-way Anosim (Table 2).

Table 2. Two-way Anosim of the AA's of the pitfall trap results in the three habitats and two seasons. G=Grassland, SS=Steep slopes, R=Riverine. Significant statistics marked *.

Groups Compared	No. of permutations	Significant Statistics	Global (R)	P Value
Summer Vs Winter	5000	0	0.221	0.0%*
Habitats	5000	0	0.323	0.0%*
G Vs SS	5000	278		5.6%
SS Vs R	5000	0		0.0%*
G Vs R	5000	6		0.0%*

There were highly significant differences both between the seasons and between the habitats (Table 2). However, the pairwise tests indicated that the difference between the grassland and steep slope habitats was insignificant. There were significant differences between the steep slope and riverine habitat, and between the grassland and the riverine habitat. Figure 3 shows a dendrogram of the results. The dendrogram shows quite clear grouping of the riverine samples, whilst the grassland and steep slope samples remain interspersed, reflecting the statistical results. In addition, grouping of the summer and winter samples is evident for samples from each habitat. Figure 4 shows the MDS plot of the pitfall data. This figure shows the same pattern, with the riverine samples being clustered discreetly. In contrast the grassland and steep slope samples show marked interspersion. It is evident that there is greater separation between season than habitat when considering the steep slope and grassland samples.

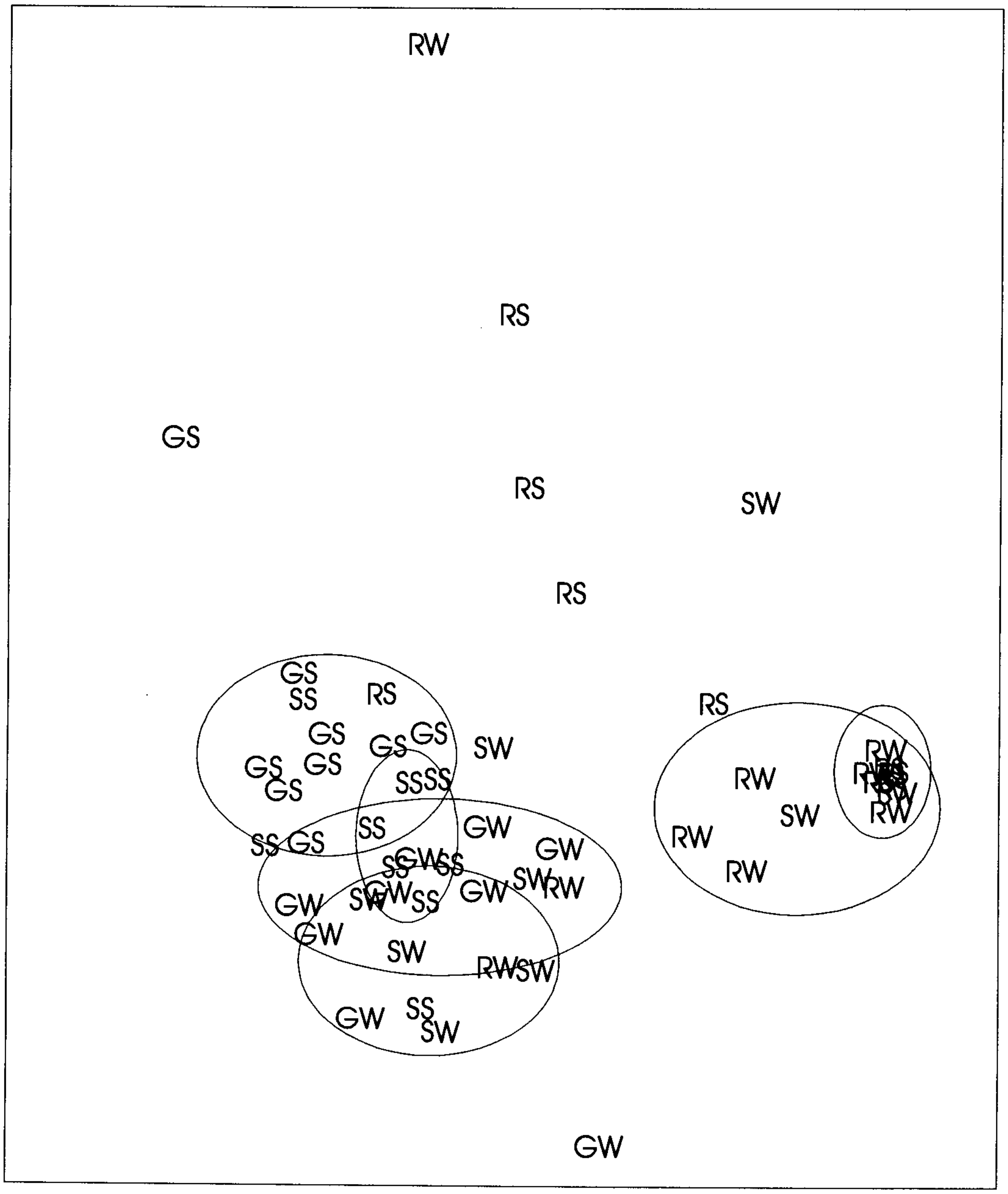
In the grassland habitat, a total of 32 species were caught in the two seasons (see Table 1). In winter, 1665 individuals of 18 different species were recorded, in contrast to the 2520 individuals of the 28 species recorded in summer. Six of the recorded species were unique to this habitat: *Monomorium* sp. 1, *T. amaurum, T. simillum, Camponotus. sp. 2. emarginatus gp.* and *Camponotus. simulans.* In winter, *M. albopilosum* had the highest RI value (67.8%), followed by *Pheidole* sp. 1 (24.7%) and *M. capensis* (3.4%) (Table 1). The three most abundant species made up 91.0% of the total numbers caught. Forty two percent of the least common species had RI's of less than one, indicating that they occurred in very few traps, in very low numbers. *A. custodiens* had an RI of only 2.2%. In summer, *A. custodiens* was by far the most important species (RI=51.8%), followed by *A. steingroeveri* (15.5%) and *M. havilandi* (10.6%).



NB. GW=Grassland winter, GS=Grassland summer, SW=Steep slope winter, SS=Steep slope winter, RW=Riverine winter, RS=Riverine summer

Figure 3

The dendrogram derived from the species within each of the nine pitfall samples taken in each season and habitat



Stress 0.11

NB. GW=grassland winter, GS=Grassland summer, SW=Steep slope winter
SS=Steep slope summer, RW=Riverine winter, RS=Riverine summer

Figure 4

The ant and termite communities recorded in the three habitats in summer and winter as suggested by pitfall trapping.

In summer, the three most abundant species made up 71.7% of the total numbers caught. Only 34% of the species recorded had RI's of less than one in this season.

In the steep slope habitat, a total of 31 species were caught in the two seasons. Seventeen species and 693 individuals were recorded in winter, compared to 27 species and 1193 individuals in summer. Five species were unique to this habitat. The winter samples in the steep slope habitat were dominated by the same two species as in the grassland habitats. *M. albopilosum* was by far the most abundant species, with a RI of 85.0%, followed by *Pheidole* sp. 1 (10.9%). In winter, the three most abundant species made up 90.9% of the total numbers, with 50% of the species having a RI of less than one. *A. custodiens* was very scarce during winter (0.1%). In summer, the most abundant species was *A. custodiens*, with a RI of 28.1%, followed by *M. havilandi* at 23.9%. In summer the three most abundant species made up 71.7% of the total numbers. Only 22% of species had RI's of less than one.

In the riverine habitat a total of 17 species were caught. Of these, 13 species and 159 individuals were caught in summer, in contrast to seven species and 116 individuals in winter. In winter, the most abundant species was *M. albopilosum* (89.3%), followed by *C.amponotus maculatis* (3.3%). In summer, the dominant species was *M. capensis* (19.2%), followed by *M. albopilosum* (16.2%), and *A. custodiens* (9.5%). As in the other habitats, the summer catches were less numerically divergent than the winter samples. In winter, the three most abundant species made up 91.4% of the total numbers caught, whereas in summer this figure was only 50.3%. *M. albopilosum* was the dominant species in every habitat during winter. In summer, *A. custodiens* was the most abundant species in the grassland and steep slope habitats and a significant constituent of the riverine samples. In each of the habitats, the dominant species made up a larger proportion of the total numbers caught in winter than in summer. In summer, a greater number of species made significant contributions to the total ant fauna.

The pitfall trapping results were analysed specifically in terms of the AA of the five most important species in the diet of the aardvark, as indicated in Chapter 2 (see Table 3).

Table 3. A two-way Anosim comparing the AAs of the species utilised by the aardvark between habitats and seasons. G=Grassland, SS=steep slope, R=Riverine. Significant statistics marked *

Groups Compared	No. of permutations	Significant Statistics	Global (R)	P Value
Summer Vs Winter	4000	5	0.145	0.1%*
Habitats	4000	0	0.366	0.0%*
G Vs SS	4000	308		10.8%
SSVs R	4000	0		0.0%*
G Vs R	4000	0		0.1%*

As with the test done on all species, there were significant differences between the habitats and the seasons in terms of the ant/termite species known to be utilised by the aardvark. However, once again there was no significant difference between the ant/termite community of the grassland and steep slope habitats. All other habitat comparisons showed highly significant differences. The AA of the species utilised by the aardvark in the three habitats and in the two seasons is illustrated in Table 4.

Table 4. The RI of each of the species in the three habitats in summer and winter, with the sum proportion of the total AA made up by species known to be utilised by the aardvark.

Species	GW	GS	SW	SS	RW	RS
A. custodiens	2.2	51.9	0.1	28.9	0	9.5
A. steingroeveri	0.1	15.5	0	0.2	0	0
C. fulvopilosus	0	0.1	0	0	0	0
C. maculatis gp	0.1	0.4	0	0.4	1.8	0
H. mossambicus	0.4	0.9	0	0.5	0	4.6
M. albopilosum	67.8	10.2	85.0	24.6	48.2	11.6
M. havilandi	0.4	10.5	0.8	24.0	0	9.5
M. capensis	3.4	0.6	0.9	5.6	0	19.2
Pheidole species. 1	24.7	5.1	10.9	7.6	0.8	5.3
T. trinervoides	0	0	0	0.4	0	0
	98.7%	84.7%	97.0%	62.3%	94.1%	56.5%

In winter, 98.7% of the individuals caught in the grassland were of species utilised by the aardvark, compared to 84.7% in summer (Table 4). These species were caught in greater numbers and in a greater proportion of traps in the grassland than in any other habitat. An exception to this rule was *T. trinervoides*, which was only recorded in the steep slope habitat. The species utilised by the aardvark contributed more to the total catches in winter than in summer in each of the three habitats, a much greater number of non-utilised species having been caught in summer. However, although the RI of the utilised species was greater in winter, greater numbers were actually caught in summer. There were some exceptions to this rule, however, an example being the greater number of *M. capensis* caught in grassland in winter than summer.

2. Dig Sampling

Dig sampling yielded a total of 23 ant species and two termite species, including two species not recorded by the other two methods *(Lepisiota* sp.4 and *Plagiolepis* sp*)*. Of these, 14 species were caught in winter, whilst 17 were recorded in summer. Figure 5, shows the number of species collected using this method, in each habitat in summer and winter. The greatest number of species was recorded in the grassland in both seasons, followed by the steep slopes and finally the riverine areas. In addition, the majority of species had a higher % occurrence in the grassland habitat than in the steep slope areas, which in turn were generally more frequent than in the riverine areas. More species were collected in

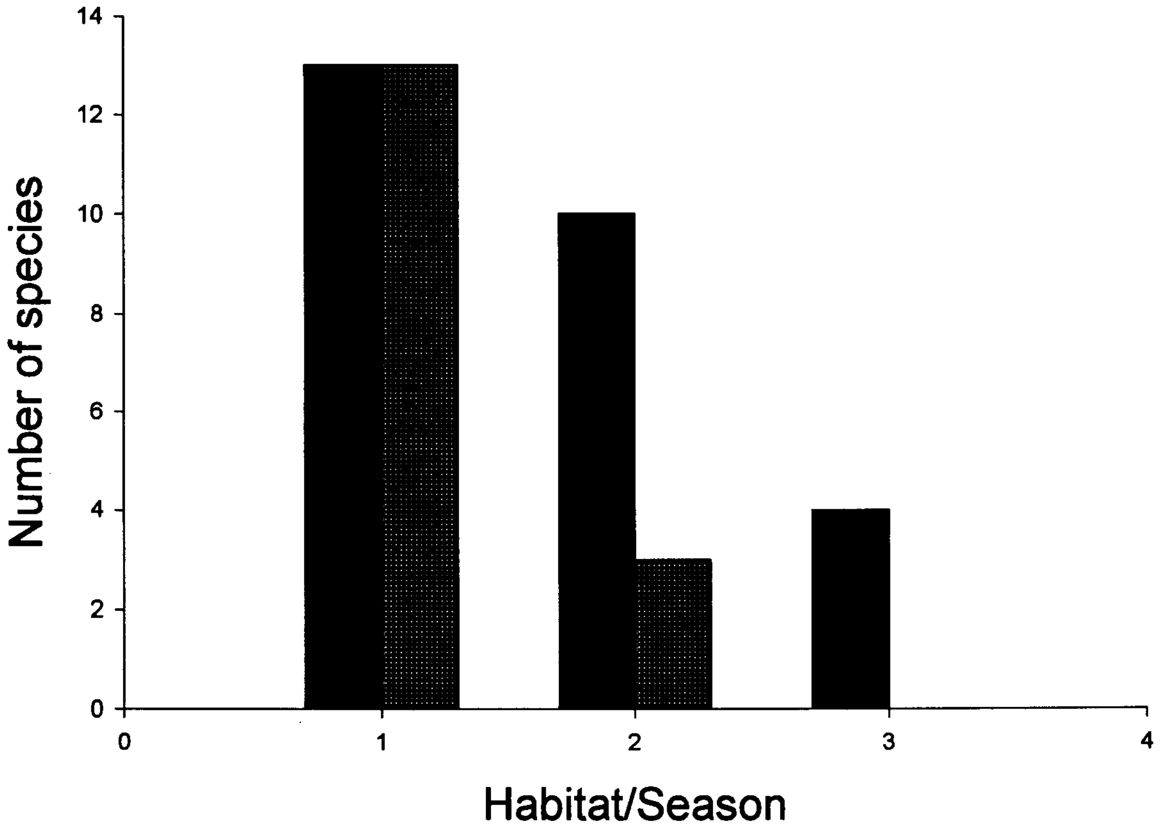


Figure 5. The number of species collected during dig sampling in the three study habitats in summer and winter

1=Grassland
2=Steep slopes
3=Riverine

■ Summer
▨ Winter.

summer than winter in the riverine and steep slope areas, whilst equal numbers were caught in the two seasons in the grassland areas. In the riverine habitat, no ants or termites were collected at all in winter.

The discontinuous point sampling nature of digs sampling meant that abundances could not be estimated with any accuracy and so the findings are described in terms of the occurrence % of the various species. Table 5 shows all of the species caught and their occurrence % in each habitat from the dig sampling.

Table 5. The occurrence % of all of the species caught in each habitat in the dig samples.

	GW	GS	SW	SS	RW	RS
Formicidae						
Anoplolepis sp. 1	5.5	0	0	0	0	0
Anoplolepis custodiens	11.1	16.6	0	8.3	0	0
Anoplolepis steingroeveri	5.5	2.7	0	0	0	0
Camponotus fulvopilosus	0	0	0	2.7	0	0
Camponotus vestitus	0	5.5	0	0	0	0
Lepisiota capensis	2.7	5.5	0	5.5	0	0
Lepisiota sp.1	5.5	0	0	0	0	0
Lepisiota sp. 4	0	8.3	0	0	0	0
Plagiolepis species.	0	2.7	0	0	0	0
Myrmicinae						
Crematogaster melanogaster	0	0	11.1	0	0	0
Messor capensis	5.5	16.6	0	0	0	0
Monomorium albopilosum	11.1	25	16.6	16.6	0	2.8
Monomorium havilandi	0	8.3	0	2.7	0	0
Monomorium notulum	2.8	0	0	0	0	0
Monomorium sp. 2	2.8	0	0	0	0	0
Monomorium sp. salomonis gp	0	8.3	0	0	0	8.3
Monomorium willowmorensis	0	5.6	0	0	0	2.8
Ocymyrmex weilzecher	0	0	0	0	0	2.8
Pheidole sp. 1	0	0	5.5	0	0	0
Tetramorium dichroum r	2.8	0	0	0	0	0
Tetramorium sericeiventre	0	0	0	2.8	0	0
Tetramorium sp1	2.8	0	0	0	0	0
Ponerinae						
Plectronectena mandibularis	0	0	2.8	2.8	0	0
TERMITIDAE						
Hodotermitidae						
Hodotermes mossambicus	2.8	2.8	0	2.8	0	0
Nasutitermitinae						
Trinervitermes trinervoides	2.8	2.8	5.5	8.3	0	0
Average % Occurrence	**2.5**	**4.4**	**1.3**	**2.1**	**0.7**	**0.6**

These results contrast with those from the pitfall trapping. The species that did occur in the dig samples occurred much less frequently, as indicated by the average occurrence % for all of the species in each habitat. In addition, the RI of the various species differed between the two methods.

In the grassland habitat, the most frequently occurring species in winter were *A. custodiens* and *M. albopilosum*, both of which occurred in 11.1% of the samples. Of the species utilised by the aardvark, the most frequently occurring species in summer were *M. albopilosum* (25%), *M. capensis* (16.6%) and *A. custodiens* (16.6%). The low frequency of occurrence of *A. steingroeveri* (2.7%) was due to the fact that high numbers caught were from one sample. The overall average occurrence % of the various species was highest in the grassland habitat. Within the grassland, the average occurrence % was higher in summer than in winter.

In the steep slope habitat in winter, only five species were recorded. Of these, *M. albopilosum* was the most frequently recorded species (16.6%). In contrast, nine species were caught in summer in this habitat, five of which were prey species of the aardvark. The most widely occurring species were *M. albopilosum* (16.6%), *A. custodiens* (8.3%) and *T. trinervoides* (8.3%), indicating that the importance of *T. trinervoides* was greater than that suggested by the pitfall trapping.

In the riverine habitat, nothing was caught in winter, whilst four species were recorded during summer, the most frequently occurring of which was *M. salomonis* (8.3%). The only aardvark prey species to be recorded was *M. albopilosum* (2.8%).

The ant and termite communities of the various habitats and the two seasons were compared using a two- way Anosim, in terms of the occurrence % of each of the recorded species (see Table 6).

Table 6. A two-way Anosim on the occurrence % of the various species between the different habitats and seasons. Significant statistics marked *.

Groups Compared	No. of permutations	Significant statistics	Global (R)	P Value
Summer Vs Winter	5000	2208	0.001	44.2%%
Habitats	5000	0	0.189	0.0%*
G Vs S	5000	763		15.3%
S Vs R	5000	0		0.0%*
G Vs R	5000	0		0.0%*

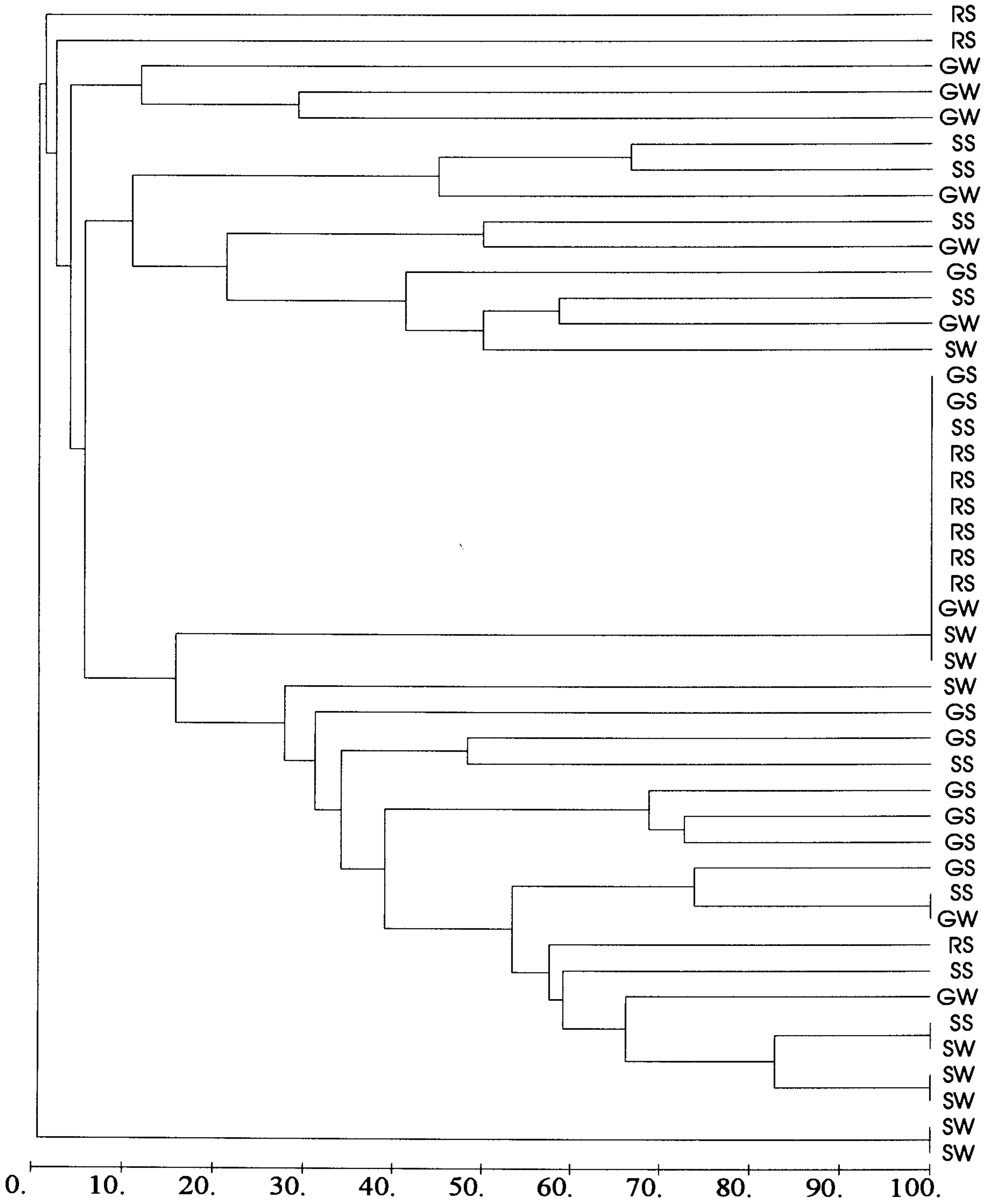
There was a highly significant difference between the habitats (Table 6). The pairwise comparisons revealed the same pattern shown by the pitfall trapping: significant differences between the grassland and riverine and steep slope and riverine, but not between the grassland and steep slope habitats.

There was no significant difference between the seasons in terms of the occurrence % of the various species in the dig samples. Although far lower numbers were caught in winter, the species tended to occur in a similar proportion of traps in both seasons. The use of occurrence % in data description tended to mask differences between the habitats in this way and, in the case of the steep slope and grassland habitat, render the differences insignificant.

Figure 6 represents a dendrogram of these results. Grouping of the riverine samples is evident, whilst the samples from the other two habitats are more interspersed with one another. The extreme clumping in the centre of the graph is caused by the fact that these samples yielded no ants or termites. Each of these samples was given an abundance of one ant of the most common species, so as to permit their inclusion on the plot. Figure 7 shows the MDS plot of the dig sample results. This plot is characterised by the extreme clustering of the riverine samples and interspersion of the grassland and steep slope samples. The samples from the two seasons in each habitat are generally interspersed.

3. Quadrat Sampling

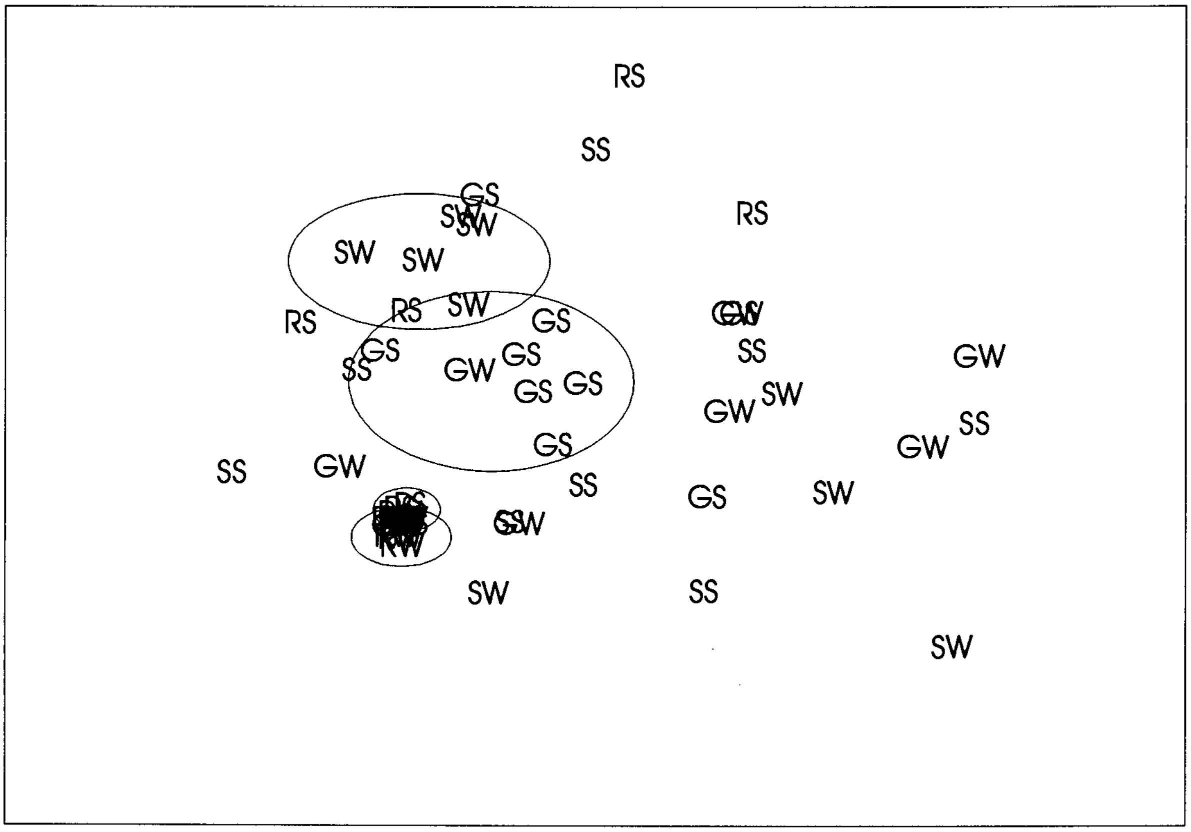
Twenty four ant species, and two termite species were recorded using this method, including three species not recorded by the other sampling techniques *(Aenictus rotundatatus, Camponotus sp. 3 emarginatus gp* and *Meranoplus spininodis.).* Twenty three species were recorded during day time sampling, compared to 19 at night. Table 7 lists the species recorded and their occurrence % at night and day in each of the home ranges.



NB. GW=Grassland winter, GS=Grassland summer, SW=Steep slope winter
SS=Steep slope summer, RW=Riverine winter, RS=Riverine summer

Figure 6.

The dendrogram derived from the species within each of the nine dig samples taken in each season and habitat



Stress 0.15

NB. GW=Grassland winter, Gs=Grassland summer, SW=Steep slope winter,
SS=Steep slope winter, RW=Riverine winter, RS=Riverine summer

Figure 7

The ant and termite communities of the three habitats in summer and winter as suggested by the dig samples

Table 7. The average occurrence % of each of the species recorded in the day and night quadrats.

ANT/TERMITE SPECIES	Mean % Occurrence DAY	Mean % Occurrence Night
Aenictinae		
Aenictus rotundatus	3.3	1.1
Formicidae		
Anoplolepis custodiens	26.6	7.7
Anoplolepis steingroeveri	15.5	6.6
Camponotus fulvopilosus	1.1	54.4
Camponotus species.2 emarginatus gp	3.3	24.4
Camponotus species. 3 emarginatus gp	0	1.1
Camponotus vestitus	1.1	0
Lepisiota capensis	0	2.2
Myrmicinae		
Crematogaster melanogaster	3.3	5.5
Meranoplus spininodis	1.1	3.3
Messor capensis	11.1	1.1
Monomorium albopilosum	5.5	26.6
Monomorium havilandi	10	6.6
Monomorium notulum	61.1	0
Monomorium willowmorense	13.3	0
Ocymyrmex weilzecher	5.5	0
Pheidole sp. 1	1.1	30
Pheidole sp. 2	13.3	1.1
Tetramorium erectum	0	1.1
Tetramorium dichroum	1.1	0
Tetramorium nr frigidum	3.3	7.7
Tetramorium sericeiventre	1.1	0
Tetramorium sp. 2 simillum gp	8.9	7.8
Ponerinae		
Plectronectena mandibularis	1.1	0
TERMITIDAE		
Hodotermitidae		
Hodotermes mossambicus	7.8	8.8
Nasutitermitinae		
Trinervitermes trinervoides	3.3	1.1

Ten of the 26 species recorded in the quadrat samples were predominantly nocturnal, whilst the remaining 15 were mainly diurnal (Table 7). Some species showed large differences in the occurrence % in the day and during the night. *Camponotus fulvopilosus*, *Camponotus sp. 2 emarginatus* and *Pheidole sp. 1* were markedly nocturnal, whereas *A. custodiens* and *M. notulum* were very diurnal in their activity. Significantly, most of the species of major importance in the diet of the aardvark were predominantly diurnal in their activity, with the exception of *M. albopilosum*.

Sampling in the home range of study animal A3 yielded the highest species count at 20, followed by A1 at 18, and finally A2 at 17. Higher species counts were found in the day in the home ranges of A1 and A3 than at night, whereas the opposite was true for A2. The number of species caught in each home range during the day and at night is illustrated on Figure 8. The ant and termite communities in the home ranges of the three study animals in the day and at night were compared using a two-way Anosim (see Table 8).

Table 8. The results of a two-way Anosim done on the quadrat results from the different home ranges in the day and at night. Significant statistics marked *.

Groups Compared	No. of permutations	Significant Statistics	Global (R)	P Value
Day Vs Night	5000	0	0.812	0.0%*
Animal	5000	0	0.229	0.0%*
A1 Vs A2	5000	2		0.1%*
A2 Vs A3	5000	0		0.0%*
A1 Vs A3	5000	9		0.2%*

There was a highly significant difference between the diurnal and nocturnal activity of ants and termites (Table 8). In addition, there was a highly significant difference between the ant and termite activity between the various home ranges. Figure 9 shows a dendrogram plot of the quadrat results Clear clustering of both home range and season groups is apparent. The MDS plot of these results is not included. The large number of samples clutter the diagram making interpretation impossible.

4. Transect Sampling: The Abundance Of *T. trinervoides* Mounds.

Table 9 summarises the numbers and characteristics of the mounds recorded in each habitat. The data represents the average findings of the transect sampling done in summer and winter.

Table 9. The number, number per Ha, size and proportion of mounds alive as determined from transects in summer and winter.

	Number	Number/Ha	Number Alive	Height
Grassland	27	120	22	17.3
Steep slope	37.5	166.6	27.5	32.6

The highest number of mounds (58.1%) was recorded in the steep slope habitat, followed by the grassland (41.9%) habitat. No mounds were recorded in the riverine transects. A t-test was carried out to compare the number of mounds between the steep slope and grassland habitats. There was no significant difference in the number of mounds between habitats (T=279.5; P=0.093).

