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THE ECOLOGY OF THE AARDVARK, *ORYCTEROPUS AFER*  
(TUBULIDENTATA – ORYCTEROPODIDAE)

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**The ecology of the aardvark, *Orycteropus afer* (Tubulidentata -  
Orycteropodidae).**

by

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## The ecology of the aardvark, *Orycteropus afer* (Tubulidentata - Orycteropodidae).

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### Abstract

Nine aardvarks were captured to have radio transmitters attached at Tussen die Riviere Nature Reserve. These aardvarks were followed using radio telemetry to investigate their activity patterns, home ranges, nightly movements, burrow utilisation and feeding ecology. Two became habituated and could be observed at close range. Activity patterns were found to vary seasonally, with aardvarks becoming active earlier, remaining active for shorter periods, and returning to their burrows earlier in winter than in summer. Home ranges were estimated between 133.1ha and 301.7ha (95% MCP), and between 147.3ha and 384ha (90% adaptive kernel). There was no apparent difference between males and females. Aardvarks utilised burrows for an average of 4.9 to 8.6 days and travelled distances between 2.11 and 4.39km per night.

Faecal analysis and feeding observations indicated that the aardvarks diets consisted entirely of ants and termites, with ants predominating over termites as the main prey source. The two most important prey species were *A. custodiens* and *T. trinervoides*. There was considerable monthly variation in prey species contributions, but in all months *A. custodiens* dominated. Seasonal trends were tenuous, with *T. trinervoides* possibly more important in winter than summer. There was a clear peak in *T. trinervoides* mound predation in winter, possibly as a result of the presence of alates in the mounds at the time. Ant populations, specifically *A. custodiens*, were considered at their lowest in winter, so predation from *T. trinervoides* mounds at the time may have supplemented the aardvarks diets.

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## CHAPTER 1

### INTRODUCTION

#### Classification and phylogeny of the aardvark

The aardvark, *Orycteropus afer* (Pallas, 1766) (Tubulidentata: Orycteropodidae), was originally assigned to the genus *Myrmecophaga* (*M. afra*), when it was described in 1766 by Pallas. This placed it in the same genus as the South American anteaters and grouped it amongst the Edentata, an Order which, at the time, comprised the armadillos, sloths, pangolins and other South American anteaters.

This misclassification was understandable due to superficially similar traits shared between the group, such as strong digging claws, elongate snouts and long, vermiform tongues. Such similar morphological and anatomical traits we now know to be the result of convergent evolution, but would have obscured their phylogeny at the time.

In 1795, Geoffroy changed the aardvarks generic name to *Orycteropus* because he realised that it was somewhat different from the South American anteaters. A new family, Orycteropidae, was then created within the Edentata for *Orycteropus*, by Gray, in 1821, which was later changed to Orycteropodidae by Bonaparte in 1852. Eventually, in 1872, Huxley separated the Orycteropodidae from the Edentata and created a new Order, the Tubulidentata. This was not, however, generally accepted until the early twentieth century, when the anatomy of the aardvark was more comprehensively studied by Mitchell (1905, 1916) on intestinal tracts, and most importantly by Sonntag (1925) on all aspects of anatomy.

Sonntag sited three features linking aardvarks with Edentata (lack of teeth in the front of the jaw, absence of enamel on the teeth, and more than one scapular head on the triceps - cited in Melton, 1976), but considered these of little significance when compared to the features separating the two groups, such as the spine, turbinate bones, ear ossicles, uterus, placenta and teeth.

Modern classification places only the South American anteaters, armadillos and sloths in the Edentata, while pangolins and other anteaters, including the aardvark, are considered separate. Pangolins, like aardvarks, now have their own Order, Pholidota.

More recently, less traditional approaches have been used to trace the phylogeny of aardvarks. De Jong *et al.* (1981) studied the amino acid sequence of the eye lens protein  $\alpha$ -crystallin A of the aardvark, and

compared it with the corresponding sequences from species representing 15 mammalian Orders. To assess the sequence relationships of the aardvark, phylogenetic trees were constructed for the available  $\alpha$  A sequences using a maximum parsimony approach. Unique similarities were observed among the sequences of aardvarks and paenungulates, suggesting that the closest relatives of the Tubulidentata are found in this Superorder, a somewhat controversial classification, which comprises the Sirenia (sea cows), Hyracoidea (hyraxes) and Proboscidea (elephants). The results also appeared to indicate that these Orders are not derived from a common stem group with the ungulates, but might be one of the first offshoots of the placental mammalian line.

Dene *et al.* (1983) compared sequences of amino acids from skeletal muscle myoglobin in aardvarks with those of 65 known vertebrate myoglobin amino acid sequences. The phylogenetic branching order was assessed by a maximum parsimony branch swapping procedure, and indicated that Tubulidentata had a very ancient separation from other members of the Eutheria. The results also suggested two possibilities as alternatives for the closest relatives of the aardvark: Proboscidea (elephants); or Erinaceidae and Chiroptera (hedgehogs and bats).

Porter *et al.* (1996) sequenced exon 28 of the gene encoding von Willebrand Factor, a glycoprotein which functions in blood clotting. Strong support was found for a monophyletic clade consisting of aardvarks, elephants, sea cows, hyraxes and elephant shrews. Virtually the same grouping was found by Springer *et al.* (1997), who sequenced DNA from mitochondrial and nuclear genes to examine relationships of insectivores to other mammals. This latter study even found evidence to include the golden moles in the clade. Studies by Madsen *et al.* (1997) and Stanhope *et al.* (1998) have further corroborated these results.

### **Fossil aardvarks**

The Tubulidentata are sometimes cited as an example of a major taxon consisting of a single evolutionary lineage. According to Patterson (1975, 1978) it has become apparent that the actual history of the group is rather more complex than this. The order first appeared in the early Miocene of Kenya, from where members spread to Europe and southern Asia during the Miocene and early Pliocene but failed to maintain themselves there. In the Holocene swamp deposits of Madagascar an aberrant form occurs. There are also fossils from the early Eocene of North and South America which have been considered for the Order, but according to Patterson (1978) the evidence for this is not convincing.

Four genera of aardvarks are known to have occurred (Patterson, 1978), three of which are now extinct. These are *Leptorycteropus*, *Myorycteropus*, *Plesiorycteropus*, and *Orycteropus*.

Reasonable reconstruction of the adaptations of *Leptorycteropus* suggests that it was the most generalised member of the order, and was not specialised for myrmecophagy (Patterson, 1975). It did not have an elongate snout, but possessed a rather large canine and a full set of cheek teeth. The limb bones were more slender than those of *Orycteropus* but were capable of digging to a lesser degree. The impression conveyed is of an omnivorous form that was a faster runner than the living species. *Leptorycteropus* did however have the characteristic tubulidentate tooth structure, leading Patterson (1975) to suggest that the acquisition of this had nothing to do with myrmecophagy. Structurally, it could represent the ancestry of *Orycteropus* and *Myorycteropus*, but its late survival indicates that its predecessors had been independent of theirs since at least Oligocene time.

*Myorycteropus* had the most advanced fore limb in respect of fossorial adaptations, in that it was relatively larger than that of *Orycteropus*. The pelvis and hind limbs were not as robustly built in *Myorycteropus*, however, and were probably not used as much in digging, but Patterson (1975) states that in all probability *Myorycteropus* constructed burrows. Very little is known of the skull other than a maxillary fragment, which indicates that the dentition was very similar to that of *Orycteropus*. In view of this, *Myorycteropus*' degree of commitment to myrmecophagy is not possible to assess. Compared to *Orycteropus*, *Myorycteropus* was precociously specialised for digging and could not have been involved in the ancestry of the living genus.

*Orycteropus* was represented by a number of species, some of which are based solely on isolated teeth or other fragments. Patterson (1975) states that these latter must be regarded with reserve until more complete specimens are found. Aside from this, there are five extinct species that can be placed in the genus with confidence, the earliest of which is *O. mauritanicus* from the middle Miocene. *O. gaudryi*, of the late Miocene, is the best known of its genus and is represented by more than 20 specimens. Through time there appears to have been a modest and late increase in overall robustness of the limb bones within the *Orycteropus*, and an increase in body size accompanied by a proportionately smaller increase in head size. There has also been a progressive enlargement of the olfactory area and lengthening of the facial region. *O. afer* is about twice as large as the known species of the other genera, and even the comparatively small *O. gaudryi* is decidedly larger. It is now the only extant member of its Order, Tubulidentata.

*Plesiorycteropus* is geographically the most isolated of the tubulidentates, known from about 50 isolated bones from Madagascar. Only becoming extinct approximately one thousand years ago, it is also morphologically the most isolated member of the Order. The skull was short, the facial region relatively short. The jaw was probably reduced as with many myrmecophagous mammals generally, and teeth were probably greatly reduced or absent (none have been found).

### **Current distribution and status**

According to Meester *et al.* (1986), the distribution of the aardvark is widespread throughout southern Africa where there is suitable habitat. Outside of the Subregion it is found in Mozambique, Malawi, Zambia, Angola, Tanzania, Uganda, Kenya, Zaire, probably Somalia, Ethiopia, Sudan, and westwards to northern Cameroon, northern Nigeria, northern Ghana, northern Sierra Leone, and Senegal.

Meester (1971) lists 18 subspecies from the entire continent, two of which are found in southern Africa. He indicates that owing to scarcity of material, neither the status nor the limits of the distribution of the subspecies are known. It is almost certain that too many subspecies are recognised (Meester *et al.*, 1986). Smithers (1971) concludes that the two subspecies thought to occur in southern Africa cannot be distinguished, therefore the distinction between them is unjustified.

According to the South African Red Data Book for terrestrial mammals (Smithers, 1986), the aardvarks status is vulnerable. This means that aardvark populations are thought to be decreasing for reasons such as the destruction or degradation of habitat, and that if this decrease continues they could become endangered. Although this status is given to the aardvark, Smithers (1986) states that they do not appear to have declined in numbers or range. It seems likely that this status was assigned as a result of its habits, which make it only appear to be uncommon. Its activity at night and solitary existence mean that it is easily overlooked.

If such a decline did exist, the most likely cause would be persecution by farmers, who may be adversely affected by the burrowing activities of the aardvarks. Aardvarks apparently dig under jackal proof fences, allowing jackals through to massacre and decimate the sheep population, they dig in the open veld, which farm vehicles can drive into and get stuck in or damaged, and they dig holes in dam walls which may cause seepage and loss of vital water. They also have the annoying, yet exaggerated habit of re-excavating holes in roads and dam walls after farmers fill them in, thus creating extra, unwanted work. The most common reason for such excavations is the presence of ants. In the Free

State, aardvarks are still common on farms, although undoubtedly farming activities keep their densities down below optimum levels.

Aardvarks are also hunted to some degree, or have been in the past, by rural people for their meat or for body parts that are considered medicinal, such as the claws, teeth and hair. Where this has occurred it will have done so for a long time, so it is unlikely that such activities could put the species under any pressure, especially when the difficulties in catching them are considered.

Although the aardvark population density is never high anywhere, its very wide distribution and broad tolerance of habitats means that it can probably be found locally at any locality in Africa south of the Sahara, except extreme areas of deserts or mountains. Kingdon (1971) states that they are very local in distribution and that this is undoubtedly determined by the abundance of termites and ants on which they feed. Skinner & Smithers (1990) suggest that their distribution is governed to some extent by the availability of food, and that there are many areas where they are locally absent within their wide distributional range as a result of either unsuitable terrain or lack of a suitable food supply.

## Objectives

The aardvark is a secretive and elusive mammal that is almost entirely nocturnal. Its evasive habits have made it difficult to study and it is, therefore, one of the more poorly understood of African mammals. There are many aspects of aardvark ecology that make it fascinating to study, including such factors as their prey selection, which requires ants and termites to be located and extracted from below ground or out of epigeous mounds, and their use of burrows as places of refuge to rest in during the day. The fact that the aardvark is so understudied and misunderstood (not in the pejorative sense) makes it an interesting study case from any point of view, made more so by the idea that it stands apart from other mammals in its own unique Order.

The aardvark has a unique appeal to many interested in natural history and, therefore, plays an important role in keeping people interested in natural history and conservation. Apart from this it also has a great influence over other members of the animal community with which it shares its home. Effective conservation of a species cannot be carried out without first having a firm background knowledge in the basics of the ecological requirements of that species. Regarding aardvarks, there is a dearth of information concerning their ecology or biology, so measures to improve their chances of survival in the long term, should they be required, cannot be implemented. Mere survival of aardvarks, which is important in its own right, would not be the only thing at stake should certain factors lead to

their reduction in numbers or even their demise. The survival of other animals which make use of the aardvarks burrow systems for their own protection might be in jeopardy.

The main objective of the present study was to gain a better understanding of aspects of the ecology of the aardvark, primarily in the areas of feeding behaviour and activity patterns (including home ranges). It is recognised that there have been previous investigations into these facets of aardvark ecology, and that this thesis is generally a continuance and development of them, but previous studies were not greatly detailed, while only one captured and radio tagged aardvarks so that individuals could be regularly followed (van Aarde *et al.*, 1992). Wild aardvarks are never easy to locate without the aid of radio telemetry equipment, and thus much past information derives from observations accumulated in a very haphazard manner. No previous studies have been able to observe closely the activities and behaviour of wild aardvarks on a regular basis, as has been possible in the present study (albeit with only two habituated individuals).

The importance of such studies of simple natural history should also not be underestimated because only once a detailed knowledge of an animals biology is attained can genuine inferences be made concerning its influence on wider reaching biological concerns, such as evolution.

Main objectives:

To investigate activity periods and nightly movement patterns

To examine home range utilisation and overlap between aardvarks

To investigate burrows and their utilisation

To investigate the diet of the aardvarks at TdR and temporal variation within this by examination of faecal samples

To investigate the feeding behaviour and temporal variation within this for comparison with faecal results

To make some inferences regarding prey selection

## CHAPTER 2

### STUDY SITE

The study was carried out at Tussen die Riviere Nature Reserve (TdR) (S 30° 30', E 26° 07') situated in the southern Free State, approximately 30km by road from the town of Bethulie (Figure 1). The main part of the reserve lies between the Orange and Caledon Rivers, at the peninsular of their confluence, while two smaller parts of the reserve lie north and south of the Caledon and Orange respectively. The total area of the reserve is approximately 22,000 hectares and it falls entirely in what Acocks (1975) classified as the False Upper Karoo. This is currently classified as part of the Eastern Mixed Nama Karoo (Hoffman, 1996), which is part of the Nama Karoo Biome. Acocks (1975) considered this the most degraded of all vegetation types in South Africa (as a result of overgrazing by Merino sheep), but according to Werger (1973) there has been a marked recovery of the veld since the withdrawal of farming and the creation of TdR in 1967.

#### Geomorphology and geology

Isolated plains of alluvium occur along the Orange and Caledon Rivers and were previously utilised as irrigated lands. A central ridge of sedimentary rocks of the Beaufort series of the Karoo system separates the riverine plains, while Karoo dolerite underlies it. Resistance to weathering of the numerous dolerite intrusions results in a rugged landscape, with both dykes and sills criss-crossing the area. The average difference in height between the rivers and the central ridge is 250m. A number of streams drain southward and northward into the main rivers, occasionally resulting in deep gullies especially in the high lying areas (Botha, Grobler and Geringer, 1971).

The green, khaki and purple mudstone, khaki and grey-yellow siltstone, and sandstone of the Etage Middle-Beaufort of the Karoo system, are the oldest geological formations of this area. The igneous dolerite is more recent, as is the alluvium (Botha *et al.*, 1971). The prevailing soil type is solonetzic, which is a fairly dense and structureless grey loam, but there are also abundant lithosols and some alluvial soils (Botha *et al.*, 1971).

#### Climate

The average monthly temperatures and rainfall for Tussen die Riviere are represented in figures 2 and 3 respectively.

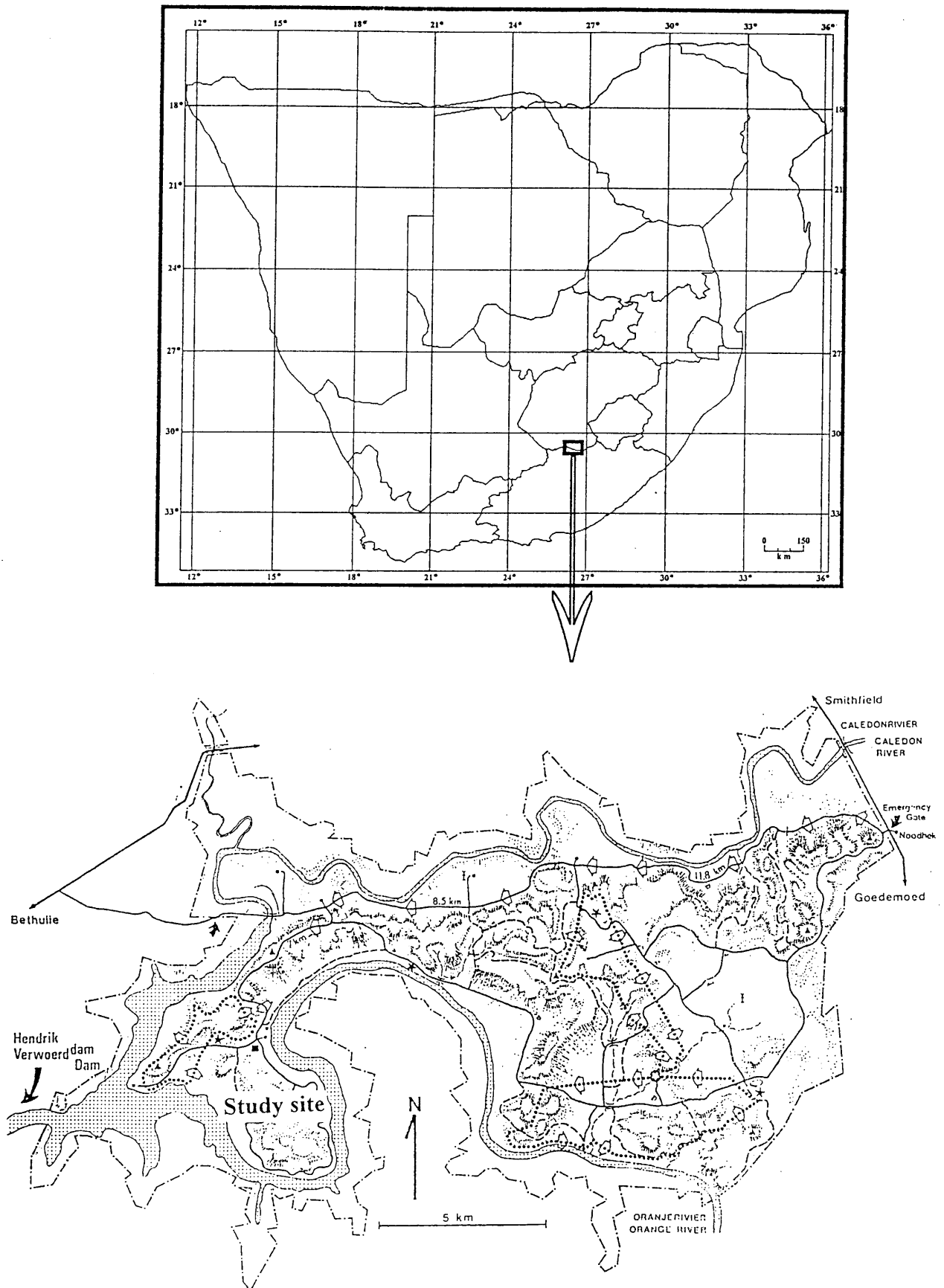


Figure 1. Tussen die Riviere Nature Reserve, South Africa.