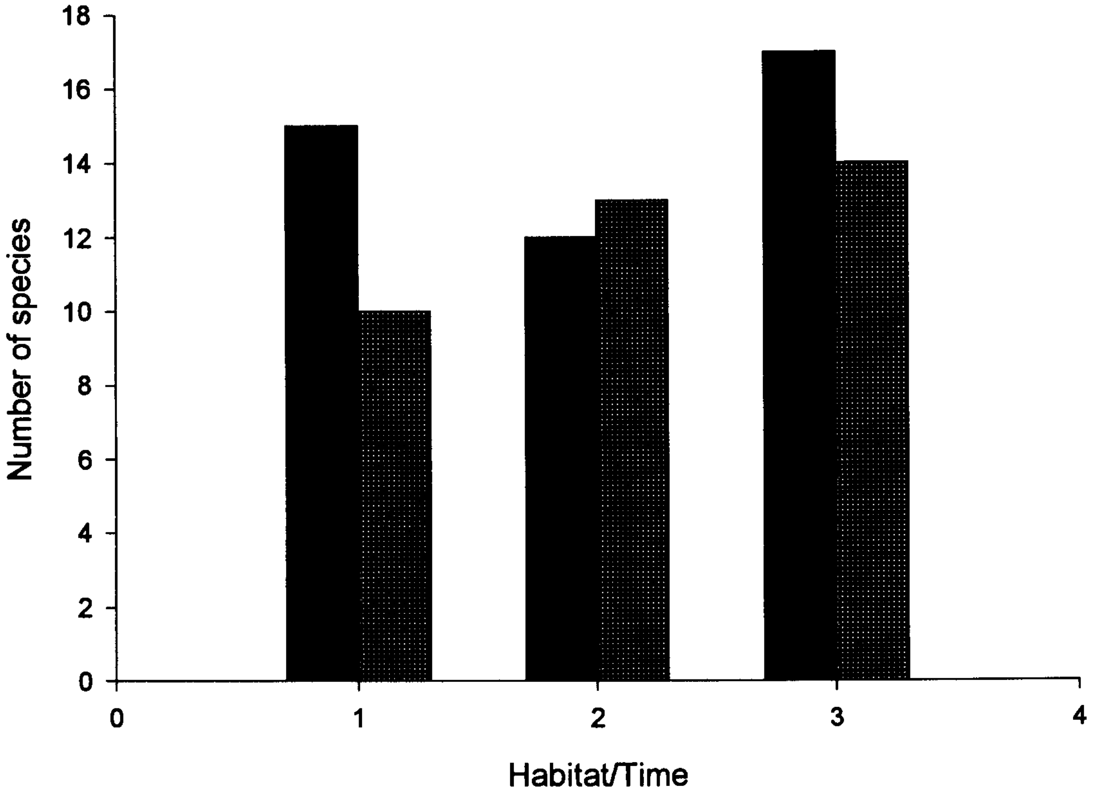
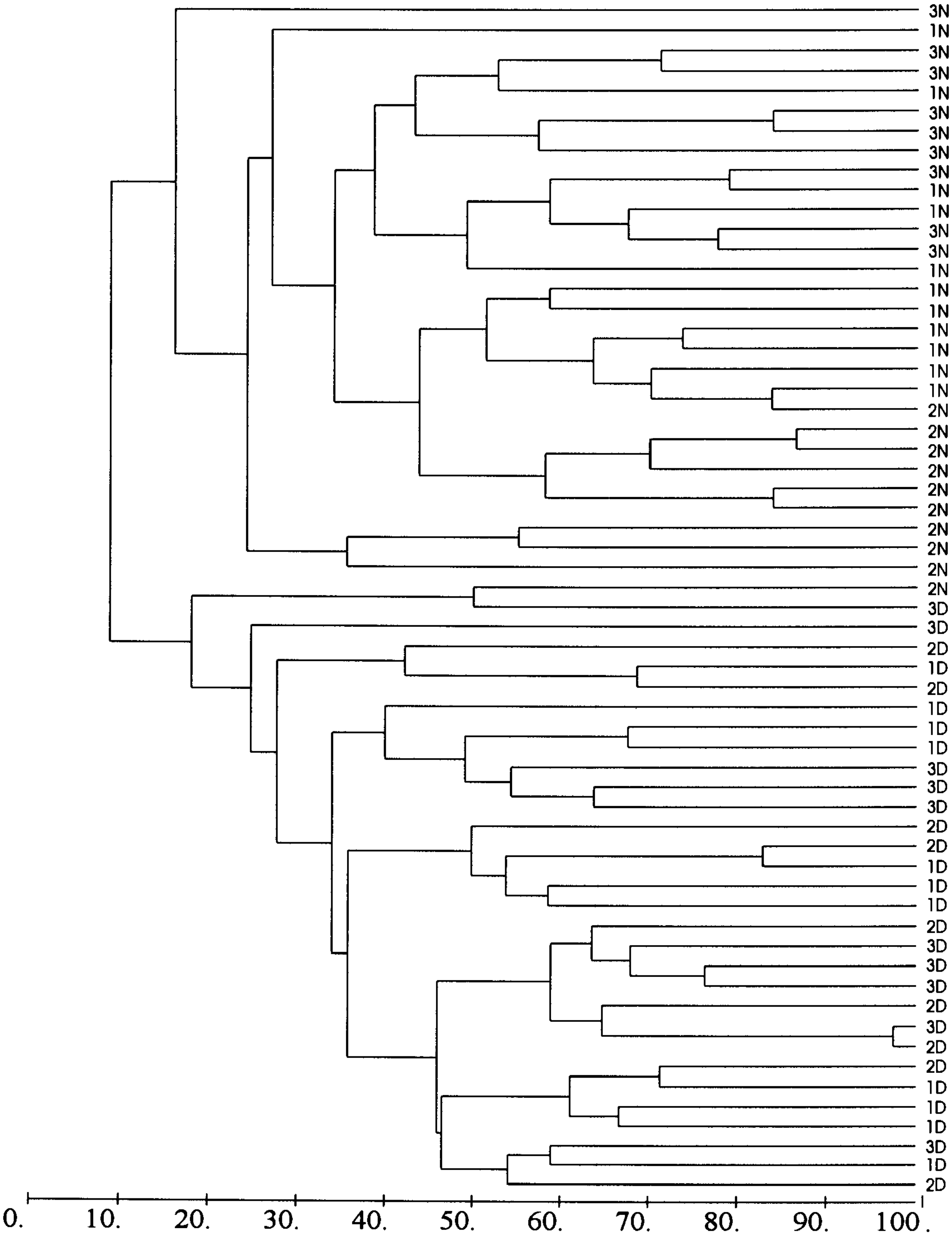


Figure 8. The number of nocturnal and diurnal species recorded in quadrat samples in each of the home ranges



NB. The numbers denote the three home ranges, whilst 'D' and 'N' denote day and night.

Figure 9.

The diurnal and nocturnal ant and termite communities in the home ranges of the three study animals, as suggested by quadrat sampling

The proportion of *T. trinervoides* mounds that were alive was compared between the habitats. A greater proportion of the mounds in the grassland habitat were alive (81.4%) than in the steep slope habitat (62.5%). However, when a t-test was conducted on these results, there was no significant difference in the proportion of mounds alive between the two habitats (T=185.00; P=0.062).

Finally, the height of the *T. trinervoides* mounds in the various habitats was recorded, in response to the finding that population size is directly correlated with this parameter (Adam, 1993). In both summer and winter, steep slope mounds were larger on average than those recorded in the grassland habitat. A t-test was carried out to compare mound size between habitats. There was a significant difference between the habitats (t=4.883; df26; P<0.001).

5. Overall Ant and Termite Diversity.

A total of 44 ant species representing five sub families and 17 genera, and two termite species were recorded using the sampling techniques mentioned above. The grassland habitat yielded 40 species, or 90.9% of the total species count. The steep slope habitat had the next highest diversity, with 34 species (77.3%) recorded. The riverine areas had by far the lowest species diversity, with only 19 species (41.3%) being recorded.

Fifteen of the 46 species recorded (32.6%) were recorded in all three of the habitats including most of the species commonly utilised by aardvark. *A. steingroeveri* and *T. trinervoides* were exceptions to this, however, not being found in the riverine areas. Twenty-one of the species (45.6%) occurred in two of the three habitats, whilst nine species (19.6%) showed strong habitat selection, occurring in one habitat type. All of the species occurring in one habitat type only occurred in the grassland. The termite species were poorly sampled by all three methods. However, transect sampling indicated that similar numbers of *T. trinervoides* mounds occurred in the steep slope and grassland habitats. The abundance and diversity of ants and termites was greater in summer than winter. Whilst 48.8% of the species were active in both seasons, 93.3% were active in summer, whilst 71.1% were active in winter. Twenty nine percent of the species were active only during summer, whilst 8.8% were active only during the winter period.

The three sampling methods gave very different representations of the ant and termite fauna. Table 10, highlights the methods responsible for recording each species.

Table 10 The species caught in all of the sampling methods, and those specific to one sampling method (donated by *).

ANT/TERMITE SPECIES	Pitfall	Digs	Quad
Aenictinae			
Aenictus rotundatus (Mayr)			*
Dolinchoderinae			
Linepthema humile (Mayr)	*		
Techonomyrmex albipes (Smith)	*		
Formicidae			
Anoplolepis sp. 1	*	*	
Anoplolepis custodiens (Smith)	*	*	*
Anoplolepis steingroeveri (Forel)	*	*	*
Camponotus fulvopilosus (De Geer)	*	*	*
Camponotus maculatus group (Fabricius)	*		
Camponotus nasutus (Emery)	*		
Camponotus simulans (Forel)	*		
Camponotus sp.2 emarginatus gp	*		*
Camponotus sp. 3 emarginatus gp			*
Lepisiota sp1	*	*	
Lepisiota sp2	*		
Lepisiota sp. 4		*	
Lepisiota capensis (Mayr)	*	*	*
Plagiolepis sp 1	*	*	*
Myrmicinae			
Crematogaster melanogaster (Emery)	*	*	*
Crematogaster sp1	*		
Messor capensis (Mayr)	*	*	*
Meranoplus spininodis (Arnold)			*
Monomorium albopilosum (Emery)	*	*	*
Monomorium havilandi (Forel)	*	*	*
Monomorium notulum (Forel)	*	*	*
Monomorium sp1	*		
Monomorium sp2	*	*	
Monomoriumsp.1 salomonis gp	*	*	
Monomorium willomorense (Bolton)	*	*	*
Ocymyrmex weilzecher (Emery)	*	*	*
Pheidole sp1	*	*	*
Pheidole sp2	*	*	*
Pheidole sp3	*		
Tetramorium clunem (Forel)	*		
Tetramorium dichroum (Santschi)	*	*	*
Tetramorium erectum (Emery)	*		*
Tetramorium nr amaurum (Bolton)	*		
Tetramorium sericeiventre (Emery)	*	*	*
Tetramorium setigerum (Mayr)	*		
Tetramorium sp1	*	*	
Tetramorium sp.nr frigidum (Arnold)	*		*
Tetramorium sp. 2 simillum gp	*		*
Ponerinae			
Pachycondyla ambigua (Andre)	*		
Plectronectena mandibularis (Smith)		*	*
Anochetus levaillanti (Emery)	*		
TERMITIDAE			
Hodotermitidae			
Hodotermes mossambicus (Hagen)	*	*	*
Nasutitermitinae			
Trinervitermes trinervoides (Sjostedt)	*	*	*

Seventeen of the above species were recorded by all of the three sampling techniques, including all of the species of major importance in the diet of aardvarks. Eleven species were recorded only in pitfall traps. Two species were found only in dig samples, and three species were recorded only in quadrats. The three techniques gave very different results in general. Tables 11 and 12 show some indication of this by highlighting how different species dominated depending upon the technique used.

Table 11. The two most important species in each habitat when using each of the methods in winter.

		GRASSLAND	STEEP SLOPE	RIVERINE
PFT	1	*M. albopilosum*	*M. albopilosum*	*M. albopilosum*
	2	*Pheidole sp. 1*	*Pheidole sp. 1*	*C. maculatis*
DIGS	1	*M. albopilosum*	*M. albopilosum*	*Zero caught*
	2	*A. custodiens*	*T. trinervoides*	*Zero caught*

Table 12. The two most important species in each habitat when using each of the methods in summer.

		GRASSLAND	STEEP SLOPE	RIVERINE
PFT	1	*A. custodiens*	*A. custodiens*	*M. capensis*
	2	*M. albopilosum*	*M. albopilosum*	*M. albopilosum*
DIGS	1	*M. albopilosum*	*M. albopilosum*	*M. salomonis*
	2	*M. capensis*	*T. trinervoides*	*M. albopilosum*
QUAD	1	*M. albopilosum*		
	2	*M. capensis*		

There was large variation in the dominant species between and within methods, between habitat and season. *M. albopilosum* was the species dominant in most combinations of sampling method, season and habitat. *T. trinervoides* was only caught in significant numbers in the dig samples and was significant in the steep slope samples. The ant communities suggested by the pitfall traps and dig samples in the various habitats in winter and summer were compared in terms of the percentage occurrence of the various species, using two-way Anosims.

Table 13. A two-way Anosim comparing the occurrence % of the various species recorded in pit fall traps and dig samples in winter. G=Grassland, SS=Steep slope, R=Riverine. Significnt statistic marked *

Groups Compared	No. of Permutations	Significant statistics	Global (R)	P Value
Pitfalls Vs Digs	5000	0	0.251	0.0%*
Habitat	5000	0	0.227	0.0%*
G Vs SS	5000	69		1.4%*
G Vs R	5000	0		0.0%*
SS Vs R	5000	30		0.6%*

Table 13 shows that there was a significant difference between the methods and the habitats. In contrast to the pitfall analysis, there was a significant difference between the steep slope and grassland communties according to the dig sampling.

Table 14. A two way Anosim comparing the pitfall trap and dig samples in summer. G=Grassland, SS=Steep slope, R=Riverine. Significant statistics marked *.

Groups Compared	No. of permutations	Significant statistics	Global (R)	P Value
Pitfalls Vs Digs	5000	0	0.386	0.0%*
Habitat	5000	0	0.283	0.0%*
G Vs SS	5000	50		1.0%*
G Vs R	5000	0		0.0%*
SS Vs R	5000	0		0.0%*

Again, there was a significant difference between the ant and termite communities between the habitats and between the two methods.

Pitfall trapping was the most effective sampling technique, yielding 38 ant species (84.4% of the total number) and two termite species. This was followed by the quadrat sampling, which yielded 23 ant species (51.1%) and two termite species, and finally the dig sampling, which produced 22 ant species (48.8% of the total caught) and both termite species. However, because quadrat sampling was only done in the summer study period, a better comparison of species counts comes from the summer results. When considering species number from the summer period only, the superiority of quadrat sampling over dig sampling in terms of species numbers caught was enhanced. Figure 10 shows the number of species recorded in summer when using each of the three sampling techniques.

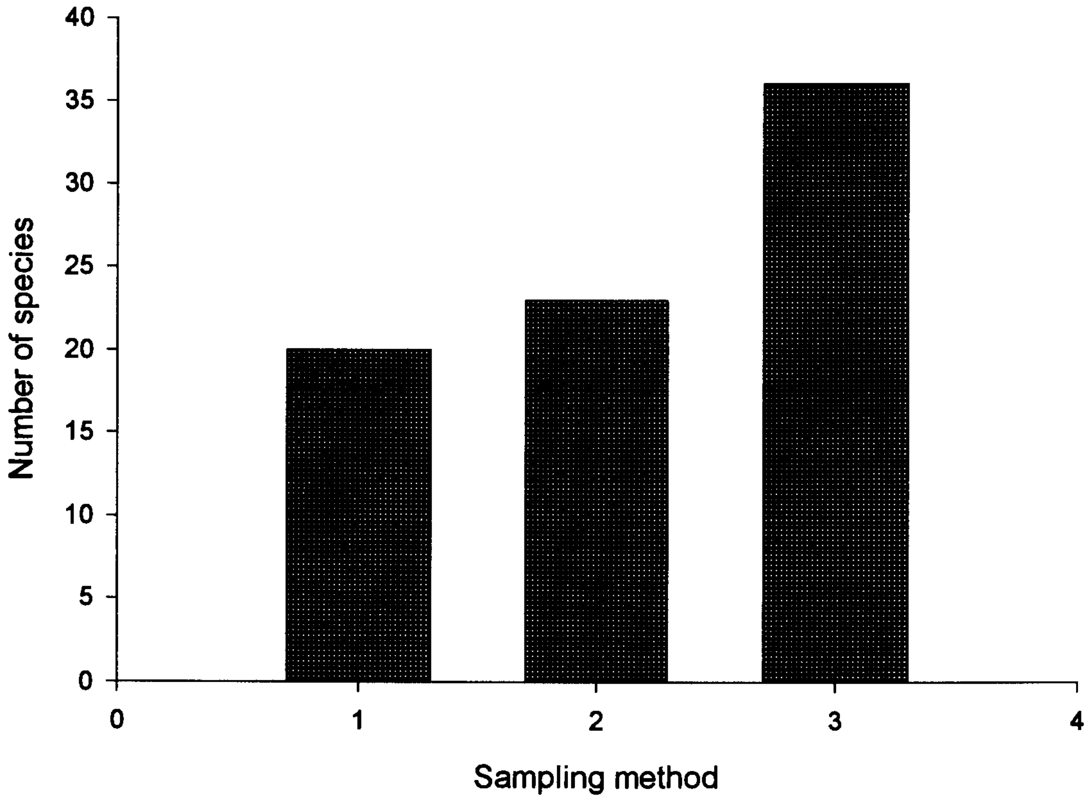


Figure 10. The total number of species recorded in summer using three sampling methods

1=Dig sampling
2=Quadrat sampling
3=Pit fall trapping

DISCUSSION

Ant and Termite Sampling

Ant and termite sampling was extremely successful, yielding high species diversity and abundances. Very little is known about the ant communities of South Africa and at this stage, broad zoogeographical patterns are the only real conclusions that can be made. Semi arid areas generally support large numbers of ant species. This is due to their well adapted physiology and behaviour, and release from competition from other insects experienced in the prevailing conditions in these areas (Andersen, 1983). However, it is widely believed that the highest ant diversity is found in tropical rain forest areas (Room, 1975).

The 44 ant species and 17 genera recorded in this study compares well with the figures obtained by other authors using pitfall traps in South Africa: For example, 21 ant species in the fynbos of the southern Cape (Koen & Brytenbach, 1988); 27 species in the Namib Desert (Marsh, 1986); 49 species and 23 genera in habitats associated with citrus (Samways, 1983); 56 species in the Eastern Transvaal, (Samways, 1990); 55 ant species in Mpumalanga (Swart, Richardson & Ferguson, 1999); and 34 ant species previously recorded at TdR (Willis, Skinner & Robertson, 1992);

However, similar surveys done in semi arid areas of Australia have generally yielded considerably higher species lists; 86 ant species in the Malle region of north-western Victoria (Andersen, 1983); 80 species in the Northern Territories, using pitfall traps and quadrats (Andersen, 1991); 111 ant species in semi arid Northern Queensland (Andersen, 1993); and 64 species in western Australia (Abensperg-Traun & Steven, 1995) .

The ant fauna was dominated by the Myrmicinae, which made up 56.8% of the total species, followed by the Formicinae, which made up 31.8%, matching well with the findings of Willis (1988), who recorded figures of 59% and 38% respectively. These two ant subfamilies are the largest, and their dominance has been reported to increase with increasing aridity (Marsh, 1986). The largest genera in the area were *Tetramorium* (nine species) and *Monomorium* (seven species), of the Myrmicinae, and *Camponotus* (seven species), of the Formicinae. Discussion of the ant distribution and abundance within the study area is hampered by the paucity of information concerning the biology of the majority of species recorded. However, where possible the results are discussed in terms of what is known about the various species.

Much consideration has been given to the merits of the various sampling techniques available (Hayes, 1970; Greenslade & Greenslade, 1971; Luff, 1975; Adis, 1979; Marsh, 1984, 1986; Andersen, 1991; Majer, 1997). Although pitfall trapping is by far the most widely used sampling method in surveys of ant fauna (Majer, 1997), there has been some contention over its validity.

Pitfall Trapping

Some authors have found the method to give reliable and accurate results (Samways, 1983; Andersen, 1991; Swart *et al.*, 1999). Indeed, the technique has several advantages. It is a convenient and cheap way in which to obtain a large number of samples, yielding high diversities and numbers of ants (Marsh, 1984). Significantly, it enables continuous sampling over a prolonged period. This avoids potential sampling bias arising from inter specific differences in activity periods that affect point sampling methods such as quadrat sampling (Marsh, 1984; Andersen, 1991).

However, several criticisms of the method have been made in the literature (Hayes, 1970; Marsh, 1986; Majer, 1997). For example it has been suggested that pitfall trapping leads to biased sampling due to inter specific differences in susceptibility to capture (Abensperg-Traun & Steven, 1995). For example, faster moving species are more prone to capture than slower species, which may have a better chance of avoiding traps (Andersen, 1991). This explains the success in capturing species such as *A. custodiens* (Pers. obs.; Swart *et al.*, 1999). Marsh (1984) noted the possible influence of body size and foraging behaviour upon the susceptibility of a species to capture. Species which forage along set trails are unlikely to be caught with any accuracy. *M. capensis* is a trail forging ant (Vorster, Hewitt & van der Westhuizen, 1991) and estimates of its abundance must be treated with caution. Majer (1997) suggested that cryptic, hypogaeic, and arboreal nesting species will tend to be under sampled by pitfall trapping. Indeed, the pitfall trapping in the present study failed to recorded the hypogaeic *Dorylus helvolus*, an important component of the aardvark diet. Majer (1997) also noted that the increased prevalence of these lifestyles with increasing complexity of the environment may lead to a corresponding decrease in the efficiency of pitfall traps. However, the habitats sampled in the present study were of low complexity and as a result, conclusions could be made with confidence.

The clumped distribution of ant nests is a big problem for avoiding bias in pitfall trapping, and many other sampling techniques (Andersen, 1991). Undoubtedly, occasional extreme values in the present study were caused by placement of traps close to nests. However, the impact of this factor was reduced by the large sample size employed and by adjusting the abundance figures for the frequency of occurrence in the depiction of the results. It is possible that some of the variation in species proportions between traps was caused by the fact that ant communities tend to occur in a mosaic fashion (Samways, 1990; Hinkley & New, 1997; Miller & New, 1997).

Despite these criticisms, pitfall trapping was by far the most successful of the three methods employed in this study, yielding 86.6% of the total recorded species. More species and more individuals were caught in each habitat and each season than by the other two techniques

Dig Sampling

The reliance upon pitfall trapping in ant community surveys has meant that the documentation on other techniques is relatively sparse. Several potential advantages of dig-sampling exist. For example, hypogaeic species ought to be adequately sampled. However, the failure of this method to record the hypogaeic ant *D. helvolus*, indicated that this may not be the case. Secondly, species with all types of foraging patterns and speeds are equally likely to be sampled. Finally, it could be argued that this method is the most relevant in terms of this study because it shows most similarity with the way in which the ant community is sampled by the aardvark.

However, dig sampling yielded only 54.3% of the ant and termite species caught overall. Although 20% fewer dig samples than pitfall traps were done and sampling was done only during the day, due to practical constraints, some of the low productivity can be attributed to the point sampling nature of the method. Epigaeic species that are inactive at the time of sampling will not be recorded. Notably, however, the effects of this disadvantage are not so great as is the case with quadrat sampling. Inactive ants and termites may be sampled if the nest lies within the dig depth. *T. trinervoides* for example, were regularly exposed from subterranean tunnels. Significantly, the point sampling nature of this method renders estimates of abundance more speculative than those generated by the pitfall trapping. In addition to suffering these constraints, some of the problems affecting pitfall trapping also affect this method. For example, the clumped distribution of most ant and termite species affects the accuracy of the results.

Quadrat Sampling

Quadrat sampling has been used successfully in a number of studies. For example, Andersen (1991) found that quadrats revealed a similar diversity of ants in similar proportions to pitfall traps. Quadrat sampling, like dig sampling removes the problems of species bias associated with pitfall trapping. The method is very convenient and quick and so large sample sizes can be achieved easily. In addition, the use of a third sampling method increases the chances of recording rare species that might not be revealed by a lower sampling effort. The quadrat sampling yielded 26 species despite having been done almost entirely in a restricted area of the grassland. This suggests that if this technique was used across each of the habitats with sampling intensity as high as that used in the pitfall trapping, the method would provide a very adequate sampling of the ant fauna of the area.

However, like dig sampling, quadrat samples do not provide continuous sampling of the population. Although ants generally have foraging periods when quadrat sampling is likely to be most successful (Briese & Macauley, 1977; Andersen, 1991), species with unusual foraging patterns are likely to be missed. For example, *H. mossambicus* has erratic and unpredictable foraging patterns (pers. obs.). This problem was minimised in the present study through the use of a large sample size and sampling through both day and night. Finally, quadrat sampling leaves more room for human error than pitfall trapping. Small and inconspicuous species are easily overlooked, especially where there is deep litter or thick ground cover (Andersen, 1983).

Abundance and Diversity: Habitat Differences

The ant communities differed markedly between the habitats. Very little is known of the habitat requirement of ants and, to a lesser extent termites (Robertson, pers. comm.). The limited research done suggests that ant assemblages are strongly influenced by certain habitat variables, including; vegetation cover; plant structural diversity; leaf litter cover; soil structure; soil texture; soil moisture content etc. (Room, 1975; Majer, 1985; Marsh, 1986; Koen & Breytenbach, 1988; Willis, 1988; Andersen, 1993; Swart *et al.* , 1999). For example, Majer (1985) found that plant species richness, % plant cover and % litter cover were highly correlated with ant species richness. Greenslade (1977) suggested that vegetation has a three-fold effect upon ant and termite community structure: Through the effects upon the microclimate, carrying capacity and structural complexity of the habitat. As a result, sites with different vegetational characteristics tend to have different ant assemblages (Andersen, 1983; Swart, 1996; Hinkley & New, 1997).

The degree of disturbance is a factor likely to be of some importance in shaping ant and termite communities (Miller & New, 1997). Differential levels of disturbance between the study habitats may provide an explanation for some of the observed variation between them. In terms of this study, it is possible to gauge roughly the degree of abiotic disturbance between the habitats and use this to suggest reasons for community patterns. Biotic disturbance such as competition is widely reported to be an important determinant of ant community structure (Davidson, 1977; Andersen, 1983; Majer, 1985; Sudd & Franks, 1987; Nonacs & Calabi, 1992). However, it is impossible to determine the extent and importance of biotic interactions without undertaking intensive manipulative study.

The Riverine Habitat

Of the three habitats, the riverine areas are the most distinct, both in terms of vegetation, and with regards to the ant/termite communities. Markedly fewer species and individuals were recorded in these areas relative to the other two habitats sampled. There are several possible explanations for this. The riverine habitat is exposed to high levels of disturbance in the form of seasonal flooding. As a result, the only species likely to survive across much of this habitat are those adapted to the rapid colonisation of available habitat. This disturbance is likely to exclude more competitive species, or those that have long term nest sites. *T. trinervoides,* for example is absent from this habitat. In addition, the cracks that appear in the fine alluvial soil on the recession of the flood water are likely to make foraging impossible, for the majority of species. A variety of shrubs and trees belonging to the *Acacia karoo-Celtis africana* community exist in this habitat (Werger, 1973) and a significant portion of the ant fauna is likely to be arboreal, and thus under sampled in the pitfall trapping (Majer, 1997).

The Steep Slope Habitat

The steep slope and grassland habitats are more similar to one another, both in terms of the ant/termite fauna and the vegetation present. The steep slope areas had a species richness just short of that found in the grassland areas, whilst Willis (1988) found this habitat to have the highest species diversity. The diversity of this habitat can be explained at least in part by the fact that in floristic and structural terms, this habitat is the richest in the reserve (Werger, 1973). In addition, the presence of a patchy litter layer, decaying wood, large numbers of small rocks and four layered vegetation provides an enormous surface area and innumerable ecological opportunities for exploitation by ants. The slightly lower diversity relative to the grassland areas may be due to the constraints imposed by the shallow, stony soils on the digging of nest holes.

The Grassland Habitat

The grassland habitat yielded the highest diversity, and by far the highest abundance of ants of the three habitats sampled. Significantly, the species utilised by the aardvark were most abundant in this habitat. Bare soil is ideal for foraging and nest construction, whilst the diversity of vegetation provides food and shelter from extreme environmental conditions (Greenslade, 1979). The high abundances recorded in this area can probably be attributed to the large areas of suitable habitat, unbroken by cracks or the presence of large numbers of rocks etc.

Some differences were noted within habitats between sites, particularly in the case of certain species. It has been suggested that ants occur in mosaic distributions, whereby in areas of apparently homogenous vegetation different species dominate (Samways, 1983; Miller & New, 1997). Such mosaics are probably the result of slight differences in habitat physiognomy. Similar findings were apparent in the present study, the distribution of *A. steingroeveri* being a prime example. This species was the dominant ant in very localised areas where *A. custodiens* (the dominant species over larger areas) was absent. In this instance, the patchy distribution appears to be related to soil type, with *A. steingroeveri* dominating on more sandy soils (pers. obs.). The degree to which competition can be implicated in this mosaic is not clear. It is known that *A. custodiens* avoid fine and crumbly soil (Steyn, 1954).

In the present study, 66.6% of the species showed some habitat specificity, 33.3% occurring in all habitats, 46.6% being absent from one habitat, and 20% occurring in one habitat. Only *A.*

steingroeveri, of the most common species, was absent from any one of the habitats, whilst the less abundant species were generally more habitat specific. This agrees with the work of Samways (1983), who found that the only species not to show habitat specificity were those most common.

Abundance and Diversity: Seasonal Differences

Marked seasonal differences were found in the ant and termite communities, in keeping with the majority of surveys done at similar latitudes (Briese & Macauley, 1977; Andersen, 1983; Majer, 1985; Willis, 1988; Andersen, 1993; Swart, 1996). In each of the habitats, greater species richness and abundance were recorded in summer than winter.

Abiotic factors such as temperature, humidity and water deficit are undoubtedly important in governing the observed seasonal activity patterns (Andersen, 1983; Steinberger, Leschner & Schmidar, 1992), whilst biotic factors such as resource availability (Samways, 1983) and inter-specific competition (Andersen, 1983) have also been suggested to play a role. Samways (1983) indicated that ant species mosaics also have a temporal dimension, with different species dominating at different times of the year. Support for this suggestion comes from the observation that 8.8% of the species were active only during the winter period when conditions in the southern Free State are extreme. The winter catches were dominated by fewer species, suggesting that relatively few species are able to cope with the harsh conditions during this period. The summer catches in contrast, were less numerically divergent, most of the species having occurred in reasonable numbers.

Species Patterns: Abundance, Distribution and Seasonality

Pitfall Trapping

The five most abundant species *(M. albopilosum, A. custodiens, M. capensis*, and to a lesser extent, *Pheidole sp. 1* and *M. havilandi)* are all species utilised by the aardvark. *Monomorium* was the most abundant genus, due largely to the high numbers of two species: *M. albopilosum* and *M. havilandi. M. albopilosum* was very abundant in all of the habitats. In contrast, Samways (1983) found this species to be very habitat selective, being typical of sparse grassland. However, the habitats compared by Samways (1983) were probably more divergent than those of this study. This species was the most abundant species overall, by some margin, contrasting with the work of Willis (1988) who found *M. albopilosum* to represent a minor component of the ant fauna. A possible explanation for this is that Willis' summer sampling was done at a different time, March, compared with December in the present study.

M. havilandi was the second most abundant *Monomorium* species, occurring in large numbers in the steep slope and grassland habitats, and at low density in the riverine areas. The species showed marked seasonality with activity being much reduced during winter. The remainder of the *Monomorium* species were numerically insignificant components of the local ant fauna.

A. custodiens, *A. steinegroeveri* and *M. capensis* all occurred at greater abundances in the grassland habitats than in the other areas. *A. steingroeveri* showed strong habitat preference, occurring at high density in the grassland areas compared to the very low numbers recorded in the steep slope areas and the riverine habitat, in which the species was not recorded. *A. steingroeveri* has not been found to nest under stones (Dean & Turner, 1990) and probably occurs at low density on the steep slopes for this reason. *A. custodiens* occurred at very high densities, being the second most abundant species overall, showing higher abundance than any other species during summer in the grassland habitat,. *A. custodiens* occurs very widely across southern Africa and is thought to be the most abundant Camponotinae species in South Africa (Steyn, 1954). The abundance of this species was significantly greater during summer than winter, when the median and major workers hibernate (Steyn, 1954). The low abundance of *A. custodiens* in winter lies in keeping with the findings of several authors (Steyn, 1954; Louw,1968; Willis, 1988; Swart, 1996).

M. capensis was well represented in the steep slope and grassland habitats, occurring at lower abundance in the riverine areas. *M. capensis* shows moderate habitat preference, preferring grassland with low basal cover (Vorster *et al.*, 1992), explaining the fact that abundance was greatest in the grassland areas. The propensity for *M. capensis* to utilise stones for nesting under (Dean & Turner, 1990) is the probable explanation for the abundance of the species on the steep slopes. *M. capensis* showed no real seasonal preference, contrasting with the findings of Vorster *et al.* (1992), who found that *M. capensis* ceases to forage during winter. Activity patterns of *Messor* spp. are determined to a large degree by temperature (Steinberger, *et al.*, 1992) and the mild conditions experienced during the winter sampling period of the present study may explain these findings.

Tetramorium was the most diverse genus in the area, with nine recorded species. However, all of the species occurred at low densities and had low RI values, in keeping with the findings of Willis (1988). However, in Willis' study, a *Tetramorium* species *(Tetramorium ackermani)* not even recorded in the present study was the sixth most abundant ant species. Willis (1988) worked in a different part of the reserve and it is possible that the absence of this species from the current survey represents an example of a mosaic distribution of ants.

The genus *Crematogaster* was represented by two species, both of which occurred in greatest abundance on the steep slopes. This can be attributed, in part, to the propensity of *Crematogaster* spp. for nesting under stones (Dean & Turner, 1990).

The two termite species were caught in low numbers in all of the habitats despite occurring abundantly in the area. Using Adam's (1993) regression on *T. trinervoides* numbers and mound sizes, one arrives at abundance figures of 15.4 X 10^6 per Ha, and 3.9 X 10^6 per Ha in the steep slope and grassland areas, respectively. In addition, *T. trinervoides* are known to forage up to 17.8

m from the mound, indicating that during foraging periods the species is distributed very widely across the veld in the steep slope and grassland areas. *H. mossambicus* can also reach incredibly high population levels (Wilson & Clark, 1977) and observations made in TdR indicate that the study site is no exception. Both species are very slow moving and thus are likely to have a low susceptibility to capture in pitfall traps. Line transect sampling is certainly more appropriate for *T. trinervoides* and in all probability would provide better population estimates of *H. mossambicus*.

Despite the inaccuracy of pitfall trapping, it is important to note that markedly fewer individuals of *H. mossambicus* were caught in the present study than in that of Willis (1988). *H. mossambicus* numbers increase during dry periods (Hewitt, van der Westhuizen, van der Linde & Mitchell, 1990; Braack, 1995). However, annual rainfall records provided by the weather bureau indicate that the year of Willis' (1988) study and those immediately preceding it were wetter on average than the year of and those before the present study. *H. mossambicus* does not occur with uniform abundance throughout TdR (pers. obs.) and is known to prefer overgrazed areas (Duncan & Hewitt, 1989). The sampling of Willis (1988) was done in a relatively restricted area and it is possible that this coincided with an area of locally high *H. mossambicus* abundance.

In the present study, *H. mossambicus* occurred in all three habitats, being most abundant in the grassland areas. In each habitat, activity was greater in the summer sampling period, contrasting with the suggestion that most foraging takes place during the winter months (Nel, 1968; Willis, 1988; Mitchell, Hewitt & van der Linde, 1993). A possible explanation for this could be found in the fact that sampling was done in early summer. *H. mossambicus* is known to swarm after the first substantial down pour of the rainy season (Nel & Hewitt, 1978) and it is possible that the production of alates prior to this requires foraging activity greater than is typical of the season as a whole. However, the very low numbers caught in this survey dictate that these findings must be treated with extreme caution for the reasons discussed previously.

Dig Sampling

The ant and termite communities indicated by the dig samples were significantly different from those suggested by the pitfall trapping. Fewer species were recorded at very much lower frequencies. The genus *Tetramorium*, was particularly poorly represented in the dig samples, with only four out of the nine species seen in the trapping having been recorded. In addition, the importance of several of the species in the community were quite different from that suggested by the pitfall trapping. For example, *A. custodiens* was under represented relative to the pitfall traps. This species is a diurnal forager (Steyn, 1954; Prins, 1981) and is therefore less likely to be recorded in underground tunnels during the day. Conversely, *T. trinervoides* was recorded more often using this method. *T. trinervoides* forages from galleries located 2.5 cm below the surface, well within the depth range of the dig samples (Adam, 1993). However, the low recorded frequencies still probably represent an inaccurate reflection of the activity of this species.

Moreover, unlike the pitfall trapping, the dig sampling was not characterised by the dominance of one or a few species. The RI of *A. custodiens* and *M. albopilosum,* for example, was less than that suggested by the trapping. This can be attributed to the fact that the use of occurrence % figures increases the importance of widespread species recorded at low density.

Despite the differences between the two methods, several patterns arose that confirm the patterns suggested by the pitfall trapping. The most frequently occurring species were those utilised by the aardvark, confirming the fact that these species are the most abundant in the area. The grassland habitat yielded greater species richness and frequencies of occurrence than the steep slopes, which in turn yielded more species more frequently than the riverine areas. As with the pitfall trapping, more species and greater frequencies of occurrence were recorded in summer than in winter. The dig sampling suggested an extreme paucity of ant and termite activity during the winter period. This is presumably because many ant species hibernate during winter and thus occur at a depth below that of the dig samples. For example, *A. custodiens* tend to hibernate in the lower half of the nests which average 45 cm in depth (Steyn, 1954), well out of reach of the dig samples.

Quadrat Samples

There were interesting differences between the quadrat data and the ant/termite communities of the grassland habitat indicated by the previous two methods. For example, the second most important species indicated by the quadrats was *Camponotus fulvopilosus.* This species is nocturnal (Skaife, 1979) and the vast majority of sightings were at night, explaining the low RI of the species in the dig samples. The low RI in the pitfall traps is probably due to the fact that this species moves relatively slowly and is therefore unlikely to be susceptible to capture. In addition, both termite species were better represented when using this method than was the case with the other techniques, although both remained under sampled. Regular sampling intervals throughout the day would doubtless provide more accurate estimates.

The Diel Activity of the Various Species

Sixty percent of the species recorded in the quadrats were predominantly diurnal, the remainder being most active during the night. Significantly, however all of the species of major importance in the aardvark diet, with the exception of *M. albopilosum*, were predominantly diurnal. These figures are similar to those of Swart (1996), who found that 58% of pangolin prey species were mainly diurnal, whilst 42% were mainly nocturnal. Willis (1988) found that a greater proportion were diurnal (69%), due probably to the inclusion of winter data. Several species are known to change their behaviour from being predominantly nocturnal in summer to being largely diurnal in winter (Briese & Macauley, 1977), a pattern typical of ant and termite communities in arid regions (Andersen 1983). *H. mossambicus,* for example, is generally diurnal during the winter and nocturnal during summer (Mitchell, *et al.,* 1992), a pattern noted in the present study.

T. trinervoides was slightly more active during the day, contrary to expectation. *T. trinervoides* lacks the pigment of *H. mossambicus* and forages predominantly at night (Adam, 1993). This finding was probably an artifact of the very low numbers recorded. In addition, the day quadrats were done in the evening and *T. trinervoides* is active during late afternoon on overcast days, which were common during the sampling period (Adam, 1993). The night quadrats were done at a time that does not coincide with the period of maximum activity found in the central Free State (Adam, 1993) and as a result are unlikely to provide an accurate representation of the abundance of this species.

A. custodiens was considerably more active during the day than at night, supporting the findings of Swart (1996) and Willis (1988), and in keeping with the work of Steyn (1954). Steyn (1954) found that in the Lowveld, *A. custodiens* has two peaks of activity, in the morning and late afternoon. *M. capensis* was predominantly diurnal, in accordance with the findings of Willis (1988).

Abundance and Diversity in the Study Animal Home Ranges

The home ranges of the three study animals that were sampled showed highly significant differences in the ant and termite communities. The vast majority of quadrat samples were done in the grassland habitat, and the differences between these areas provides support for the existence of a mosaic of ant communities. Notably, the most important species in the diet of the aardvark were present in the home ranges of each of the study animals. An exception was *M. capensis,* which was missing from the home range of A1. However this animal was recorded eating this species in this area, so it obviously occurs there. The quadrat sampling supported the conclusion that these species were some of the most important in the local communities.

Line Transects: Counts Of *T. trinervoides* Epigeous Mounds

The density of *T. trinervoides* mounds was highest in the steep slope areas (166.6 per Ha), followed by the grassland areas (120 per Ha). These results contrast with those of Willis (1988), who found mound densities to have been higher overall, and higher in the grassland areas than in the steep slopes. Willis' (1988) study was done in a different part of the reserve where conditions may be more favourable for the species. Conversely, much lower mound densities were recorded at Bultfontein, in the central Free State (Adam, 1993). Mound density at Bultfontein, was correlated with soil depth and grass composition. In this study, however, greatest mound density was recorded on the steep slopes typified by shallow soil. It is possible that the mounds on the slopes were located only at sites with deeper soil. In addition, the soils on the steep slopes have a higher clay content than the grasslands (Schulze pers. comm.), a factor which may promote mound construction.

Total Ant and Termite Diversity of TdR

Despite the intensity and variety of sampling used, the survey failed to record all species known to occur in the area. Two species known to be of significance in the diet of the aardvark in the area, *D. helvolus,* and *Solenopsis punctaticepes* (Taylor, 1999) were not recorded. The pitfall survey and extended searching of Willis (1988) yielded 13 species not recorded in the present study. Although a wide variety of visual searching methods were used, several of these species were recorded in pitfall traps, lending further support to the temporal mosaic theory suggested above.

The additional species were: *Monomorium* sp.1 *boerorum* complex, *M. disertum* (Forel) *M. drapenum* (Bolton), *M. scultzei* (Forel) and *M. anceps* (Emery), *Tetramorium ackermani* (Arnold), *T. occulatum* (Forel), *T.* sp. 3 *occulatum* complex, *T. sp. poweri* complex and *T. n.* sp. *squaminode* gp, *Camponotus mystaceus* (Emery) and *C. perersi janus* (Forel). These species brings the total number of recorded ant species in the area to 56, which relative to other areas in South Africa, represents a high diversity.

In conclusion, the ant and termite sampling yielded 44 ant species representing five subfamilies and 17 genera, and two termite species of two subfamilies. *M. albopilosum* and *A. custodiens* were the two most abundant species. Distinct differences were found between the habitats and the seasons. The greatest abundance and diversity occurred in the grassland habitat in both summer and winter, the lowest being recorded in the riverine areas. The summer communities were richer in species and individuals in each habitat. The species utilised by the aardvark were numerically dominant in each habitat and each season. The majority of these species were diurnal, with the exception of *M. albopilosum,* which was nocturnal.

Chapter 2

BEHAVIOURAL OBSERVATION

Foraging Patterns, Dietary Composition and Faecal Content

INTRODUCTION

Redford (1987) recorded 216 mammals as being myrmecophagous, feeding predominantly upon ants and termites. Ants and termites provide a ubiquitous and enormously abundant food source and as a result, the diversity of mammals and other species that depend upon them is not surprising. However, a suite of problems is associated with the utilisation of this food supply. These problems have resulted in the extreme specialisation and convergent evolution seen in many mammalian myrmecophages (Melton, 1976; Redford, 1987). The morphology, physiology and even behaviour of many mammalian myrmecophages show similarities associated with the utilisation of this food source (Abensperg-Traun, 1990). The guild is largely dominated by ancient species which radiated into the niche at an early stage and have since become extremely specialised (Richardson, 1987). The aardvark is no exception, being a very ancient species and showing marked morphological and physiological adaptations to its semi-fossorial myrmecophagous habit. A major focus of this study is to determine how the behaviour of the aardvark is related to the problems associated with myrmecophagy and the extent to which it is moulded by prey species biology.

Until quite recently research upon mammalian myrmecophages had been neglected (Redford, 1983). The situation has improved and research upon myrmecophages in Australia, South America and southern Africa has rectified this to some extent. In terms of the aardvark, prior to recent work done at TdR, most accounts of the diet were based upon limited stomach contents data (Smithers, 1971) and faecal analyses (Melton, 1976; Melton & Daniels, 1986). However, since then the work of Willis (1988) and particularly Taylor (1998) have improved knowledge considerably from detailed observational and faecal analysis.

It is clear that the diet of the aardvark is made up almost entirely of ants and termites. Several other items have been recorded, but these seem to be of very limited importance. For example, Melton (1976) found large numbers of red seeds in some faecal samples. Smithers (1971) found considerable quantities of melon seeds and pulp in one stomach sample. Meeuse (1962) reported that the aardvark is responsible for the dispersal and germination of the seeds of the 'aardvark cucumber' *Cucumis humifructis*. However, this report remains to be verified. The consumption of the underground fruits and the deposition of the seeds in a convenient seed-bed made up by the buried faeces was quoted as an example of symbiosis. Kingdon (1971) however, reported that the aardvark feeds solely on insects, cockroaches, grasshoppers and insect larvae complementing the staple diet of ants and termites. The same author reported large quantities of *Scarabaeidae* larvae in one aardvark stomach. Personal observation from Lowveld Zimbabwe offers support to this record.

There has been a gradual realisation of the fact that ants are generally more important in the diet of the species than are termites. For example, Smithers (1971) reported that Formicidae dominated in stomach sampling of eight animals. Termites occurred in four, making up 100% in one of the samples. The recent work by Willis (1988) and Taylor (1998) have reinforced this idea.

The diet of the aardvark has clearly been the subject of some attention. However, the degree of selectivity in the diet, and the factors driving prey selection have been largely ignored to date in aardvark research, as has been the case in work on other myrmecophages. The present study examines in detail, prey choice relative to availability and a suite of other prey species characteristics. The patterns of foraging and feeding are considered and the degree to which these are influenced by various aspects of prey species biology is examined.

METHODS

Radio tracking and Behavioural Observation

The location of the focal animals was achieved using a Telonics © receiver and a four bar Yagi antenna. During behavioural observation, the animals were followed at a distance of approximately three metres, using a small torch. Extreme care was taken to avoid obstructing or affecting the focal animals in any way. The torch beam was kept well clear of the eyes of the aardvark and observations were made from the sides and the rear of the animal rather than from the front. The habituation of the aardvarks prior to the study was sufficient to permit observation without eliciting abnormal behaviour. Indeed, the study animals ignored the presence of a researcher entirely. Observations were recorded in shifts of two hours, with 4-6 hours watching each night. An effort was made to ensure that observations were evenly distributed throughout the activity periods of each animal. This ensured that any variation in foraging activity throughout the course of the night was taken into account. A number of behaviour variables were recorded during each study period:

- The habitat in which each feed occurred.
- The species of prey eaten at each feed. This was determined by looking closely at the feed site after the departure of the study animal. Identification of the prey species was made by Robertson (pers. comm.) and Taylor (pers. comm.).
- The time was recorded every ten minutes, so as to enable accurate determination of feeding intensity.
- The length of each feed. This was considered to be the length of time when the aardvark actually collected food, as was indicated by the movement of the hyomandibular apparatus as the tongue was moved in and out of the feeding site. This made a very distinct noise, and there was clearly visible motion of the facial muscles and bones. Timing was done using a stop watch. Digging times and chewing times were not recorded, in order to reduce ambiguity and increase accuracy.
- The depth of each dig. This was recorded with a tape measure after the departure of the study animal. The deepest area of the dig was measured at each site to ensure consistency. Feeding done on the surface of the soil was recorded as such.
- The distance between feeds. When the feeds were close to one another, measuring was done with a tape measure. When larger distances were involved, the distance was measured through counting the number of paces. The paces were made to be as constant as possible. The route taken was exactly that of the aardvark, without cutting corners. The distance was then recorded to the nearest metre.
- Finally, a record was taken as to whether the feed was taken from a previously undisturbed site, or from a site with sign of aardvark activity already present.

Faecal analysis

Faecal analysis was carried out in order to give a more accurate impression of the diet of the aardvark in TdR, by reducing the reliance upon the relatively small sample size of habituated animals. Faeces were collected from the focal animals as they were deposited. In addition, faeces were collected from the home ranges of other individuals, in other areas of the reserve. Information from previous studies on home range sizes (Willis, 1988; van Aarde, Willis, Skinner & Haupt, 1992; Taylor, 1998) was used to ensure that faeces was collected from the home ranges of different individuals and that independence of samples was maintained. Faeces were found by searching for defecation scrapes. Only very fresh faeces were collected in order to enable valid seasonal comparisons, in light of the fact that aardvark faeces are likely to persist for long periods in the veld.

Analysis of the faeces was done using a method adapted from Willis (1988). Samples were soaked in water for a period of 24 hours. Following this, the sample was gently broken up under the water using a pestle and mortar. This resulted in the separation of the organic material from the denser inorganic material, the former tending to float on the surface. The organic material was then removed using a sieve. The remaining material was re-mixed and sieved again so as to ensure that all of the organic material was removed. This was then dried in absorptive paper for a period of at least 24 hours. A sample of the organic matter was taken and analysed. The ant and termite heads were removed carefully from the other faecal remains and identified under a dissection microscope, using the heads of sample ants caught and identified in the field as a reference. Where identification was not possible, samples were sent to Dr Robertson of the South African Museum. The proportions of the heads of the various species were then calculated.

The purpose of this part of the study was to determine the seasonal diet of the aardvark in the area and, to highlight feeding patterns relative to aspects of prey availability and prey species biology.

RESULTS

Behavioural Observation

The feeding behaviour of the aardvark was observed for two months in winter (July-August) and two months in summer (November- December). In the former, they fed upon a total of ten ant species and two termite species, but in winter, only seven ant species and two termite species were utilised.

The Relative Importance (RI) of the various prey species in the aardvark diet was calculated using two different methods. First, the % time spent feeding upon each prey species and secondly, the number of different feeds made upon each prey species.

RI of Prey Species as a Function of Percent Time Spent Feeding.

The most important species overall in terms of the time spent feeding are listed below.

Table 15. The average time % spent feeding on the various prey species in winter, summer and overall. NB The two *Camponotus* spp are clumped to give a genus figure. *M. havilandi* was consumed in negligible proportions and is excluded.

	Winter	Summer	**Overall**
A. custodiens	18.8	54.6	**36.7**
M. capensis	24.3	4.5	**15.8**
T. trinervoides (Mound)	29.4	1.4	**15.4**
A. steingroeveri	7.1	14.6	**10.8**
H. mossambicus	1.2	19.7	**10.5**
T. trinervoides (Ground)	18.4	1.4	**9.9**
M. albopilosum	0.4	2.3	**1.4**
D. helvolus	0.01	1.1	**0.6**
Camponotus spp	0.3	0.5	**0.4**
C. melanogaster	0	0.1	**0.05**
Pheidole species.1	0	0.01	**0.001**

In terms of the time spent feeding, the Formicidae (62.2%) were considerably more important in the diet than were the Isoptera (37.8%). The most important species overall was *A. custodiens*, followed by *T. trinervoides* and *M. capensis*. *H. mossambicus* was fed upon for 10.5% of the time in total and *M. albopilosum* for 1.4% of the time. The remaining species were responsible for less than 1% of time spent feeding. Figure 11. highlights the RI of the various prey species in both summer and winter. A one-way Anosim revealed a significant difference between the two seasons in terms of the time spent feeding on the various species (Table 16).

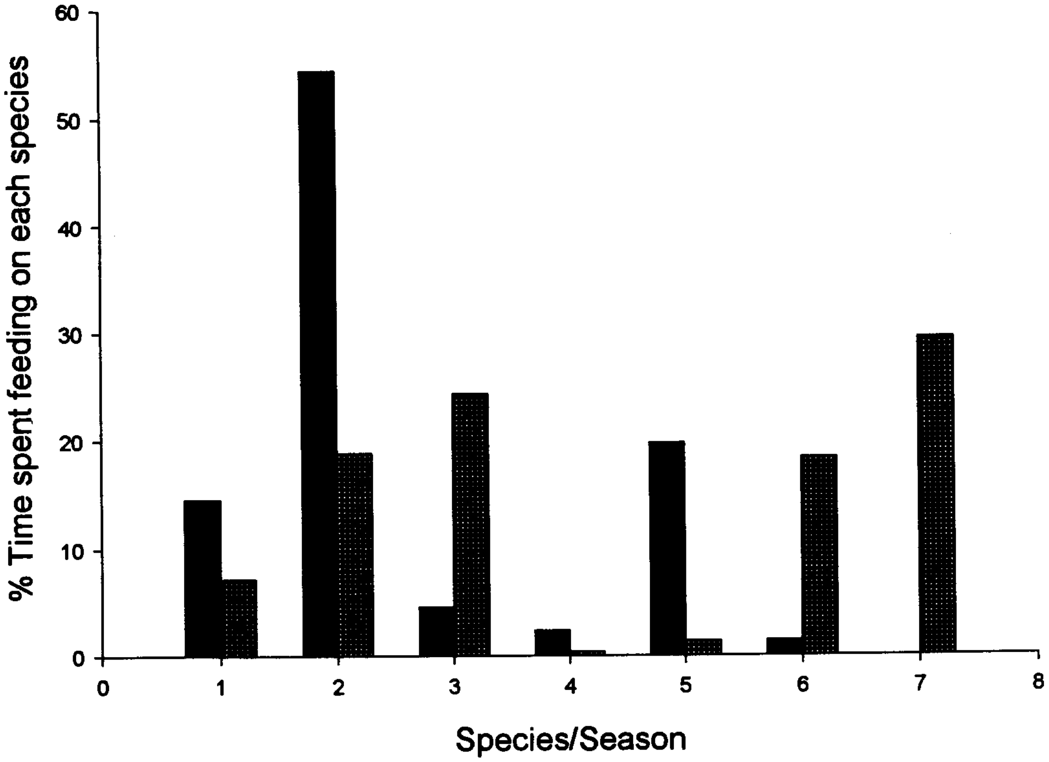


Figure 11. The diet of the aardvark in summer and winter as a function of the time % spent feeding on each species.

1= A.steines
2=A.custodiens
3=M.capensis
4=M.albopilosum
5=H.mossambicus
6=T.trinervoides
7=T.trinervoides mound feed

■ Winter
▨ Summer

Table 16. The results of a one-way Anosim analysis comparing summer and winter diets of the aardvark in terms of the time % spent feeding. Significant statistics marked *.

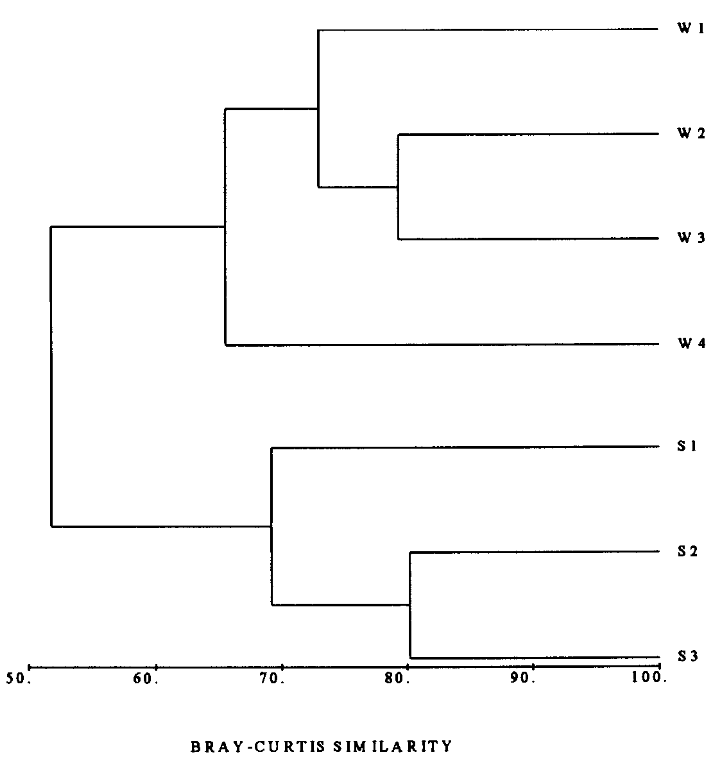
Groups Compared	No. of permutations	Significant Statistics	Global (R)	P Value
Summer Vs Winter	35	1	0.907	0.029*

Figure 12 represents a dendrogram of these results. The samples are clearly clumped in season groups. Figure 13 shows a MDS plot of these results. Equally clear clustering is apparent from this figure.

Several species show large differences in the extent to which they were utilised between summer and winter. *A. custodiens* had an RI of only 18.8 in winter, compared to 54.6 in summer. *M. capensis* was more important in winter (RI=24.3) than in summer (4.5). The utilisation of *T. trinervoides* also varied to a great extent between seasons. In winter ground feeds on this species had an RI of 18.4, with mound feeds at RI 29.4. In summer however, *T. trinervoides* had a far lower RI, both ground and mound feeds having had an RI of 1.4. *H. mossambicus* also showed a large discrepancy between the seasons. In summer, the RI was 19.7, whereas in winter the species had a RI of only 2.3. *M. albopilosum* was slightly more prevalent in the diet of in summer, though in terms of time spent feeding the species was not a significant component of the diet. The seasonal variation in diet was compounded by the difference in the number of species utilised overall, as mentioned above. In addition to the seasonal variation in time spent feeding, there were large differences between the feeding patterns of individual animals in both seasons (Table 17).

Table 17. Time % spent feeding on the various prey species by the study animals in winter.

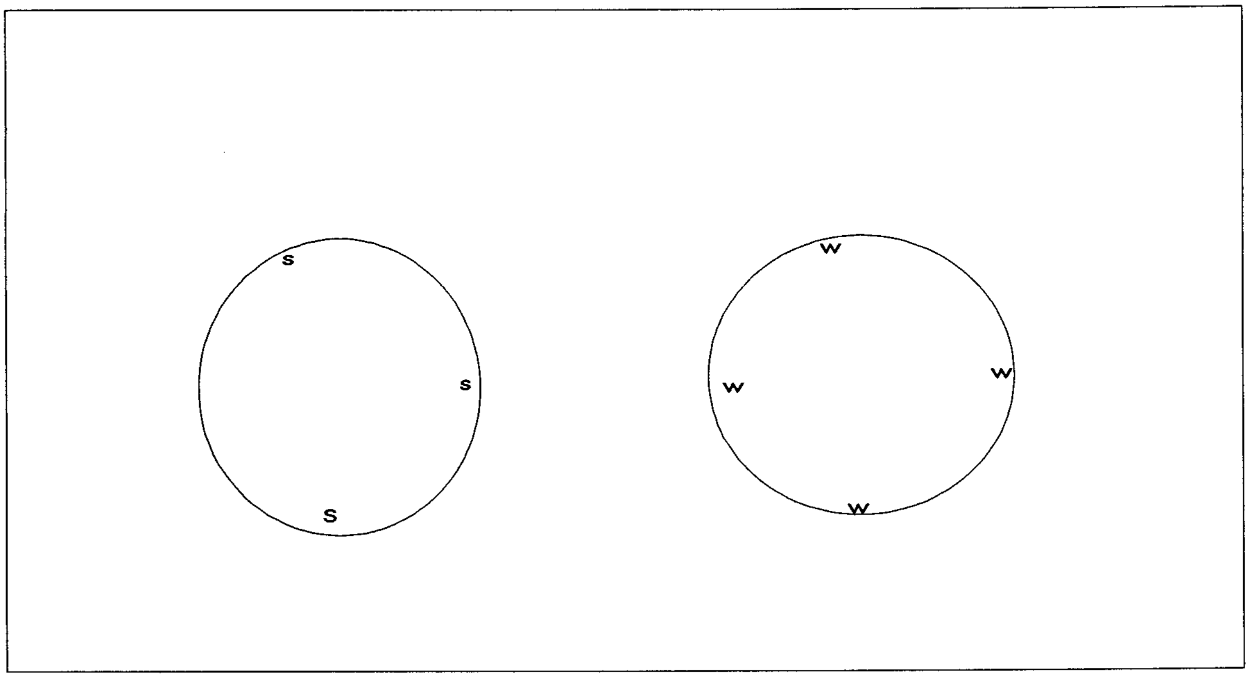
	A1	A2	A3	A4
A. custodiens	8.9	12.3	9.3	44.8
A. steingroeveri	11.2	0	17.4	0
Camponotus sp.	0.002	0.6	0	0.7
C. melanogaster	0	0	0	0
D. helvolus	0	0	0.03	0
H. mossambicus	4.4	0.03	0.2	0.04
M. albopilosum	0.3	0.9	0.2	0.2
M. capensis	40.6	12.3	7.5	37.0
Pheidole sp. 1	0	0	0	0
T. trinervoides (Ground)	0.2	35.3	30.5	7.2
T. trinervoides (Mound)	34.7	38.3	34.8	10.2



NB. S = summer, W = winter samples

Figure 12

The diet of the aardvark in summer and winter in terms of the time spent feeding on the various species



Stress = 0.2

NB. S = summer, W = winter samples

Figure 13

The diet of the aardvark in summer and winter in terms of the % time spent feeding on the various species

Marked differences occurred in the time spent feeding on some of the species by some of the animals. For example, *T. trinervoides* mound feeds made up over 30% of the time spent feeding by study animals A1, A2 and A3, whilst animal A4 invested only 10.4% of time feeding from mounds. Likewise, with the ground feeds on *T. trinervoides*, two of the animals invested >30% of the time, whilst the other two animals spent 0.2% and 10.2% respectively. *A. steingroeveri* made up a considerable portion of the diet of two of the study animals, despite having been absent from that of the other two. *M. capensis* varied in importance from 40.6% in study animal A1, to 7.5% in the diet of A3.

Table 18. The time % spent feeding on the various prey species by the study animals in summer.

	A1	A2	A3
A. custodiens	26.5	79.8	59.8
A. steingroeveri	15.2	10.1	18.3
Camponotus sp.	1.0	0.3	0.2
C. melanogaster	0.22	0	0.1
D. helvolus	0	2.9	0.5
H. mossambicus	48.4	3.2	7.4
M. albopilosum	1.9	2.4	2.6
M. capensis	6.2	0	7.3
Pheidole sp. 1	0.01	0	0
T. trinervoides (Ground)	0.6	1.0	1.2
T. trinervoides (Mound)	0.02	0.3	2.6

The summer diet of the three study animals showed considerable variation, as in winter. Note that study animal A4 went missing and so the data recorded for this animal were negligible. *H. mossambicus* showed the largest variation in terms of its RI in the total time spent feeding. Study animal A1 spent 48.4% of its feeding time preying upon this species, whilst the other two animals invested less than 10% of their time feeding upon it. *A. custodiens* varied in RI from 78.8% of feeding time in animal A2, to 26.5% in study animal A1.

The RI Of Prey Species as a Function of the Percentage of the Total Number of Feeds.

The number of feeds made upon the various species is another way in which the diet of the aardvark can be expressed. The number of feeds made on each species by the aardvarks in summer and winter is shown in Figure 14. As with the percentage time data, there were large differences between the number of feeds on most of the species between the seasons (see Table 19).