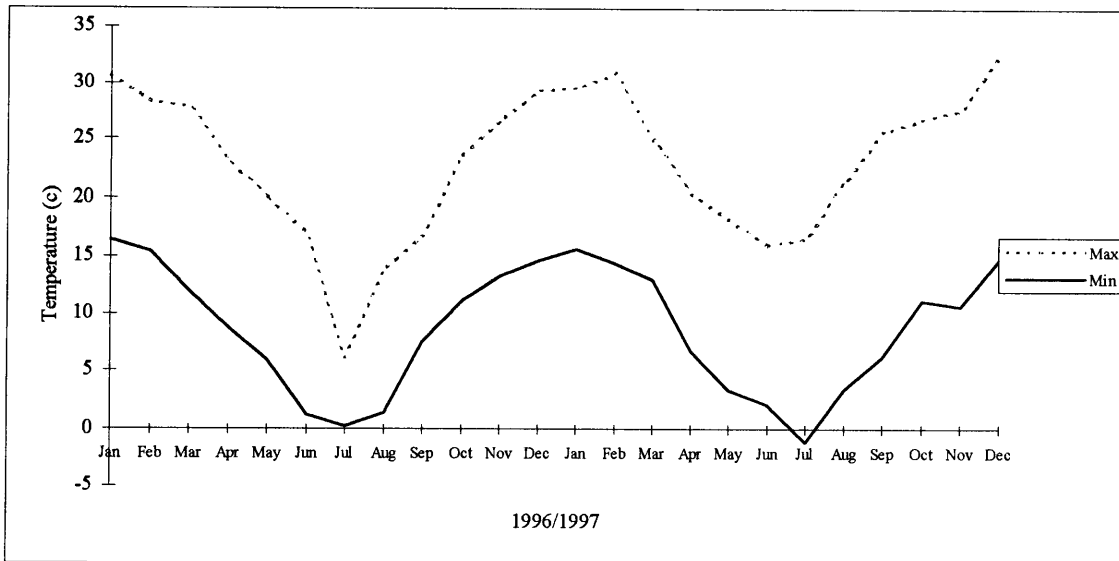


**Figure 2.** Average maximum and minimum temperatures for 1996 and 1997, recorded at Goedemoed, just west of Tussen die Riviere.

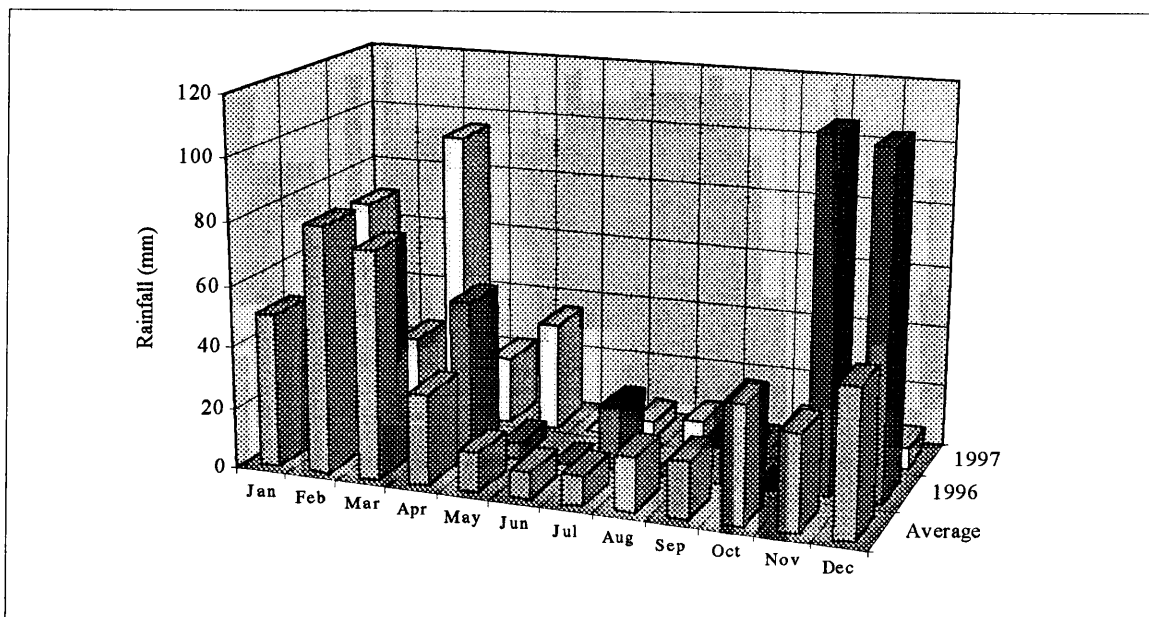


**Figure 3.** Average monthly rainfall for Tussen die Riviere and monthly rainfall for the period of the study (1996 and 1997).

## Plant Communities

According to Werger (1973), the vegetation of TdR can be divided into three major groups of communities:

- 1) Riverine communities. These are mostly made up of the *Acacia karoo* - *Celtis africana* community on the levees of fine alluvial sand with a pH between 6.5 and 7.5. They are usually three-layered consisting of a tree layer from 6 to 10m with an average cover of 75%; an open 2 to 4m tall shrub layer with an average cover of 40-50%; and a field layer up to 0.6m consisting of grasses, herbs and small shrubs, with a greatly varied cover depending on the amount of grazing. Where the levee drops away into the river channel one often finds a community mixture of the *Acacia karoo* - *Celtis africana* community with *Salix capensis*, *Nicotiana glauca*, *Agrostis lachnantha* and even *Salix babylonica*.
- 2) Communities of the flats and gently sloping terrain. These are usually two-layered, with the most important being the grass and dwarf shrub layer between 0.15 and 0.6m high with a cover up to 50%. The communities of the flats are floristically poorer than those of the sloping terrain. Werger separates this community into four main parts: a) *Eragrostis lehmanniana* - *Chrysocoma tenuifolia* community; b) *Chrysocoma tenuifolia* - *Lessertia pauciflora* community; c) *Chrysocoma tenuifolia* - *Nenax microphylla* community and; d) *Chrysocoma tenuifolia* - *Polygala leptophylla* community.
- 3) The communities of the steep slopes. This is the richest community both floristically and structurally, consisting of three or four layers. These are: a sparse layer of creeping and rosette plants up to 0.05m high; a grass, dwarf shrub and small shrub layer up to 0.8m covering between 35 and 50%; a tall shrub layer between 1 and 4m covering from 10 to 30%; and sometimes an open tree layer up to 6m high. Important trees in this community include *Rhus erosa* and *Olea africana*.

## CHAPTER 3

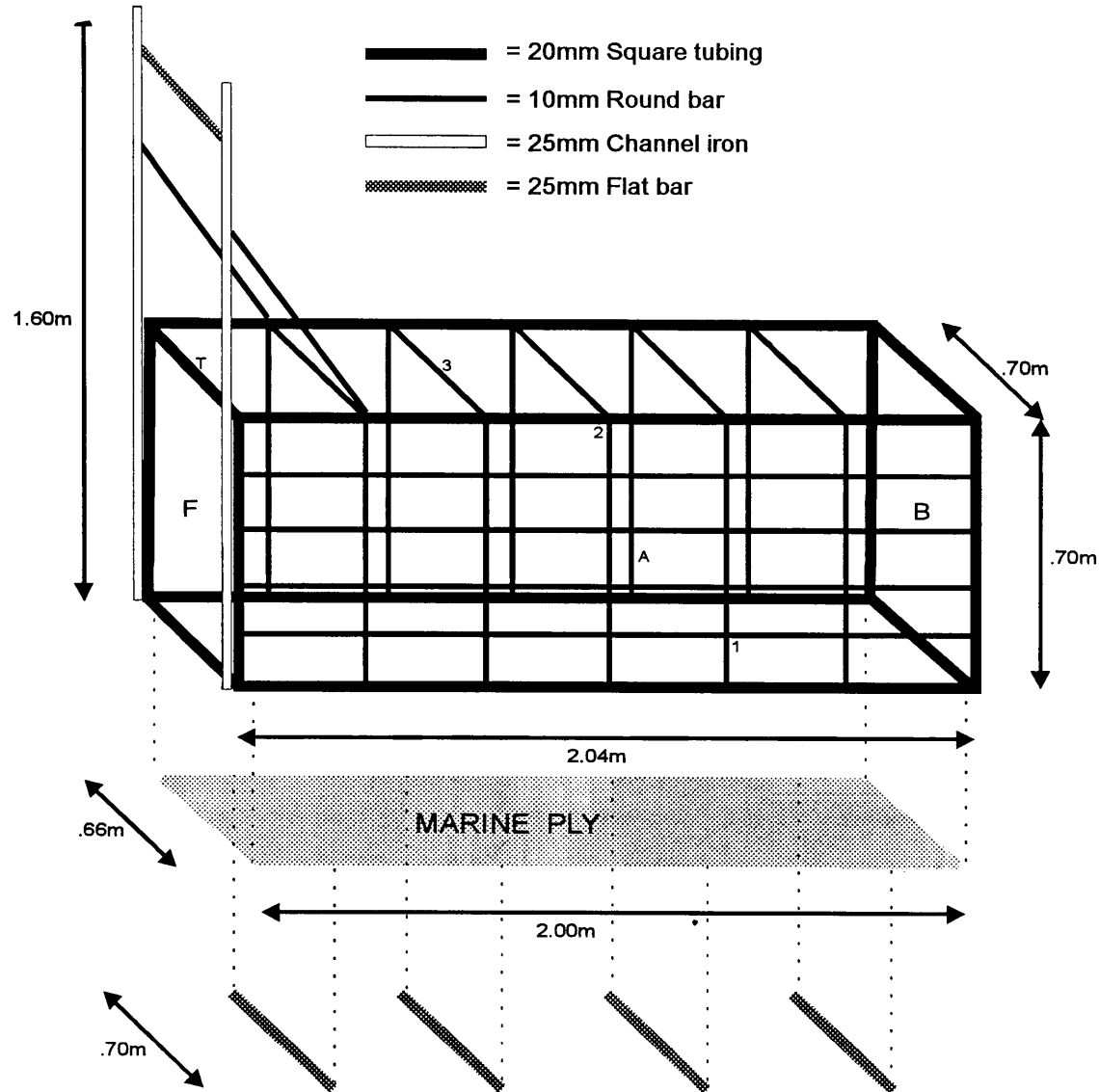
### CAPTURE

Aardvarks were located from the back of a four wheel drive vehicle, driven slowly both on and off road, while spotters scanned the surroundings with the aid of hand held spotlights (Coleman 1 million candlepower halogen lamps). Once an aardvark was sighted the driver drove straight towards it while the spotters kept the light on it (when possible). Unfortunately, the most common response of the aardvarks to this was to take flight, so the best tactic was to pursue them until they entered a hole, preferably without getting too close. It was considered important to submit the aardvarks to as little stress as possible, so when an individual did not bolt away quickly, it was not chased hard. Rather, it was followed at the slowest feasible pace until entering a hole. However, as most of the aardvarks sighted ran quickly away, it was normally necessary to drive faster and this sometimes led to a long pursuit. There is a misconception that aardvarks are ungainly and slow moving, but this is far from true. They are surprisingly agile and have a turn of speed that can exceed 40km/h. Hence, once sighted, it was never a certainty that the aardvark would be successfully seen into a burrow, and indeed, approximately half of those spotted were lost in the chase.

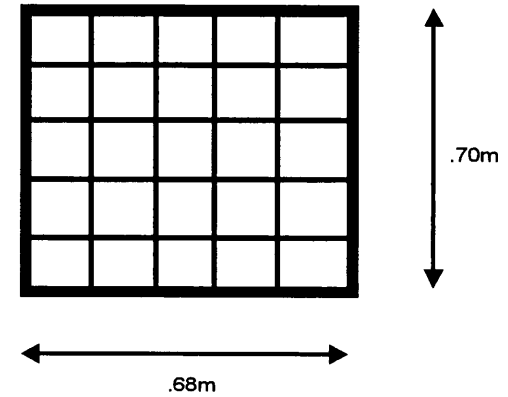
Once an aardvark was successfully chased into a burrow a trap was set directly outside with its open end facing into the hole (Figure 4). A corrugated iron “funnel” was placed over the hole to guide the animal from the tunnel entrance into the trap itself, leaving no escape route above ground. The trigger mechanism was a trip wire which released a gravity driven trap door.

Occasionally aardvarks dug their way out underneath the funnel and consequently avoided the trap, so care was taken to dig the funnel in well and weigh it down with rocks and soil. After the trap was set it was checked regularly (or continuously) and this often involved a lot of waiting as the aardvarks rarely came out the same night they were chased. It was more common for them to come out the night after the chase, but occasionally they waited even longer before emerging. Once the aardvarks were trapped inside the cage, they were immobilised as quickly as possible, because they underwent considerable stress and sometimes injured themselves by running into the sides of the trap. Consequently, the trap had to be strong to contain the animal. To prevent the aardvarks from running up and down the cage and make it easier to inject the drugs, the trap was turned up on its end.

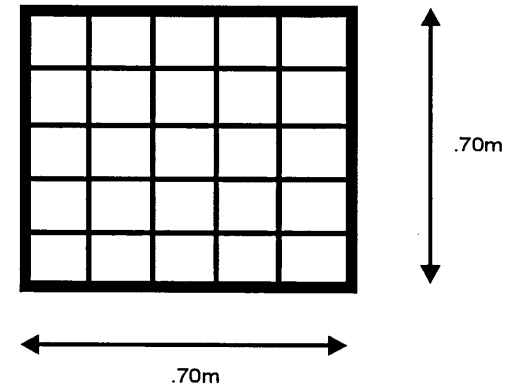
Although the trap method was the most successful, it was also possible to catch the animals directly by hand when they ran away. To do so it was necessary to drive alongside the moving animal so catchers



FRONT (F)



BACK (B)



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Figure 4. The cage trap used to capture aardvarks

could jump off next to it. This proved an unacceptable method as there was some risk of running the aardvark over with the vehicle. One aardvark was, however, captured successfully in this way and was injected immediately with the immobilising drugs (see below). As aardvarks are strong animals, considerable strength is required to restrain them like this.

### **Immobilisation - Drug protocol for attaching radio collars**

The drugs and drug doses administered were altered and improved with increasing experience and with the change over from radio collars to implants.

The first five aardvarks captured were fitted with radio collars and hence only required to be drugged for long enough periods to fit the collars and record biological measurements. They were administered with doses fitting their estimated body weights.

1) Adult male (M1), 42kg, 5<sup>th</sup> June 1996:

6ml Ketamine HCL (Ketalar ®), intramuscular (IM)

0.6ml Azaperone (Stresnil ®) IM

2ml Comprapen (antibiotic) IM

The animal became unconscious within eight minutes and was easily worked on to attach the radio collar. The animal woke up slowly and kept falling about. It was placed outside the capture burrow, which it crawled into by itself. Later in the day the aardvark had moved from the hole and the procedure proved to be successful. However, although the trap had been checked regularly, it was not reached quickly enough because the aardvark cut its face on the bars as it ran up and down inside. The normal unease or panic demonstrated by aardvarks when trapped was probably confounded in this case because it was getting light when the animal was found. Fortunately, this turned out to be the only occasion of capture in daylight, but even so, more frequent trap checks were undertaken after this.

2) Sub-adult/adult male (M2), 32.5kg, 6<sup>th</sup> June 1996:

5ml Ketamine HCL (Ketalar ®) IM

0.6ml Azaperone (Stresnil ®) IM

2ml Comprapen IM

The animal became unconscious within seven minutes for radio collar attachment. As with the first animal, it recovered slowly and repeatedly fell over, so was placed outside the capture burrow. Again it crawled inside by itself and recovered successfully.

3) Male (M3), 48kg, 26<sup>th</sup> June 1996:

3ml Ketamine HCL (Ketalar ®) IM

0.5ml Azaperone (Stresnil ®) IM

Re-dose 2ml Ketamine HCL IM

The drug dosage was reduced in an attempt to improve the recovery time (and therefore reduce stress) of the aardvark. This proved insufficient to fully immobilise the animal, so a second dose was administered. Even with the top up, the animal recovered quickly, allowing only enough time to attach a radio collar. The animal recovered successfully.

4) Adult male (M4), 45kg, 16<sup>th</sup> August 1997:

4ml Ketamine HCL (Ketalar ®) IM

1.5ml Midazolam (Dormicum ®) IM

2ml Comprapen IM

Re-dose 2ml Ketamine HCL IM (due to animal waking up)

Midazolam was used with the aim of inducing amnesia in the aardvark, as it is known to do with human patients. Human patients usually have no recollection of events during and immediately prior to administration of Midazolam and it was hoped that by using this drug, the aardvark would not remember the traumatic capture experience. A radio collar was attached and the animal recovered slowly, so was allowed to enter the capture hole. It recovered successfully.