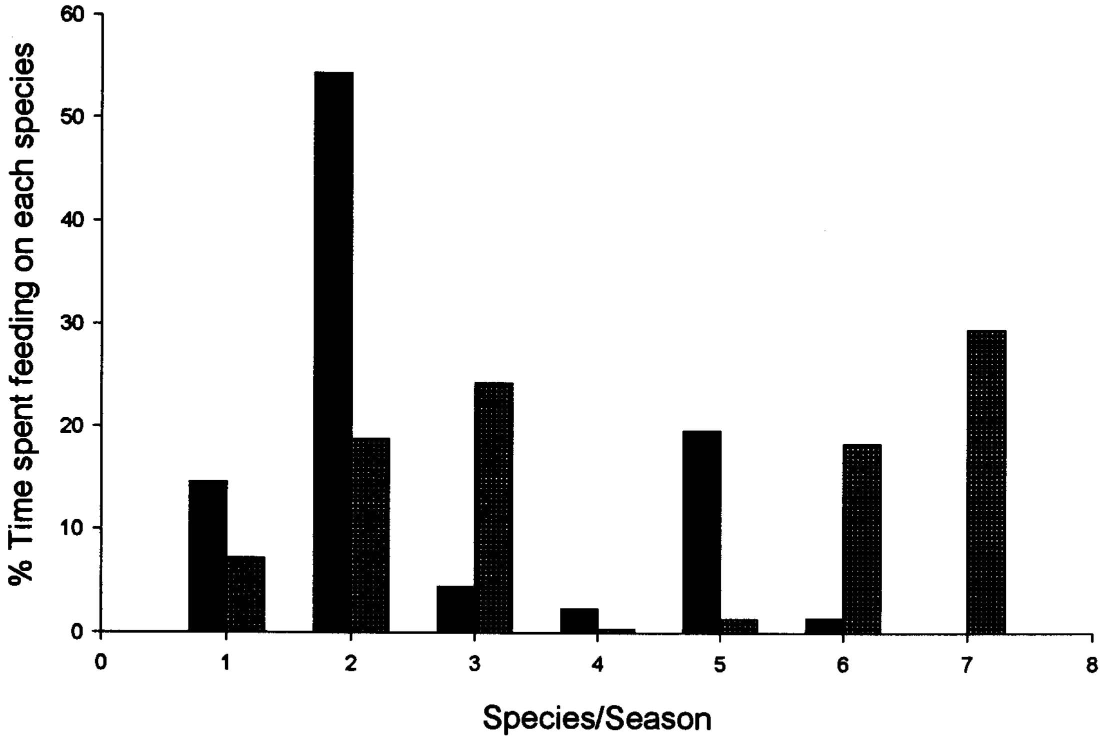


Figure 14. The diet of the aardvark in summer and winter as a function of the number % spent feeding on each species.

1= A.steines
2=A.custodiens
3=M.capensis
4=M.albopilosum
5=H.mossambicus
6=T.trinervoides
7=T.trinervoides mound feed

■ Winter
▨ Summer

Table 19. The percentage number of feeds made upon each of the species in winter summer, and overall.

	Winter	Summer	**Overall**
A. custodiens	19.3	52.0	**35.7**
T. trinervoides (Ground)	39.3	1.2	**20.3**
M. capensis	25.8	3.5	**14.7**
H. mossambicus	6.9	20.1	**13.5**
A. steingroeveri	5.6	17.2	**11.4**
T. trinervoides (Mound)	2.1	0.4	**1.3**
M. albopilosum	0.4	2.2	**1.3**
Camponotus spp	0.5	1.5	**1**
C. melanogaster	0	0.4	**0.2**
D. helvolus	0.03	1.8	**1.0**
Pheidole sp. 1	0	0.003	**0.001**

The number of feeds on the various species in summer and winter were compared using a one-way Anosim, which revealed a significant difference in number of feeds made upon the various prey species between summer and winter (Table 20).

Table 20. The results of a one-way Anosim analysis comparing the diet in terms of the number of feed on the various species, between season. Significant statistics marked *.

Groups compared	No. of permutations	Significant Statistics	Global (R)	P Value
Summer Vs Winter	35	1	0.722	0.029*

Comparison between the percentage time and percentage number of feeds made on the various prey species provides a clearer picture of the feeding patterns of aardvarks in the area (Figures 15 and 16). Although in summer there was little discrepancy between the two parameters, in winter, there were some notable differences: *T. trinervoides* ground feeds made up 18.4% of the time, but 39.3% of the number of feeds. Conversely, feeds from *T. trinervoides* mounds made up 29.4% of the feeding time, but only 2.1% of the number of feeds. Finally, *H. mossambicus* represented 1.8% of the time spent feeding, but 6.9% of the number of feeds. These discrepancies were clearly related to the average lengths of the feeds upon the various species.

The Average Length of Feeds on the Various Prey Species.

The average lengths of feeds in the two seasons are shown in Figure 17. The average length of feeds on all species in winter was 13.2 seconds. *T. trinervoides* ground feeds and *H. mossambicus* feeds were on average 5.9 and 2.9 seconds respectively, considerably lower than the overall average.

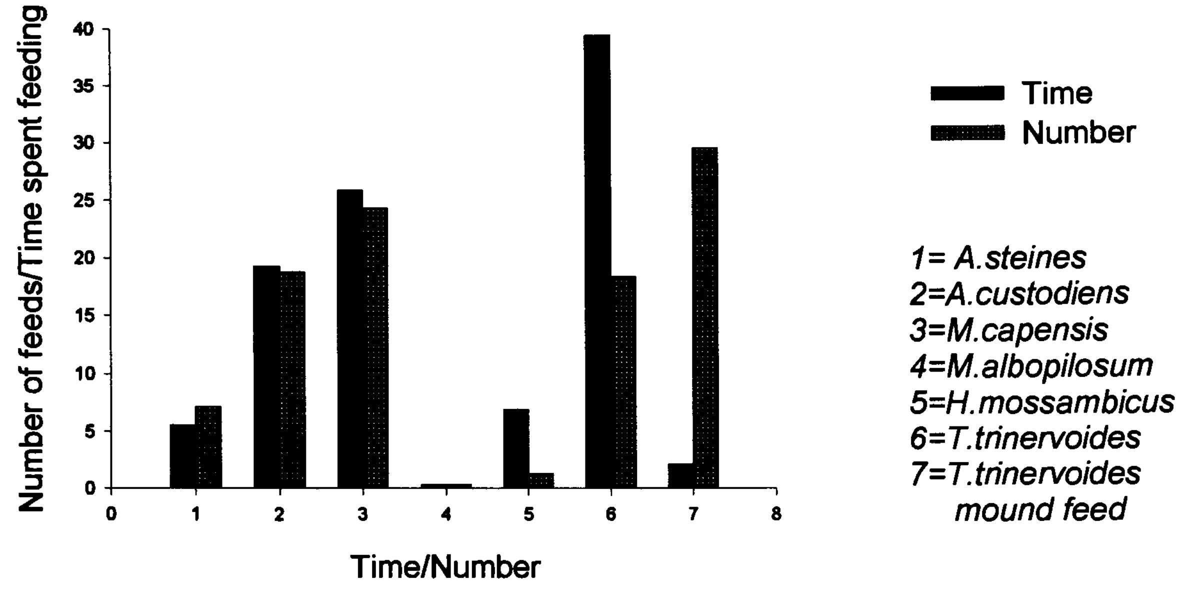


Figure 15. The winter diet of the aardvark as a function of both the number of feeds and the time spent feeding on each species.

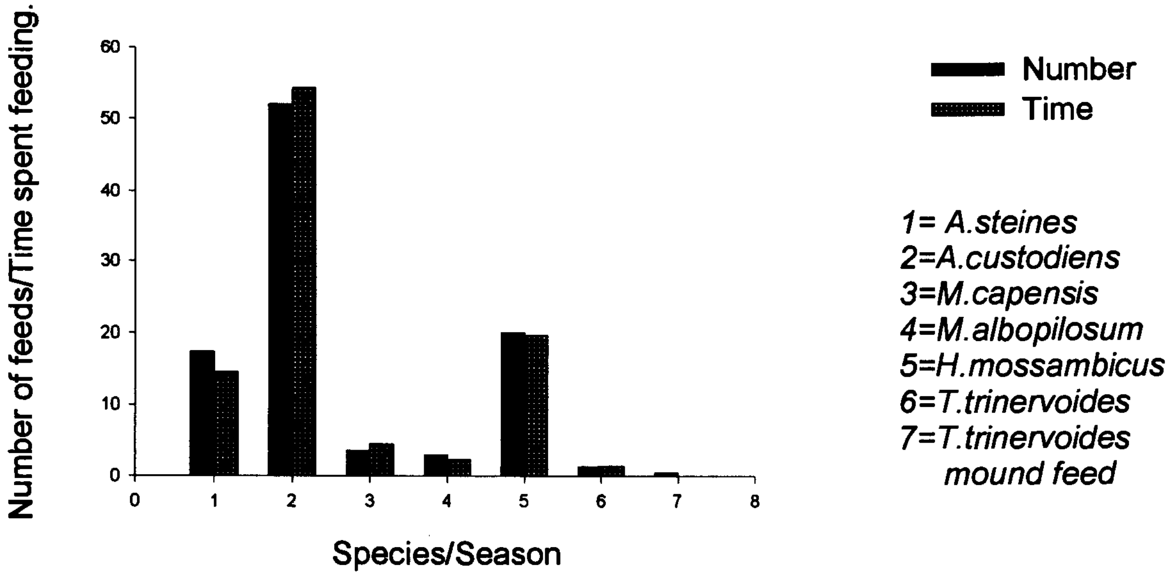


Figure 16. The summer diet of the aardvark as a function of both the time spent feeding and the number of feeds on each species.

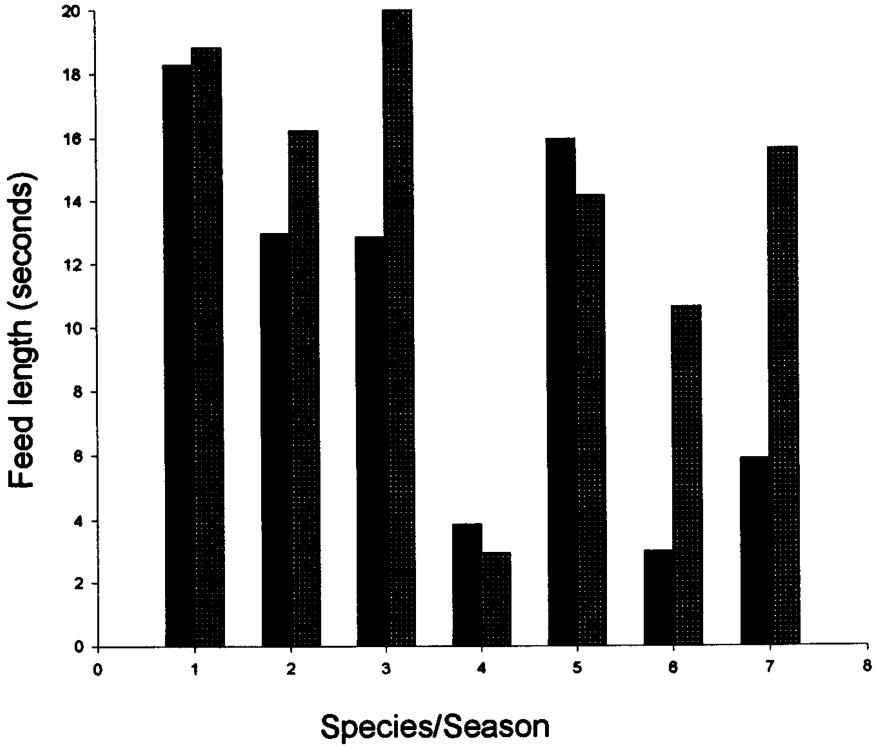


Figure 17. The average length in seconds of feeds on the various prey species in winter and summer

1=A.steines
2=A.custodiens
3=M.capensis
4=Camponotus
5=M.albopilosum
6=Hodotermes
7=Trinervitermes

■ winter
▨ summer

In contrast, *T. trinervoides* mound feeds were on average 238.1 seconds long which was much longer than the overall average. This variation was reflected in a high standard deviation (SD=89.6). In summer, the average length of feeds for all the species was 16.5 seconds, with a standard deviation of 17.9.

The summer feeds were, on average longer than in winter, with the exception of *M. albopilosum* and *Camponotus* spp. Although several species showed little difference (e.g. *A. steingroeveri*, *Camponotus* spp. and *M. albopilosum)*, large discrepancies between the summer and winter feed lengths were found for *M. capensis,* (12.8 and 20.0 sec's, respectively), *H. mossambicus* (3.0 and 10.6 sec's) and *T. trinervoides* (5.9 and 15.6 sec's).

The length of feeds was analysed statistically, using two two-way Anovas. The difference between the diets in summer and winter prevented the use of an adequate single test. In winter, there was a highly significant difference between the species in terms of feed lengths (Anova: F=62.196; df=3; P<0.001). A pairwise multi comparison post hoc test showed that the only significant differences in the feed lengths were between those made upon *T. trinervoides* on the ground (5.9 seconds) and those from mounds (238.1 seconds) when compared with all of the other species. There was no significant difference in the average feed lengths between the study animals Anova: F=2.391; df=3; P=0.071).

In summer, there was a highly significant difference between the feed lengths on the different species (Anova: F=26.805; df=4; P<0.05). There was a significant difference between the length of feeds upon *Camponotus* spp. (2.9 seconds) and all other species. In addition, there was a significant difference between the length of feeds upon *H. mossambicus* (10.6 seconds) compared with *A. custodiens* (16.2 seconds), and *M. albopilosum.* (14.1 seconds), As with winter, there was no significant difference in the average feed lengths between the study animals (Anova:F=3.700; df=2; P=>0.05). There was a significant interaction between the animal and prey species (Anova:F=5.756; df=8; P<0.001). Table 21 highlights the between-animal differences. *A. custodiens* (11.6-21.9 seconds) and *A. steingroeveri* (5.7-24.4 seconds) were two of the most variable species in terms of feed lengths by the various study animals.

Table 21. The average feed lengths on the major prey species by the various study animals in summer. Coefficients of variation in parentheses.

ANIMAL SPECIES	A1 Average	A2 Average	A3 Average
A. custodiens	11.6 (45.7)	17.9 (52.5)	29.0 (62.1)
A. steingroeveri	24.4 (68.4)	5.7 (100)	21.9 (73.1)
Camponotus sp.	2.7 (66.6)	3.0 (23.3)	3.0 (43.3)
M. albopilosum	18.7 (48.1)	13.4 (97.7)	16.0 (81.8)
M. capensis	13.0 (99.1)	-	21.0 (87.4)
H. mossambicus	13.6 (81.6)	10.1 (106.9)	7 (151.4)
T. trinervoides	13.8 (93.5)	4.7 (42.5)	17.2 (76.7)

Faecal Analysis.

A total of 57 faecal samples from the home ranges of eight animals were analysed in winter, whilst 35 samples from the ranges of ten animals were analysed in summer. The results of the faecal analysis are summarised in Table 22. Note that because *A. custodiens* and *A. steingroeveri* are indistinguishable in the faecal remains, they are listed together as *Anoplolepis* spp.

Table 22. The RI of the various species in the faeces of the aardvark in summer and winter. Coefficients of variation in parentheses.

	Winter	Summer	Overall
Anoplolepis spp.	63.8 (47.6)	67.3 (43.8)	65.6 (46.3)
T. trinervoides	22.7 (135.7)	0.7 (342.8)	11.7 (217.9)
M. capensis	2.0 (265)	0.5 (200)	1.3 (307.7)
H. mossambicus	3.9 (374.4)	11.7 (258.9)	7.8 (296.2)
M. albopilosum	4.4 (127.3)	9.6 (100)	7 (112.9)
D. helvolus	1.9 (221.0)	8.4 (1.2)	5.2 (242.3)
C. melanogaster	0.02 (500)	0.03 (33.3)	0.03 (333.3)
Camponotus spp.	0.5 (200)	1.7 (182.4)	1.1 (200)
Pheidole Sp. 1	0	0.06 (333.3)	0.03 (666.6)

Table 22 highlights the large differences between the two seasons in the faecal content. In both seasons, *Anoplolepis* spp. had by far the highest RI in the faeces, at 63.8 in winter, and 67.3 in summer, followed by *T. trinervoides* in winter, with an average RI of 22.7. Of this, 42.1% were soldiers and 57.9% workers. In summer, however, this species had a RI of only 0.7, of which 82% were workers, and 18% soldiers. In summer, the second most important faecal constituent on average was *H. mossambicus* at 11.7%. In the winter faeces, the same species had an average RI of only 3.9. The high coefficients of variation indicate that there was considerable variation between the faecal samples. Significantly, *Anoplolepis* spp. had SD figures considerably lower than the mean, indicating that the RI of this species was relatively consistent. Figure 18 represents percentage content of the various species in the faeces in summer and winter. A one-way Anosim on the overall faeces (Table 23) indicated that there was a significant difference between the two seasons, as was suggested by the behavioural observations.

Table 23. The results of a one-way Anosim on all faeces collected in the two seasons. Significant statistics marked *.

Groups Compared	No. of Permutations	Significant Statistics	Global (R)	P Value
Summer Vs Winter	5000	0	0.340	0.0%*

The extent of dietary variation between aardvarks and between seasons was determined using a two-way Anosim analysis on the faeces of the study animals (Table 24). Unequal numbers of samples from animals other than the study animals prevented the inclusion of these data into a two way Anosim. The limited data for study animal A4 during the summer period precluded the inclusion of this animal in the test.

Table 24. The results of a two-way Anosim analysis on the faecal content of the study animals in the two seasons. Significant statistics marked *.

Groups Compared	No. of Permutations	Significant Statistics	Global (R)	P Value
Summer Vs Winter	5000	0	0.464	0.0%*
Animals	5000	14	0.136	0.3%*
A1 Vs A2	5000	127		2.6%*
A1 Vs A 3	5000	4		0.1%*
A2 Vs A3	5000	1422		28.5%

There was a significant difference between the seasons and between the animals in the faecal content. The pairwise tests indicated that there were significant differences between two of the three comparisons; A1/A2, and A1/A3. The faecal contents of the various study animals in summer and winter are summarised in Tables 25 and 26. Study animal A4 disappeared during summer and for this reason the data for this animal were not included in the summer analysis. However, the winter data are included in Figures 19 and 20. The dendrogram (Fig. 19) shows marked clustering of the season groups. In addition, some clustering of individual groups is also apparent. The interspersion of the samples from study animals A2 and A3 is indicative of the insignificance of the difference between them. Figure 20 represents an MDS plot of these data. Some clustering is apparent, particularly with regard to season groups, and certain individual animal groups.

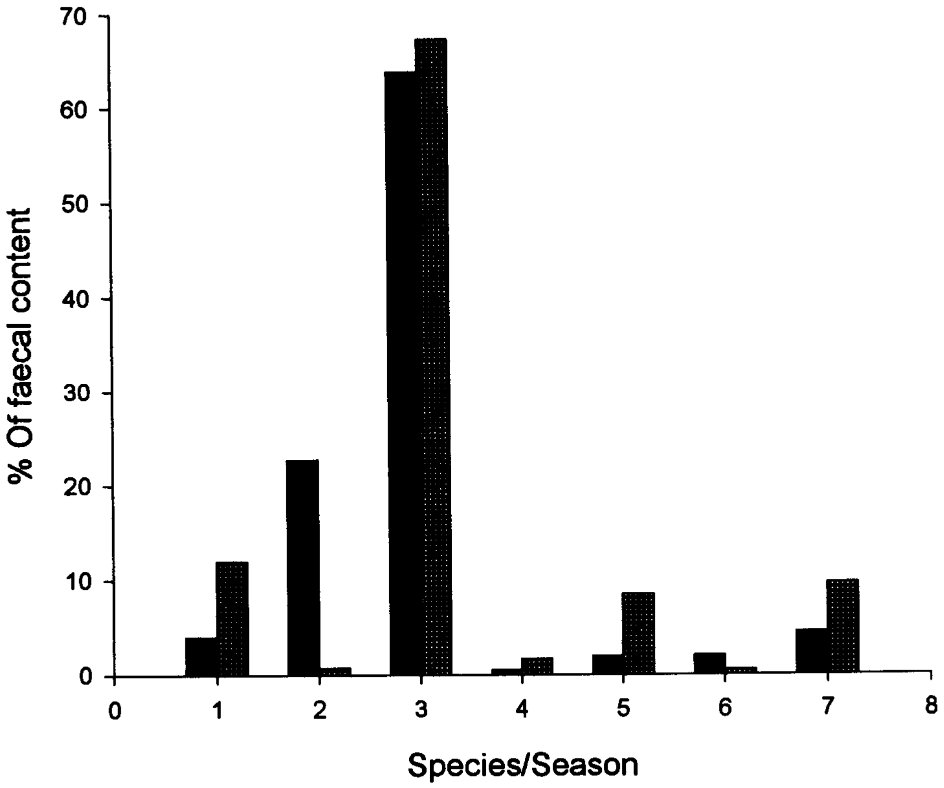
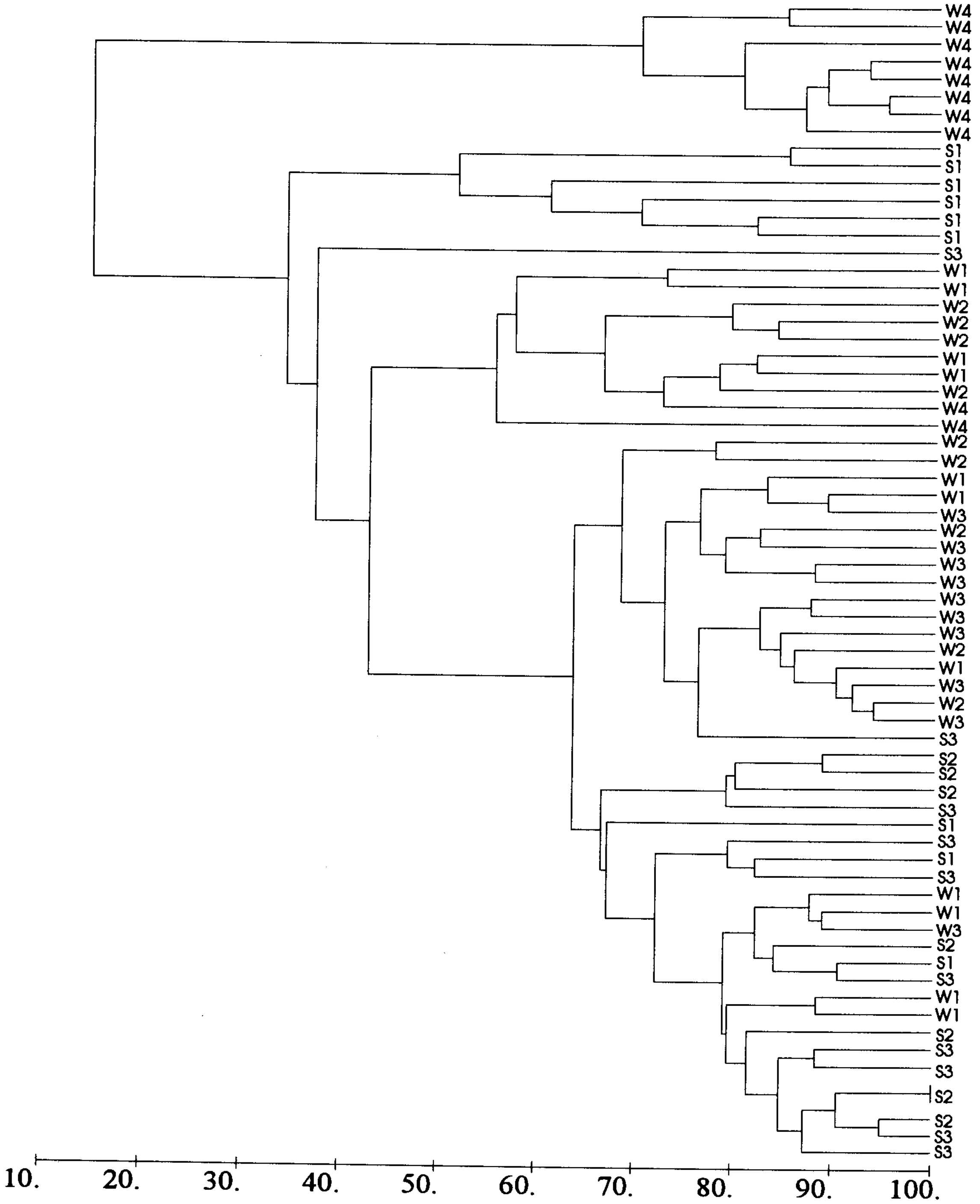


Figure 18. The faeacal content of the aardvark in summer and winter

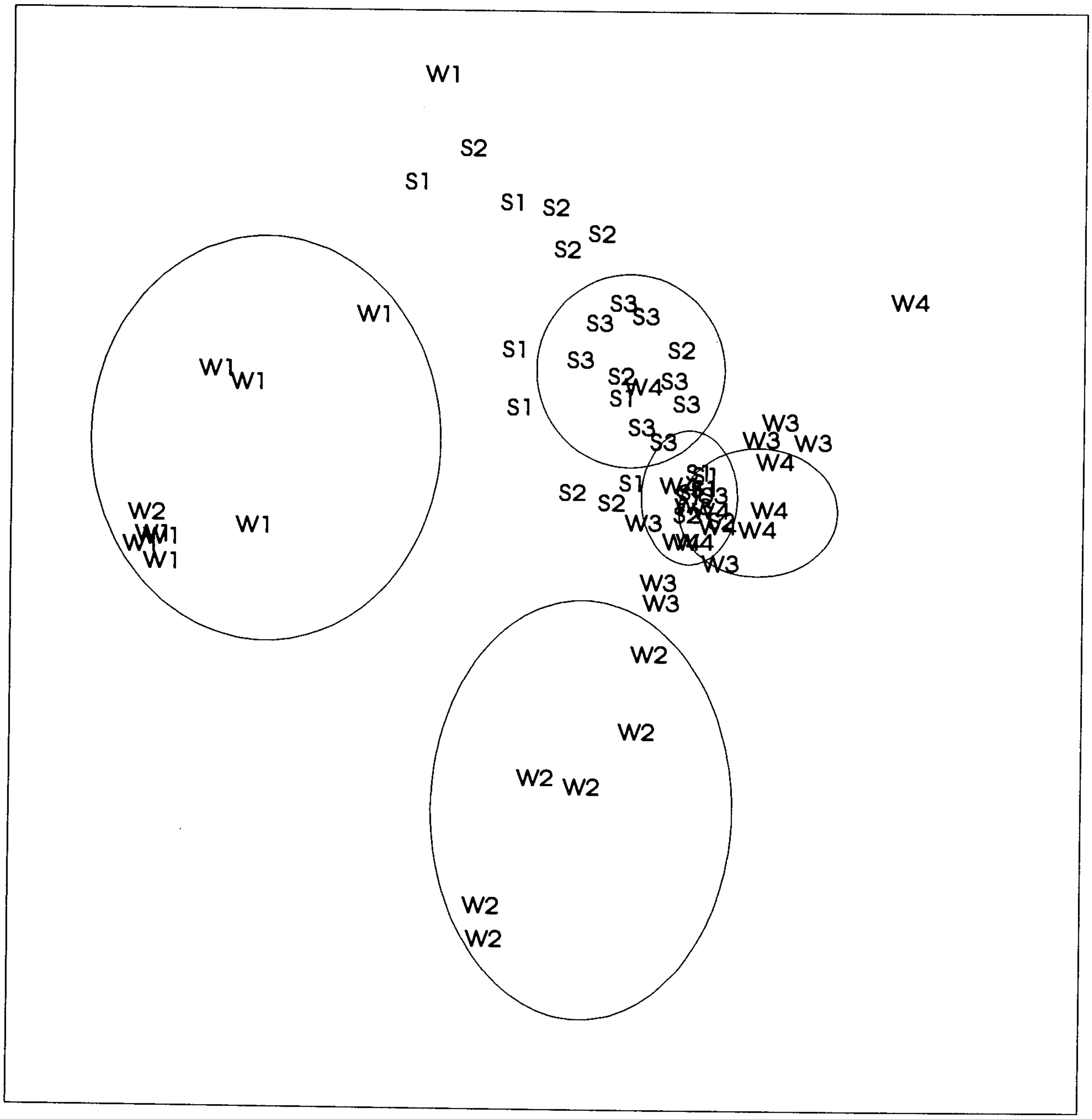
1=H.mossambicus
2=T.trinervoides
3=Anoplolepis spp
4=Camponotus spp
5=D.helvolus
6=M.capensis
7=M.albopilosum

■ Winter
▨ Summer



NB. W1, W2, W3 & W4 donate the faecal samples from the four study animals in winter
S1, S2 & S3 donate the faecal samples for the three study animals in summer

Figure 19
The faecal content of the study animals in summer and winter



Stress 0.13

NB. W1, W2, W3 & W4 donate the faecal samples for the 4 study animals in winter

S1, S2 & S3 donate the faecal samples from the three study animals in summer

Figure 20

The faecal content of the study animals in summer and winter

Table 25. The percentage faecal contents of the various study animals in winter.

	A1	A2	A3
Anoplolepis spp	60.4 (33.5)	48.3 (27.4)	71.8 (16.0)
Camponotus sp.	0.7 (1.6)	0.8 (1.7)	0.1 (0.2)
C. melanogaster	0.5 (1.0)	0.2 (0.5)	0
D. helvolus	0.1 (2.9)	4.8 (6.6)	3.5 (4.9)
H. mossambicus	1.7 (4.7)	2.7 (5.5)	0.1 (0.1)
M. albopilosum	8.1 (8.9)	2.8 (3.7)	4.8 (3.7)
M. capensis	2.2 (2.7)	0.9 (1.7)	0.9 (0.9)
M. havilandi	0	0.05 (0.2)	0.09 (0.2)
Pheidole sp. 1	0	0	0
T. trinervoides	26.4 (34.3)	39.4 (31.9)	18.6 (14.8)

Table 26. The percentage faecal contents of the various study animals in summer.

	A1 Summer	A2 Summer	A3 Summer
Anoplolepis spp	37.9 (32.0)	81.9 (7.9)	77.5 (20.5)
Camponotus sp.	4.3 (5.6)	0.7 (0.7)	0.9 (1.3)
C. melanogaster	0.1 (1.6)	0.1 (0.2)	0.1 (0.4)
D. helvolus	0.7 (2.3)	7.3 (8.5)	9.4 (23.7)
H. mossambicus	41.7 (51.3)	0.5 (2.5)	0.2 (1.3)
M. albopilosum	12.3 (12.5)	6.6 (7.5)	8.2 (7.0)
M. capensis	0.5 (1.7)	0.3 (0.8)	0.1 (0.2)
M. havilandi	0.4 (0.9)	0.1 (0.2)	0.2 (0.3)
Pheidole sp. 1	0.2 (0.4)	0	0 (0)
T. trinervoides	0.05 (0.05)	0.3 (0.4)	1.8 (4.1)

Although there was general agreement between the animals in terms of the contribution of the various species, several large differences do exist. Study animal A1 showed greater differences with A2 and A3 than either did with one another. For example, the contribution made by *H. mossambicus* in the summer faeces of A1 was considerable, whilst the importance of this species in the faeces of the other animals was negligible. *Anoplolepis spp.* had a much lower RI in the faeces of A1 than either A2 or A3 in summer. The RI of *T. trinervoides* in the winter faeces was considerably higher for A2 than for the other animals.

The faecal content was also considered in terms of the percentage occurrence of the various species. This is shown in Figure 21. A one-way Anosim revealed a significant difference between the seasons in the occurrence of the various species (see Table 27).

Table 27. The results of a one-way Anosim on the occurrence of the various species in the summer and winter faeces. Significant statistics marked *.