5) Adult female (F1), 40.5kg, 17<sup>th</sup> August 1996:

6.5ml Ketamine HCL (Ketalar ®) IM

0.5ml Azaperone (Stresnil ®) IM

2ml Comprapen IM

Re-dose 1ml Ketamine HCL + 0.25 ml Azaperone IM

The animal was worked on easily for radio collar attachment. This time the aardvark recovered relatively well, with little falling about. It re-entered its capture hole and recovered successfully. This aardvark had many mites (Hybophtheridae) on its back legs and ventral surface area.

The following two aardvarks were captured and collared after the first four implant operations were carried out. The timing of the drug effects and the animals consequent recovery from these were recorded for female F3.

6) Adult female (F3), 37.5kg, 22<sup>nd</sup> October 1996:

|                        |                                                                                        |
|------------------------|----------------------------------------------------------------------------------------|
| T <sub>0 min</sub> :   | 6ml Ketamine HCL (Anaket-V ®) IM<br>0.5ml Azaperone (Stresnil ®) IM<br>2ml Procopen IM |
| T <sub>6 min</sub> :   | Drugs visibly taking effect                                                            |
| T <sub>10 min</sub> :  | Animal immobilised, radio collar attached                                              |
| T <sub>76 min</sub> :  | Leg movements                                                                          |
| T <sub>85 min</sub> :  | Animal sitting                                                                         |
| T <sub>90 min</sub> :  | 2-3 steps before falling over                                                          |
| T <sub>110 min</sub> : | Semi-continuous walking, but unsteady                                                  |
| T <sub>135 min</sub> : | Walking steadily                                                                       |
| T <sub>139 min</sub> : | Enters hole, digs in.                                                                  |

The animal recovered successfully but could not be recaptured for the implant operation. When trapped down a burrow it remained inside for periods of up to seven days until the trap was removed, when it was deemed necessary to do so for the sake of the animal.

7) Juvenile/sub-adult male (M5), 22kg, 26<sup>th</sup> October 1996:

4ml (approx.) Ketamine HCL (Anaket ®) IM  
0.5ml Azaperone (Stresnil ®) IM  
2ml Procopen IM

This animal would not walk completely into the trap for five nights so the trap was eventually triggered manually when the aardvark was just inside. A collar was attached and the animal was held until it was considered safe to let it re-enter the burrow. Recovery was successful.

## Drug protocol for radio implant operations

Once implantable radio transmitters were available, a vet was enlisted to carry out the operation and administer the relevant anaesthetising drugs. The first four operations were carried out without the use of a halothane machine and the dosage regimes were varied experimentally with the aim of identifying the most reliable and safest procedure possible. The timing of the drug effects, the aardvarks vital signs, and the time to recovery were recorded.

a) Adult male (M1) recapture, 42kg, 29<sup>th</sup> August 1996:

|                               |                                                                                                                                                        |
|-------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------|
| T <sub>0 min</sub> :          | 71µg/kg Medetomidine (Domitor ®) IM<br>2.4mg/kg Ketamine HCL (Anaket-V ®) IM<br>0.2 mg/kg Atropine IM                                                  |
| T <sub>50 min</sub> :         | Operation started                                                                                                                                      |
| T <sub>70 min</sub> :         | Body temperature decreased to 34.3°C                                                                                                                   |
| T <sub>80 min Post-op</sub> : | 4ml Peni LA ® and 3ml Arthridine ® IM                                                                                                                  |
| T <sub>90 min</sub> :         | Animal woke up without warning while on the operating table while injecting antibiotic and had to be restrained and re-dosed with 75mg Ketamine HCL IM |
| T <sub>100 min</sub> :        | Animal began to wake again, re-dosed 50mg Ketamine HCL which had little effect                                                                         |
| T <sub>120 min</sub> :        | Animal awake and strong while carried to burrow for release.<br>Implant operation successful.                                                          |

b) Sub-adult/adult male (M2) recapture, 32kg, 30<sup>th</sup> August 1996:

|                              |                                                                                                       |
|------------------------------|-------------------------------------------------------------------------------------------------------|
| T <sub>0 min</sub> :         | 14mg/kg Ketamine HCL (Anaket-V ®) IM<br>0.94mg/kg Xylazine HCL (Rompun ®) IM<br>0.03mg/kg Atropine IM |
| T <sub>20 min Pre op</sub> : | 150mg Ketamine HCL IM<br>Body temperature 37.5°C                                                      |
| T <sub>30 min</sub> :        | Body temperature 35.4°C                                                                               |
| T <sub>40 min</sub> :        | 100mg Ketamine HCL intravenous (IV)<br>0.03mg/kg Atropine IM                                          |

|                       |                                                     |
|-----------------------|-----------------------------------------------------|
|                       | Body temperature 33.7°C                             |
| T <sub>50 min</sub> : | 100mg Ketamine HCL IM                               |
| T <sub>55 min</sub> : | 50mg Ketamine HCL + 1mg Medetomidine (Domitor ®) IM |

On release the animal was still under the effects of the drugs. It was placed outside its burrow, which it crawled into on its own. This release technique was exactly the same as that used previously for the first five animals collared, but this time the aardvark did not recover. After three days it had not exited the hole and was dug up dead. It was found in a small tunnel away from its main chamber and an autopsy revealed it had died of asphyxiation. It was resolved for future operations that aardvarks would not be released until they had fully recovered.

c) Adult female (F1) recapture, 37kg, 19<sup>th</sup> September 1996:

|                        |                                             |
|------------------------|---------------------------------------------|
| T <sub>0 min</sub> :   | 20mg/kg Ketamine HCL (Anaket-V ®) IM        |
|                        | 0.68mg/kg Midazolam (Dormicum ®) IM         |
| T <sub>30 min</sub> :  | Response to deep pain reflex                |
|                        | 300mg Ketamine HCL IM                       |
|                        | Body temperature 35.4°C                     |
|                        | Oxygen administered by mask                 |
| T <sub>40 min</sub> :  | Body temperature 35.5°C                     |
| T <sub>45 min</sub> :  | Deep pain reflex caused limb movement       |
|                        | 200mg Ketamine HCL IM                       |
| T <sub>50 min</sub> :  | Body temperature 33.7°C                     |
| T <sub>60 min</sub> :  | At release site, but kept in heated vehicle |
| T <sub>165 min</sub> : | Animal difficult to hold, so released       |

It displayed compulsive digging and sniffing behaviour and the movements of its hind legs were not well co-ordinated. It could not be constrained, however, and was allowed to enter its burrow. The next night it did not exit the burrow, so was dug out the following morning. It was barely alive and very cold when found, and died after 15 minutes.

The animal had been in relatively poor condition with many external parasites (Hybophtheridae) covering its body. It had been captured one month previously to have a collar fitted. In the following time it had lost 4kg in body weight. Autopsy showed multifocal disseminated yellow-white hard nodules

between 1 and 3mm in diameter throughout the lungs. There were areas of severe superficial congestion in the caudal lobes of the left lung. The pathological lesions were described as a sub-acute, multifocal disseminated pneumonia. Bacteria culture of the lungs identified *Actinobacillus suis* as the causative agent of the pneumonia (P. Nel, pers. comm.<sup>1</sup>).

d) Adult female (F2) new animal, 45kg, 20<sup>th</sup> September 1996:

|                       |                                                                                                           |
|-----------------------|-----------------------------------------------------------------------------------------------------------|
| T <sub>0 min</sub> :  | 15.5mg/kg Ketamine HCL (Anaket-V ®) IM<br>0.28mg/kg Midazolam (Dormicum ®) IM                             |
| T <sub>7 min</sub> :  | 4.4µg/kg Medetomidine (Domitor ®) IM                                                                      |
| T <sub>25 min</sub> : | Operation started, oxygen administered by mask                                                            |
| T <sub>30 min</sub> : | Response to deep pain reflex<br>300mg Ketamine HCL IV                                                     |
| T <sub>35 min</sub> : | Animal went into apnoea due to rapid injection of Ketamine<br>2ml Doxapram (Dopram ®) IV Animal recovered |
| T <sub>45 min</sub> : | Operation completed<br>4mg Betamethasone (Betsolan ®) IV<br>3ml Arthridine ® IM<br>6ml Peni LA ® IM       |
| T <sub>50 min</sub> : | In vehicle with heater on                                                                                 |
| T <sub>85 min</sub> : | Movements of aardvark too strong to hold, so released                                                     |
| T <sub>190</sub> :    | Aardvark walking normally and enters hole of own accord.<br>Operation successful.                         |

### The use of Halothane gas

e) Sub-adult female (F4) new animal, 25.5kg, 25<sup>th</sup> November 1996:

|                       |                                                                                                                        |
|-----------------------|------------------------------------------------------------------------------------------------------------------------|
| T <sub>0 min</sub> :  | 2ml Medetomidine (Domitor ®) IM<br>0.75ml Ketamine HCL (Anaket-V ®) IM<br>2.5ml Atropine IM<br>Body temperature 35.2°C |
| T <sub>20 min</sub> : | 1.5% Halothane administered with oxygen                                                                                |

---

<sup>1</sup> Nel, Dr P, Free State Nature Conservation

|                       |                                                                                        |
|-----------------------|----------------------------------------------------------------------------------------|
|                       | Operation begins                                                                       |
|                       | Body temperature 36.3°C                                                                |
| T <sub>40 min</sub> : | Operation ends                                                                         |
|                       | Body temperature 35.6°C                                                                |
| T <sub>50 min</sub> : | Body temperature 35.4°C                                                                |
| T <sub>57 min</sub> : | Body temperature 35.6°C                                                                |
| T <sub>75 min</sub> : | Body temperature 35.0°C                                                                |
|                       | Animal still on operating table, kept on Halothane to allow Ketamine time to wear off. |
| T <sub>120</sub> :    | Animal at release site.                                                                |
|                       | Antisedan iv. (antidote for Dormitor)                                                  |
| T <sub>125</sub> :    | Animal wide awake, bolts away very quickly.                                            |
|                       | Operation successful.                                                                  |

This aardvark became habituated to humans in January 1997, the second animal to do so.

f) Juvenile/sub-adult male (M5) recapture, 22.5kg, 25<sup>th</sup> November 1996:

|                   |                                                   |
|-------------------|---------------------------------------------------|
| T <sub>0</sub> :  | 2ml Medetomidine (Domitor ®) IM                   |
|                   | 150mg Ketamine HCL (Anaket-V ®) IM                |
|                   | 2ml Atropine IM                                   |
| T <sub>30</sub> : | 1.5% Halothane administered with oxygen           |
|                   | Body temperature 34.7°                            |
| T <sub>35</sub> : | Body temperature 34.3°                            |
| T <sub>40</sub> : | Body temperature 33.9°                            |
| T <sub>45</sub> : | Body temperature 33.9°                            |
| T <sub>50</sub> : | Body temperature 34.1°                            |
|                   | Animal kept on Halothane for Ketamine to wear off |
|                   | At release site animal given Antisedan iv.        |
|                   | Animal wakes up, bolts away quickly.              |
|                   | Operation successful.                             |

This aardvark became habituated to humans in December 1996, the first of the group to do so.

In January 1998, four new aardvarks were captured for implant operations. This took place after the field work for the current thesis was completed so is not of relevance to the results based on data from the aardvarks mentioned here. However, it is worth mentioning that very similar protocols were used on all four animals, following closely that of the last two above. Medetomidine (Domitor ®) IM and Ketamine HCL (Anaket-V ®) IM were administered to all animals at the capture sites, followed by Halothane on the operating table. All four operations were successful and all four animals recovered fully. Two of these became habituated to humans.

In addition to the first round of implants, two animals have since been recaptured to have the implants replaced after these stopped working. The two aardvarks were F4 (December 1997) habituated for the period of 11 months prior to recapture, and M5 (October 1998) habituated for the period of 22 months prior to recapture. Both were captured by hand with the aid of a net because they could be approached easily. Again the operations were successful and neither animal showed signs of losing their habituated status. In the case of M5, this was his third capture.

### Study animals

In total, nine aardvarks were captured to have radio transmitters attached. Five of these were males and four were females. They were mentioned in the section above on immobilisation, but are listed together here for easier comparison. The two aardvarks that were habituated during the study are indicated by an asterisk (\*).

Adult male (M1) 42kg Captured June 96

Sub-adult/adult male (M2) 32.5kg Captured June 96

Adult male (M3) 48kg Captured June 96

Adult male (M4) 45kg Captured August 96

Juvenile/sub-adult male (M5) 22kg Captured October 96 \*

Adult female (F1) 40.5kg Captured August 96

Adult female (F2) 45kg Captured September 96

Adult female (F3) 37.5kg Captured October 96

Sub-adult female (F4) 25.5kg Captured November 96 \*

## Radio transmitters

The radio collars were home-made using Telonics transmitters (Telonics, Telemetry-Electronic Consultants, 932 E. Impala Avenue, Mesa Arizona 85204-6699, USA) powered by Lithium C-cell batteries (Uniross Batteries, SAFT Lithium). The transmitter and battery were encased in dental acrylic which in turn was held in place with 2 ply industrial belting, 25mm wide and 2.5mm thick. The belting was made two layers thick to enclose the transmitters aerial, which needed to extend well beyond the transmitter body without being exposed to the elements to be knocked about. The double layer added strength to the collar as well. The mass of the collars were approximately 160g each.

As an aardvarks head tapers away from its neck, the only things stopping a collar from falling off were the ears. Consequently, the collars had to be fitted snugly to keep them on. Although this was done without restricting the animals ability to move and breath, it did result in a build up of mud and dirt between the inside of the collar and neck. This was found to be the case with two of the animals recaptured for radio implant operations. In wet conditions this would have been worsened and would probably have caused some irritation to the animal. This was the main reason for the change over from collars to implants. A second, and important reason for the switch, was that implants cannot fall out, whereas collars can fall off.

Radio implants were attained ready made from Telonics. Their specifications were as follows: IMP/400/L, length 9.7cm, diameter 3.3cm, weight 85-90g, operational life 20-36months at 35-75 pulses/min. They were inserted intra-abdominally while the aardvarks were anaesthetised by a vet. It was intended to tie them into the fat layers of the abdominal wall, but when the operations commenced it was discovered that there was not enough fat to do this. They were, instead, placed freely into the peritoneal cavity. The frequencies of all transmitters ranged from 146Mhz to 151Mhz, although most were concentrated in the 148Mhz region.

## Location and habituation

A whip antenna placed on top of a vehicle allowed signals from the transmitters to be detected while driving in the general vicinity of the aardvarks, and once one was detected a hand held directional antennae used to find its direction. Two types of directional antennae were used throughout the study, one a home made, 4 prong yagi antenna based on the design of W. F. Ferguson (department of Zoology and Entomology, UP), the other a Telonics antenna. Both were very efficient at locating the positions of individual aardvarks.

The average distance from which the signal of a transmitter could be detected was approximately 1km on flat, open ground. This would have been greater if the aardvarks were larger animals, but the positions of their necks and abdomens meant that the transmitters were virtually at ground level. The strength of the signals varied slightly between transmitters but were affected mostly by the terrain. A low rise between the tracker and aardvark weakened the signal, while a larger hill or gully sometimes cut off the signal completely, even if the animal was only 200m away. The distance from which a signal could be detected was increased substantially if one climbed a hill and gained some height. From hill tops overlooking open ground, signals were received from as far as 5km away.

When an aardvark was in a burrow, the strength of the signal was reduced significantly, sometimes to the extent that the antenna had to be within 10m of it to receive a signal. This meant that to locate an aardvark during the day was almost impossible unless one had a good approximation of its burrows location.

When active, the aardvarks were followed on foot as continuously as possible with the aim of getting them used to human presence. For the first six months, none of the aardvarks allowed human observers close to them and they mostly stayed out of sight. Some of the animals were more wary than others and bolted away at the slightest hint of disturbance, and could not be approached again the same night. Others, although they did not allow humans to approach closely, would keep just out of sight without running away. These animals would be seen fortuitously at a distance several times per night if the tracker was persistent.

In the period of the current study only two aardvarks out of nine became habituated, allowing close observation, while the rest continued to keep their distance. These two animals (male M5, female F4), the smallest of the nine, eventually became so tame that they were apparently undisturbed by physical contact. A further two animals became habituated after the field work for this thesis was completed, so were not included in the data analysis. These latter two individuals, also a male and female, were captured in January 1998.

The habituation of aardvarks required persistence on the part of the trackers, but was also very much dependant on the individual animals themselves. The first three to be habituated were all individuals under 25kg, so it appeared that younger animals were relatively easier to tame than adults. This fact only indicated correlation of course, not necessarily cause, but it appeared to play a genuine role in the process. All three were habituated in less than three weeks. The fourth aardvark habituated was a female weighing 33kg (an intermediate mass) and it took approximately three months to tame her. This

individual was the first one hand caught and, therefore, only suffered stress for a few minutes while the immobilising drugs took effect. The smallest armadillo (19kg) was also hand caught, indicating that this method of capture may have played an important role in their eventual habituation. It should be recognised, however, that catching by hand is very difficult and primarily a result of good fortune. It also contains the risk of driving over the animal while trying to get close to it.

Animals M1, M3, M4, F1, F2 and F3 were all followed regularly in 1996 or 1997, but did not become habituated at all, while F6 was followed almost continuously from February to June 1998 with no success. Some of these individuals were more shy than others, and entered burrows immediately after detecting that they were being followed, while others, although staying above ground, simply kept out of sight of their pursuers. The ability of the armadillos to escape their followers at such times by entering burrows meant that they were never exposed to the sounds or smells of humans for long periods. They did not, therefore, have sufficient time to get used to being followed or realise that the humans represented no threat, so there was little chance of them being habituated.

Part of the reason for their evasive behaviour was probably due to the stressful capture experience, but the fact that most armadillos ran away at their first contact with humans, even without being captured and immobilised, indicates that this was natural behaviour and could not be blamed entirely on the capture methods. Melton (1975) described the same problem of fleeing armadillos when trying to observe them in the wild in Uganda, an area totally separate from the Free State. This is further proof that evasive behaviour is instinctive in armadillos.