Groups Compared	No. of Permutations	Significant Statistics	Global (R)	P Value
Summer Vs Winter	126	1	0.756	0.8%*

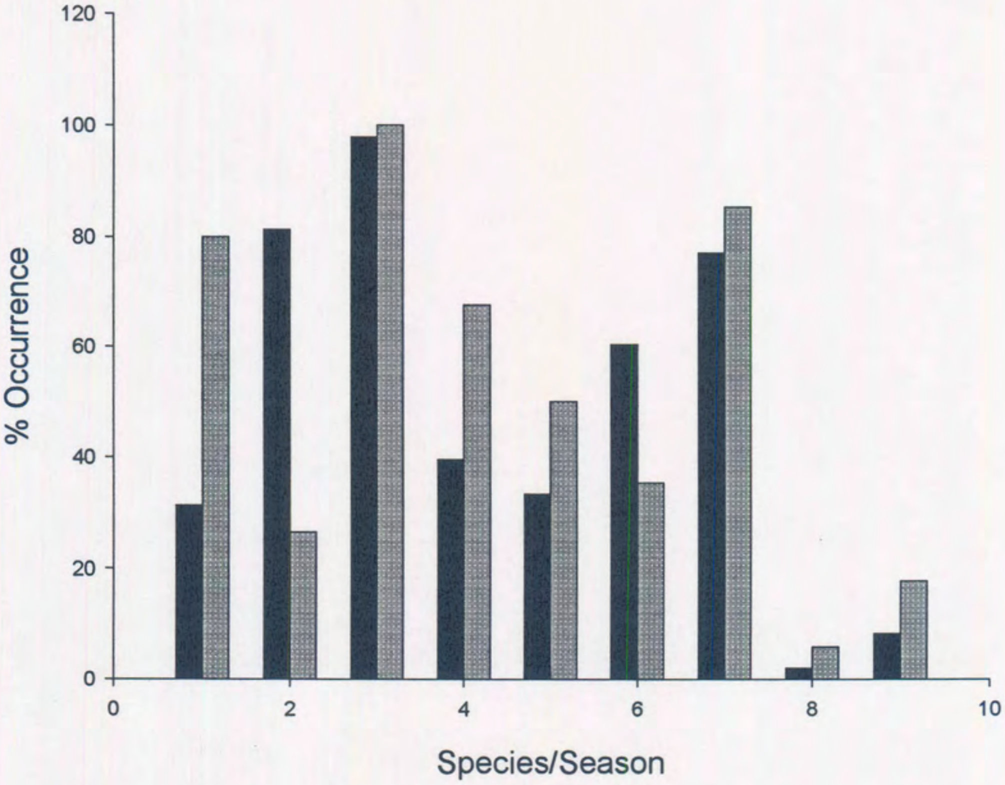


Figure 21. The average % occurrence of the various species in the faeces of the aardvark in summer and winter

1=H.mossambicus
2=T.trinervoides
3=Anoplolepis spp
4=Camponotus spp
5=D.helvolus
6=M.capensis
7=M.albopilosum
8=C.melanogaster
9=M.havilandi

■ Winter
▨ Summer

T. trinervoides occurred in 81.3% of faecal samples in winter, but only 26.5% in summer. *H. mossambicus* occurred in only 31.3% of samples in winter, but 80% in summer. *Anoplolepis* spp. had the highest occurrence %, at 97.9% in winter, and 100% in summer. *M. albopilosum* also had a very high occurrence % in both winter (85.3%) and summer (77.1%).

A comparison between the occurrence % and the content % provides an insight into the patterns of feeding. Figures 22 and 23 show both the occurrence % of prey species and content % of the faeces made up by each species in winter and summer, respectively. There were large discrepancies between the two parameters. For every species the occurrence % is considerably greater than the content %. In both seasons, *Anoplolepis* spp. was the only species category that had a figure for content % approaching that of occurrence %. *T. trinervoides, H. mossambicus, M. capensis* and *Camponotus* spp. all had very low RI's despite having high rates of occurrence, indicating that low numbers of ants were eaten despite fairly regular feeds upon the species.

The RI of the Various Species in the Faeces and Behavioural Observations

The diet suggested by the faecal analysis (faecal content) was compared to that suggested by the behavioural observations (percent time spent feeding). This is represented graphically in Figures 24 and 25 for winter and summer respectively and is summarised in Table 28.

Table 28. The average time % spent feeding on the various species and the average content % of the faeces, of the three study animals in summer and four animals in winter.

	Winter Faeces	Winter Time	Summer Faeces	Summer Time
Anoplolepis spp.	60.2	26.0	65.8	69.2
T. trinervoides	28.1	47.9	0.7	2.6
M. capensis	1.3	24.3	0.3	4.5
H. mossambicus	1.5	1.2	14.1	19.7
M. albopilosum	5.2	0.4	10.3	2.3
D. helvolus	2.8	0.01	0.6	1.1
C. melanogaster	0.3	0	5.6	0.1
Camponotus spp.	0.5	0.3	2.0	0.5
Pheidole sp. 1	0	0	0.1	0.01

In winter, the RI of *Anoplolepis* spp. in the faeces (60.2) was much greater than in the feeding time (26.0). Other discrepancies also occurred. With the very notable exception of *M. capensis* and *T. trinervoides*, which had a considerably higher RI in the feeding

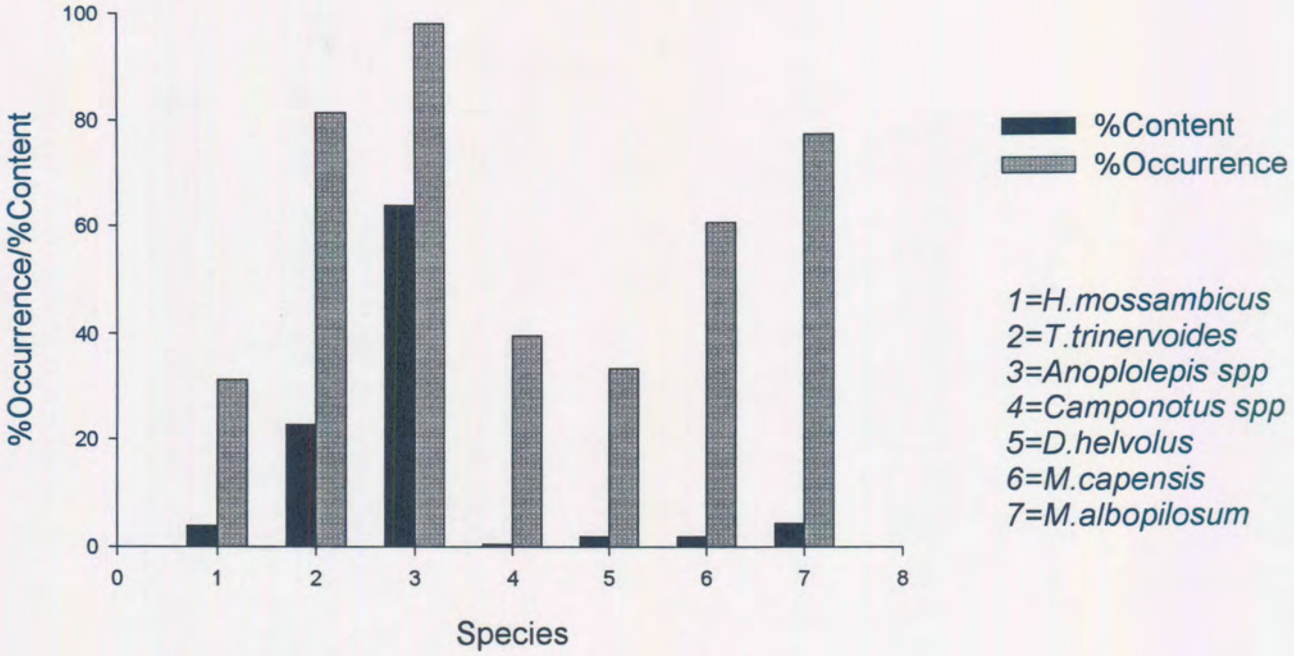


Figure 22. The occurrence % and content % of the various prey species in the winter faecal samples

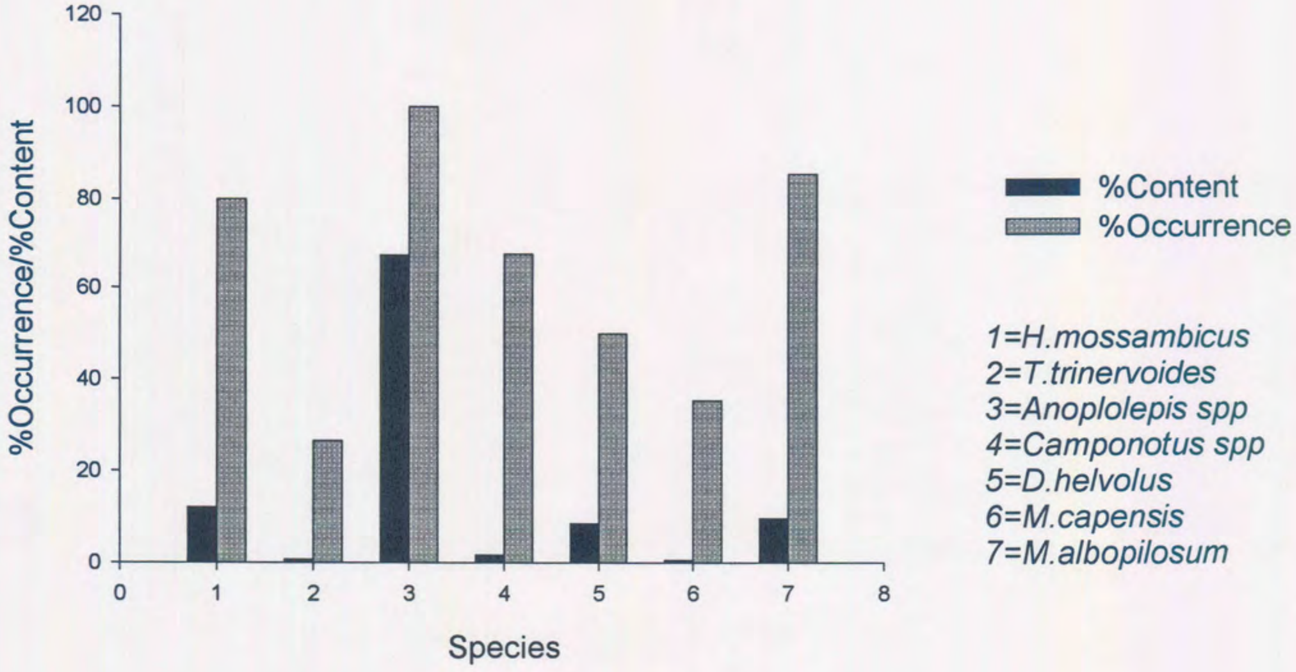


Figure 23. The occurrence % and content % of the various prey species in the summer faecal samples

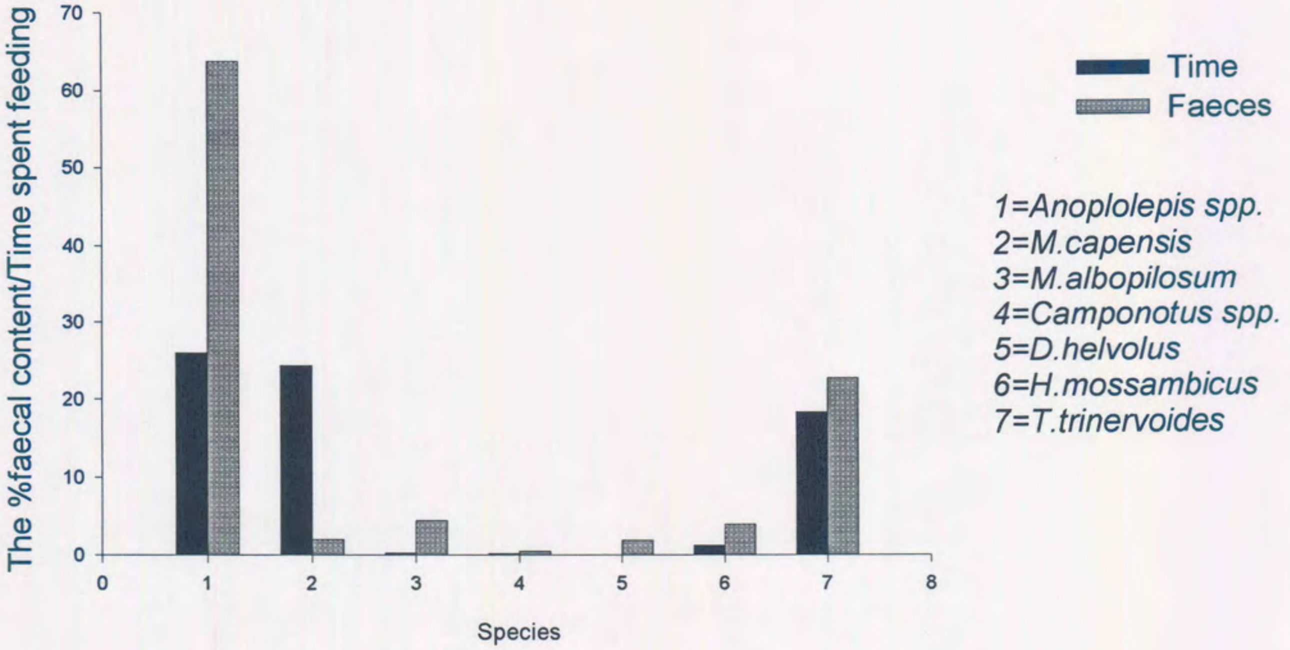


Figure 24. The faecal content % and time spent feeding on each prey species in winter.

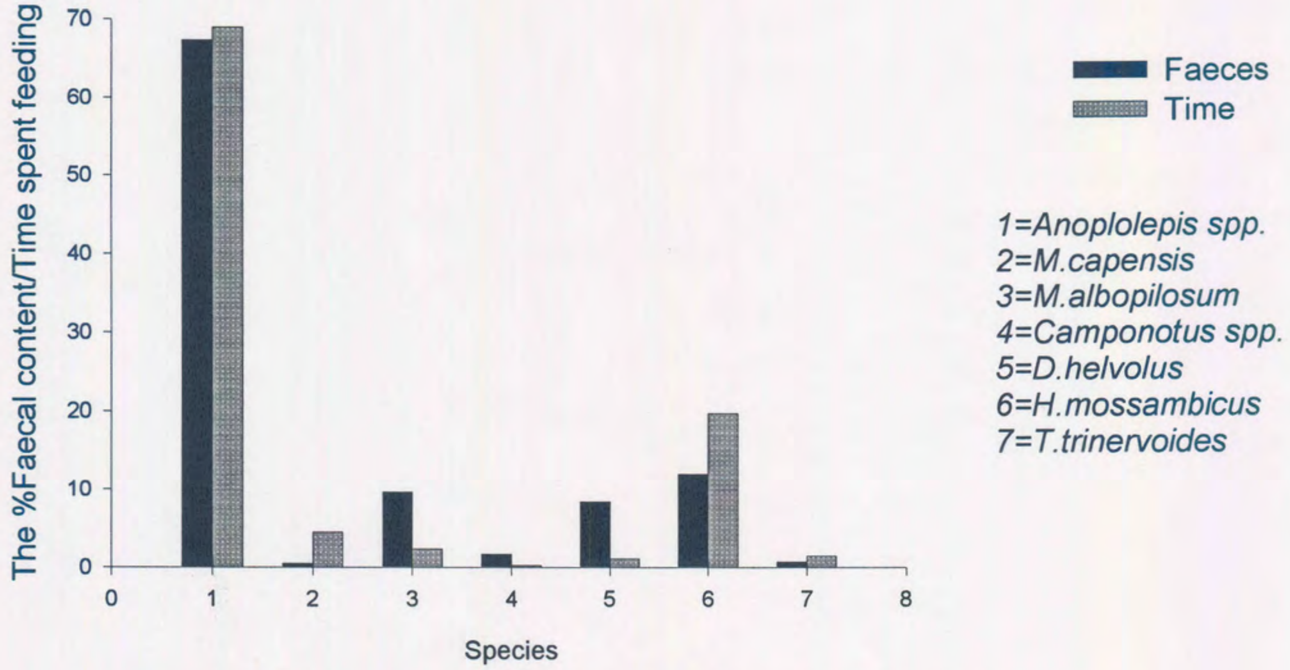


Figure 25. The Faecal content % of the aardvark and the time spent feeding on each prey species in summer.

observations than in the faeces, all species had a higher RI in the faeces than in the observations in winter observations. The differences between the faeces and behavioural observations in summer were less pronounced. For example, *Anoplolepis* spp. had a RI of 69.2% in the observations and 65.8% in the faeces. *M. capensis, H. mossambicus* and *T. trinervoides* each had a higher RI in the observations than in the faeces, whilst the converse was true for *M. albopilosum, Camponotus* sp. and *D. helvolus.* The largest discrepancies between the two parameters were for *H. mossambicus* (14.1% faeces, 19.7% of time) and *M. albopilosum* (2.3% time, 10.3% faeces).

The Number of Consecutive Feeds on the Same Species.

The average number of consecutive feeds made upon the various species would indicate the degree of clumping in the feeding. A three-way Anova was done to look at the effects of season and species upon the average number of consecutive feeds upon a single species. There were no significant differences between the seasons (Anova: F=6.086; df=1; P>0.05) and between the animals (Anova: F=10.709; df=2, p<0.001), but there was a significant difference between the species (Anova; F=25.5; df=3; p<0.05) in terms of the average number of consecutive feeds. The three way interaction between each of the terms was significant (Anova: F=3.983; df=6; P<0.001). In summer, *A. custodiens* was fed upon 6.7 times in a row on average compared to 3.5 in winter. The opposite pattern is shown by *M. capensis* (2.2 and 6.4 for summer and winter respectively), *H. mossambicus* (3.8 and 6.8), *T. trinervoides* ground feeds (1.3 and 18.1). However, because of missing data points, all of the data for both seasons could not be included in a single test. As a result, two separate tests were done on the data. This enabled consideration of the full data set for summer and winter.

In winter, the highest average number of consecutive feeds was made upon *T. trinervoides* (18.1), whilst feeds upon *M. albopilosum* (1) and *T. trinervoides* from mounds (1.3) were generally singular events. *A. steingroeveri* , *H. mossambicus* and *M. capensis* were all fed upon in bouts of just over six consecutive feeds. A two way Anova on ranks indicated that there was a significant difference between the species (Anova: F=15.411: df=3 P<0.001), but no significant difference between the study animals in the number of consecutive feeds made on each species (Anova: F=1.813; df=2 P=0.149). In summer there was a significant difference between the species (Anova: F=15.636; df=5; P<0.001) and between the study animals in the number of consecutive feeds made (Anova: F=4.212; df=2; P=0.016). *A. steingroeveri* was the species fed upon the greatest number of times in a row on average, at 9.3, followed by *A. custodiens* at 6.7. Figure 26 shows the average number of consecutive feeds made upon the various prey species in summer and winter. The means for the various prey species were more variable in summer than winter. The biggest

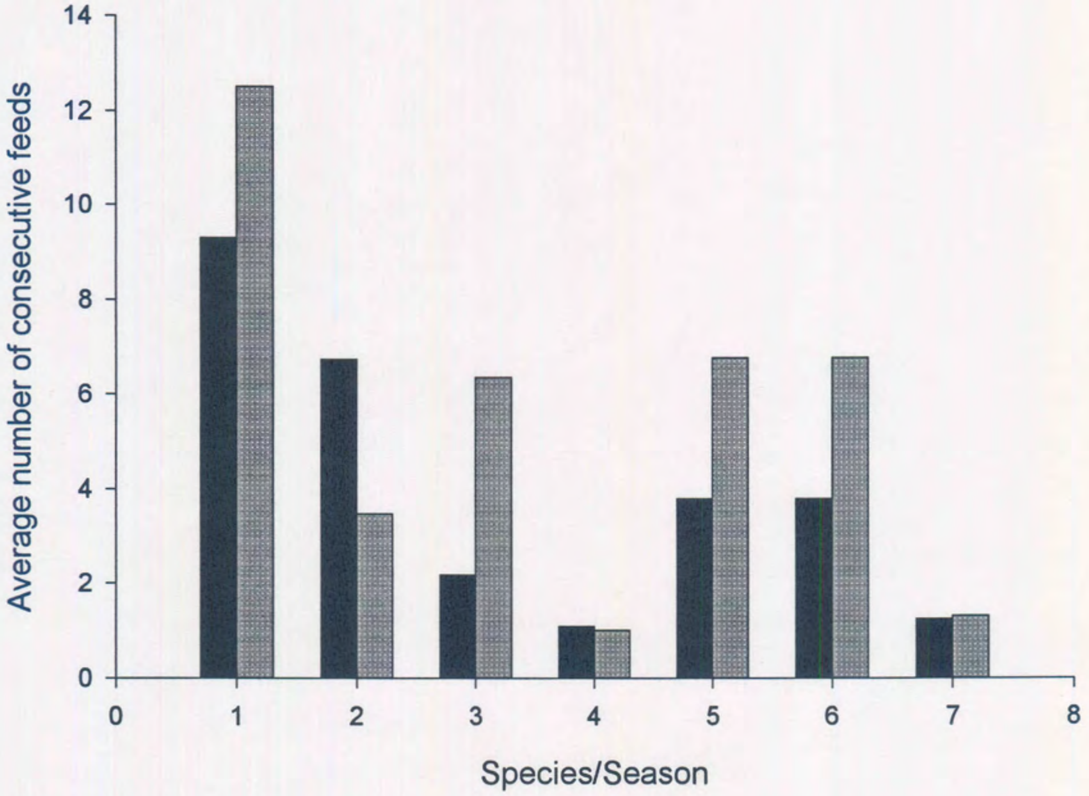


Figure 26. The average number of consecutive feeds made upon the prey species in summer and winter.

1=A.steines
2=A.custodiens
3=M.capensis
4=M.albopilosum
5=H.mossambicus
6=T.trinervoides ground feed
7=T.trinervoides mound feed

■ Summer
▨ Winter

differences in the number of consecutive feeds were between *A. steingroeveri* and *T. trinervoides* and *A. custodiens*. These results indicate that the aardvarks generally fed upon the various species in bouts. Seasonal differences in the average number of feeds to some extent reflect seasonal differences in utilisation of each species. *T. trinervoides*, for example was utilised far more in winter than summer, and was fed upon more times consecutively on average during this time. However *H. mossambicus* was fed upon in a more clumped fashion in winter despite the fact that this species was utilised considerably less during this season. In addition, despite being a relatively minor dietary component, *A. steingroeveri* had high numbers of consecutive feeds in both seasons. At the other extreme, *T. trinervoides* feeds from mounds make up a significant portion of the winter diet and yet in this season the feeds were generally singular events with no clumping.

The Distances Between Feeds on the Same and Different Species

A comparison between the distance walked between feeds on the same species, and between feeds on other species provides another method of determining the pattern of feeding. Figures 27 and 28 show the average distances walked between feeds on the same ('intra distance') and different species ('inter distance'), for each species in summer, and winter respectively. Three-way Anovas were done on both the summer and winter data, to determine the effects of animal, prey species and whether the movement was within or between prey species feeds, on distance walked. There was a significant difference between the intra and inter species distances in summer (Anova: F=14.132; DF=1; $P<0.001$), and in winter (Anova: F=62.24; df=1; $P<0.001$).

In winter, there was no difference between the animals (Anova, F=2.38, df=3 P=0.095), or between the species (Anova: F=2.43; df=3; P=0.094) in terms of the distance walked. The longest average distance between feeds upon the same species in winter was recorded for *M. albopilosum* (22.3m), followed by *A. custodiens* (15.8 m), whilst the shortest distance on average was recorded between feeds upon *T. trinervoides* (2.0m). *H. mossambicus* feeds were also generally very close together, with an average of 2.7 m between them.

Due to missing data points, the analysis for summer was conducted on the data for two animals. As with winter, there was no difference between the animals (Anova: F=3.533; df=1; P=0.062), or between the species (Anova: F=3053, df=4, $P>0.05$). The interaction between species and inter/intra distance was significant (Anova; F=2.612; df4; P=0.037). The only differences found in the distances walked between feeds on the same species were between *M. albopilosum* and *M. capensis*. Feeds upon *M. albopilosum* were farther apart than consecutive feeds upon *M. capensis*, which were generally very close together. As in winter, the longest average distance walked between feeds upon the same species was recorded for *M. albopilosum* (16.7 m). This was followed by *A. custodiens,* with an average of 10.7 m between feeds.

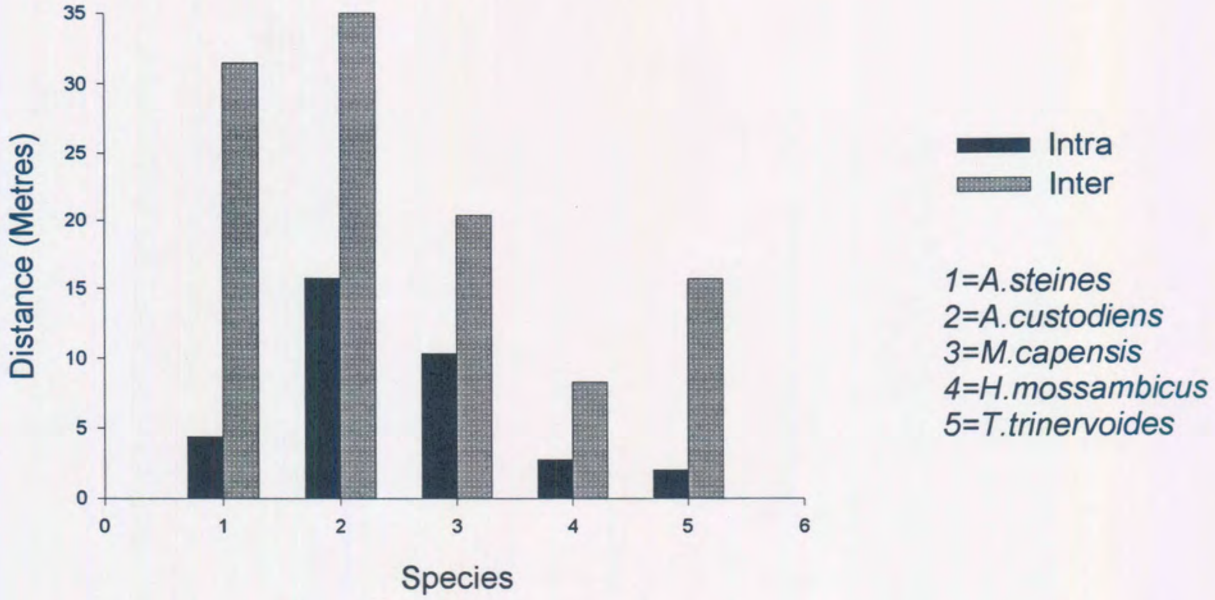


Figure 27. The distance walked between feeds on the same and different species by the aardvark in winter.

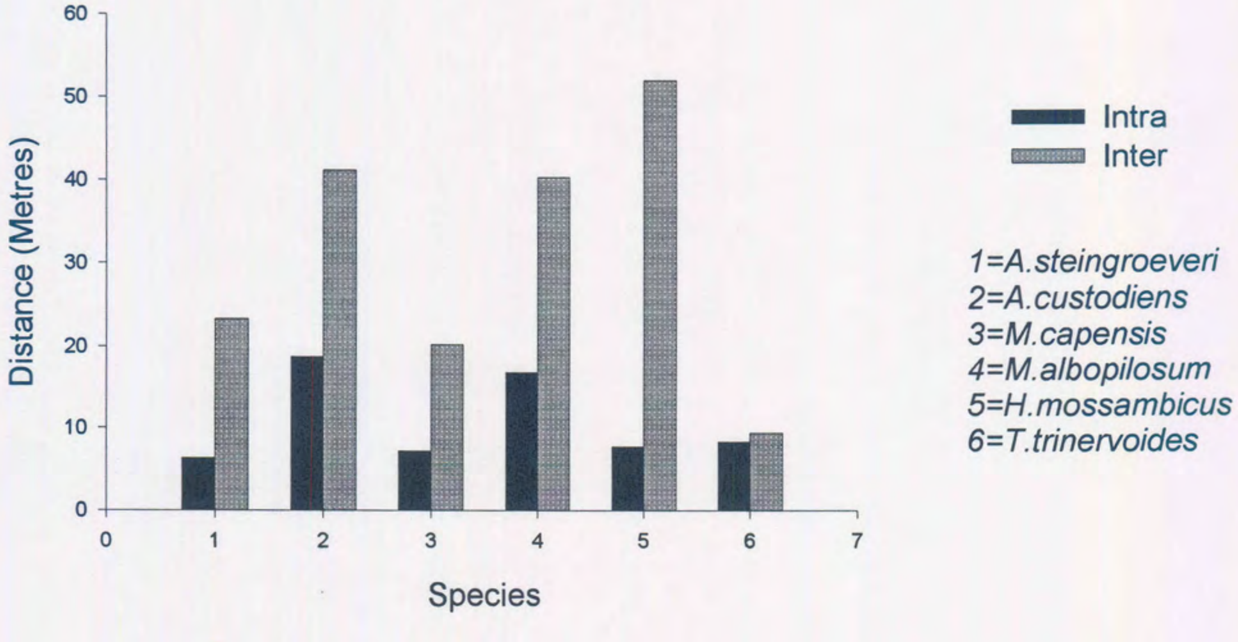


Figure 28. The distance walked between feeds on the same and different species by the aardvark in summer.

The Feeding Rates per Hour

The average number of feeds per hour, seconds spent feeding per hour and the distance walked per hour was calculated for each of the study animals in summer and winter. Two-way Anovas were done to determine how these variables differed between the seasons and between the study animals, and whether the relationships were linear (see Table 29).

Table 29. The mean seconds feeding, number of feeds and distance walked per hour.

	Seconds Feeding	Number of Feeds	Distance walked
Winter	761.5	73.9	647.6
Summer	731.9	45.0	679.5

The number of feeds was significantly greater in winter, than in summer (Anova: F=9.130; df=1; P=0.004). There was no significant difference between the study animals in terms of the numbers of feeds (Anova: F=2.505; df=3; P=0.067). In the number of seconds spent feeding per hour, however, there was no significant difference between summer and winter (Anova: F=0.0516; df=3; P=0.813), or between the animals (Anova: F=0.374; df=3; P=0.772). In addition, there was very little difference between the average distance walked per hour between summer and winter (Anova: F=0.102; df=1; P=0.751), or between the study animals (Anova: F=1.910; df=3; P=0.131).

The Proportion of Feeds Made at Fresh Sites.

This aspect of feeding behaviour provides further insight into the feeding patterns of the species in the area (see Table 30).

Table 30. The proportion of feeds made at fresh sites in summer and winter.

	Winter	Summer
A. custodiens	97.1	98.3
A. steingroeveri	99.0	97.4
Camponotus spp.	99.0	100
H. mossambicus	94.9	84.4
M. albopilosum	100	98.3
M. capensis	98.3	93.0
T. trinervoides	77.5	95.5
T. trinervoides (mound)	28.6	50

In both seasons, the vast majority of feeds were made at fresh sites. However, a significant proportion of the feeds made upon *T. trinervoides* were at ready-dug sites. In summer, 4.5% of ground feeds and 50% of mound feeds on this species were from non-fresh sites, whilst in winter the figures were higher still at 22.5% and 71.4%. In winter, only 1.3% of feeds upon *M. capensis* were at non-fresh sites, whilst in summer the figure was much higher at 7.0%. *H. mossambicus* is a third species which was fed upon a considerable number of times from non-fresh sites. In winter 5.1% of feeds were at pre-dug sites, whereas in summer the figure was higher at 15.6%

The Depth of Digs.

Digging is energetically very costly and the depth of the digs on each of the species correlates with the energy expenditure required to obtain that prey species. Figure 29, shows the average depths for the various prey species in winter and summer. The average depth of digs in winter across all species was 6.12 cm, whilst the figure for summer was 11.7 cm, a pattern which is apparent from the graph.

A three-way Anova on ranks was carried out to determine the effects of species and season upon the mean depth of digs. There was a significant difference between the seasons (Anova: F=19.924; df=1; P=<0.001), the average depth in summer being significantly greater than in winter. For example, *A. custodiens* was fed upon from digs with an average depth of 8.5 cm in winter, compared with 12.3 cm in summer. *H. mossambicus* was fed upon from an average depth of 0.9 cm in winter, compared with 9.4 cm in summer. *T. trinervoides* also showed large differences between the seasons, being fed upon from digs of 4.2 cm on average in winter, and 9.4 cm in summer. There was also a significant difference between the species in terms of the depths of digs (Anova: F=10.705; df=3; P<0.001) and study animals (Anova: F=3.673; df=2; P=0.027) in terms of the dig depth. In addition, there were significant interactions between study animal and species (Anova:F=2.78; df=6; P=0.013) and between season and species (Anova: F=3.6; df=3; P=0.015) in terms of their effect upon dig depth.

The relationship between the dig depth and the length of the feeds in summer and winter was tested using linear regression. In both seasons, there was no significant correlation between these parameters (Winter: R=0.202; df4; P=0.745), (Summer: R=0.35; df6; P=0.429).

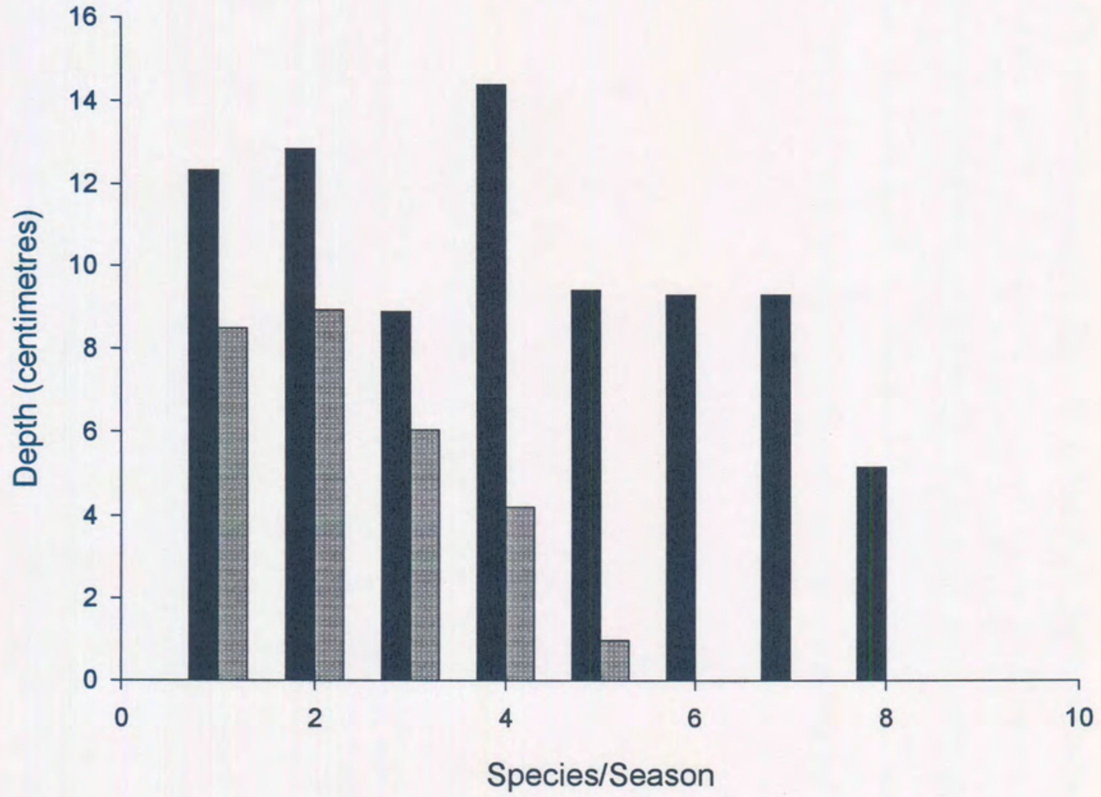


Figure 29. The average depths of the digs made on the various prey species in summer and winter

1=A. steingroeveri
2=A. custodiens
3=M. capensis
4=T. trinervoides
5=H. mossambicus
6= M. albopilosum
7=Camponotus spp.
8=C. melanogaster

■ Summer
▨ Winter

Prey Selection

In this section, the prey selection of the aardvark is considered, first relative to the availability of the various species. This is intended to establish the degree of selectivity in the diet. Following this, an attempt is made to determine which factors are of importance in dictating prey choice.

Pit Fall Trapping

Chi-Square tests were done to compare the diet of the aardvark expressed as the percentage of the faecal content made up by each of the prey species, with the RI of the various species in the pitfall trapping. The RI figure is the same as was used in Chapter 1, the abundance adjusted for the frequency of occurrence. Chi-Square Tests were done for the winter and then the summer data.

Table 31. The Observed, and Expected values for the utilisation of the species caught in the pitfall traps in winter, and the calculated Chi Square Statistic.

ANT/TERMITE SPECIES	Observed Winter	Expected Winter	Chi Square Statistic
Dolinchoderinae			
Linepthema humile	0.35	1	0.4
Total	**0.35**	**1**	**0.4**
Formicidae			
Anoplolepis species.	2252.1	32.8	150 159.2
Camponotus fulv/macu/nasut	52.9	0.2	13 925.3
Lepisiota sp1	0.4	0.2	0.1
Total	**2305.4**	**34.4**	**164 084.6**
Myrmicinae			
Messor capensis	69.4	48.2	9.4
Monomorium sp1	0.4	0.2	0.1
Monomorium sp2	0.4	0.8	0.2
Monomorium albopilosum	155.4	958.4	672.8
Monomorium havilandi	2.4	5.6	1.8
Monomorium notulum	0.4	2	1.4
Pheidole sp1	0.4	349.6	348.9
Tetramorium clunem	0.4	7	6.3
Tetramorium erectum	0.4	0.4	0.01
Tetramorium sericeiventre	0.4	0.2	0.1
Tetramorium setigerum	0.4	1	0.4
Tetramorium sp1	0.4	0.2	0.1
Total	**230.4**	**1373.6**	**1041.6**
TERMITIDAE			
Hodotermitidae			
Hodotermes mossambicus	143.0	6	3129.5
Nasutitermitinae			
Trinervitermes trinervoides	800.6	2066	775.0
Total	**943.6**	**2072**	**3904.5**
OVERALL TOTAL	**3479.8**	**3479.8**	**169 031.1**

There was a highly significant difference between the observed and expected values for the utilisation of the various species caught in the pitfall traps in winter (X2=169 031.1; df18; P<0.001). Large differences occurred between the observed and expected values for a number of species. *Anoplolepis spp.* and *H. mossambicus* were highly preferred in the diet relative to the availability. In contrast, *M. albopilosum*, *Pheidole* sp. 1 and *T. trinervoides* were highly under-utilised relative to availability. A significant number of the available species (particularly the myrmicines) were absent from the diet. Overall, the Myrmicines and Isoptera were highly under-utilised, while the Formicines were highly preferred. Summer availability was also compared with the utilisation indicated by the faecal results.

Table 32. The Observed, and Expected values for the utilisation of the species caught in the pit fall traps in summer, and the calculated Chi Square Statistic.

ANT/TERMITE SPECIES	Observed Winter	Expected Summer	Chi Square Statistic
Formicidae			
Anochetus levaillanti	0.5	1	0.3
Anoplolepis sp. 1	0.5	17	16.1
Anoplolepis spp	3076.6	1111	3477.7
Camponotus fulv/macu/nasut	76.3	10.2	428.9
Camponotus sp.2 emarginatus gp	0.5	1.2	0.5
Camponotus simulans	0.5	0.2	0.3
Lepisiota capensis	0.5	0.2	0.3
Total	**3155.3**	**1140.8**	**3924.2**
Myrmicinae			
Crematogaster melanogaster	1.4	0.01	185.4
Messor capensis	22.9	13	7.5
Monomorium albopilosum	438.9	217.4	225.6
Monomorium havilandi	7.3	224.8	210.4
Monomorium notulum	0.5	11.8	10.9
Monomorium willomorense	0.5	3	2.1
Monomorium sp.1 salomonis gp	0.5	7.4	6.6
Ocymyrmex weilzecher	0.5	35.8	34.9
Pheidole sp1	2.7	109.6	104.2
Pheidole sp3	0.5	0.2	0.3
Tetramorium erectum	0.5	0.8	0.1
Tetramorium nr amaurum	0.5	0.2	0.3
Tetramorium sp1	0.5	0.2	0.3
Tetramorium sp. nr frigidum	0.5	0.4	0.01
Tetramorium sp. 2 simillum gp	0.5	7.8	6.9
Tetramorium sericeiventre	0.5	15.2	14.3
Tetramorium setigerum	0.5	1.6	0.8
Total	**478.6**	**398.0**	**810.7**
TERMITIDAE			
Hodotermitidae			
Hodotermes mossambicus	214.9	20.2	1875.9
Nasutitermitinae			
Trinervitermes trinervoides	27.4	2066	2011.5
Total	**242.3**	**2086.2**	**3887.4**
OVERALL TOTAL	**3876.2**	**3876.2**	**8622.3**

As with the winter data, there was a highly significant difference between the observed and expected utilisation of the available species (X2=10 8622.3, df26, P<0.001). Again, *A. custodiens* and *H. mossambicus* were highly preferred. In summer, *M. albopilosum* was also slightly over-utilised relative to availability. In contrast, *T. trinervoides* was highly under-utilised. As in winter, the Formicines were preferred in general, whilst the Isoptera were highly under-utilised. In contrast to he winter data, the Myrmicines were preferred slightly.

Prey Availability in the Home Ranges of Individual Animals: Quadrat Sampling

The diets of the individual study animals were looked at relative to the estimates of availability gained from quadrat sampling. Quadrat sampling was done only during the summer months and so comparisons are limited to this period. In addition, the quadrat data were collected in terms of the percent occurrence of the various species. As a result, this enabled direct comparison of the percent occurrence of the various species in the faeces.

Table 33. The expected utilisation of the various species as indicated by the occurrence % in the quadrats in the home range of study animal A1, and the observed occurrence in the faeces of this animal.

ANT/TERMITE SPECIES	Observed Occurrence	Expected % Occurrence	Chi Square Statistic
Formicidae			
Anoplolepis spp	80.7	16.6	247.6
Camponotus spp	62.8	70	0.7
Lepisiota capensis	0.01	6.6	6.6
Total	**143.5**	**93.2**	**254.9**
Myrmicinae			
Meranoplus spininodis	0.01	3.3	3.3
Messor capensis	26.9	0.01	72 181.8
Monomorium albopilosum	71.8	73.3	0.04
Monomorium havilandi	17.9	10	6.3
Monomorium notulum	0.01	13.3	13.3
Monomorium willowmorense	0.01	6.6	6.6
Ocymyrmex weilzecher	0.01	6.6	6.6
Pheidole sp. 1	17.9	46.6	17.7
Tetramorium dichroum	0.01	3.3	3.3
Tetramorium nr frigidum	0.01	3.3	3.3
Tetramorium sp. 2 simillum gp	0.01	6.6	6.6
Total	**134.5**	**172.9**	**72 248.6**
Ponerinae			
Plectronectena mandibularis	0.01	3.3	3.3
Total	**0.01**	**3.3**	**3.3**
TERMITIDAE			
Hodotermitidae			
Hodotermes mossambicus	80.7	20	184.3
Nasutitermitinae			
Trinervitermes trinervoides	9.0	75	58.2
Total	**89.7**	**95.0**	**242.4**
OVERALL TOTAL	**735.42**	**735.42**	**72 749.3**

There was a highly significant difference between the percentage occurrence of the various ant and termite species in the quadrats in the home range of study animal A1, and the observed occurrence in the faeces of this animal (X2 68 148.4, df=15, P<0.001). The majority of available species were not utilised at all, whilst some species were very under-utilised. *T. trinervoides* and *Pheidole* sp. 1, for example occurred less frequently in the faeces than in the quadrat samples. Conversely, *Anoplolepis spp* and *H. mossambicus* were highly preferred. The Myrmicines and Isoptera were under utilised overall, whilst the Formicines were preferred.

The diet of study animal A2 was compared with the availability of the various ant and termite species within the home range area (see Table 34).

Table 34. The expected utilisation of the various species as indicated by the percent occurrence in the quadrats in the home range of study animal A2 and the observed occurrence in the faeces of this animal.

ANT/TERMITE SPECIES	Observed% Occurrence	Expected % Occurrence	Chi Square Statistic
Formicidae			
Anoplolepis spp	68.4	33.3	37.1
Camponotus sp.2 emarginatus gp	60.8	20	83.2
Camponotus fulvopilosus	60.8	66.6	0.5
Lepisiota capensis	0.01	13.3	13.3
Total	**190.1**	**133.2**	**134.1**
Myrmicinae			
Crematogaster melanogaster	7.6	10	0.6
Messor capensis	22.8	23.3	0.01
Monomorium albopilosum	60.8	60	0.01
Monomorium havilandi	15.2	10	2.7
Monomorium notulum	0.01	13.3	13.3
Pheidole sp. 1	0.01	30	29.9
Tetramorium erectum	0.01	3.3	3.3
Tetramorium nr frigidum	0.01	20	19.9
Tetramorium sericeiventre	0.01	3.3	3.3
Tetramorium sp. 2 simillum gp	0.01	6.6	6.6
Total	**106.4**	**179.8**	**79.7**
TERMITIDAE			
Hodotermitidae			
Hodotermes mossambicus	68.5	3.3	1286.6
Nasutitermitinae			
Trinervitermes trinervoides	26.4	75	31.5
Total	**94.8**	**78.3**	**1318.2**
OVERALL TOTAL	**391.3**	**391.3**	**1532.0**

There was a highly significant difference between the observed utilisation of the various species and availability in the home range of A2 as indicated by the quadrat samples (X2=1532.0; df14; P<0.001). Again, *Anoplolepis* spp, and *H. mossambicus* were highly preferred, whilst *T. trinervoides* was highly under-utilised relative to the availability suggested by the quadrats. The Formicines were preferred, whilst the Myrmicines and Isoptera were under-utilised.

Table 35. The expected utilisation of the various species as indicated by the percent occurrence in the quadrats in the home range of study animal A3 and the observed occurrence in the faeces of this animal.

ANT/TERMITE SPECIES	Observed% Occurrence	Expected % Occurrence	Chi Square Statistic
Aenictinae			
Aenictus robustus	0.01	3.3	3.3
Total	**0.01**	**3.3**	**3.3**
Formicidae			
Anoplolepis spp	90.8	39.9	64.9
Camponotus sp.2 emarginatus gp	0.01	6.6	6.6
Camponotus spp	62.0	73.3	1.7
Lepisiota capensis	0.01	3.3	3.3
Total	**152.8**	**123.3**	**76.5**
Myrmicinae			
Crematogaster melanogaster	0.01	6.6	6.6
Meranoplus spininodis	0.01	10	10.0
Messor capensis	24.8	23.3	0.01
Monomorium albopilosum	74.3	43.3	22.2
Monomorium havilandi	16.5	20	0.6
Monomorium notulum	0.01	3.3	3.3
Monomorium willowmorense	0.01	3.3	3.31
Pheidole sp. 1	0.01	16.6	16.6
Pheidole sp. 2	0.01	3.3	3.3
Tetramorium dichroum r	0.01	6.6	6.6
Tetramorium nr frigidum	0.01	13.3	13.3
Tetramorium sericeiventre	0.01	6.6	6.6
Tetramorium sp. 2 simillum gp	0.01	13.3	13.3
Total	**115.7**	**169.5**	**105.6**
TERMITIDAE			
Hodotermitidae			
Hodotermes mossambicus	54.5	6.6	347.4
Nasutitermitinae			
Trinervitermes trinervoides	54.5	75	5.6
Total	**109.0**	**81.6**	**353.0**
OVERALL TOTAL	**377.5**	**377.5**	**538.4**

There was a highly significant difference between the expected and observed utilisation of the various ant and termite species in the home range of study animal A3 (X2=538.5; df=19, P<0.001). *Anoplolepis spp, M. albopilosum* and *H. mossambicus* were preferred, whilst *T. trinervoides* was under-utilised relative to the availability suggested by the quadrats. The Formicines and Isoptera were preferred in general, whilst the Myrmicines were under-utilised.

It is apparent that aardvarks don't feed at random upon the ant and termite community. First, of 44 recorded ant and termite species, only 12 (27.3%) were utilised. There were significant differences between the expected utilisation derived from pitfall trapping and quadrats and the actual utilisation in both seasons. One species, *D. helvolus*, occurred in the diet, despite not having been recorded in the pitfall traps.

Several patterns arose in terms of utilisation versus availability of the species. The Formicines, and especially the *Anoplolepis* spp, were preferred both in terms of the faecal content and percent occurrence of the faeces. *H. mossambicus* was also markedly preferred. Conversely, *T. trinervoides* was grossly under-utilised relative to the estimated availability. The Myrmicines were under-utilised overall, with the exception of *M. capensis,* which in terms of numbers was preferred.

Prey Choice and Prey Value

The abundance of the prey is one of many potential determinants of prey selection by the aardvark. Using methods adapted from Swart *et al.* (1999), the major prey species in the diet of the aardvark were considered in terms of a number of variables considered most likely to be important in affecting prey choice. Six parameters were included to generate a prey value figure.

The abundance of each species as suggested by the pitfall trapping results from the grassland (the habitat in which >95% of feeding occurred) was included. The abundance figures were scaled from 1-20, with an increase of one on the scale indicating an increase in abundance of 50 ants. A figure of 1 therefore, indicates an abundance of 1-49, 2 = 50-99, 3= 100-149 etc. One species (*D. helvolus*) was not recorded in the sampling due to its subterranean habits. A low abundance figure of two was given, though this remains speculative. In addition, an abundance figure for *T. trinervoides* was generated by comparing the number of *T, trinervoides* per Ha (see page 43) with an approximation of *A. custodiens* numbers per Ha, as derived from Steyns (1954) nest density counts. This provided a ratio of *T. trinervoides* to *A. custodiens,* which was then applied to the abundance figure for *A. custodiens* derived from the pitfall traps. This gave an abundance figure of 41 for *T. trinervoides* in both prey value models.

The size of each ant species was incorporated. The length was included without alteration as it was thought that the volumetric measurement used by Swart *et al* (1999) was less accurate. The calorific values obtained from the recent work of Taylor (1998) in the same area were included as absolute values. The average dig depth made upon each of the species was included in order to represent the effort expended in obtaining these species. Finally, the aggressiveness and mobility of the various species were included. Following the methods of Swart et al (1999), a figure of 1-5 (1 low, 5 high) was given to each species to represent the mobility and defensive capabilities in the event of an attack on the nest by an aardvark. These figures were based upon personal observation and review of the available literature. These parameters were combined to generate a figure for Prey Value, using the following equation:

$$\text{Prey Value} = {}_{\text{-}}\text{Log}\left(\frac{\underline{(\text{Size*Abundance*KJ per g})}}{(\text{Defence*Mobility*Depth})}\right.$$

The dietary RI used in this part of the study was derived from the faecal data, due to the fact that these data are drawn from a larger sample size than the observational data. These variables and the resultant prey value for each species is summarised in Tables 36 and 37 for winter and summer, respectively.

Table 36. The value of each factor determining the prey value in winter. A=Abundance; mm=size; D=Depth (cm); Agg=aggression; M=mobility.

	RI	A	mm	KJ/g	Cm	Agg	M	PV
A. custodiens	46.3	1	6	20.2	8.9	4	5	**-0.02**
A. steingroeveri	17.5	1	5	22.0	8.5	4	4	**-0.09**
Camponotus sp.	0.5	1	9	21.1	3	3	3	**0.85**
D. helvolus	1.9	2	6	21.8	9	5	3	**0.28**
H. mossambicus	3.9	1	11	19.2	2.7	1	4	**1.29**
M. albopilosum	4.4	19	3.5	23.2	9.8	2	2	**1.60**
M. capensis	2.0	1	7	20.8	6.0	1	2	**1.08**
T. trinervoides	22.7	41	4	20.2	3.8	3	1	**2.46**

According to Table 36, *T. trinervoides*, followed by *M. albopilosum* had the highest Prey Value in winter. As indicated by the pitfall traps, *T. trinervoides* had by far the highest abundance in the grassland in winter, whilst the abundances of the other species were low. Note that the two *Anoplolepis* spp. were indistinguishable in the faeces, and so the RI of these two species was generated by breaking the *Anoplolepis* spp. into two proportions, relative to the average time spent feeding on each of them during the observations. The two *Anoplolepis* spp showed the lowest prey value figures as a result of their high aggression and mobility values. *H. mossambicus* is by far the largest species eaten by these aardvark, whilst of the major species, *M. albopilosum* was the smallest. The two termite species, and the *Camponotus* spp. were fed upon from shallow digs on average, whilst the other species required deeper digs of similar proportions. *D. helvolus* is the most aggressive, and *M. capensis* and *H. mossambicus*, the least aggressive of the important species in the diet of the aardvark. *A. custodiens, A. steingroeveri* and *H. mossambicus* are highly mobile, whilst *T. trinervoides* is very slow moving indeed. Taking into account each of these factors, *T. trinervoides* had the highest prey value in winter, followed by *M. albopilosum* and *H. mossambicus. A. custodiens, A. steingroeveri* and *D. helvolus* each had low prey values (see Table 36).

Table 37. The value of each factor determining the prey value in summer. A=Abundance; , mm=length; D=Depth (cm); Agg=aggression; M=mobility.

	RI	A	mm	Kj/g	Dcm	Agg	M	PV
A. custodiens	53.8	20	6	20.2	12.9	4	5	**0.97**
A. steingroeveri	13.8	7	5	22.0	12.3	4	4	**0.59**
Camponotus species.	1.7	1	9	21.1	2.7	3	3	**0.89**
D. helvolus	8.4	2	6	21.8	9	5	3	**0.29**
H. mossambicus	11.9	1	11	19.2	9.4	1	4	**0.74**
M. albopilosum	9.6	5	3.5	23.2	9.3	2	2	**1.04**
M. capensis	0.5	1	7	20.8	8.9	1	2	**0.91**
T. trinervoides	0.7	41	4	20.2	14.4	3	1	**1.88**

As in winter, *T. trinervoides* had the highest prey value figure in summer. The prey value of *A. custodiens* showed a big increase due to the increase in abundance seen during this season, and despite an increase in the average dig depth. The value of *A. steingroeveri* increased, also as a function of an increased abundance. The value of *M. albopilosum* decreased significantly, due to the decrease in abundance in the summer period.

So far, it has been assumed that each of the parameters used in the calculation of a prey value figure is important to the aardvark in terms of its prey selection. This assumption was tested with the use of a backwards stepwise regression on the summer, and winter data. A threshold F value of 4.00 was used to determine which parameters were removed from the model.

In winter, the results of the backwards stepwise regression are summarised in Table 38.

Table 38. Backwards stepwise regression on the winter data, and the variables remaining in the final model.

Group	**DF**	**F**	**P**
Regression	2	4.921	0.066
Residual	5		
Group	**Coeff**	**P**	
Abundance	1.104	P=0.044	
Mobility	14.196	P=0.028	

The abundance and mobility of the various species were the factors found to be of value in predicting the diet of the aardvark in winter (Rsq=0.663).

The same analysis was conducted for the summer data, the results of which are summarised in Table 39.

Table 39. Backwards stepwise regression on the summer data and the variables remaining in the final model.

Group	**DF**	**F**	**P**
Regression	2	8.120	0.027
Residual	5		

Group	**Coeff**	**P**
Abundance	0.451	0.105
Mobility	0.900	0.011

The stepwise regression provided a highly accurate prediction of the utilisation of the various species (Rsq=0.765). Once again the final model indicated that the diet of the aardvark was best predicted by the inclusion of only abundance and mobility, of which the latter had the best predictive power.

DISCUSSION

Feeding Ecology

The diet of the aardvark in TdR has been discussed in detail by three authors. Agreement between the studies would enable conclusions to be drawn with confidence. The present study had the advantage of four habituated study animals compared to two in the study of Taylor (1998) and none in that of Willis (1988). In addition, the intensive sampling of the resource base available to the aardvark provides a strong basis for discussion.

Ants and termites provide an extremely abundant and widespread food source in an enormous variety of habitats and niches. Their eusocial habit ensures that they exist in a concentrated form. However, the abundance and ubiquity of this food source are balanced by a suite of problems incurred during its' exploitation. Ants and termites represent a nutritionally poor food source and their small size dictates that enormous numbers must be consumed daily. A variety of stinging, biting and chemical spraying defence mechanisms exist, the efficacy of which is enhanced by the colonial lifestyle (Redford, 1987). Animals are sensitive to the costs of foraging (Cowie, 1977) and myrmecophage prey is often subterranean, or located beneath hard protective nests requiring considerable effort to expose. These prey are frequently highly mobile and can disperse rapidly. In addition, the size difference between predator and prey precludes accurate selection with the tongue. During each feed, a decision must be made as to when to cease feeding based upon changing value of prey at the feeding patch. These factors have been overcome to some extent by morphological, physiological and behavioural adaptation. This discussion deals with the way in which the behavioural patterns of the aardvark have been tailored to problems associated with utilisation of this food source. First, the effects of the seasonal variation in prey abundance, availability and behaviour upon the feeding patterns of the aardvark are discussed. Following this the diet of the aardvark is considered relative to various facets of prey species biology. Finally, the factors driving the prey selection of the aardvark are considered, relative to the findings of other studies done upon mammalian myrmecophages.

Seasonal Variation in Feeding Patterns

Summer and winter in TdR show extreme differences in climatic conditions and in the availability of resources. Ant and termite abundance and diversity decline markedly in winter. In addition, the activity, foraging patterns and consequently the susceptibility to predation of many of these species varies seasonally. Consequently, the feeding ecology of the aardvark differed, both in terms of the RI of the prey species and in aspects of foraging behaviour.

In winter, feeding was characterised by large numbers of short feeds, whilst in summer the feeds were generally longer and less frequent. However, there was no difference in the amount of time spent feeding between the two seasons. In other words, the type of feeding differed, although the intensity did not. This differs from the findings of Taylor (1998) who found that a greater proportion of time was spent feeding in winter than in summer. Two possible explanations for the difference between the two studies exist. First, Taylor (1998) measured digging and 'handling time' as feeding time, whilst the present study recorded only the time spent feeding on each dig. There was a greater number of feeds per hour in winter than in summer in the present study and so logically one would expect that if one considered digging time as feeding time, the time spent feeding in winter would also be seen to be greater. Secondly, it is possible that the prey abundance was greater and that nutritional stress was less due to the milder conditions experienced.

The average length of feeds was shorter during winter than summer, except for the extremely long feeds upon *T. trinervoides* mounds. The majority of species significant in the diet of the aardvark were considerably more abundant in summer than in winter. Reduced numbers of prey individuals per nest would encourage shortened feeds per nest and an increased number of different feeds. In summer, when the numbers were generally higher, the greater densities of ants per nest would encourage longer feeds per nest.

The phenomenon of shorter feeds in winter was reflected in the difference between the representations of the diet in terms of percentage time spent feeding and percentage number of feeds on the various species. In summer, the two parameters were very similar. However, in winter several species were over represented in their contribution to the percentage total number of feeds and under represented in the percentage time spent feeding. This was because the average feed lengths on these species were less than the overall mean in winter. Ground feeds upon both *T. trinervoides* and *H. mossambicus* were examples of this. Conversely, feeds upon *T. trinervoides* mounds were far longer than the average and were under represented in terms of numbers and over represented in terms of percentage time. The reasons for these patterns will be discussed shortly.

The average depth of digs was greater in summer than in winter. This may be because the softer, wetter soil would render digging easier and less energetically costly than in winter. In addition, the greater concentration of ants per nest in summer may have made the greater effort in terms of exposing the nest worthwhile.

The distance walked did not differ between seasons. During food shortage it may be expected that foraging would occur over a greater area. However, it is likely that the ant nests of the various species persist with reduced numbers, despite the effects of climate. *A. custodiens* nests for example, persist throughout winter despite significant reductions in numbers (Steyn, 1954). As a result the density of nests would be similar between the seasons and so an increase in the area covered per night would not necessarily yield greater returns.

In both seasons, distances between feeds upon nests of the same species were shorter than those between feeds upon different species. This indicated that feeding was clumped. The aardvarks fed on most species in bouts. The majority of species were fed upon several times consecutively before feeding upon other species commenced. An extreme example of this was the average of 18 consecutive feeds made upon *T. trinervoides* from the ground in winter. The reason for this clumped feeding is probably two fold. First, several of the species have clumped distributions. *A. steingroeveri* was a clear example of this, being very abundant in localised areas with predominantly sandy soils (pers. obs.). In these areas this species is the most abundant and as a result the majority of feeds were made upon *A. steingroeveri*. Secondly, multiple feeds on the same nest or colony were often made. For example, *A. custodiens* nests have several openings (Steyn, 1954).

The diet of the aardvark differed between the seasons. The observation results and the faecal analysis agreed in terms of the overall seasonal difference in the diet. However, the two methods conflicted in terms of the RI of several species. These findings are similar to those of Taylor (1998), who discussed reasons for this phenomenon in detail: Differential rates of intake per unit time spent feeding could result in over or under representation of the species in the faeces. This could partly explain the low numbers of *M. capensis* heads in the faeces because they were observed in very low numbers at the feeding site, relative to other species. Secondly, differential rates of digestibility of the various species might be the cause of under representation of a prey species in the faeces. However, the heads in the faeces never showed evidence of partial digestion and the chitinous remains were usually intact. Conversely, the fact that larvae were never observed in the faeces despite almost certainly having been ingested, suggests that larval forms were totally digested. Finally, the under representation of *M. capensis* in the faeces may be due to the fact that this was the only species that was seen to be masticated. Broken fragments of *M. capensis* head capsules were observed in the faeces. Each of these very plausible suggestions remain untested and speculative.

The Diet of the Aardvark: Feeding Patterns Associated with the Various Prey Species.

The diet of the aardvark varies considerably between different localities within southern Africa (Smithers, 1971; Melton, 1976; Smithers, 1983; Melton & Daniels, 1986; Willis, 1988; Taylor, 1998). The present study, in keeping with all of the studies done in southern Africa, indicated that the Formicidae form a more important dietary component than the Isoptera. The contribution of the Isoptera to the diet was greatest during the winter months, as found by Taylor (1998), but contrary to the findings of Willis (1988).

Anoplolepis spp.

A. custodiens has been recorded in the diet of the aardvark in all of the studies done in this region (Smithers, 1971; 1983; Melton & Daniels, 1986; Willis, 1988; Taylor, 1998). *Anoplolepis* spp. were the most important dietary constituents in both seasons in terms of both faecal results and behavioural observations, in keeping with the findings of Willis (1988) and Taylor (1998). *A, custodiens* and *A. steingroeveri* were indistinguishable in the faeces and as a result the findings of this analysis can be discussed only in terms of the genus. However, the observations indicated that *A. custodiens* was three times more important in the diet than *A. steingroeveri.*

The faecal results indicated that *Anoplolepis* spp. were the most frequently occurring species in the diet, having occurred in 97.5% of the samples analysed. The RI values recorded in this study were similar to those of Taylor (1998), but considerably higher than those recorded by Willis (1988). Willis' (1988) work was done several kilometres away from the site of this study and that of Taylor (1998). Given the mosaic distribution of ants and termites indicated by the sampling, it is likely that the availability of prey differed slightly from one part of the reserve to the next, so some differences are to be expected.

The RI of *Anoplolepis* spp. in the faecal samples was slightly higher in summer. However, the behavioural observations indicated that this genus was of far greater importance in summer. In summer, *A. custodiens* and *A. steingroeveri* both had high prey value figures. During this period the abundance of both species was very high and there was the potential for additional nutritional benefit from the high numbers of developmental stages (Steyn, 1954). In winter the two species had very low prey values due to the low abundances and the high aggressiveness and mobility values.

The numbers of workers and developmental stages are at their lowest during the winter months (Steyn, 1954) and it is logical that feeding upon these species was reduced during this period. However, in both seasons and especially in winter, the *Anoplolepis* spp. were preferred, suggesting that the winter prey value figure was inaccurate. Importantly, although the abundance of *A. custodiens* was low relative to the most abundant species *(M. albopilosum)*, it was the second most abundant species greater than 0.5 cm in length. The significance of size in prey choice is discussed shortly. In addition, both species are predominantly diurnal as indicated by the quadrat sampling, and by the work of Steyn (1954). As a result, during the foraging hours of the night, both species are likely to be highly concentrated in the nest and very available to the aardvark.

The two species were given high aggressiveness figures in the prey value model, the behaviour of the two species reflecting their "pugnacious" tag. Both species have the habit of swarming over the aardvark as it feeds, biting fiercely. Although uncomfortable for a human, aardvarks appear to be unaffected by these defences, continuing to feed despite the presence of many individuals on the face and back (pers. obs.). As a result, the aggressiveness of the two species is unlikely to decrease their attractiveness as prey species to the aardvark.