## CHAPTER 4

### ACTIVITY PATTERNS, HOME RANGES, NIGHTLY MOVEMENTS AND BURROWS

#### Introduction

Aardvarks have been considered exclusively nocturnal mammals that may be seen during daylight hours under exceptional circumstances (Skinner & Smithers, 1990). They are recorded as being late movers, seldom being seen before 21h00 and are known to forage on both dark and moonlit nights (van Aarde *et al.*, 1992). Kingdon (1971) states that they usually leave their holes at about 20h00 and return to them or dig a fresh one before dawn. He records them as being very active in bright moonlight. There have been observations of them coming out to sun themselves (Kingdon, 1971) with one free-ranging tame aardvark regularly sunning itself for about an hour each day at 10h00. As with many aspects of aardvark behaviour, the knowledge above comes mostly from chance or even anecdotal sightings (with the exception of van Aarde *et al.*, 1992) and needs to be investigated more thoroughly. This was possible with the availability of radio tagged aardvarks.

Home ranges consist of a more or less restricted area within which an animal moves when performing its normal activities. The home range of aardvarks have mostly been estimated in the past from their tracks, which has the potential for quite serious inaccuracies when the animals are not actually observed (especially when their behaviour has only been described from chance sightings, as was the case for aardvarks). The only substantial home range study carried out to date on aardvarks which involved catching and radio collaring animals was that of van Aarde *et al.* (1992) and was carried out at the same site as the present study. Positions were estimated using triangulation every hour, a good method except for the times when aardvarks move into areas where they cannot be detected, such as behind hills or in gullies. Because aardvark home ranges have been little studied, it was considered worthwhile to collect additional data and improve on the current knowledge. For this reason, and because positional fixes could be gained during the normal course of research during the present study, home ranges were investigated for the radio tagged aardvarks during 1996 and 1997.

Most estimates of the nightly distances travelled by aardvarks come from observations of their tracks. They range from 10km (Kingdon, 1971) to as much as 30km (Shoshani, 1988). Melton (1975) calculated a mean nightly distance travelled as 9.6km, with a maximum estimated distance of 14.7km. The only recorded estimates of distances travelled per night derived from radio tagged aardvarks came from the work of van Aarde *et al.* (1992), who calculated a mean distance covered from sunset to

sunrise of 2.21km, with a range of 0.5km to 6.97km. Apart from the interest value of knowing nightly distances travelled by aardvarks on TdR, it is useful to know how much ground an animal has to cover to locate sufficient food to maintain itself. Such knowledge leads to implications about the ant and termite communities, about the energy budgets of the predator, and ultimately about carrying capacities of the area.

Burrows are vital in the life of aardvarks due of their role in providing protection from the elements and from predators. Aardvarks remain in their burrows the whole day (except at certain times in winter, as will be shown later) which means they spend at least two thirds of their life underground. There has been much interest in the burrow systems of aardvarks because of the effect they have on the veld, on farm land, and the influence they have on the lives of other animals. Also, there have been many descriptions of burrow structure and stories of how people went down holes to catch aardvarks and were never seen again. Somehow the aardvark and its burrow holds a fascination with many people. Elaborate burrow systems have been described by a number of authors, including Hediger and Verschuren (1948), Kingdon (1971), Smithers (1971) and Melton (1975), and references have even been made to how females make use of the larger burrows as permanent sites while the males are more nomadic. How this last fact was inferred without really knowing anything about the behaviour of the different sexes and their burrowing habits is unknown.

There is much anecdotal knowledge concerning aardvark burrow systems and their usage which needs to be redressed, so with the availability of radio tagged aardvarks, and the opportunity of making observations of burrow usage during the course of normal observations, the burrowing habits of aardvarks were investigated.

## **Materials and Methods**

All data used to estimate activity patterns, nightly movements, burrow usage and home ranges were recorded during the normal course of a nights research, while making observations on the feeding behaviour.

### **Activity periods**

The times at which aardvarks emerged from their holes were recorded regularly, although not every night. The positions of the burrows of the two habituated aardvarks were often known so the timing of emergence could be recorded. This was done either by checking the radio frequencies regularly until the

signals were obtained, indicating that the aardvark(s) had emerged, or by waiting near the burrow entrance and watching. Standing too close to the burrow, however, appeared to delay the exit of the animal, even when habituated, so this was not often done. Aardvarks that were not tame were extremely sensitive to noise and movement near their burrows, and did not emerge if the observer was close. It was, therefore, standard practise to remain slightly away from the entrance to get an undisturbed exit time.

The time of re-entry of a hole was recorded either by observing the aardvarks until they became inactive (in which case the position of the hole was also recorded) or by waiting for the signal to disappear while at another position. The position of the burrow could often be checked at a later stage to confirm that the aardvark had in fact entered a hole, and not simply moved out of range.

### **Home range analysis**

The majority of aardvark positions, including all those of the two habituated animals, were fixed by sight, while some (namely for the unhabituated aardvarks) were judged by the sounds of their movements as they ran away because they were not observed. Two methods were used estimate these positions. The first involved estimating the position of the aardvark as a distance and bearing from known landmarks dotted throughout the study site. The positions of all landmarks were fixed previously with a GPS (Garmin ®) and the distance from the aardvark to the landmark estimated by pacing between the two. The second method was to fix the position immediately using a GPS. Practical constraints meant that a GPS was not carried continuously.

Built in to any home range study is a certain amount of inaccuracy, and the present study was no exception. Three sources of inaccuracy for the distance/bearing method of positional estimation were the estimated distance from the animal to the landmark, the GPS position of the landmark, and the plotting of the position on a map to obtain a cartographic position.

The inaccuracy of the distance estimation was calculated by pacing against an accurately measured distance (100m) and determining the difference between the two. From six repetitions it was determined that the author underestimated the 100m distance by an average of 6m (range 3m-8m). The nearest possible landmarks to the animals were always used with the aim of keeping the distance estimate inaccuracy to a minimum. To be safe, an error of 10m per 100m, was used, so a maximum inaccuracy of 30m occurred with landmarks 300m away from the aardvark.

The estimated positional error (EPE) of the GPS was usually found to lie between 19 and 34m, depending on the satellite coverage. Landmark positions were only recorded when satellite coverage allowed an EPE of less than 30m. Accumulating the potential errors of positional fixes gives a maximum inaccuracy of 72.5m (30m distance + 30m GPS + 12.5m map plotting error), and an area inaccuracy of less than one hectare.

Except for the two tame animals, all the aardvarks kept their distances from the observers. The degree to which they evaded contact varied between individuals, with some keeping just out of sight but remaining above ground, and others running away at the slightest disturbance and immediately entering a burrow for safety. Whatever the reaction, once an aardvark knew it was being followed its behaviour changed from foraging to escape, and, therefore, their positions while being followed were influenced by the human pursuer. Only positions recorded before evasive behaviour occurred were used in the analysis.

Positions were recorded discontinuously for both habituated and unhabituated aardvarks, as opposed to continuously, which involves taking fixes at very short intervals, usually between five and 15 minute intervals. Continuous locational positions were recorded occasionally for analysis of nightly movement patterns, but these data were not used for home range analysis. An important consideration when estimating home ranges is the frequency with which positions are fixed. If positions are recorded too frequently there is a problem of auto-correlation (non-independence).

Independence between successive observations is an implicit assumption in most statistical analyses of animal movements (Swihart & Slade, 1985). Independence occurs when an animal's position in its home range at time  $t + k$  is not a function of its position at time  $t$ . In studies that use long intervals between positional fixes, independence of successive observations is likely to be achieved (unless the animals carry out the same routine and follow the same routes every day), but frequent monitoring of an individual's position severely jeopardises the validity of the independence assumption. Frequent successive observations will tend to be positively correlated so sample variances of locations will be underestimates of the true values, and statistical estimates of home range size will underestimate the true size of the home range by an amount related to the covariance between successive observations (Swihart & Slade, 1985). Erroneous descriptions of range utilisation will also occur (Rooney *et al.*, 1998).

The simplest methods of dealing with autocorrelated data are based on rates of movement (Rooney *et al.*, 1998). The most straight forward of these supposes that a time to independence for successive fixes

(i.e. the shortest time interval between two non-autocorrelated data points) would be the time taken for an animal to cross its entire range. Because an average foraging speed was estimated (see below), this was used to estimate the time it would take an aardvark to traverse its entire range. Actual walking speed (without foraging) could also be calculated, but aardvarks rarely just walk for long periods of time without stopping to feed, so this measure of speed of movement would be inappropriate because it would underestimate the time to independence.

The foraging speed was estimated from data from both habituated aardvarks and a large number of sub-samples covering many random periods of different nights. This estimate, therefore took into account periods of lesser and greater activity (i.e. times when the aardvarks moved quite a lot, times when they moved slowly, and times when they stayed in one place for long periods feeding at one site). Neither of the two habituated aardvarks ever showed any resting periods in which they just stood or sat without feeding (neither did the other two aardvarks habituated in 1998, Lindsey pers. comm.), so the only periods when they stayed in the same place for long periods and when they were not kept there by feeding behaviour was when they were in their burrows.

Before calculating the home ranges of any aardvarks, the approximate limits to their individual ranges were familiar. Therefore, an approximate estimation of the greatest diameter of their ranges could be calculated and this used to estimate the time to independence for locational fixes. If a distance of 3km was taken as the greatest distance across a home range (this was probably higher than average), and an estimate of average foraging speed of 600m per hour (from ~ 50m /5mins), then an aardvark could cross its home range in approximately five hours.

In an activity period of eight hours, two positional fixes could in theory be taken which would be over five hours apart, although one of these might not be considered independent of the animal's sleep hole at the time. In other words, if the positional fix was taken ten minutes after emergence from the burrow for example (or ten minutes before re-entering the burrow), the aardvark would not have moved very far and its position would be highly dependent on the position of the burrow. With this in mind, and the fact that the activity periods of the aardvarks were shorter in winter than summer, one positional fix was generally taken per night, although two were taken when the activity period of the animal was long enough for locations to be independent.

Regarding the unhabituated aardvarks, practical constraints often meant that locations were not obtained every night, and sometimes as little as once or twice a week. Such longer time periods between locations obviously do not suffer from the problems of autocorrelation, but they do mean that less

locations are made in the time period available, which means that the full range of the animal may be underestimated.

When starting a home range study it is recommended to carry out a “trial run” first, which includes estimating the number of fixes needed from each individual animal to determine home range size, by calculating the point at which the home range reaches an asymptote (Harris *et al.*, 1990). Because home range estimation was only part of the present study and following the aardvarks was a necessity anyway, positional fixes could be gained during the course of a normal nights work, so they were recorded without knowing the minimum amount required. However, *post hoc* estimations of the number of fixes required per animal were carried out to check whether the home range estimations for each aardvark were calculated with enough points.

The two methods used to estimate the home ranges of the radio tagged aardvarks at TdR were minimum convex polygon (MCP) and adaptive kernel. Both were calculated using the computer software package CALHOME (U.S. Forest Service, Pacific Southwest Research Station). The MCP method is the most frequently used of all home range estimation methods, and as such is useful for comparison with other studies, including the one on aardvarks by van Aarde *et al.* (1992). Disadvantages are that it includes areas that may never be visited by the subject animals (this can be reduced by using 95% or less of fixes which removes extreme outliers) and that it gives no indication of intensity of use of areas within the range (in other words it does not examine core areas).

The kernel method is an elegant and powerful technique representing range configuration (Cresswell and Smith 1992). It is an approach to home range analysis based on probability density estimations, that is the home range of an animal is described in terms of a probabilistic model. It is very useful for estimating the utilisation distribution density (the name given to the distribution of an animal’s position in the plane) because there are no constraints placed on the form of the utilisation distribution (Worton, 1989).

### **Nightly movements**

Nightly movement patterns were recorded at irregular intervals in 1997 for the two habituated aardvarks. The aardvark being followed was located in its burrow before emerging and once out was followed for the majority of the night. Every ten minutes the position of the animal was recorded with a GPS. The accuracy of the GPS was recorded as within 30m or less so the results should be treated with caution. The distances between GPS points were used to estimate nightly distances moved. Aside from

the potential positional inaccuracy of the GPS locations, taking positions every ten minutes only allows for straight line distances between consecutive locations and does not take into account any meandering of the animal between such fixes. They were, therefore, underestimates.

As well as overall nightly movements, a general foraging speed was estimated by walking directly in the foot steps of the habituated aardvarks and pacing out the distance covered in a given unit of time (five minutes). Multiple sub-samples were obtained to achieve a reliable estimate. This was then used in conjunction with the GPS data for estimated nightly distances moved.

## **Burrows**

As described briefly above, the positions of the burrows of the two habituated aardvarks were recorded regularly while following them at night. Locations were fixed using a GPS. Because they tended to use burrows on consecutive nights for periods of days to weeks (this will be shown properly in the results) the position of a burrow on a day when the animal was not observed to enter a hole could be judged from past knowledge of burrow use. It was rare for an aardvark (one of the two habituated ones at least) to reuse a burrow after it had started using a different one, unless a long period of time had elapsed. The only times they stopped using a hole for brief periods before reusing the same hole was when they were disturbed somehow at the burrow.

Only one other aardvark had its burrows positions located regularly (aardvark M2) and this was only for the period of three months at the beginning of the study. The remaining unhabituated animals burrows were located irregularly throughout the study period because to do so required long periods of following at a distance, which was impractical. Often when following an unhabituated aardvark with the aim of habituating it, the animal would enter a burrow to escape its pursuer. Such utilised holes were not generally considered their sleeping burrows of the time and were therefore not recorded as such. Locating burrows when the aardvarks were already inside (in the daytime) was virtually impossible.

Burrow temperatures were recorded at two different sites in June 1996, at a time when air temperatures were consistently below freezing at night. Temperature loggers were placed at approximately 2m depth for nine days and 11 days in the two separate burrows. Both ground and burrow temperatures were concurrently recorded every two hours for a period of 20 days.

## Results

### Activity periods

Figure 5 shows the burrow emergence and re-entry times for aardvarks M5 and F4 during 1997. Emergence and re-entry times in the chart did not necessarily correspond to the same days because sometimes only one or the other were recorded during the course of a night. Although there was variation both within and between the aardvarks, there was a very clear trend in both emergence and re-entry times through the course of the year. From January to June/July 1997 there was a gradual change, with the timing of both emergence and re-entry times becoming earlier. After July the timing reversed, with both emergence and re-entry times gradually becoming later again until they reached similar levels (in time) during December 1997 as they had in January 1997.

Not only did both aardvarks show the same trends, but both also showed very similar timing of those trends and both emerged from and re-entered their holes at very similar times throughout the year. Another fact that can be deduced from the chart was that the activity periods of both animals, that is the time they were active above ground, shown as the periods between the curves of exit time and re-entry time, were longer in January and December than they were in July. The two habituated aardvarks were, therefore, out of their burrows for less time on average in winter than they were in summer.

The activity periods of the unhabituated aardvarks, although not recorded as frequently as the two tame animals, are shown in Table 1. Occasions when these aardvarks entered burrows while being followed for habituation purposes were not included, as their behaviour was clearly evasive and the reasons for them entering burrows was escape. Included in the Table are the range of times recorded for three male and two female aardvarks, during the periods when they were available. None of the months comprise data from all five animals at the same time.

A similar pattern to that of Figure 5 occurred for the unhabituated animals, in that both emergence and re-entry times were earlier in winter than they were in summer. However, none of the animals represented in Table 1 emerged from their burrows before nightfall, even in the winter months.

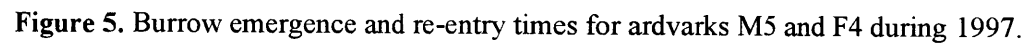


**Table 1.** Ranges of emergence and re-entry times for the unhabituated aardvarks from June 1996 to June 1997. Contributing animals were: M1, M2, M4, F2 and F3.

|                | Emergence time | Re-entry time |
|----------------|----------------|---------------|
| June 1996      | 17h50 - 18h40  | 01h10 - 02h40 |
| July 1996      | 18h10 - 19h40  | 00h30 - 02h20 |
| August 1996    | 18h10 - 20h00  | 01h00 - 03h30 |
| September 1996 | 19h00 - 20h10  | 01h30 - 04h10 |
| October 1996   | 19h30 - 20h20  | 02h20 - 04h20 |
| November 1996  | 20h00 - 20h50  | 02h00 - 04h40 |
| December 1996  | 20h40 - 21h40  | 03h10 - 05h10 |
| January 1997   | 20h30 - 21h30  | 02h50 - 05h20 |
| February 1997  | 20h40 - 21h20  | 03h00 - 04h40 |
| March 1997     | 19h50 - 21h00  | 02h40 - 04h10 |
| April 1997     | 18h20 - 19h50  | 00h40 - 03h00 |
| May 1997       | 18h20 - 19h10  | 00h40 - 02h40 |
| June 1997      | 18h20 - 19h00  | 00h20 - 02h50 |

Sometimes, both emergence and re-entry times were recorded for one or both of the habituated aardvarks in the same night, allowing the length of the nights activity period to be calculated. Monthly averages are shown in Figure 6.

It is clear that both aardvarks activity periods were shorter in winter than in summer. Both animals showed a similar increase in activity period from February to March, followed by a sharp decrease until May. Both aardvarks were on average active for the least period of time per night in June 1997. From July onwards the average activity period for both aardvarks increased steadily until October for F4 and November for M5. The change from October to November was the only period when the lengths of the activity periods for the two aardvarks diverged.