Both species are highly mobile and disperse rapidly from the attack site. It is possible that this is the factor that causes a cessation of the feeding bouts, despite the fact that in many cases hundreds of ants remain at the site. The average length of feeds on *A. steingroeveri* was longer that for *A. custodiens* in both seasons. *A. custodiens* is a faster moving species, quicker to disperse from the feeding site than *A. steingroeveri* and this may be the reason behind the difference in average feed lengths. The length of feeds on both species were greater in summer than in winter, possibly due to the reduced ant numbers in the nests during winter (Steyn, 1954).

The average depths of feeds upon both species were very similar in both seasons, being deeper on average in summer, presumably due to the softer soil. Steyn (1954) noted that queen cell chambers are found as close to 5 cm from the surface, occurring successively to a depth of 45 cm, indicating that the digs were made to a depth sufficient to expose large numbers of prey.

Feeds upon the two species differed markedly in the degree of clumping. The aardvark fed upon *A. steingroeveri* in bouts in localised areas. This was probably a result of the restricted distribution of this species. *A. steingroeveri* was fed upon an average 10.9 times consecutively, compared to 5.1 times for *A. custodiens*. In addition, the average distance between feeds upon *A. steingroeveri* was 4.4 m, in comparison to 15.8 m for *A. custodiens*. Whilst foraging in areas in which *A. steingroeveri* occur, the animals fed almost exclusively on the species until they moved out of the area. In contrast, *A. custodiens* is more widely distributed and common within the area. Probability dictates that two consecutive feeds would likely be upon *A. custodiens*, even if there was a long period of walking in between. This factor inflated the average distance between feeds upon this species.

Trinervitermes trinervoides

T. trinervoides was the second most important dietary component overall, in keeping with the findings of Taylor (1998). Several factors make this species a highly valuable prey item to the aardvark and it's prey value was the highest in both seasons. *T. trinervoides* is extremely abundant and accessible, being concentrated in the mounds or foraging tunnels. In addition, the alates, which can make up 4% of mound numbers during certain times of the year (Adam, 1993), have the highest calorific value of any of the prey species measured (Taylor, 1998). On the other hand, nasute termites have well documented defences (Lubin & Montgomery, 1981; Prestwich, 1983; Redford, 1987). However, the feeding behaviour indicates that these defences have little effect upon the aardvark or its behaviour.

T. trinervoides was utilised to a much greater extent in winter than in summer. Whilst the numbers of most prey species decrease drastically during the winter months, the numbers of *T. trinervoides* remain constant (Adam, 1993) and therefore provide a plentiful food source during a period of nutritional stress. In contrast, Willis (1988) and Melton & Daniels (1986) found termites to be utilised more during the summer months.

In congruence with the findings of Taylor (1998), the majority of time spent feeding upon this species in winter was from the epigeal mounds (61.5%), although a significant amount of time was spent feeding upon the species from shallow scrapes (38.5%). In summer, the same proportion of time was spent feeding upon *T. trinervoides* from the ground and from the epigeal mounds. It has been suggested that the reduced foraging of these termites in winter results in their being concentrated in the mound in large numbers (Taylor, 1998). In addition, during July and August large numbers of alates are present in the mounds whilst during the summer months they are absent (Adam, 1993). These factors explain the increased utilisation of the mounds in winter.

The large number of feeds upon *T. trinervoides* from the ground during winter is contrary to the findings of Taylor (1998) and the observations of Henning (pers. comm). However, the species is known to inhabit the subterranean tunnels during winter (Adam, pers. comm.) and the mild conditions of the winter study period probably increased numbers in the tunnels, possibly explaining the anomaly.

T. trinervoides was under-utilised relative to availability in both seasons. In summer, the abundance of other prey species is extremely high. In addition, the higher activity levels of the termites during this time probably reduces concentrations in the foraging tunnels and epigeous mounds. In winter however, the reasons behind this under utilisation are less clear. It is possible that the clumped nature of the epigeous mounds ensures that large numbers of other prey species are eaten between mound feeds. Montgomery (1985) noted that the vermilingua fed upon a variety of species to avoid excessive intake of defensive chemicals. This mechanism may be employed by the aardvark to avoid excessive intake of *T. trinervoides* terpenoids.

The feeds upon *T. trinervoides* from the ground and from the mounds were different in character. Feeds from the ground were short during winter (5.9 seconds), increasing in length to 15.9 seconds during summer. In summer, it is possible that termite foraging parties are larger and justify longer feeds. The short duration of feeds can be explained by the fact that the foraging parties consist of relatively low numbers of termites, which are likely to be depleted rapidly. Indeed, the aardvarks were often observed to feed upon a tunnel before feeding close by for a short period and returning to the original site. Although the workers flee on attack (pers. obs.), the soldiers are known to be attracted to the site of attack and the return of the aardvark to the site may be in response to this 'replenishment' of numbers at the site. The attraction of soldiers to the site is unlikely to be the cause of the initial cessation of feeding because the low speed of movement prevents an effective change in caste proportions within 30 seconds (Richardson & Levitan, 1994). The ground feeds were shallow scrapes, aimed at exposing the foraging tunnels 2.5 cm beneath the surface (Adam, 1993). Feeding occurred from the surface when large foraging parties were located. In summer, the digs were deeper, averaging 9.4 cm. There is no evidence of a change in the depth of the foraging tunnels with season and this phenomenon was probably a result of the softer soil.

Feeding upon *T. trinervoides* from the ground was clumped, with an average of 18.1 feeds being made upon the species before attention was turned to others during winter. The average distance between feeds was short (2.3 m.) and probably a function of the extreme density of the species in the area. The foraging tunnels extend up to 15 m from the mounds, and foraging areas of different mounds overlap (Adam, 1993). In addition, feeds were frequently made on the same tunnel at different sites. These factors explain the proximity of the feeds and the high numbers of consecutive feeds. Significantly, however, the same species was only fed upon 1.3 times consecutively on average in summer, a result of the low numbers of feeds that were made overall during this period.

Feeds on the mounds were long, averaging 238.1 seconds in winter. The digs into the mounds were often very deep, targeting the centre of the mound where the termites concentrated during the cold winter nights (Adam, 1993). The termites are present in large numbers in these parts of the mound, justifying lengthy feeds. These feeds were usually singular events, due to the relatively large distance between neighbouring mounds.

Hodotermes mossambicus

The next most important species in the diet of the aardvark in the area was *H. mossambicus. H. mossambicus* is the largest prey species in the area and, in terms of the mass of food consumed, *H. mossambicus* made up a greater proportion in winter than indicated by the observations or faecal results. Willis (1988) also found this species to be a significant dietary component, in contrast to Taylor (1998). The additional two animals monitored in this study utilised *H. mossambicus* much more than the two animals observed in Taylor's (1998) study. The present study differed from that of Willis (1988) in that *H. mossambicus* was utilised to a much greater extent during summer than winter. *H. mossambicus* is more active during winter (Nel, 1968; Mitchell *et al.*, 1993) and the concentration of individuals in the nest during summer probably increased their availability as prey to the aardvark.

Seasonal differences in the forging behaviour of *H. mossambicus* was reflected in seasonal differences in the foraging behaviour of the aardvark when feeding upon this species. In winter, the feeds were generally made from the surface or from foraging ports, as indicated by the mean depth of 0.9 cm. The feeding was highly clumped with large numbers of feeds being made on termites foraging from a single port. This was highlighted in the short distance between feeds (2.7 m). In summer, however, the feeds were longer (10.6 seconds) from shallow nests (9.4 cm) where *H. mossambicus* were congregated and more irregular in occurrence with only 3.8 consecutive feeds occurring on average, at a mean distance of 7.6 m from one another.

The calorific value of *H. mossambicus* is slightly lower than that of the other prey species of the aardvark in the area (Taylor, 1998). However, Skinner (unpubl.) showed that the species is a richer source of various essential amino acids than *T. trinervoides* and it is suggested that the species may be selected by mammals for this reason.

The defensive capabilities of the species are poor, consisting of a snapping response by the soldiers, which reside underground (Wilson & Clarke, 1977). Hodotermitid soldiers often flee from mammalian predators (Redford, 1987) and appear to be totally ineffective against the aardvark. *H. mossambicus* are highly, mobile and rapid dispersal is co-ordinated through the release of pheromones following attack (Wilson & Clarke, 1977). This factor, is likely to be the most important in limiting mammalian predation. In summer, over 16% of feeds were made upon digs that had been opened several seconds or minutes before, suggesting that feeding had ceased temporarily as a result of prey dispersal. Leaving a feeding site for a short period may result in the termite density at the attack site being replenished to the extent that further feeding is profitable.

However, as with *T. trinervoides*, the abundance of *H. mossambicus* was under estimated in this study and is known to occur in huge numbers in the area. As a result, the apparent preference of the aardvark is likely to have been an artefact. A more accurate estimation of numbers would probably show that this species is under-utilised by the aardvark. The distribution of the species in the area appears to be very patchy (pers. obs.) indicating that the importance of the species is likely to vary between different areas. In addition, Nel (1968) has indicated that the species is prone to population fluctuations and as a result variation in the contribution to the diet of the aardvark probably has a significant temporal component. This could possibly explain the findings of Taylor (1998).

Monomorium albopilosum

M. albopilosum also made up a relatively insignificant portion of the aardvark diet. Although this species occurred in 83% of the faecal samples, it occurred in low numbers and it was fed upon infrequently, making up a small proportion of the percentage time spent feeding. Feeds were irregular and generally singular events, despite the extreme abundance of the species, particularly during winter when the abundance of most other species was highly reduced. Relative to the availability indicated by all three sampling methods, *M. albopilosum* was highly under utilised.

Explanation for this under utilisation cannot be found in terms of the calorific value of the species as this species has the highest calorific value of any of the local species tested (Taylor, 1998). In addition, the mobility of the species was low relative to the other species and the aardvark showed no signs of irritation caused by the defence of the species. The most likely reason for the under utilisation of the species is its small size; *M. albopilosum* was the second smallest species after *M. havilandi* in the diet of the aardvark.

The Factors Driving Prey Choice

The feeding of the aardvark was non-random. Of the 44 species recorded in the area, only 27.3% were recorded in the diet of the aardvark. The Formicines were highly preferred, whilst the Myrmicines were under-utilised, conforming to the findings of Redford (1987), who noted that in terms of the number of genera consumed by myrmecophages, myrmicines were less preferred than the Formicines. The Isoptera were under-utilised in terms of relative numbers in the faeces relative to those available. The prey choice and feeding patterns of the aardvark are driven by a variety of factors, of varying significance.

Abundance

It has been suggested that the relative abundance of prey is an important factor in determining prey choice in myrmecophagous mammals (Redford, 1987; Abensperg-Traun, 1990). Abundance was predictive of utilisation and was included in both final models. However, the various species were not all utilised in proportion to their abundance. *M. albopilosum* and *T. trinervoides* being particularly clear examples of this.

The haphazard mode of foraging makes abundance likely to be important in determining utilisation. For example, the fact that *A. custodiens* is more widespread and numerous than *A. steingroeveri* probably explains why it is utilised to a much greater extent than the more localised species. All of the species of major importance in the diet of the aardvark are extremely abundant in the area and it seems likely that above a certain threshold of abundance other factors drive prey selection.

Prey Activity

The activity patterns of the prey species may be of some importance in determining utilisation by the aardvark. *H. mossambicus,* for example exhibits unpredictable activity patterns as an anti-predator strategy (Wilson & Clark, 1977). In addition, the nocturnal activity of *M. albopilosum* probably decreases availability as prey to the aardvark by decreasing the concentration of ants in the nest. Most other species utilised by the aardvark are predominately diurnal and as a result during the nocturnal foraging hours of the aardvark, are concentrated within the nests. However, prey activity was not included in the model because the activity of some species was unpredictable and activity affected the availability of species in different ways.

Prey Defences

The defences of ants and termites are reported to be of importance in affecting prey choice in a number of myrmecophages (Lubin & Montgomery, 1981; Redford, 1985; Richardson, 1987). Evidence for this has been found for a variety of myrmecophages, including the aardwolf, *Proteles cristatus* (Richardson, 1987), the pangolin, *Manis temminckii* (Swart, 1996), the giant anteater, *Myrmecophaga tridactyla* (Redford, 1985), the Vermilinguas *Cyclopes didactylus* and *Tamandua mexicana* (Montgomery, 1985), the echidna, *Tachyglossus aculeatus* (Abensperg-Traun, 1990) and the numbat, *Myrmecobius f. fasciatus* (Calaby, 1960). Prey defences cause irritation and premature cessation of feeding bouts in a number of species (Redford, 1987). It has been suggested that the preference of myrmecophages for Formicines over Myrmicines can be explained in terms of prey defences. In this study however, this preference appears to be more a function of prey size than prey defence.

Mammals are the second most important predators of ants and termites, after other ants (Redford, 1987) and there has likely been strong selective pressure to develop defences designed to reduce mammalian predation. Conversely, the evolutionary age of the aardvark and many other mammalian myrmecophages has provided ample time for the development of counter adaptations through co-evolution. There is some evidence for prey defences affecting the aardvark. For example, considerable discomfort and frantic grooming behaviour was observed when the aardvark fed upon *D. helvolus*. In addition, Taylor (1998) suggested that the selection for larger *T. trinervoides* mounds by the aardvark may be due to the lower proportions of soldiers relative to smaller mounds. However, several factors suggest that the effect of prey defences upon the feeding patterns of the aardvark is limited. First, this factor was not predictive of utilisation and was dropped from both summer and winter models. Only *D. helvolus* caused visible discomfort on a regular basis during feeding bouts. In addition, in contrast to the pangolin (Swart, 1996), *H. mossambicus* caused no discomfort to the aardvark. The hard mounds of certain termite species are an effective barrier to a number of myrmecophages (Calaby, 1960; Redford, 1983; Richardson, 1987; Abensperg-Traun, 1990; Swart, 1996) whilst the aardvark penetrated *T. trinervoides* mounds with consummate ease. The frontal glands of nasute termites (including *T. trinervoides*) secrete a highly noxious terpene-based substance (Richardson, 1987) and it has been suggested that the aardwolf is the only mammal species able to tolerate large numbers of *T. trinervoides* soldiers in the diet (Andersen, 1994; Richardson & Levitan, 1994). However, the proportions of the soldiers in the aardvark faeces were much higher than in the mounds indicating that the aardvark is not too careful to avoid their ingestion. In addition, the aardvark fed freely from foraging parties, despite the presence of higher proportion of soldiers than in the mounds (Adam, 1993). This evidence indicates that the aardwolf is by no means unique in its tolerance.

Some behavioural features of the aardvark probably reduce the effect of prey defences. First, on reaching prey nests they dig very rapidly and then feed frantically, enabling consumption of prey to occur before the concentration of soldiers can increase significantly. Secondly, frequent digging during feeding probably has the effect of removing any build up of soldiers. Finally, the absence of chewing reduces the release of chemical defences. For example, the head capsules of *T. trinervoides* containing most of the terpenoids tend to pass into the faeces intact.

Redford (1983) showed that the efficacy of prey defences depends upon the size of the predator and the aardvark is likely to be less affected than smaller species. In addition, the thick skin is probably largely impenetrable to the jaws of most ants and termites.

Prey Mobility

Prey mobility was highly predictive of prey utilisation in both seasons and was included in both final models. The mobility of a species has the potential to rapidly reduce the value of a 'prey patch' (Abensperg-Traun, 1990) and encourage the aardvark to move to a fresh site. The mobility of *H. mossambicus* and *A. custodiens,* for example, rapidly reduces the prey density at the feeding site (pers. obs.). This seems to be a plausible explanation for the fact that aardvarks frequently leave feeding sites despite the presence of hundreds of ants around the nest exit. The aardvark tongue is vermiform, adapted for insertion into holes and tunnels, not for lapping ants up from the surface. As a result, once the ants had dispersed from the tunnel they are largely unavailable to the aardvark. In contrast, the low mobility of *T. trinervoides* is probably a major reason behind the length of feed upon the mounds.

Calorific Value of the Various Prey Species

The degree to which energy is limiting will remain unknown in the absence of detailed energetic studies. However, the aardvark is a very large mammal and it feeds upon very small prey items of relatively low nutritional value. The vast majority of time is spent foraging for food and logically the aardvark might select species richer in calories.

Invertebrates generally show little variation in calorific value (Redford & Dorea, 1984) and the prey species of the aardvark in TdR are no exception (Taylor, 1998). Calorific value was not predictive of utilisation in either season and was dropped from both models. However, increased numbers of *T. trinervoides* alates in the mounds appears to be important in causing the increased importance of this species in winter. To this extent, calorific value may be of importance in driving prey choice.

Prey Size

Given the similarity of the calorific values of the various species, one might expect the size of the various prey species to be of significance in prey choice. Most of the species included in the model were large and correspondingly, this factor was not predictive of utilisation of the species included in the model. However, there was strong selection for large prey species. All of the species of major importance in the diet were over 0.5 cm in length (with the exception of *T. trinervoides*) and only one large species *(O. weilzecher)* was absent from the diet. In contrast, the vast majority of species recorded in the area were much smaller.

Dig Depth

If energy is limiting, one would expect the cost of exposing the prey to be of importance in prey selection. Digging is energetically costly and differences in the depths of the various prey species may affect their value as prey items. However, several points suggest that this factor is of little importance in prey choice by the aardvark. For example, the depth at which the various species were fed upon was not correlated with utilisation or feed length in either season, suggesting that digs were made to the depth required to expose prey regardless of value. In contrast, the pangolin has been shown to make longer feeds upon species where the depth of the digs is greater, indicating that more effort was expended for species of higher value (Swart, 1996). In addition, the difference between the average depths of the feeds upon the various species of major importance in the diet was small and in energetic terms, probably insignificant. Finally, the aardvark spent much of its time when not feeding, excavating old holes, a pastime which involved digging effort greater than that expended during most feeds by several orders of magnitude.

The digging ability of the aardvark is renowned and several factors suggest that the species is less limited by digging constraints than other species. As mentioned previously, the aardvark is the only myrmecophage in southern Africa capable of penetrating the hard mounds of many termite species. In addition, the average dig depth for the aardvark was also much deeper than that of the pangolin. For example, the pangolin made digs of 3.6 cm on average when feeding upon *A. custodiens* (Swart, 1996) which is insufficient to expose the shallowest queen cells (Steyn, 1954). In contrast the aardvark made digs of 10.9 cm on average when feeding upon this species.

Constraints Upon The Myrmecophagous Lifestyle: Patterns.

The characteristics of social insects as prey have resulted in considerable specialisation in the aardvark and many other myrmecophagous mammals. There has been marked convergent evolution between mammals within this feeding guild (Melton, 1976). This convergence has been both morphological and apparently physiological, with most mammalian myrmecophages having lower metabolic rates than predicted by body size (Schmidt Nielsen *et al.,* 1968, in Abensperg-Traun, 1990, McNab, 1984). Much less well documented however, is the behavioural convergence.

Mammalian myrmecophages frequently show a meandering, almost haphazard foraging pattern, reflecting the often ubiquitous distribution of their prey. Location of the subterranean prey is typically olfactory, in response to the subterranean or cryptic nature of their prey. The small size and poor nutritional quality of the prey often results in the vast majority of time being spent foraging. Chewing is absent in many myrmecophages, a feature thought to be an adaptation enabling rapid ingestion of food in response to the high mobility of the prey (Redford, 1987). Correspondingly, the teeth are often greatly reduced. The feeds are typically short due to prey dispersal or defences. The short feeds generally cause little prey value depression, a factor which is probably the cause of the absence of territoriality in many myrmecophages (Redford, 1983). Finally, myrmecophages tend to be very flexible, showing large variations in the diet across their geographical range. This flexibility is a major contributor to their success and many of these species, including the aardvark have extremely wide distributions as a result.

In conclusion, the feeding ecology of the aardvark is affected by several aspects of prey species biology. Seasonal variation in feeding patterns occurs as a result of variation in abundance and activity of the prey species. Seasonal prey choice is affected by a great variety of factors, none of which operate in isolation. Several factors that do not directly affect the selection of a species, may affect the RI of a species in the diet indirectly through affecting feeding patterns such as the length of feeds. The aardvark is highly specialised, and is arguably better adapted to myrmecophagy than many other species, the aardwolf and pangolin in particular.

Chapter 3

Habitat Use

Introduction

The habitat selection of the aardvark has largely been neglected. Smithers (1971) found evidence of activity throughout Botswana, from riverine, bushveld and open grassveld habitat. Evidence of aardvark activity was absent only from rocky hills or areas liable to seasonal flooding. In addition, Willis (1988) measured aardvark sign in the three major habitats of TdR and found that riverine and steep slope areas were largely devoid of sign. However, no study to date has combined behavioural observation with rigorous quantification of aardvark sign relative to food availability and habitat variables. The main objectives of this part of the study were to determine the seasonal habitat selectivity of the aardvark and the factors influencing this selection. In addition, the feeding patterns exhibited in each of the habitats were compared.

Materials and Methods

1. Habitat Availability

The availability of habitat in the area was determined using 1/50 000 aerial photographs of the area, supplied by the Department of Regional and Land Affairs. The different habitats were readily distinguishable in these pictures and the proportion of land area made up by each was calculated. Once the habitat availability was established, the next step was to determine the extent to which the aardvark utilised the various habitats.

2. Behavioural Observation

The first measure of habitat use was behavioural observation, as discussed in the previous chapter. Recording the habitat in which each feed was made enabled the quantification of habitat use. In addition, the characteristics of the feeds, such as depth, length and distance could also be compared between habitats.

3. Line Transects

Line transects were used to quantify the usage of the various habitats. Again, this reduced the reliance upon the low sample size of habituated aardvarks. The use of a second technique also gave increased credence to the results obtained. Line transects were used to give a comparative measure of aardvark activity between the habitats. In addition, various habitat characteristics, both physical and biological were quantified to increase the explanatory power of the results obtained.

Nine transects were done in each of the three habitats. The design of transect sampling was based upon that of Willis (1988). The sites and directions of transects were chosen at random. Each line was 100 m in length and 2.5 m wide. The centre of the transect line was marked by placing stakes at ten metre intervals. This enabled the accurate measurement of objects from the centre of the line. Items were recorded if more then 50% of their surface area lay within the designated 2.5m width (Willis, 1988). The following aspects of aardvark activity were recorded:

- Number of aardvark food digs. Aardvark food digs were distinguished from those of porcupine (*Hystrix africaeaustralis)* sign by the broad claw marks made by the digging of the study species. In addition, personal familiarity with the appearance of aardvark sign made identification simple. A field guide was used to increase certainty. Only those diggings that could be identified unambiguously as those of the aardvark were recorded.

The validity of the comparison of dig numbers between habitats was tested by comparing the erosion rates of artificial aardvark digs between habitats using a method adapted from that of De Villiers & van Aarde (1994). This was achieved by observing the erosion rate of equally proportioned artificial digs. Nine sites were selected randomly in each habitat. At each of these sites three artificial digs were placed. The dimensions of each dig were made as similar as possible, in a quarter ellipsoid shape with a maximum depth of 12 cm, a maximum width of 22 cm and a length of 22 cm. These proportions were based upon measurements of aardvark diggings. Measurements were taken from each of the digs four months after their creation.

- Number of aardvark defecation digs. On defecating, aardvarks leave a very distinctive broad scrape next to a small heap of soil, containing the faeces. This is created by the claws of the hind feet whilst the animal covers the scat.

- Number of aardvark burrows. Again only holes that were unambiguously those of the aardvark were recorded. As such, semi-collapsed holes or those of a different size were not counted.

In addition, a number of habitat characteristics were quantified using the line transects:

- Degree of rockiness. This was determined by placing a 1m^2 quadrat every ten metres along the transect. Within each quadrat, the percentage of the ground surface covered by rocks was estimated carefully.

- Grass cover. This was determined in the same fashion as above.

- Number of bushes, shrubs and trees. This was determined by counting all woody vegetation above 50 cm in height.

RESULTS

Habitat Availability and Utilisation

The availability and seasonal utilisation of the three habitat types is expressed in Tables 40 and 41.

Table 40. The habitat availability in the study area and the habitat utilisation of the study animals in winter.

	Available	Utilisation	Utilisation	Utilisation	Utilisation
		A1	A2	A3	A4
Grassland	**58.6%**	99.7	100	97.1	100
Steep slopes	**24.3%**	0.3	0	2.9	0
Riverine	**17.1%**	0	0	0	0

Table 41. The habitat availability in the study area and the habitat utilisation of the study animals in summer.

	Available	Utilisation	Utilisation	Utilisation	Utilisation
		A1	A2	A3	A4
Grassland	**58.6%**	94.2%	100%	94.8%	100%
Steep slopes	**24.3%**	5.8%	0%	5.2%	0%
Riverine	**17.1%**	0%	0%	0%	0%

The grassland habitat covered the greatest area in the study site, followed by the steep slope areas and finally the riverine. Each of the three habitats made up a substantial portion of the area of the reserve. However, it can be seen from the table above that only the grassland habitat was utilised to any significant extent. The steep slope areas were highly under-utilised relative to availability, whereas the riverine habitat was not used at all during the study period. The available habitat and the utilisation of the various habitats in summer and winter is expressed on Figures 30, 31 and 32, respectively.

A Chi-square test was performed to compare the expected habitat use with the observed habitat use in winter and in summer. There was a highly significant difference between these two parameters in both tests (X2; df2=67.84; P<0.001) and (X2; df3=61.56; P<0.001) for winter and summer, respectively.

Two of the study animals were not seen to utilise habitats other than the grassland areas in summer or winter. In winter, the 2.9% of time spent in the steep slope habitat by study animal A3 was the greatest amount of time spent feeding in another habitat. In summer, study animals A1 and A3 used the steep slope habitat for 5.8% and 5.2% of time, respectively.

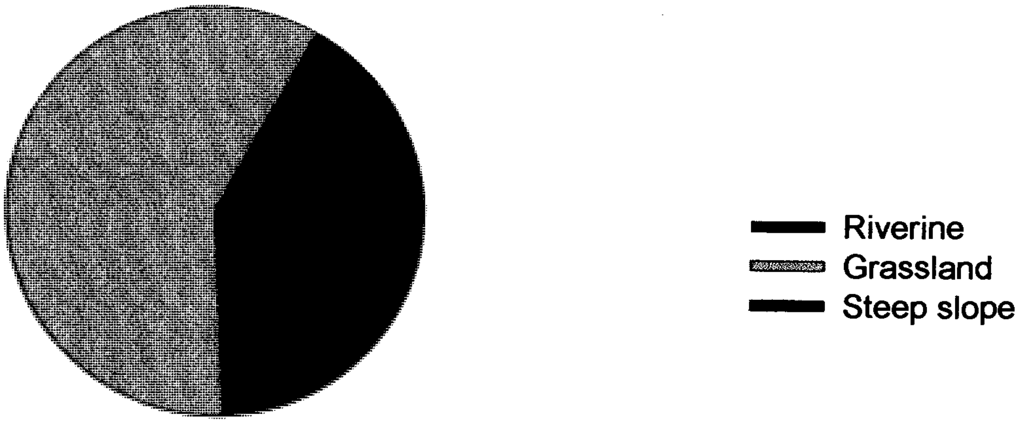


Figure 30. The habitat availability within the study area

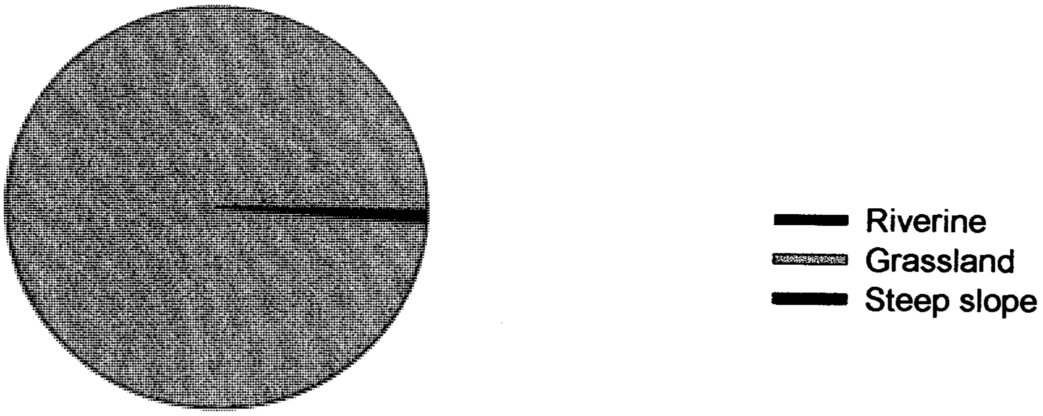


Figure 31. The average winter habitat use

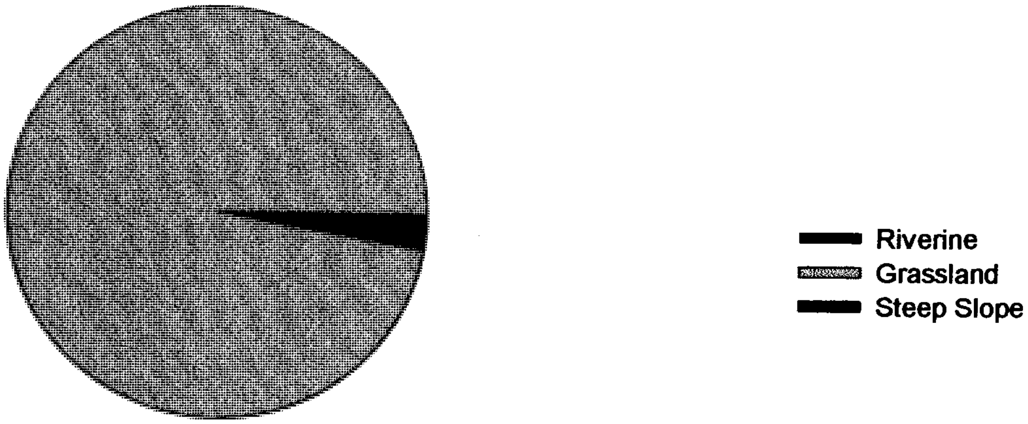


Figure 32. The average summer habitat use

The identity of the prey species taken during feeds in the steep slope habitat was recorded. A total of seven ant species and two termite species were recorded as being fed upon in the steep slope habitat, in contrast to the ten ant species and two termite species recorded in the grassland habitat. The proportion of feeds made upon the various species in the steep slope habitats during summer is illustrated in Table 42.

Table 42. The time spent feeding upon the various prey species in the steep slope habitat summer.

	A1	A2
A. steingroeveri	56.0	5.9
A. custodiens	3.5	82.2
M. capensis	2.9	2.9
T. trinervoides	7.7	0
M. albopilosum	7.7	6.2
H. mossambicus	17.3	0.9
Camponotus spp.	0.4	0.3
Pheidole sp. 1	4.1	0
	0.4	0

The two study animals show large differences in the proportions of the diet made up by the various prey species in the steep slope habitat. Study animal A1 fed predominantly upon *A. steingroeveri* (56.0%) in this habitat, followed by *H. mossambicus* (17.3%). In contrast, study animal A3 fed largely upon *A. custodiens* (82.2%), followed by *M. albopilosum*..

The RI of the various species in the steep slope feeds relative to the overall feeds was very different. However, due to the low sample size and very low number of feeds made in the steep slope habitats this is unlikely to be representative of feeds in this habitat overall. In addition, the low number of feeds made in habitats other than the grassland made accurate calculation of feeding parameters such as average depths, lengths etc. impossible.

Transect Sampling

Erosion Rates in the Three Habitats

The depths of 27 artificial aardvark digs were measured four months after they were created. A two-way Anova was carried out on the depths of the four-month-old digs in each habitat in order to show whether there was a difference in erosion rates. There was no significant difference between the habitats in this regard (Anova; F=1.105; df2; P=0.369). As a result, comparison of the extent of aardvark sign found in the three habitats is valid.

The Number of Feeding Digs in Each Habitat

The number of feeding digs in each habitat was recorded and is expressed in Table 43.