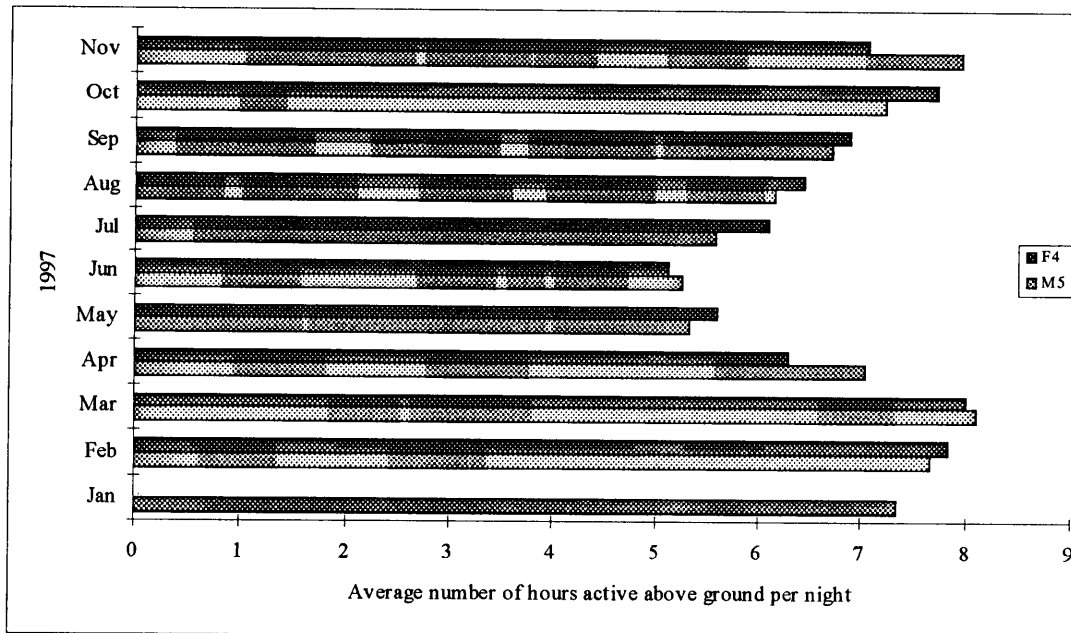


**Figure 6.** Monthly variation in average nightly activity periods for aardvarks M5 and F4 during 1997.

It was considerably more difficult to estimate the activity periods for the unhabituated aardvarks, because to do so required following them (to obtain their burrow re-entry time), and this often forced them into a burrow earlier than they would normally cease surface activities. Hence, the range of emergence and re-entry times given in Table 1 should be used as a guide to their activity periods. If there was a difference in the length of activity periods for these other aardvarks between summer and winter, then it was that activity was shortened in winter, but the pattern was not as clear as it was for aardvarks M5 and F4.

Table 2 shows the temperature ranges at which the two habituated aardvarks ceased surface activities through the winter and early summer of 1997. In July and August 1997, the two habituated aardvarks were active at temperatures as low as 2.1°C, and it is probable that other aardvarks were active at even colder temperatures. In other months the aardvarks ceased surface activities at higher temperatures. From October 1997 onwards this corresponded with dawn, after which aardvarks always went back to their burrows, but surface activity ceased as early as 24h00 in May 1997, when the average temperature was 7.5°C. This obviously did not correspond to the approaching daylight hours.

**Table 2.** Burrow re-entry times and corresponding ambient temperatures for aardvarks M5 and F4. Re-entry times are taken from Figure 5.

| 1997      | Range of burrow re-entry times | Temperature range at burrow re-entry |
|-----------|--------------------------------|--------------------------------------|
| April     | 22h00 - 02h00                  | 12.5 - 9.9°C                         |
| May       | 21h30 - 24h00                  | 10.1 - 7.5°C                         |
| July      | 22h00 - 02h00                  | 3.7 - 2.2°C                          |
| August    | 23h00 - 03h00                  | 4.3 - 2.1°C                          |
| September | 01h00 - 04h00                  | 8.5 - 7.4°C                          |
| October   | 01h00 - 05h00                  | 10.4 - 8.3°C                         |

Other environmental factors that may potentially have exerted an influence on the activity patterns of aardvarks were rain, wind and moonlight. Without looking for evidence of correlation between activity with any of these, it is enough to state that the two habituated aardvarks were active every single night they were searched for. They were active in the rain and in strong winds, although both types of weather appeared to make the animals more skittish. Moonlight appeared to exert no influence on activity either, with animals active at times of full moons and new moons. There were nights, even weeks when one or two of the unhabituated aardvarks could not be located, but these invariably turned out to be the result of them being active in unexpected areas, not because they remained inactive.

### Home range estimation

Home range estimates were made for five aardvarks, including the two habituated animals. The aardvarks were M2, M4, M5, F2 and F4. Ninety five percent MCP’s and two levels of adaptive kernel (90% and 50%) were estimated for each individual. The results, in hectares, are shown in Table 3.

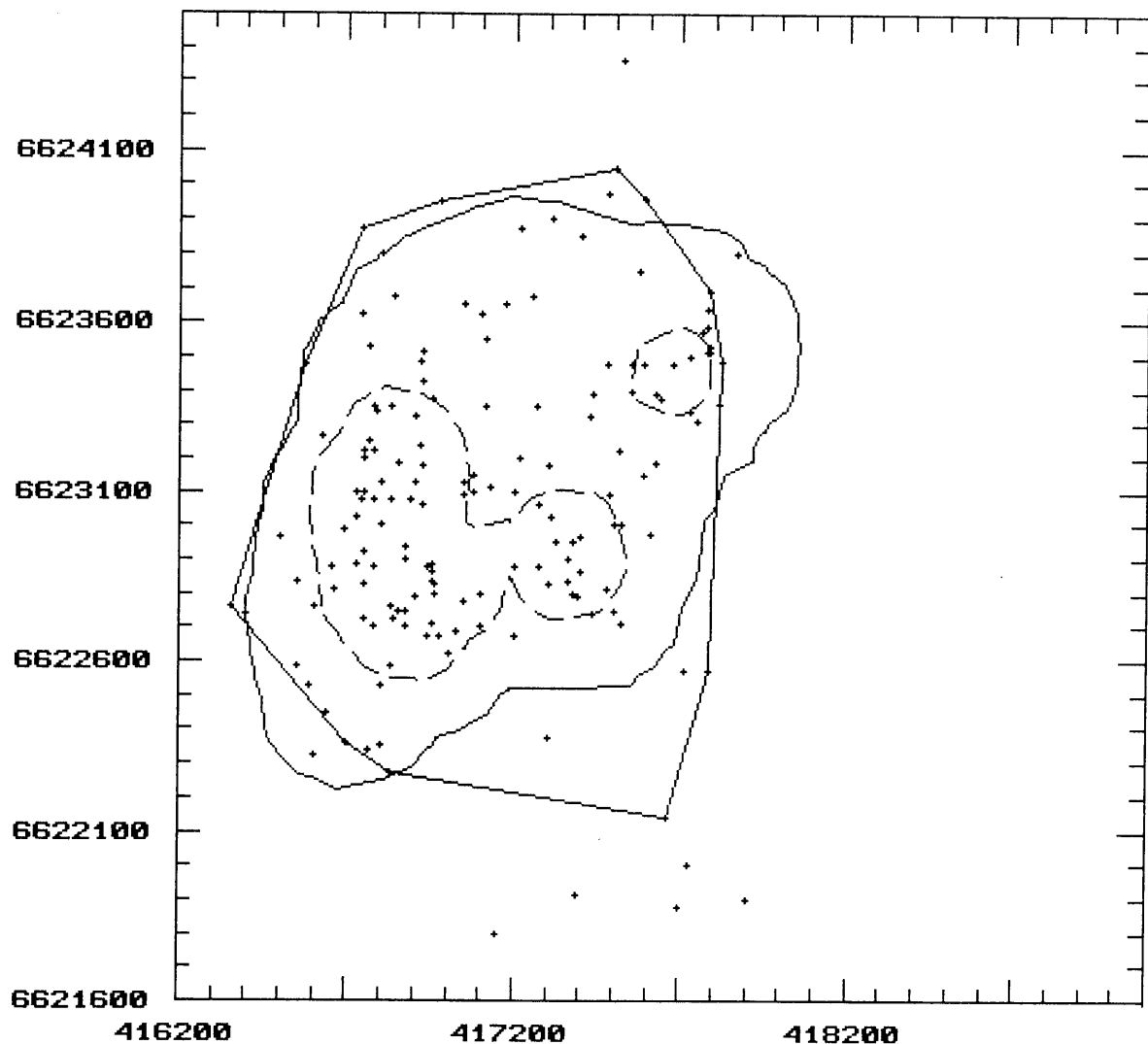
**Table 3.** Home range estimations for five aardvarks (3 males, 2 females), including the two habituated animals. All home range estimates are given in hectares.

| Aardvark | Months of positions | Number of positions | MCP 95%  | Adaptive kernel 90% | Adaptive kernel 50% |
|----------|---------------------|---------------------|----------|---------------------|---------------------|
| M2       | Jun 96 - Aug 96     | 50                  | 133.1 ha | 147.3 ha            | 40.5 ha             |
| M4       | Aug 96 - Jun 97     | 80                  | 301.7 ha | 384.4 ha            | 92.4 ha             |
| M5       | Nov 96 - Oct 97     | 162                 | 213.6 ha | 198.8 ha            | 53.1 ha             |
| F2       | Oct 96 - Oct 97     | 82                  | 239.3 ha | 274.7 ha            | 65.7 ha             |
| F4       | Dec 96 - Oct 97     | 160                 | 271.5 ha | 248.0 ha            | 85.4 ha             |

Asymptotic home range graphs for four of the aardvarks are shown in appendix I. These represent the number of positional fixes required to obtain asymptotic home range estimates. Aardvark M2 is not shown because only 50 positions were obtained before the animal died, although the area curve did apparently reach an asymptote between 40 and 50 positions. Of the other four animals, only M4 did not satisfactorily reach an asymptote, although its home range area did dip between 50 and 60 positions before increasing again. F2’s home range area reached an asymptote earlier than the rest, at 30 positions.

Regarding the two habituated animals, M5’s area reached an asymptote between 70 and 80 positions, although it did increase slightly after this, while F4’s area reached an asymptote between 80 and 90 positions, increased sharply again between 100 and 110 positions, then evened off a second time at approximately 120 positional fixes. This increase in area between 100 and 110 fixes can be attributed to the aardvark shifting her home range quite considerably at this time. After the focus of her activities had changed, she occasionally revisited the previous areas of her original focus, but did so only rarely.

Figures 7 shows the entire home range of aardvark M5 for the period of one year (162 positions), while Figure 8 shows his home range split into two 6 month blocks. Figure 9 shows the entire home range of aardvark F4 for one year (160 positions), while Figure 10 shows her home range split into two 6 month blocks. The home ranges were split in this way to indicate the shift in their ranges, which should be apparent for F4. The scale in all the home range Figures is given as Universal Transverse Mercator (UTM), and can be read as metres.



Display units (x and y co-ordinates) = metres

Number of data points = 162

Minimum convex polygon      95% = 213.6 ha ———

Adaptive Kernel                      90% = 198.8 ha ———

50% = 53.1 ha - - -

**Figure 7.** Home range estimation for aardvark M5 for the period from November 1996 to October 1997, using the UTM scale.

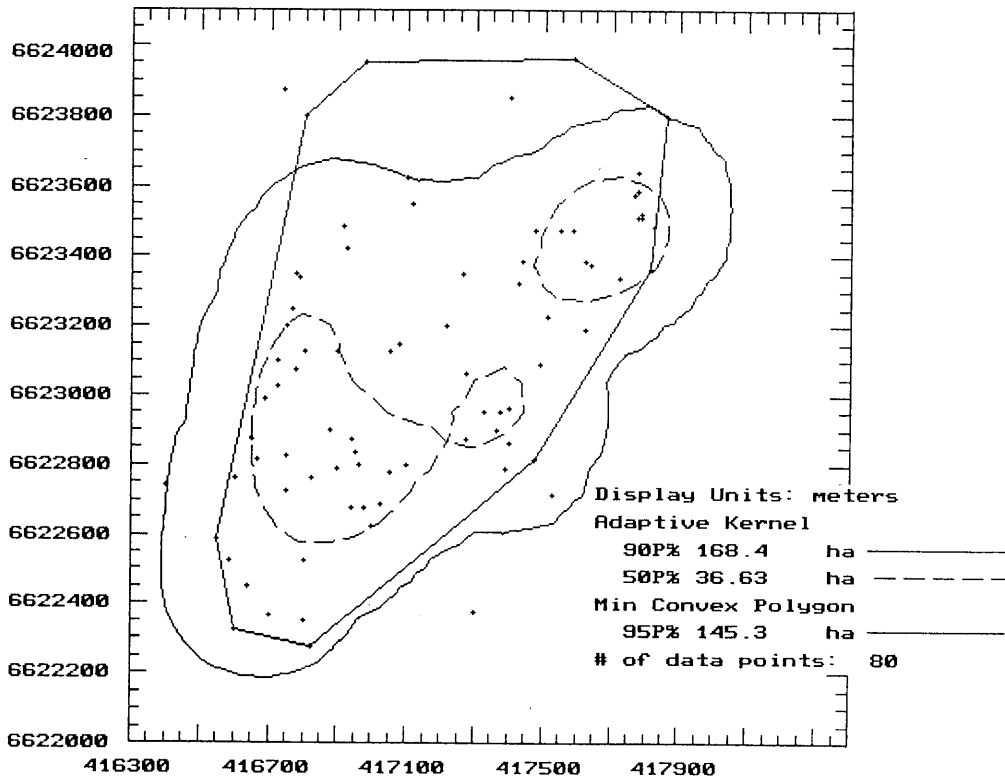
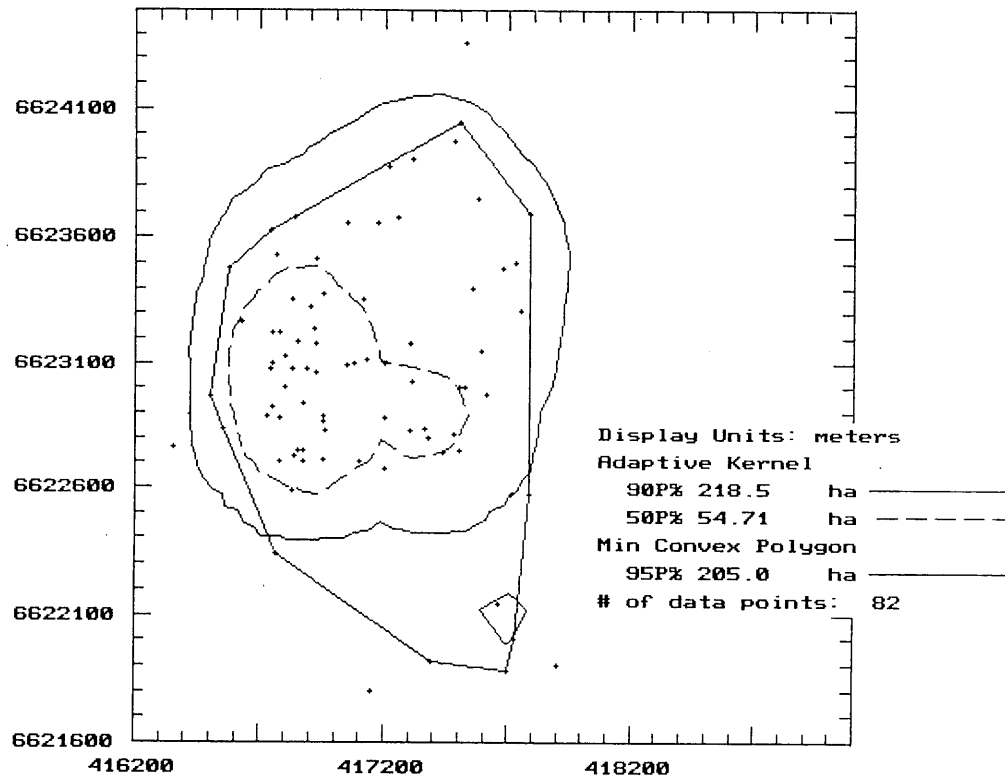
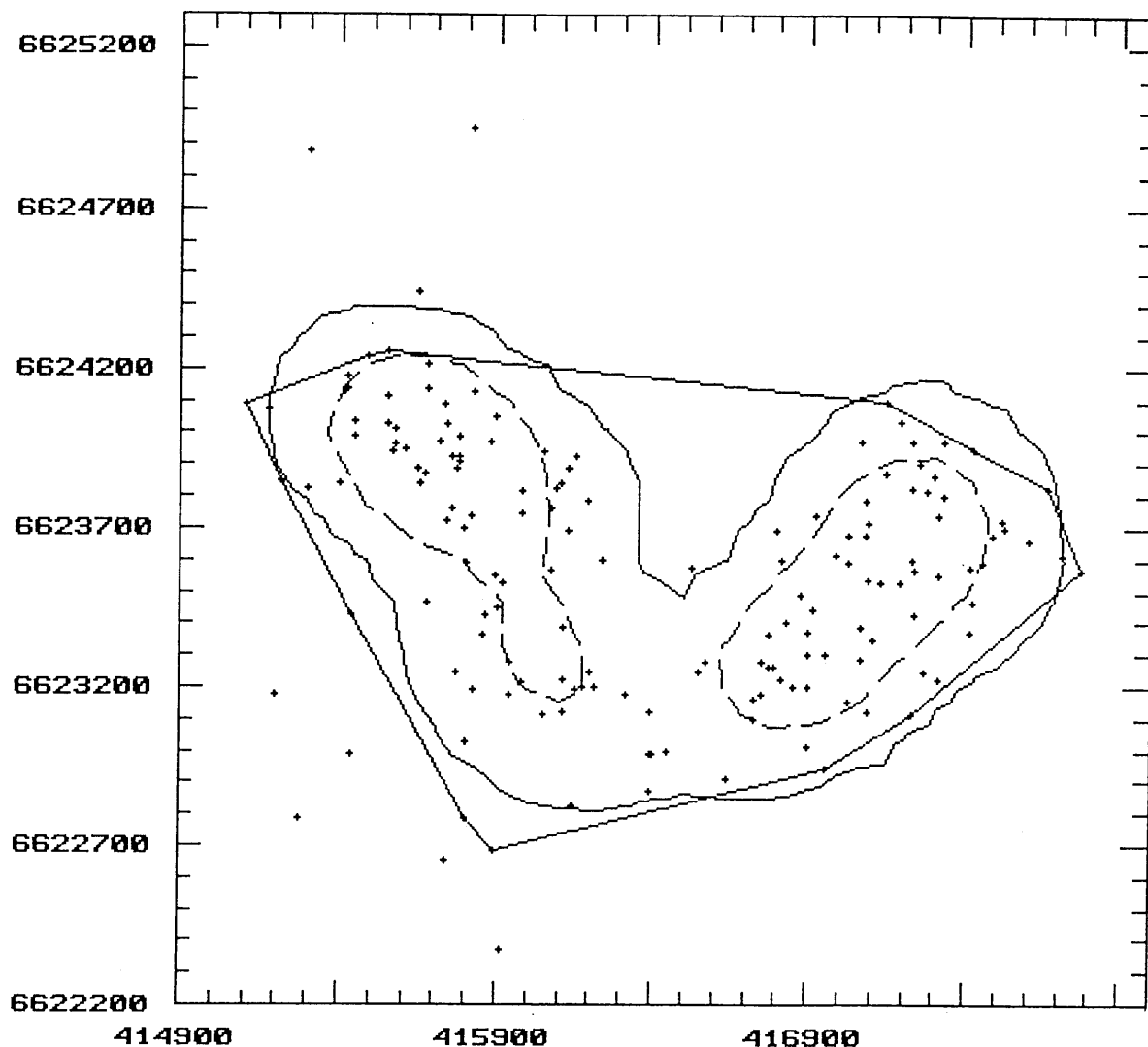


**Figure 8.** Home range estimation for aardvark M5 using the UTM scale. a) November 1996 to March 1997 (80 positions); b) April 1997 to November 1997 (80 positions).