Table 43. The number of food digs recorded in the three habitats in summer and winter.

	Grassland	Steep slopes	Riverine
Winter	410	16	136
Summer	185	6	3

In winter, the grassland habitat had the most recorded digs (78.7%), followed by the riverine habitat (18.3%). A Kruskal-Wallis test indicated that this difference was significant (KW; H=4.010, df1; P=0.045). The high numbers recorded in the riverine habitat in winter were largely from one transect, the vast majority of transects having been devoid of aardvark activity. This is reflected in the figure of three recorded during summer in this habitat. The steep slope areas had low numbers in both seasons, with the grassland areas being the only sites where evidence of aardvark activity was widespread.

The Number of Sleeping Burrows and Defecation Scrapes in Each Habitat.

The number of sleeping holes and defecation scrapes recorded was low, but highest in the grassland habitat (Table 44).

Table 44. The number of defecation scrapes and sleeping burrows in the three habitats in both seasons.

	Grassland	Steep slope	Riverine
Sleeping Burrows	4	0	2
Defecation scrapes	6	0	0

Very low numbers of either holes or defecation scrapes were recorded in any of the habitats. For this reason the summer and winter counts are combined in Table 43.

The Proportions of *T. trinervoides* Mounds Affected by Aardvark

The proportion of mounds affected by aardvark activity is summarised in Figure 33. In winter, a greater proportion of mounds was affected by aardvark activity in the grassland habitat (66.7%), than in the steep slope habitat (7.5%). In summer, the difference between the two habitats was less, with 44.4% of grassland mounds being affected by aardvark activity, compared with to 22.8% in the steep slopes.

A two-way Anova was done to look at the effects of season and habitat upon the proportion of mounds affected. There was a highly significant difference between the habitats (Anova; F=9018; df1; P=0.007), but no significant difference between the seasons in this regard (Anova; F= 1.948, df1; P=0.177).

The Ground Cover of the Study Habitats.

A number of habitat variables were measured and compared between the sites of interest.

The grass cover in the three habitats was quite similar, with the exception of the riverine habitat in summer. Here the average percentage cover was 53% compared with 34% in the grassland and 24.5% in the steep slopes. A Kruskal-Wallis test was performed to compare grass cover between the habitats and revealed no significant difference (KW; H=4.032; df2; P=0.133). However, when the seasons were compared using the same test, there was a significant difference (KW; H=15.784; df1; P=0.016). It is apparent that the grass cover was higher in summer than winter in all three habitats.

The second vegetation characteristic to be measured was the number of bushes in each habitat. More bushes were recorded in the steep slope habitat than elsewhere, followed by the grassland areas.

A Kruskal-Wallis test was used to compare numbers between the habitats. This indicated that there was a significant difference (KW; H=19.390; df2; P<0.001). Significant differences existed between all habitat combinations, except steep slope and grassland, in the number of bushes recorded.

Finally, the rock cover was recorded along transects in each of the three study habitats (see Table 45).

Table 45. The average rock cover % in the three study habitats.

Steep Slopes	Grassland	Riverine
52.5	0.1	0

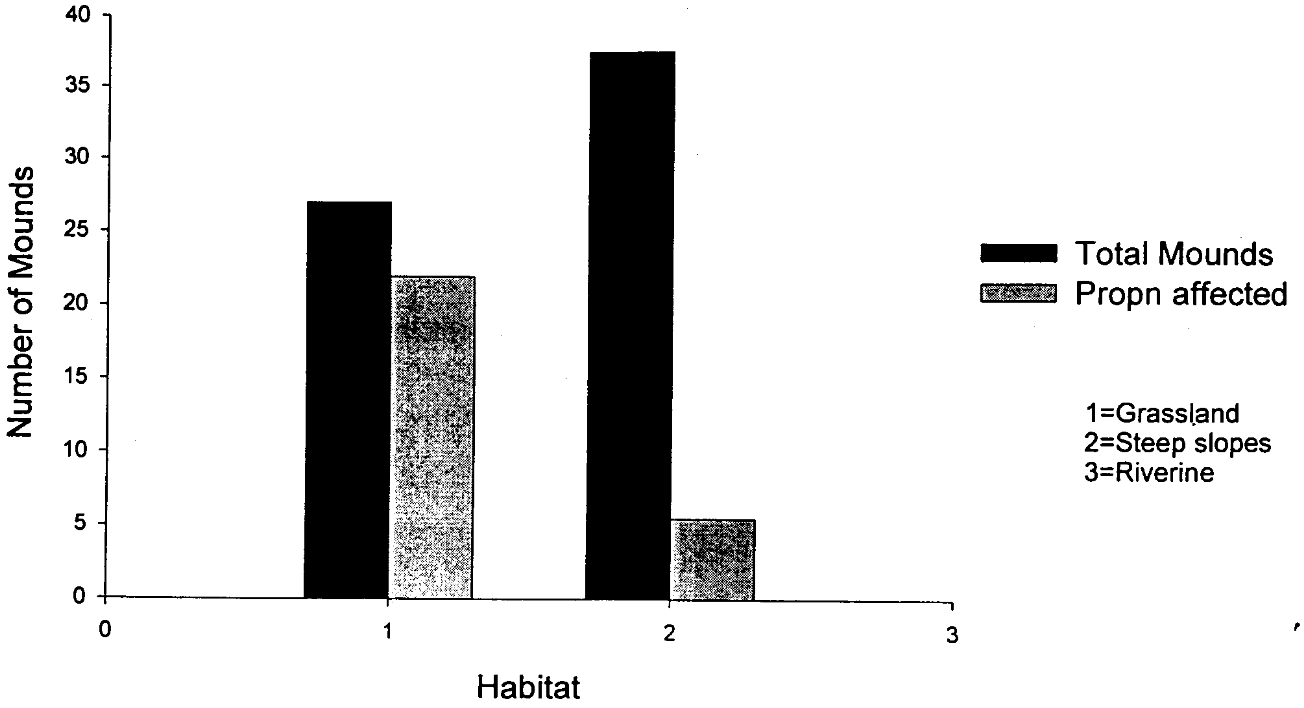


Figure 33. The average number of mounds and the proportion affected by aardvark activity in the three habitats

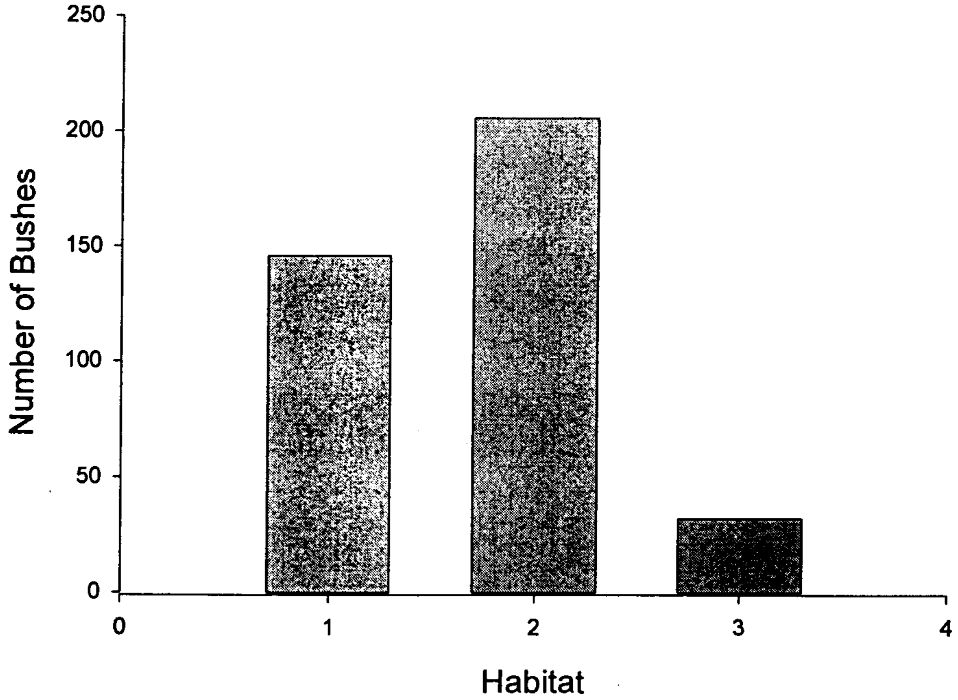


Figure 34. The average number of bushes recorded in the three habitats

DISCUSSION

Habitat Utilisation

The aardvark was highly selective in terms of its habitat utilisation. The vast majority of time was spent in the grassland areas, with two of the study animals not having been recorded in any other habitat. The aardvarks were not seen to utilise the riverine habitat at all during the study, the steep slope habitat having been used very sparingly by the two animals that ventured out of the grassland area. However, during preliminary observations, two of the study animals were observed feeding in the riverine area. Furthermore, Taylor and Henning (pers. comm.) have both reported feeding occurring in this habitat. In addition, a fifth study animal was frequently followed over steep slope areas during habituation (Henning, pers. comm.). However, this animal was apparently stressed and so this is unlikely to have been typical behaviour. The animals clearly selected against foraging in the steep slope and especially the riverine areas. This is despite the fact that these habitats formed a significant portion of the available land area. The transects confirmed the observations, indicating that aardvark sign was mainly concentrated within the grassland areas, negligible evidence having been recorded in the other two habitats. Although a significant number of feed digs were recorded in the riverine habitat on one transect during winter, the vast majority of riverine transects were totally devoid of aardvark sign. These findings agree with those of Willis (1988) who also recorded significantly greater activity in the grassland areas.

Several possible explanations for this extreme habitat selectivity exist. The first is that of food availability. The grassland habitat yielded higher numbers of all of the prey species significant in the diet of the aardvark, in both seasons. However, in statistical terms, this difference was not significant. In addition, the line transects indicated that the steep slope habitat had a higher concentration of *T. trinervoides* mounds, which were larger on average than in the grassland areas. It is clear therefore, that although there was a reduced abundance of food within the steep slope areas, there were high populations of most prey species. If food was limiting, one would expect this habitat to have been utilised to a greater extent. However, several factors suggest that food within the grassland areas was not limiting. First, a fraction of nests of the major prey species showed signs of aardvark predation and those that had been affected are unlikely to have been destroyed by short feeding bouts (Redford, 1987). In addition, the large majority of *T. trinervoides* mounds also remained untouched and available for predation. The extreme paucity of food found in the riverine areas is very probably the reason why these area were not utilised at all.

Abensperg-Traun (1990) found that habitat choice in the echidna was influenced by the distribution of shelter sites. The sleeping burrows of the aardvark were entirely concentrated within the grassland habitat. However, the absence of sleeping burrows in the steep slope areas is unlikely to dissuade the aardvark from utilising this habitat. Feeding upon the slopes would have increased the distance to a hole to a very minor extent. When the aardvark ceased foraging, they tended to walk straight to their current hole without stopping to feed, a distance frequently as much as several hundred metres. The distance from the sleeping burrow does not seem to be a factor which influences foraging patterns.

The habitat choice of several species has been found to be influenced by predation or competition. For example it the side striped jackal (*Canis adustus*) has been shown to modify habitat use due to competition with the black backed jackal, *(Canis mesomelas)* (Lindsey, 1997). However, species such as the pangolin which one might expect to compete with the aardvark, are absent from the area. The aardwolf is also unlikely to compete with the aardvark given its reliance upon *T. trinervoides* and its inability to penetrate the mounds (Richardson, 1987). In addition, there are no predators capable of killing adult aardvark in the area. As a result, both of these explanations can be ruled out. The characteristics of the vegetation are unlikely to explain the lack of use of the steep slope habitat. The difference in the grass cover in the steep slope and grassland areas was not significant and there is no logical reason to suspect that the greater, but low, density of bushes in the steep slope areas would deter the aardvark. However, the high density of rocks in the steep slope areas are probably a very significant problem associated with foraging in these areas. The soil in this habitat is very shallow and rocky, making digging very difficult. The difficulty associated with inserting pitfall traps in the steep slopes bears testimony to this! In addition, when the aardvark was seen feeding in these areas, they showed signs of difficulty during digging, ceasing to dig altogether when even relatively small rocks were reached. Dean & Turner (1990) have suggested that ants nesting under stones offers freedom from, or reduced risk of, predation by the aardvark. In contrast, the grassland areas have much deeper soils (Werger, 1973) and the paucity of rocks makes digging much easier. Finally the incline of the slope areas and the increased effort required to traverse these areas is another very plausible reason for the avoidance of this terrain.

In conclusion, the aardvark shows a marked preference for the gently sloping grassland areas, avoiding the steep slope areas and especially the riverine areas. This was despite the fact that these habitats make up a significant portion of the available land area. The riverine areas are almost totally devoid of prey, a factor that explains the absence of aardvark activity in these areas. The steep slope areas yielded high prey abundance, but have extremely shallow, rocky soils which make digging very difficult. In addition, the incline of these areas is likely to have increased foraging costs. The grassland areas in contrast, have the highest levels of prey availability, deep, rock-free soils and gentle inclines making movement easy and unhindered.

SUMMARY

The aim of the present study was to determine the seasonal diet, feeding patterns and habitat selection of the aardvark. The factors driving prey selection were determined through estimating abundance and consideration of various aspects of prey species biology. Habitat selection was considered relative to the prey availability and various biotic and abiotic characteristics of the steep slope, riverine and grassland areas.

The ant and termite sampling yielded 44 ant species of five subfamilies and 17 genera, and two termite species of two subfamilies. Distinct differences in the ant and termite communities occurred between the habitats and the two seasons. Pitfall trapping was the most successful sampling method, yielding 40 species, compared to 25 during both the quadrat and dig sampling. *M. albopilosum* was the most abundant species overall, followed by *A. custodiens*. The species utilised by the aardvark were the most abundant in all of the habitats. The proportion of the catch made up by these species was greatest in the grassland habitat.

The riverine areas were the most distinct in terms of the ant and termite communities, yielding the lowest abundance and diversity of ants. The steep slope and grassland communities were more similar to one another than either was to the riverine communities. The greatest abundance and diversity was recorded in the grassland areas. Fifteen of the 25 species were recorded in all three habitats, 21 were found in two of the three, and nine were recorded only in the grassland areas. In each of the habitats, the abundance and diversity was significantly lower during winter. Ninety three percent of the species were active during summer, whilst only 71.1% of the species were recorded in winter. In terms of diel patterns, 60% of the species were predominantly diurnal, whilst 40% were mainly nocturnal in their activity. Of the ant species utilised by the aardvark, all were mainly diurnal, with the exception of *M. albopilosum.*

There were large differences in the diet and foraging behaviour between the seasons. In winter, *T. trinervoides* was the second most important dietary component after *Anoplolepis* spp. In summer, however, this species was barely utilised, *H. mossambicus* having been the second most important after the *Anoplolepis* spp. Feeding during winter was characterised by a large number of short feeds from relatively shallow digs. In summer, the feeds were longer, fewer in number and from relatively deeper digs. These patterns were the result of differences in prey activity, abundance and availability between the seasons. In both seasons, feeding was typically clumped with bouts of feeds upon a certain species prior to switching prey species. The distance between intra-species feeds was

significantly less than that between feeds on different species. The average distance walked per hour did not differ between seasons.

The feeding of the aardvark was non-random. Of the 46 species recorded in the area, only 27.3% were recorded in the diet of the aardvark. The Formicines were highly preferred, whilst the Myrmicines were under-utilised. The Isoptera were generally under-utilised relative to availability. There were significant differences between the availability and utilisation of most species.

A variety of factors affected the prey choice and feeding patterns of the aardvark. The abundance of prey was very important and was correlated with utilisation in both seasons. However, the various species were not utilised in relation to their relative abundance and above a certain abundance threshold, other factors were probably responsible for prey choice. Prey size was a second factor important in aardvark prey choice. With the exception of *T. trinervoides*, all of the major prey species were over 0.5cm in length and only one species of this size in the area was not eaten by the aardvark. Finally, prey activity was important in affecting prey selection. This factor explains the unimportance of *T. trinervoides* in summer despite very high populations of the species. Prey activity, prey abundance, prey defences and prey mobility are factors that are likely to have been of importance in causing the characteristic feeding patterns observed when the aardvark fed upon the various species.

The aardvark was also highly selective in terms of habitat use. The vast majority of aardvark activity was recorded in the grassland areas, a finding that was corroborated by behavioural observation. Only two of the four study animals ventured out of this habitat during the study period. The riverine areas were completely avoided, whilst negligible amounts of time were spent in the steep slope areas. Although the food eaten in these areas was different to the overall diet, the low number of feeds in this habitat renders these findings extremely dubious. An extreme paucity of potential aardvark prey was recorded in the riverine areas, whilst the steep slopes were characterised by shallow rocky soils which render digging very difficult. In contrast, the grassland areas yielded the highest concentrations of prey, the deep soils and light vegetation making foraging and digging very easy.

References

Abensperg-Traun, M. 1990. Patch selection and patch use in the Echidna *Tachyglossus aculeatus* Shaw 1792 (Monotremata: *Tachyglossidae)*, in western Australian wheatbelt reserves. Unpublished Ph.D., Thesis. University of Western Australia.

Abensperg-Traun, M. & Steven, D. 1995. The effects of pitfall trap diameter on ant species richness (Hymenoptera: *Formicidae)* and species composition of the catch in a semi arid eucalypt woodland. *Aust. J. Ecol.* **20:** 282-287.

Adam, R.A. 1993. Aspects of the biology of the harvester termite (*Trinervitermes trinervoides*). Unpublished Ph.D. Thesis, University of the Orange Free State.

Adis, J. 1979. Problems of interpreting arthropod sampling with pitfall traps. *Zool. Anz.* **202:** 177-184.

Anderson, D.R., Laake, J.L., Crain, B. R. & Burnham, K.P. 1979. Guidelines for line transect sampling of biological populations. *J. Wildl. Mgmt.* **43:** 70-78.

Anderson, A.N. 1983. Species diversity and temporal distribution of ants in the semi arid Malle region of north west Victoria. *Aust. J. Ecol.* **8:** 127-137.

Anderson, A.N. 1991. Sampling communities of ground foraging ants: Pitfall catches compared with quadrat counts in an Australian tropical savannah. *Aust. J. Ecol.* **16:** 273-279.

Anderson, A.N. 1993. Ant communities in the gulf region of Australia's semi arid tropics: Species composition, patterns of organisation, and biogeography. *Aust. J. Zool.* **41:** 399-414.

Anderson, M.D. 1994. The influence of seasonality and quality of diet on the metabolism of the aardwolf, *Proteles cristatus* (Sparrman 1783). Unpublished M.Sc. Thesis, University of Pretoria.

Arnason, U., Gullberg, A. & Janke, A. 1999. The mitochondrial DNA molecule of the aardvark, *Orycteropus afer*, and the position of the Tubilidentata in the eutherian tree. *Proc. R. Soc. Lond. B.* **266:** 339-345.

Bothma, J. & Nel, J.A.J. 1980. Winter food and foraging behaviour of the aardwolf, *Proteles cristatus*, in the Namib-Naukluft Park. *Madoqua* **12:** 41-149.

Braack, L.E.O. 1995. Seasonal activity of savannah termites during and after severe drought. *Koedoe* **38:** 73-82.

Briese, D.T. & Macauley, B.J. 1977. Temporal structure of an ant community in semi arid Australia. *Aust. J. Ecol.* **5:** 121-134.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community. *Aust. J. Ecol.* **18:** 117-143.

Clarke, K. R. & Warwick, R. M. 1994. Change in a marine community: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory. Bourne Press Ltd. Bournemouth, UK.

Calaby, J.H. 1960. Observations on the banded ant eater *Myrmecobius f.fasciatus* Waterhouse (Marsuipialia), with particular reference to its food habits. *Proc. zool. Soc. Lond,* **135:** 183-207.

Coulson, I. 1989. The pangolin (*Manis temminckii* Smuts, 1832) in Zimbabwe. *Afr. J. Ecol* . 27: 149-155.

Cowie, R.J. 1977. Optimal foraging in great tits *(Parus major)*. *Nature* **268:** 137-139.

Davidson, D.W. 1977. Foraging ecology and community organisation in desert seed eating ants. *Ecology* 58: 725-737.

Dean, W. R. & Turner, J. S. 1990. Ants nesting under stones in the semi arid Karoo, South Africa: predator avoidance or temperature benefits. *J. arid. Environ.* **21:** 59-69.

De Jong, W.W., Zweers, A. & Goodman, M. 1981. Relationship of aardvark to elephants, hyraxes and sea cows from alpha-crystillin sequences. *Nature* **292:** 538-540.

Dene, H., Goodman, M., Walz, D.A. & Romero-Herrera, A.E. 1983. The phylogenetic position of the aardvark *(Orycteropus afer)* as suggested by its myoglobin. *Z. Physiol. Chem.* **364:** 1585-1595.

De Villiers, M.S. & van Aarde, R.J. 1994. Aspects of habitat disturbance by cape porcupines *(Hystrix africaeaustralis)* in a savannah ecosystem. *S. Afr. J. Zool.* **29:** 217-220.

Dene, H., Goodman, M., Walz D. A. & Romero-Herrera, A. E. 1983. The phylogenetic position of aardvark (*Orycteropus afer*) as suggested by its myoglobin. *Z. Physiol. Chem.* **364:** 1585-1595.

Duncan, F.D. & Hewitt, P.H. 1989. Observations on the foraging behaviour of the harvester termite, *Hodotermes mossambicus* (Hagen) (Isoptera: *Hodotermitidae). Bull. Ent. Res.* **79:** 631-642.

Grafen, A. 1994. Quantitative methods. Unpublished Final Honour School Course Guide. University of Oxford. UK.

Greenslade, P.J.M. 1973. Sampling ants with pitfall traps: digging in effects. *Insectes. Soc.*. 20: 343-353.

Greenslade, P.& Greenslade P.J.M. 1971. The use of baits and preservatives in pitfall traps. *J. Aust. ent. Soc.* **10:** 253-260.

Greenslade, P. & Greenslade P.J.M. 1977. Some effects of vegetation cover and disturbance on a tropical ant fauna. *Insectes Soc* . 24: 163-182.

Hayes, W.B. 1970 The accuracy of pitfall trapping for the sand beach isopod *Tylos punctatus. Ecology* **51:** 514-516.

Heath, M.E. & Coulson, I.M. 1997. Home range size and distribution in a wild population of Cape pangolins, *Manis teminckii,* in north west Zimbabwe. *Afr. J. Ecol.* **35:** 94-109.

Hewitt, P.H., van der Westhuizen, M.C., van der Linde, K. & Mitchell, J. 1990. The dry matter, energy and nitrogen budget of the harvester termite *Hodotermes mossambicus* (Hagen). *S.Afr.J.Sci.* **86:** 30-34.

Hinkley, S. & New, T.R. 1997. Pitfall trapping for surveying ant assemblages: lessons from a study at Mount Piper. *Memoirs of the Museum of Victoria* . **56::** 369-376.

Hoffman, M.T. 1996. Upper Nama Karoo, in *Vegetation of South Africa, Lesotho and Swaziland.* (Eds. Louw, A.B. & Rebelo, T.G). Department of tourism and environmental affairs, Pretoria.

Jacobsen, N.H.G., Newberry, R.E., de Wet, M.J., Viljoen, P.C & Pietersen, E. 1991. A contribution to the ecology of the steppe pangolin *Manis teminckii* in the Transvaal. *Z. Saugetierk.* **56:** 94-100.

Kingdon, J. 1971. East African Mammals. *An Atlas of Evolution in Africa.* Vol. 1. Academic Press, London. 378-387.

Koen, J.H. & Breytenbach, W. 1988. Ant species richness of fynbos and forest ecosystems in the southern Cape. *S. Afr. J. Zool.* **23:** 184-188.

Lindsey, P.A. 1997. Niche differentiation between sympatric jackals species (*Canis adustus, Canis mesomelas*) in north west Zimbabwe. BA (Hons) thesis, University of Oxford, UK.

Low, A.B. & Rebelo, T.G. 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental affairs and Tourism, Pretoria.

Lubin, Y.D. & Montgomery, G.G. 1981. Defences of *Nasutitermes* termites (*Isoptera, Termitidae*) against Tamandua anteaters (*Edentata, Myrmecophagidae*). *Biotropica.* **133:** 66-76.

Luff, M.L. 1975. Some features influencing the efficiency of pitfall traps. *Oecologia*. **19:** 345-357.

Majer, J.D. 1978. An improved pitfall trap technique for sampling ants and other epigaeic invertebrates. *J. Aust. ent. Soc.* **17:** 261-262.

Majer, J.D. 1985. Re colonisation by ants of rehabilitated mineral sand mine on North Stradbroke Island with particular reference to seed removal. *Aust. J. Ecol*. 10: 31-48.

Majer, J.D. 1997. The use of pitfall traps for sampling ants - a critique. *Memoirs of the Museum of Victoria.* **56:** 323-329.

Marsh, A.C. 1984. The efficacy of pitfall traps for determining the structure of a desert ant community. *J. Ent. Soc. Sth. Afr.* 47: 115-120.

Marsh, A.C. 1986. Ant species richness along a climatic gradient in the Namib desert. *J. arid. Environ*. **11:** 235-241.

McNab, B.K. 1984. Physiological convergence amongst ant-eating and termite-eating mammals. *J. Zool. , Lond,* **203:** 485-510.

Meeuse, A.D.J. 1962. The *Curcubitaceae* of southern Africa. **8:** 1-11.

Melton, D.A. 1976. The biology of aardvark *(Tubilidentata-Orycteropidae). Mammal Rev.* **6:** 75-88.

Melton, D.A. & Daniels, C. 1986. A note on the ecology of the aardvark *Orycteropus afer. S. Afr. J. Wildl. Mgmt* **16:** 112-114.

Miller, L.J. & New, T.R. 1997. Mount piper grasslands: pitfall trapping of ants and interpretation of habitat variability. *Memoirs of the Museum of Victoria* **56:** 377-381.

Mitchell, J.D., Hewitt, P.H. & van der Linde, T.C. 1993. Critical thermal limits and temperature tolerance in the harvester termite *Hodotermes mossambicus* (Hagen). *J. Insect. Physiol.* 6: 523-528.

Montgomery, G.G 1985. Impact of vermilinguas *(Cyclopes, Tamandua :Xenartha = Edentata)* on arboreal ant populations. In *The evolution and ecology of armadillos, sloths and vermilinguas.* (Ed. Montgomery, G.G.). Smithsonian Institution Press, Washington & London. 1-451.

Nel, J.J.C. 1968. Aggressive behaviour of the harvester termites *Hodotermes mossambicus* and *Trinervitermes trinervoides. Insectes Soc.* **15:** 145-156.

Nonacs, P. & Calabi, P. 1992. Competition and predation risk: their perception alone affects colony growth. *Proc. R. Soc. Lond .B* . **249:** 95-99.

Prestwich, G.D. 1983. The chemical defences of termites. *Sci. Am.* **249:** 68-75.

Prins, A.J. 1981. Review of *Anoplolepis* with reference to male genitalia, and notes on *Acropyga* (Hymenoptera: Formicidae). *Ann. S. Afr. Mus.* **89:** 215-247.

Redford, K.H. 1983. Mammalian myrmecophagy: Feeding, foraging and feeding preference. Ph.D. Thesis, University of Harvard, Cambridge Massachusetts.

Redford. K.H. 1985. Feeding and food preference in captive and wild giant anteaters. *J. Zool., Lond* . **205:** 559-572.

Redford, K.H. 1987. Ants and termites as food: patterns of mammalian myrmecophagy. In: *Current Mammalogy.* Vol. 1. Genoways, H.H.(Ed.).Plenum Press, New York.

Redford, K.H. & Dorea, J.G. 1984. The nutritive value of invertebrates, with emphasis on ants and termites as food for mammals. *J. Zool. ,Lond* . 203: 385-395.

Richardson, P.R.K. 1987. Aardwolf: The most specialised myrmecophagous mammal? *S. Afr. J. Sci.* **83:** 643-646.

Richardson, P.R.K. & Levitan, C.D. 1994. Tolerance of aardwolves to defence secretions of *Trinervitermes trinervoides*. *J. Mammal.* 75: 84-91.

Room, P.M. 1975. Diversity and organisation of the ground foraging ant faunas of forest, grassland and tree crops in Papua New Guinea. *Aust. J. Zool.* **23:** 71-89.

Samways, M.J. 1983. Community structure of ants *(Hymenoptera: Formicidae)* in a series of habitats associated with citrus. *J. Appl. Ecol*. **20:** 833-847.

Samways, M.J. 1990. Species temporal variability: epigaeic ant assemblages and management for abundance and scarcity. *Oecologia*. **84:** 482-490.

Skaife, S.H. 1979. African insect life. Revised edition. Struik, Cape Town.

Skinner, J.D. The nutritive value of *Trinervitermes trinervoides* and *Hodotermes mossambicus (Isoptera: Termitidae).* Unpublished.

Skinner, J.D. & Smithers, R.H.N. 1990. The Mammals of the Southern African Subregion. University of Pretoria press.

Smithers, R.H.N. 1971. The Mammals of Botswana. *Mus.mem.Natl Mus.Monum.Rhod*. 4: 1-340.

Smithers, R.H.N. 1983. The mammals of the southern African subregion. University of Pretoria.

Steinberger, Y., Leschner, H. & Shmida, A. 1992. Activity patterns of harvester ants (*Messor* spp.) in the Negev desert ecosystem. *J. arid. Environ.* 23: 169-176.

Steyn, J.J. 1954. The pugnacious ant *Anoplolepis custodiens* (Smith) and its relation to the control of citrus scales at Letaba. *Mem. Ent. Soc. Sth Afr.* **3:** 1-96.

Sudd, J.H. & Franks, N.R. 1987. The behavioural ecology of ants. Blackie, Glasgow.

Swart, J.M. 1996. Foraging behaviour of the Cape pangolin *Manis teminckii* in the Sabi Sand Wildtuin. Unpublished M.Sc. thesis, University of Pretoria.

Swart, J.M., Richardson, P.R.K. & Ferguson, J.W.H., 1999. Ecological factors affecting the feeding behaviour of pangolins (*Manis temminckii*) *J. Zool., Lond.* **247:** 281-292.

Sweeney, R.C.H. 1956. Some notes on the feeding habits of the ground pangolin, *Smutsia teminckii* (Smuts). *Ann. Mag. Nat. Hist. 12 ser.* **9:** 893-896.

Taylor, W.A.1998. The ecology of the aardvark, *Orycteropus afer* (Tubilidentata - Orycteropodidae). Unpublished MS.c thesis, University of Pretoria.

Van Aarde, R. J., Willis, C. K., Skinner, J. D. & Haupt, M. A. 1992. Range utilisation by the aardvark, *Orycteropus afer* (Pallas 1766) in the Karoo, South Africa. *J. Arid Environ* . **22:** 387-394.

Vorster, H., Hewitt, V.H. & van der Westhuizen, M.C. 1991. Polymorphism and the foraging behaviour of the granivorous ant, *Messor capensis* (Mayr) (*Formicidae: Myrmicinae*). *J. Afr. Zool.* 105: 485-492.

Vorster, H., Hewitt, V.H. & van der Westhuizen, M.C. 1992. Nest density of the granivorous harvester ant *Messor capensis* (Mayr) (*Hymenoptera: Formicidae*) in semi arid grassland of South Africa. *J. Afr. Zool.* **106:** 445-450.

Werger, M.J.A. 1973. An account of the plant communities of Tussen die Riviere game farm, Orange Free State. *Bothalia.* 11: 165-176.

Willis, C.K. 1988. Relative importance of ants and termites in the feeding ecology of the aardvark *(Orycteropus afer).* Unpublished BSc. (Hons) thesis, University of Cape Town.

Willis, C.K., Skinner, J.D. & Robertson, H.G. 1992. Abundance of ants and termites in the False Karoo and their importance in the diet of the aardvark, *Orycteropus afer*. *Afr. J. Ecol.* **30:** 322-334.

Wilson, D.S. & Clark, A.B. 1977. Above ground predator defence in the harvester termite, *Hodotermes mossambicus*. *J. Ent. Soc. Sth Afr.* **40:** 271-282.