Display units (x and y co-ordinates) = metres

Number of data points = 160

Minimum convex polygon      95% = 271.5 ha ———

Adaptive Kernel                      90% = 248.0 ha ———

50% = 85.4 ha - - - -

**Figure 9.** Home range estimation for aardvark F4 for the period from December 1996 to October 1997, using the UTM scale.

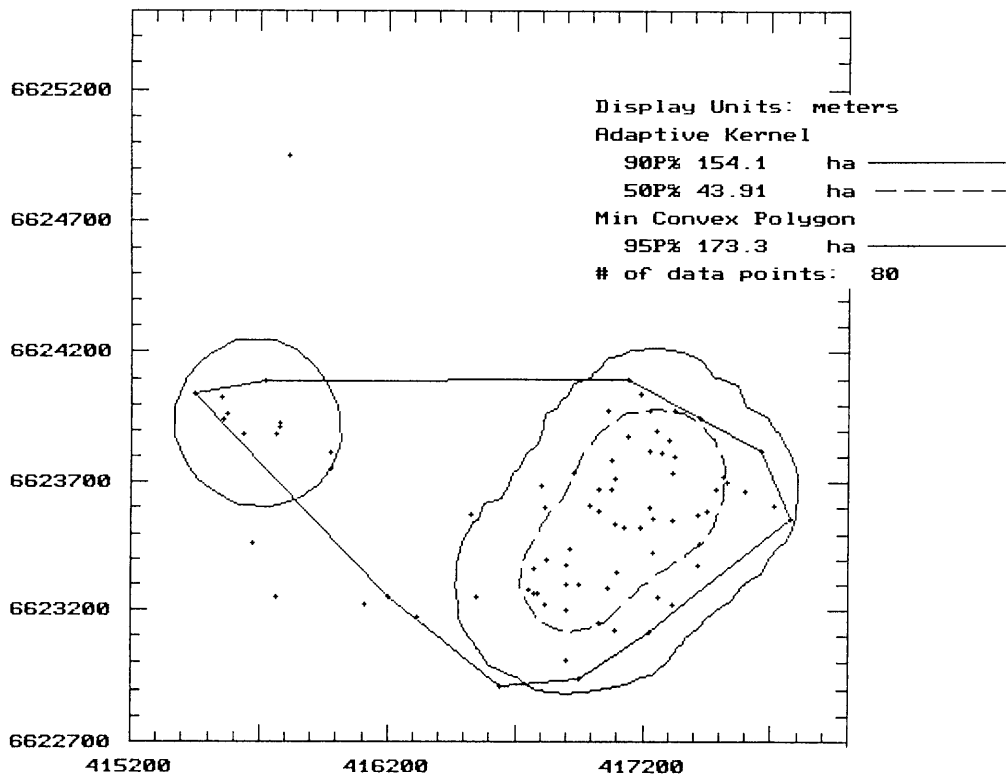
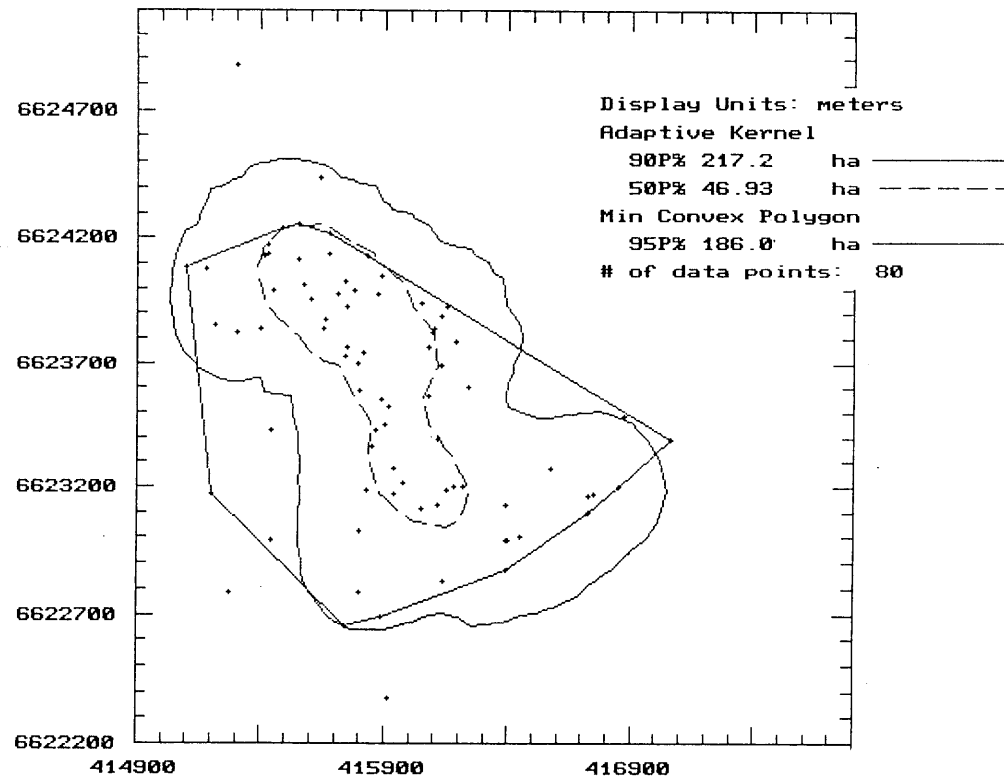


**Figure 10.** Home range estimation for aardvark F4 using the UTM scale. a) December 1996 to mid April 1997 (80 positions); b) mid April 1997 to October 1997 (80 positions).

Both aardvarks showed bivariate distributions at the 50% utilisation distribution level, either when the complete years positions were used, or when only six months data were used. This indicated that at the 50% level, these two aardvarks used two separate areas preferentially over other areas. Although not represented in diagrammatic form, the home range of aardvark F2 also showed a bivariate distribution at the 50% level for adaptive kernel, while that of M4 did not.

Figure 11 shows the overlap in home ranges for eight radio tagged aardvarks. Aardvarks M1, F1 and F3 were not included in the home range estimations of Table 3 because insufficient numbers of positions were obtained to make reasonable estimations. However, the limits to their home ranges were known, so could be used as a comparison with the other aardvarks, using 100% MCP. It is recognised that 100% MCP includes areas not visited by the animals (including the Orange River in M1's case), but they were represented this way to give an overall idea of the potential overlap. Outlying positions may have been visited infrequently, but they do represent areas where the aardvarks went to at some stage. The areas within the ranges shown in Figure 11 should not, however, be treated as such, they are merely representative of overlap. Also, although most of these aardvarks were at some stage known to be active within their respective home ranges concurrently, they were captured at different times in the study period and vanished or died at different times later in the study period, so temporal overlap was not complete. The home ranges of aardvarks M2 and F1 were recorded concurrently only with aardvarks M1 and M4.

There was considerable overlap between a number of the aardvarks, including male-male, male-female, and female-female overlap. There was even an area where three female overlapped together (F2, F3 and F4). It should be remembered that these were 100% MCP areas, so should be treated as maximum potential overlaps.

Figure 12 shows the overlap between aardvarks M4, M5, F2 and F4, using 75% MCP. These animals were chosen because they showed the most overlap in Figure 11, and 75% MCP was used to indicate whether core area overlap occurred. As with 100% MCP's, 75% MCP areas showed overlap, including male-male, male-female and female-female overlap.

### **Nightly movements and foraging speeds**

Nightly distances travelled by aardvarks M5 and F4 are represented in Table 4. There was no evidence of statistical differences between the two aardvarks ( $t = -0.034$ ,  $df = 14$ ,  $p = 0.973$ ).

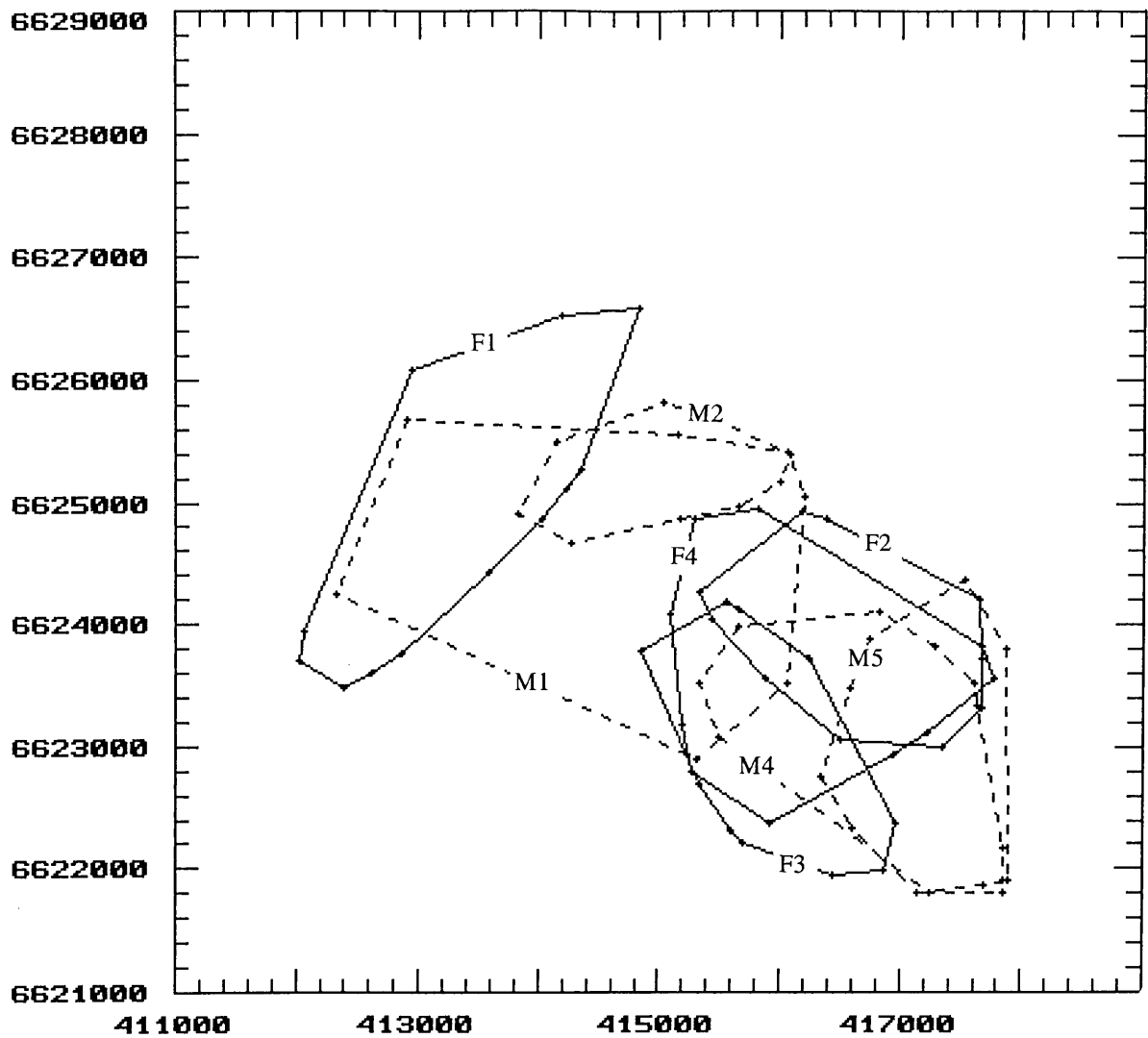


**Figure 11.** Estimated home range overlap for aardvarks M1, M2, M4, M5, F1, F2, F3 and F4 (UTM scale: display units = metres). Areas enclosed are 100% MCP for each aardvark.

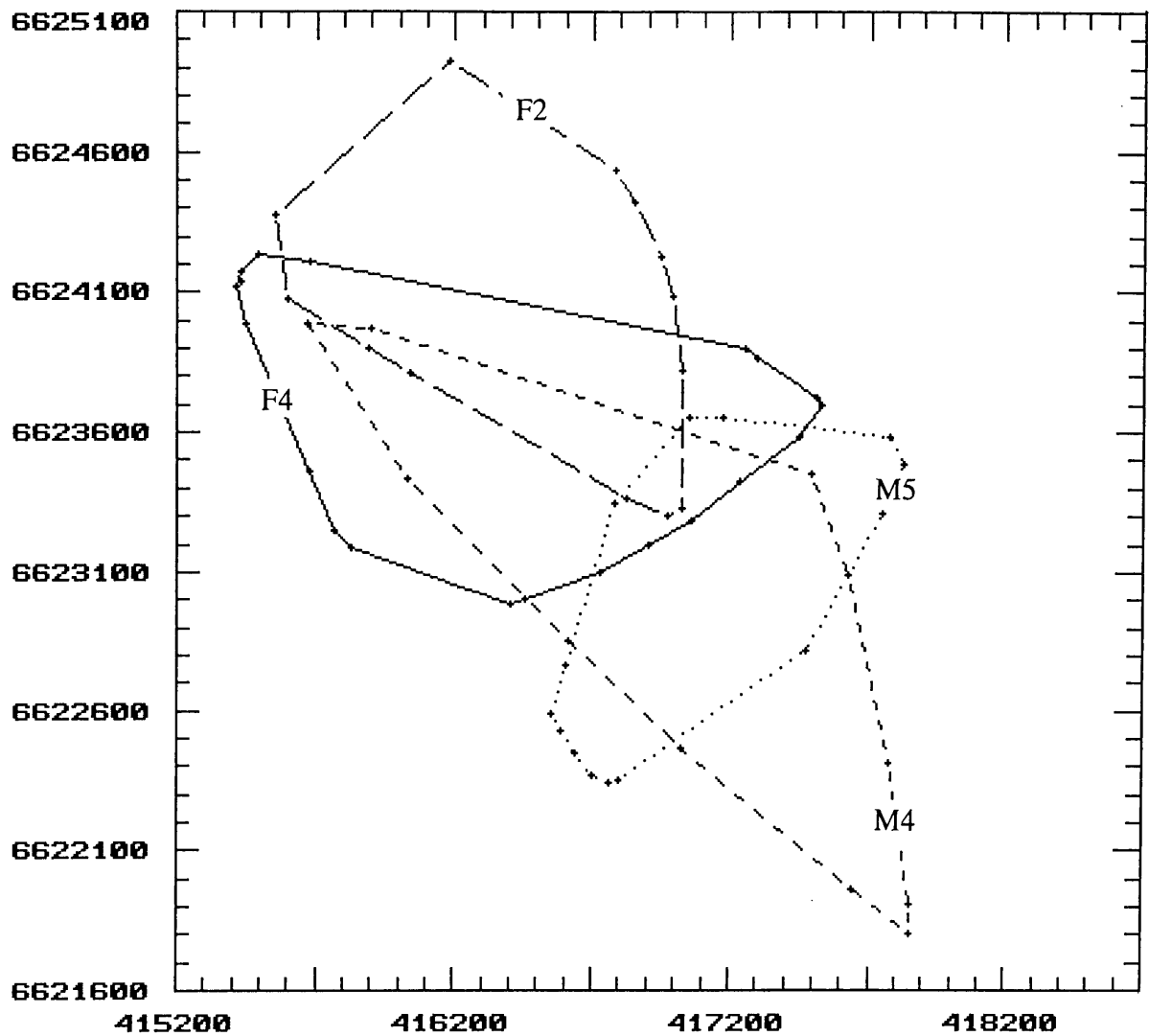


**Figure 12.** Estimated home range overlap for aardvarks M4, M5, F2 and F4 (UTM scale: display units = metres). Areas enclosed are 75% MCP for each aardvark.

**Table 4.** Nightly movements of aardvarks M5 and F4 recorded at irregular intervals during 1997. (for M5: n = 5; F4:n = 11)

|       | M5                | F4                |
|-------|-------------------|-------------------|
| Mean  | 3.258 km          | 3.272 km          |
| Sd    | 0.692 km          | 0.778 km          |
| Range | 2.17 km - 3.93 km | 2.11 km - 4.38 km |

Foraging speeds were estimated for five minute periods and the results were as follows:

Aardvark M5: Mean = 42.6m, Sd = 16.7m (n = 54)

Aardvark F4: Mean = 50.6m, Sd = 22.2 (n = 34)

There was no evidence that foraging speeds differed between the two aardvarks ( $t = -1.24$ ,  $df = 86$ ,  $p = 0.22$ ). Data was  $\text{Log}_{10}$  transformed because an  $F_{\text{max}}$  test indicated variances were not homogeneous, and the variances were greater than the mean.

Combining an average foraging speed with average activity periods gives a second method of estimating nightly distances travelled by an aardvark. Taking the average foraging speed as 45.7m in five minutes (M5 and F4 average), and minimum and maximum activity periods of five hours and eight hours respectively, the minimum and maximum nightly distances travelled were 2.74km and 4.39km respectively

These distances do not preclude the possibility of aardvarks walking further than this, because the habituated animals were known to occasionally walk continuously for longer than ten minutes (especially at the end of their activity periods when they moved back to their holes), in which time they would cover a distance of over 0.5km (assuming the estimated walking speed of approximately 3km/h). Bursts of continuous walking like this, although not common, increased the distance covered.

Figure 13 shows the movements of aardvark F4 for two consecutive nights in August 1997. Nightly movement patterns like these were typical, although they went in all directions, so it is unnecessary to

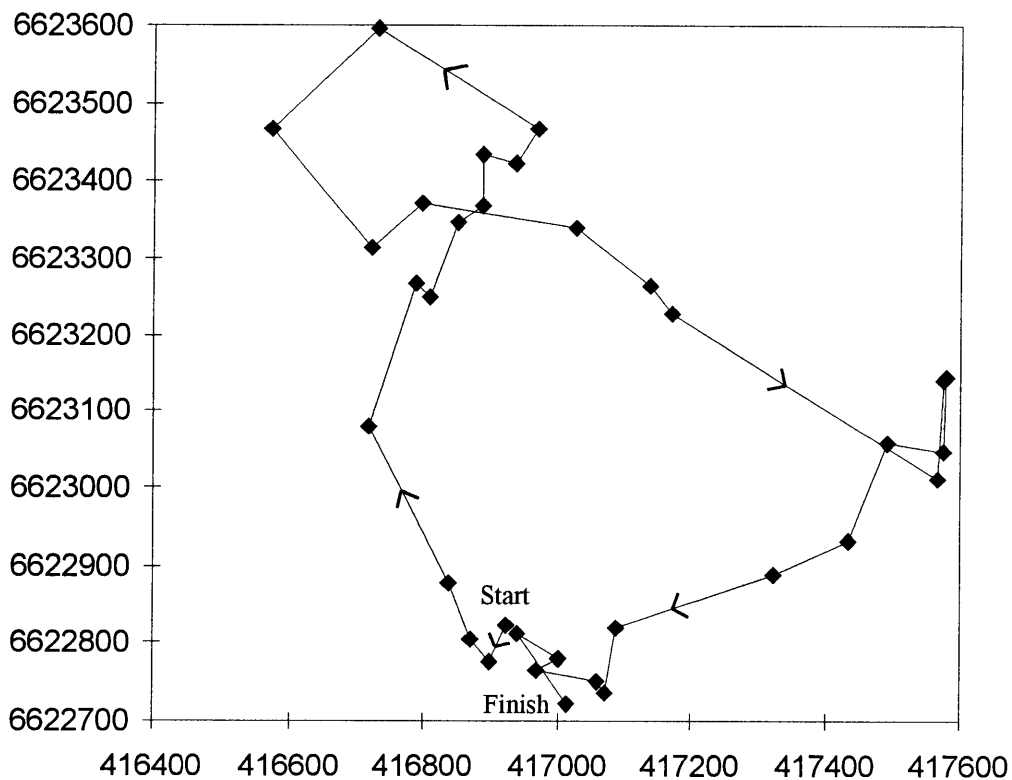
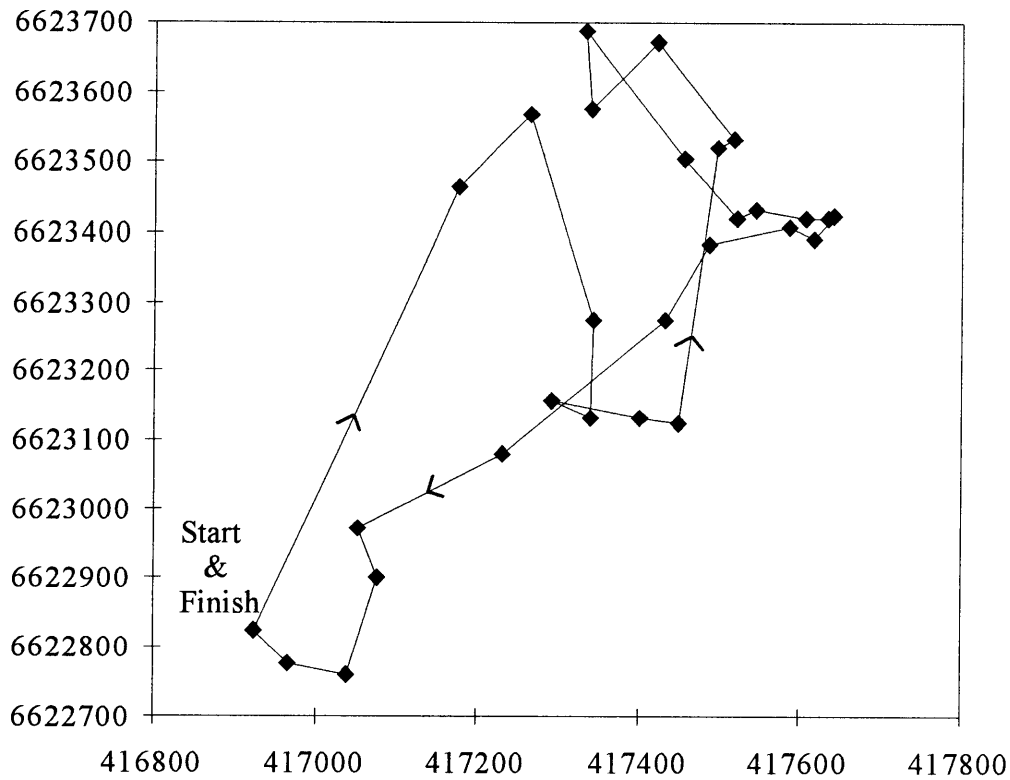


**Figure 13.** The nightly movement patterns of aardvark F4 during two consecutive nights in August 1997. UTM scale used (units = metres). a) 27 August, b) 28 August.

represent more nights. As was the case with the home range diagrams, the movements are plotted on a UTM scale, and the distances are, therefore, in metres.

### Burrows

Burrows used by the radio tagged aardvarks were recorded whenever possible, but for the unhabituated animals it proved impossible to locate them on any regular basis. Regular burrow use was only recorded for the two habituated aardvarks and for animal M2 when it was alive (at the beginning of the study). Table 5 shows this burrow use in terms of numbers of known burrows and number of consecutive days spent per burrow. It should be noted that even for the habituated aardvarks, burrows could not always be located, so the total number of burrow days were less than that of the total observation period.

**Table 5.** Burrow usage by aardvarks M2, M5 and F4.

| Aardvark | Time period | Number of burrows | Number of consecutive days per burrow |     |         |         |
|----------|-------------|-------------------|---------------------------------------|-----|---------|---------|
|          |             |                   | mean                                  | Sd  | maximum | minimum |
| M2       | 3 months    | 8                 | 6.9                                   | 5.7 | 16      | 1       |
| M5       | 12 months   | 34                | 4.9                                   | 6.2 | 23      | 1       |
| F4       | 12 months   | 26                | 8.6                                   | 9.6 | 38      | 1       |

Comparing the two habituated aardvarks, the female (F4) used less burrows than the male (M5) over the same time period and used the same burrows on average for longer consecutive time periods. However, when comparing all three animals, there was little statistical evidence of any difference between the average time periods spent consecutively in burrows (ANOVA:  $F = 2.6$ ,  $df = 67$ ,  $p = 0.082$ ). Both males and females were known to use burrows for time periods as short as one day, while the longest period of consecutive use of one burrow was 38 days, by aardvark F4.

Although there were many days when burrow locations were unknown, it is considered likely that on most of these days the aardvarks were in burrows other than the ones recorded.

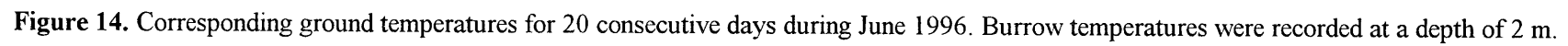
Aardvark F4 only returned to two burrows after ceasing to use them for the first time, while aardvark M2 was known to reuse only one burrow. Aardvark M5 was never observed to reuse a burrow after vacating it and moving to a separate one. Regarding the unhabituated aardvarks, returning to burrows after they had ceased using them was known to occur, but on most occasions this took place while they were being tracked and may have been the result of escape behaviour, rather than selecting to return to these burrows by choice.

Burrows were never observed to be shared by two aardvarks at the same time, although on one occasion a large porcupine was seen emerging from a burrow that a radio tagged aardvark was known to be in. The only occasion when burrow sharing almost occurred was when the female F4 took over a burrow being used by M5. When M5 returned to the burrow, just before dawn, and after F4 had already entered, he entered as normal, but then emerged after about 30 seconds and moved to a new burrow.

Neither of the two habituated aardvarks were ever observed digging fresh new burrows during the course of the present study. Instead, when they ceased activities at the end of a night, they either returned to the burrow they were already using, or moved to a pre-existing burrow (which was new to them) and renovated it. Renovations involved flicking soil out of the entrance of the hole with their hind feet, and much of this was often pulled out from deeper in the burrow with their fore feet. On occasion, new burrows were found in the study area which had not been seen before, so some aardvark must have dug them. It may have been one of the habituated animals, but the event was never witnessed.

Burrows used were spread throughout the aardvarks home ranges, with some being located on the peripheries and others situated well within the boundaries and into the centre. This was the case for all the radio tagged animals, including the unhabituated ones for which regular burrow locations could not be made.

Burrow and ground temperatures recorded in June 1996 are shown in Figure 14. Ground temperatures fluctuated considerably between 20°C during the day and -5°C at night, but burrow temperatures were buffered between 10°C and 5°C in the first burrow, and 9°C and 3°C in the second burrow.



## Discussion

### Activity periods

The most important pattern to be taken from the results of activity periods should be that aardvarks became active earlier in winter than summer, ceased activities earlier in winter than summer, and on average were active for shorter periods in winter than summer. Van Aarde *et al.* (1992) found that aardvarks on TdR were active from 19h30 to 05h30 in summer and from 18h00 to 01h30 in winter. This compares favourably with the findings of the present study.

The trend that aardvarks M5 and F4 showed by foraging in the mid- to late afternoon in the winter of 1997 was repeated in 1998 (pers. obs.; Henning pers. comm.), so was not aberrant behaviour for one year. Although none of the other radio tagged aardvarks were ever detected out of their burrows before dusk during the present study, there have been numerous observations of unknown aardvarks active above ground in the middle of the afternoon on TdR over the last few years (Roods, pers. comm.; Vrahimis, pers. comm.; Groeneveld, pers. comm.). As well as these random sightings, one of the aardvarks captured and habituated in 1998 (an adult female which was not used as a focal animal for the present study) was known to become active from about 16h00 in the winter months (Le Roch, pers. comm.). It appears, therefore, that limited diurnal activity in winter months is quite a common occurrence at TdR, although it also appears that it is behaviour restricted to certain individuals while many aardvarks remain strictly nocturnal.

This diurnal activity was also restricted to the afternoon at TdR, while none of the radio tagged aardvarks were ever detected on the surface in the morning. Kingdon (1971) reports a tame animal that regularly sunned itself at about 10h00, although no mention was made of the time of year this occurred or where this individual usually lived. There are also reports of bushmen in the Kalahari spearing aardvarks as they sit in the sun outside their burrows, although this was partly the result of flooding (Skinner & Smithers, 1990).

Possible explanations for the cyclic activity patterns exhibited by the aardvarks during the course of the study are season related. Seasonal changes that take place at TdR include earlier onset of nightfall, longer periods of darkness, and colder temperatures as winter approaches. The opposite trend occurs at the end of winter with the onset of summer. For strictly nocturnal mammals, earlier darkness affords the opportunity of becoming active at an earlier time in the evening, while later sunrise should allow them to remain active until later. The aardvarks did make use of the earlier darkness by becoming

active earlier, but they did not exploit the opportunity of extended foraging periods that the longer nights made possible. Instead they ceased activities earlier in winter than in summer and even had shorter overall activity periods in winter.

The primary cause of earlier activity periods in winter was probably, therefore, lower temperatures. The southern Free State regularly attained temperatures below freezing at night between May and July, partly as a result of continuously clear skies. The lowest temperature recorded during the present study was  $-12^{\circ}\text{C}$ , and temperatures have been known to fall below this. Such cold temperatures would be expected to have considerable effects on the activities of many mammals, including the aardvarks, which do not have the insulating fur that most terrestrial mammals inhabiting cold regions have.

The temperatures at which the two habituated aardvarks ceased activities, as shown in Table 2, do not give much insight into the effect of ambient temperatures on burrow re-entrance times, except that aardvarks were still active in July and August at temperatures near freezing ( $2.1^{\circ}\text{C}$ ). Temperatures in May were cold, often below  $5^{\circ}\text{C}$  before sunrise, but aardvarks ceased surface activities during this period at temperatures well above these, and well above the minimum of July and August. It is, therefore, difficult to explain why the aardvarks did not remain active for longer during May. It may be that because the aardvarks became active earlier during this period by emerging from their burrows in the late afternoon, that they had obtained enough food to satiate their appetites, allowing them to return to their burrows earlier.

The activity of the aardvarks ant and termite prey was also considerably affected by ambient temperatures and might have been expected to affect the behaviour of the predator to a certain extent. The activities of the ants and termites are discussed in the next chapter, so will not be discussed here, except to say that aardvarks preyed on ants and termites out of the ground, not on the surface, and continued foraging after the prey became inactive, both in warm and cold months. The aardvarks did not appear to be dependent on whether their prey were active. The most likely cause of cessation of activities was, therefore, the temperature effects on the aardvarks themselves. Night time temperatures were coldest in the early morning before sunrise, but by these times aardvarks were already in their burrows (at least in winter). Early morning temperatures in summer were not nearly as cold as early evening temperatures in winter, so the aardvarks were not forced to their burrows in summer by cold temperatures.

The age of the aardvarks might be considered relevant when interpreting activity period lengths, because older and larger animals might be expected to require more food to sustain themselves. A

possible counter argument to this is that wild aardvarks take a long time to reach full size (whatever that may be: out of 15 aardvarks weighed during the study period, the heaviest was 48kg) and young individuals may require as much food as older ones. Aardvark M5 increased from 22.5kg in November 1996 to 35kg in October 1998. He gained only 12.5kg in two years, and was still considerably below what would be considered a large mass (40kg+).

It is highly probable that aardvarks elsewhere in Africa, especially nearer the equator, have activity patterns that differ from those in the southern Free State. As mentioned in the introduction, Kingdon (1971) stated that aardvarks became active at about 20h00, but he did not make any distinction between seasons. His observations were made in east Africa, and it is likely that aardvarks there exhibit more consistent activity periods due to less variation in seasonal temperatures and night lengths. It is also possible that periods of above ground activity are altered in areas where predators occur (specifically lions), although what influence this has, and how it manifests itself is unknown.

Aardvarks were not influenced in their activity patterns by other environmental effects, such as moonlight, rainfall and windy conditions. This is contrary to the belief that they are active on dark nights to avoid predation, or that they are particularly active at times of bright moonlight (Kingdon, 1971). As they have poor eyesight, it should make little difference to them whether the moon is full or not.

### Home ranges

The home range estimates can be considered satisfactory for four of the animals, with that of the fifth aardvark (M4) possibly being an underestimate (as indicated by its observation-area curve not reaching an asymptote). Van Aarde *et al.* (1992) found observation-area curves attained asymptotic values between 80 and 102 radio relocations. This agreed favourably with the asymptotic level for the two habituated aardvarks, but was higher than the number of required positional fixes for aardvarks M2 and F2. Aardvark M4 was inconclusive. Van Aarde *et al.* (1992) obtained positional fixes as regularly as every hour, while the present study recorded a maximum of two positions a night (normally one). As mentioned in the methods section, autocorrelation, caused by locations being non-independent, leads to an underestimate of home range size if insufficient points are obtained. This might have been the reason van Aarde *et al.* (1992) required as many as 102 radio fixes from one aardvark to achieve an asymptotic observation-area curve. Less frequent positional fixes may have allowed an asymptote to be reached with less fixes.

What was apparent in the present study, specifically in the case of aardvark F4, was that 80 positions were sufficient only until the aardvark shifted its home range. It is possible that if positions were recorded regularly over an extended period (years) for certain aardvarks, their home ranges would continually increase, and this would be the result of them shifting their home range rather than a general increase in their age and size with possible corresponding increase in food requirements.

A juvenile aardvark captured and habituated in 1998, after the field work for the present study was complete, shifted its entire home range from one side of the central ridge of sedimentary rocks (the Orange River side) to the other (the Caledon River side), a distance of approximately 3km (Le Roch, pers. comm.) and has never since returned to its original area of capture. It was habituated before it dispersed, so it is unlikely that the cause was human interference. The exact reason for the dispersal was unknown, but it appeared that heavy rains that caused large areas of its original home range to be flooded (predominantly the flood plain of the Orange River) may have played a significant role. The age of this aardvark may have also played a role in its dispersal, because it was a young animal (the smallest captured during the present study at 19kg), but because no means of age estimation exists for aardvarks, the age of this individual could not be judged and the possibility of age related dispersal could not be assessed.

Aardvark M5 did not shift its home range during the entire study. Although it may not have visited certain areas within its range for a few days to weeks, it never moved the entire focus of its activities for extended periods in the same way that aardvark F4 or the juvenile animal in 1998 did. However, from October 1998, this animal did apparently extend its foraging area quite considerably, into part of the range that F4 previously used in the first six months that she was followed. It appears, therefore, that assessment of an aardvark's home range over a period of approximately six months may be adequate, but that it must be remembered that the focus of their area utilisation may change with time and their home range areas will then regularly change.

As only 80 and 82 positions were recorded for aardvarks M4 and F2 respectively, it could not be determined whether they shifted their home ranges, but non-empirical estimation indicated that they did not. Rather they appeared to use all areas within their respective ranges throughout the course of the study.

Van Aarde *et al.* (1992) found that mean estimates of home ranges for five aardvarks on TdR varied from 1.8, 2.4 and 3.5km<sup>2</sup>. These estimates were calculated using the restricted polygon technique, MCP's excluding excursions, and MCP's including excursions (100%) techniques respectively. The

percentage of outlying positions left out of the restricted polygons is unknown so the results are not exactly comparable with those of the present study, but they are favourable. Of the three aardvarks that were found to reach observation-area asymptotes (van Aarde *et al.*, 1992), the home range estimates from the restricted area method were 1.3, 1.8 and 3.0km<sup>2</sup> for an adult male, sub-adult male, and adult female respectively. No sex specific differences were suggested, and this agrees with the findings of the present study.

Ninety five percent MCP results from the present study were 133ha (sub-adult male), 302ha (adult male), 214ha (sub-adult male), 239ha (adult female), and 272ha (sub-adult female). The first area was obtained from only 50 positions, although an area-observation asymptote was apparently reached, while the second area did not quite reach an asymptote. Although the largest area was for an adult male, the second and third largest were for the females, with the larger of the two being the younger animal. Although the sample size was small, these results do not indicate any sex specific or age specific differences in home range. Nothing is known about very young aardvarks, so no inferences can be made concerning the size of their home ranges.

The area encompassed by some of the home ranges included substantial areas of steep slopes and high lying hilltops, which the animals did not frequent. This was particularly the case for M1, M4, M5 and F1 (see Figure 11 of 100% MCP comparisons of all eight aardvarks). Aardvarks were known to cross over hills to reach other areas within their ranges, and there was evidence in many steep areas of aardvark activity, such as excavated *T. trinervoides* mounds. Many of the times aardvarks were known to traverse these steep areas were during ongoing attempts to habituate them, and were, therefore, times of evasive behaviour, but they were also known to do this when uninfluenced by any human presence. Whether traversed or not, these areas were infrequently visited and, therefore, increased the home range sizes of some of the aardvarks without contributing to the usefulness in terms of foraging space. However, as such landforms are part of the natural landscape, they form valid parts of the home ranges of the animals which encompass them.

Only two animals out of five overlapped in the 1992 study, and this was very limited (van Aarde *et al.*, 1992). This was in contrast to findings in the present study, where considerable overlap was indicated. The simple explanation for the previous study finding no overlap was that not all the aardvarks in the area were captured, and those were too far apart.

The fact that there was overlap between all three combinations of sexes, male-male, male-female, and female-female during the present study, gives some insight into possible conspecific relationships, but

much still remains to be found. With the four best known aardvark home ranges, and these were the ones that overlapped the most, 75% MCP's still showed some degree of overlap, indicating that even when core areas were considered, the animals did not maintain individual territories (although this might depend on what percentage of a home range is considered a core area).

The Kernel method is a more recent technique than MCP and incorporates the idea of a utilisation distribution, or core area, in a more meaningful way than can be done by using a restricted polygon. The kernel method has not been used previously to estimate home range utilisation for aardvarks, but van Aarde *et al.* (1992) did illustrate heterogeneity in the range of aardvarks by 3-D imagery, where the intensity of utilisation of grid squares was indicated by the heights of peaks on 3-D graphs.

Ninety percent and 50% home range areas were estimated using the adaptive kernel technique to give an estimation of the utilisation distribution with outliers removed (90%) and an estimation of a core area (50%). The difference between the 95% MCP and 90% kernel method was mainly that the latter gave a better representation of the way in which the aardvarks utilised the space within their respective home ranges. The former simply removed outlying positions until 95% of the original locations remained.

The 50% adaptive kernel method provided some insight into core areas utilised by aardvarks within their complete home ranges. Fifty percent was possibly a somewhat subjective value to represent a core area, but the whole issue of deciding what percentage of a home range constitutes a core area could be considered subjective itself. Figures 7 to 10 indicate that when 50% home ranges are analysed using the adaptive kernel technique, there appears to be a bivariate distribution, with the areas encompassing 50% utilisation distributions split into two distinct areas. Van Aarde *et al.* (1992) also found that aardvarks used certain areas of their home ranges more frequently than others, which is in agreement with the findings of the present study.

The cause of an animal having two distinct areas of favoured utilisation should be related to resource distribution. In the case of the aardvarks, such a resource was probably the ant and termite prey. If the distribution of ants and termites was at all clumped, in other words if some areas within the study area contained more ants and termites than other areas, then this could have been a direct cause of aardvarks favouring certain areas over others. However, no quantification of aardvark prey resources was made at a scale that could have identified areas of differing ant and termite abundance, so no conclusions can be drawn from the aardvarks bivariate distributions. Nevertheless, as the predominant habitat utilised by the varying aardvarks were the communities of flats and gently sloping terrain between the rivers (see

chapter 2), it seems improbable that such heterogeneity in ant and termite communities would exist. Observations made during the present study did not indicate specific areas where ant and termite densities were relatively lower than other areas, although this would need to be tested empirically. Pitfall trapping techniques carried out on TdR by Willis (1988), Willis *et al.* (1992) and by Lindsey (pers. comm.), only examined variation between different habitats and did not indicate differences within habitats, especially at a scale that would be required to explain bivariate core area utilisation.

In the case of aardvark F4, she was known to shift her range in the middle of the study, and this would have resulted in her core area being bivariate. The cause of the observed shift might have been prey resource related, but cannot legitimately be assessed with the current knowledge about the ant and termite fauna of TdR.

### Nightly movements

Van Aarde *et al.* (1992) found that aardvarks spent less time foraging and traversing their home ranges during the cold, dry months (May-August) than during the warm, wet months (September-April). No obvious activity peaks were found. Mean foraging speeds were lower during winter than summer, and distances covered per night were shorter in winter. The average distance covered per night was 2.21km, with a range of 0.5km - 6.97km. Average distances travelled per hour were 0.18-0.83km for males and 0.46-0.94km for females

Although seasonal comparisons of foraging speeds and nightly distances moved were not made during the present study, the overall results were generally in agreement with those of van Aarde *et al.* (1992). The average of 2.21km found in 1992 was approximately 1km less than that found by regular positional fixes with a GPS during the present study for the two habituated aardvarks. These GPS results were considered underestimates as well because they did not take into account possible zigzagging of the aardvarks between each ten minute fix. The GPS data need to be treated with caution anyway due to the potential 30m error of every reading. The estimates of average foraging speeds calculated from pacing behind the aardvarks might be considered more accurate. The minimum distance travelled in one night estimated by van Aarde *et al.* (1992) seems too low for a normal nights foraging and could be the result of the animal remaining close to its burrow for the entire night but at the same time zigzagging considerably. A second possible reason could be that something disturbed the aardvark and caused it to enter a burrow.

Movements by the unhabituated aardvarks were more difficult to investigate. Because positions of the animals were attained by sight, and the primary reasons for following these animals was to habituate them, the animals movements were influenced by the human tracker. At these times they walked continuously giving the impression of covering much greater distances than the habituated animals. However, when these aardvarks were left alone they remained much more stationary and did not traverse large areas of their known home ranges in short spaces of time.

## **Burrows**

Although the female F4 was observed to use burrows for longer average periods than the male M5, this difference was not significant. This is the first real evidence of the length of time that wild aardvarks use burrows and the first that males do not use “temporary” burrows, while females use more permanent burrows, as quoted by some authors (see introduction).

Although the longest time periods spent using a single burrow on consecutive nights was as long as 38 days for F4 and 23 days for M5, the average periods were considerably shorter (between 4.9 and 8.6 days). Possible reasons why the aardvarks stopped using burrows after only a few days include that the burrows became infested with parasites after a certain time (although this would not explain how one individual could use a hole for as long as 38 days without being overrun) and that burrows in certain areas are convenient for foraging in some areas but not others. If this latter were the case, then aardvarks might change burrows when they change foraging areas (temporarily). The problem with this argument is that at the end of their activity periods the habituated aardvarks often walked over 500m back to their burrows from all ends of their home ranges without stopping to forage, indicating that it was not important whether they foraged far from their burrows. There was no evidence that burrows were separated from so called foraging grounds anyway, because aardvarks often started feeding in close proximity to their burrows.

The fact that aardvarks rarely reused burrows once they had stopped using them might simply reflect the numerous burrows available to them. They had no reason to reuse a burrow when there were so many available. It might be that selection of a new burrow is a random event and this would mean that the chances of using a burrow for a second period of time is statistically improbable. The most likely reason aardvarks do not share burrows with other aardvarks is a lack of space within them although their natural solitude may be the underlying cause.

Temperature fluctuations within burrows were found to be considerably buffered from local environmental temperatures. It is highly probable that the temperatures right at the end of a burrow, where the aardvarks rest during the day, would be even less variable, especially if the aardvarks displace soil behind them while moving to their sleeping chamber. This would be of great benefit to the aardvarks, or any other animals inhabiting disused burrows, in terms of body temperature regulation. In winter, when temperatures are regularly below freezing, especially in the early hours of the morning before sunrise, the aardvarks would have a place of refuge from the cold. As aardvarks have been shown to return to their burrows much earlier in winter than summer (see above), that is as early as midnight or before, buffered burrow temperatures are put to considerable use by them. In summer, when daytime temperatures often exceed 30°C, the burrow temperatures would be considerably lower, thus protecting the animals from unnecessary heat (as well as direct sunlight).

In conclusion, aardvarks of TdR were found to be predominantly nocturnal but became partially diurnal during the coldest months. Even in summer, aardvarks were not late risers, but instead became active soon after dark. They were active for shorter periods during the colder months, and in the coldest times appeared to have their activity patterns driven by local temperatures, seeking refuge earlier in the buffered comfort of their burrows. Home ranges were found to overlap between all sexes indicating that strict territories were not maintained. However, further research should be undertaken to investigate scent marking behaviour which was observed on numerous occasions during the study, and which might indicate the possibility of a certain degree of territoriality. Aardvarks were not found to traverse large distances per night as was inferred in the past by observations of spoor, and females did not use burrows for significantly longer periods than males, dispelling the idea that males are more nomadic. As no births were witnessed during the study, no added information was gained regarding burrow use or other activity patterns of females at times when they have young to look after. Aardvark behaviour at this time is still a mystery.

## CHAPTER 5

### THE FEEDING ECOLOGY OF THE AARDVARK

#### Introduction

Many mammals, ranging from elephant shrews to antelope, are myrmecophagous, which means they eat ants and termites, and as such are the second most important class of animals, behind ants, to do so (Redford, 1983). The abundance of the Formicidae (ants) and Isoptera (termites) is the primary reason for the high degree of exploitation to which they are exposed. Redford (1983) lists 216 myrmecophagous mammalian species, of which 36% eat ants, 17% eat termites, and 47% eat both. The list is not exhaustive because there are probably many species whose diets are not well recorded and in which ants or termites are represented to a limited extent. Of the species listed, many eat other food types as well, and many are opportunistic, only eating ants and termites when the chance arises. Ants can be taken by predators foraging both arboreally and terrestrially, although in the tropics most ant eaters are arboreal. Termite eaters on the other hand, are mostly terrestrial.

Prey selection within a myrmecophagous species can vary considerably, with individuals in some areas predating mostly ants, while individuals of the same species in other areas take mainly termites. Examples of such geographic variation can be found in the giant anteater (*Myrmecophaga*) from South America and the echidna (*Tachyglossus*) from Australia. Variation in prey selection can also be temporal (seasonal), as has been found in the *Myrmecophaga*, or may occur within a population, such as the *Tamandua* anteaters of South America (Lubin & Montgomery, 1981) and the bat-eared fox, *Otocyon megalotis*, of southern Africa (Nel, 1978). Despite this widely documented variation in prey selection within myrmecophagous species, there has been much disagreement in the literature regarding whether ants are more important than termites, or vice versa. Rather than arguing which of the two orders is most important, Redford (1983) suggests that most mammals that eat large quantities of ants also eat large quantities of termites, and that they are not specialised on prey of a particular taxonomy, but of a certain type: small, fairly homogeneous, social arthropods.

The aardvark is a myrmecophagous mammal and, as has been the case for other mammals sharing their diet, there has been some confusion regarding which Order, ants or termites, is the most important. It appears that initial ideas favoured termites over ants as the predominant prey (FitzSimons, 1919; Shortridge, 1934; Skinner, Pers. Comm.), but with time this has reversed and now ants are considered more important (Melton, 1975; Melton & Daniels, 1986; Smithers, 1971; Willis, 1988; Willis *et al.*,

1992). Most disagreement about the preferred prey is probably due to geographical, temporal and individual variation within the aardvark, as described above for other species, but a further reason is that diggings in termitaria are normally more obvious than diggings on flat ground, and this biases observations and confounds the idea that termites are the preferred food (Skinner & Smithers, 1990).

Shortridge (1934) stated that the food of the aardvark is exclusively termites and ants, but placed more emphasis on termites as the prey species. He quoted Stevenson-Hamilton: “The Ant-Bear exists practically everywhere in South Africa where there are white ants (termites)...”. “Its method of procedure is to break into one of the big dome anthills from one side and, having sufficiently disturbed the inmates, to introduce its long sticky tongue”. Powell-Cotton was also quoted: “They appear (in Abyssinia) to prefer a sort of white ant that lives in the ground but throws up no hill”.

Kingdon (1971) indicated the importance of termites and ants by suggesting that the aardvarks local distribution was determined by their (termites and ants) abundance. Moreover, he alluded to less evidence of aardvark activity in the dry season (winter), coinciding with the time when termites become quiescent, citing an example of an area where aardvarks became more common as a result of an increased biomass of termites. This took place on the slopes of Mt Elgon (Uganda) where there had been a recent build up of large herds of livestock, thus increasing the amount of trampled grass and dry dung which some termites thrive on. However, this thesis is unlikely to have been well grounded with data on ant and termite numbers, let alone aardvark numbers, so is probably anecdotal.

On the other hand, Smithers (1971) found that Formacid ants constituted the principal contents of three stomach contents from Botswana, while only traces of termites were found. This was stated to parallel a sample from the then Rhodesia (Smithers & Wilson, 1979), consisting of eight stomach contents. Seven of these contained ants in varying proportions, four of which were entirely ants, while four contained varying proportions of termites. In addition, in Uganda, while working on the relations of vertebrates and termite mounds, Melton (1975) analysed aardvark faecal samples for insect remains and found that ants formed the bulk of the diet in the dry season whilst termites were taken mainly at the height of the wet season. In the Umgeni Valley Nature Reserve, Natal, Melton & Daniels (1986) found that both ants and termites were predated, but that ants were the predominant prey.

Willis (1988) and Willis *et al.* (1992) compared the occurrence of ants and termites in 20 aardvark faeces (10 summer, 10 winter) with the seasonal abundance of ant and termite species sampled by pitfall trapping, at Tussen die Riviere Game Farm, Free State. He found that during the wet season (summer), 64% of the diet consisted of ants while termites contributed 29% (the remainder was made

up by seeds and fly pupae). In the dry season (winter) ants were more important in the diet than in summer, while termites showed the opposite trend. Seventy eight percent of the diet in winter consisted of ants, while termites contributed 13% (again, seeds and fly pupae made up the rest). Thirteen species of ant and two species of termite were recorded in the faeces. There was a greater diversity of ants in the summer samples compared with the winter ones, with summer consisting of 12 species and winter 6 species.

Other than ants and termites, there are records of other items in the diet of the aardvark which are worth noting. The stomach contents of one aardvark in East Africa contained over 40 scarabaeid pupae (Coleoptera) (Kingdon, 1971). Scarab beetles lay their eggs in large quantities in dung stored up to 40cm below the surface and it was thought that the aardvark must have located them by smell and dug them up deliberately. It seems likely that a large number of pupae such as this precludes the possibility that they were ingested by accident. Kingdon (1971) also reported that locusts are occasionally eaten, but as this was never observed during the present study or any evidence ever found for it, this source of dietary intake appears improbable.

An individual collected on the Kwaai River was said to have two fat mice, *Steatomys pratensis*, in its mouth, both considerably crushed through mastication (Smithers, 1971). This report (not observed directly by Smithers himself) is almost certainly invalid.

A somewhat different dietary component was first reported for the aardvark by Meeuse (1958), when it was found that a member of the Cucurbitaceae, *Cucumis humifructus*, was often located growing at the entrances of aardvark burrows. Mitchell (1965) independently reported the same association, and it has since been assumed that this cucurbit, due to its unique geocarpic habit, is reliant on the aardvark for dispersal.

*C. humifructus* is a normal cucumber plant with stems running up to three metres along the ground and very small, yellow flowers typical of the family. When the flowers are fertilised the flower stems turn downwards and force their way 20-30cm into the ground, with the result that the fruit is formed underground (geocarpy). The fruit, which is spherical, pale greenish-yellow, and the size of a small orange, contains within it a colourless, tasteless, watery flesh. It is thought that the aardvark is the only animal with the ability to locate, dig up and eat the fruit and then disperse the seeds, which are quite hard, in its faeces.

Mitchell (1965) reported that the plant was found growing at the entrance of five aardvark burrows, and that the roots of each plant arose directly from the recognisable droppings of an aardvark. Seeds from *C. humifructus* have also been found in aardvark faecal samples (Hollmann *et al.*, 1995), evidence which gives the association, although never proven, some validity. The range of *C. humifructus* also falls within that of the aardvark, although there are probably many plants for which this is true. However, for this symbiotic relationship to exist, as some authors have called it, it must be assumed that the aardvark has a reason to dig up and eat the fruit. The reason given is that the cucurbit acts as a source of water for the aardvark especially in areas where there is little or no standing water, but all the evidence indicates that aardvarks obtain sufficient water from their diet of ants and termites. As aardvarks have not been observed actually feeding on this plant, direct observations are required to validate the theory. There is also no good evidence to assume that other animals cannot dig up and help disperse these plants, rendering *C. humifructus* less reliant on aardvark for survival than some authors have suggested.

## Aims

Much of our current knowledge of the aardvarks diet is anecdotal and has come from chance sightings. In the cases where faeces were analysed, the actual number of faeces examined were often small and gave little idea of any variation. Where sample sizes were larger, such as the 20 stomach contents from Zimbabwe, no indication of seasonal variation was given, while the technique allowed no means of examining individual variation (because the animal was dead). The most extensive seasonal study to date was that of Willis (1988), which included ten summer and ten winter samples. No studies up to the present have had access to habituated wild aardvarks, and it has not been possible to observe their feeding behaviour closely under natural conditions.

In view of these shortcomings, the objective of the present study was to improve the current knowledge of aardvark feeding ecology. The aims were as follows:

- a) To examine faecal samples in a regular manner for the period of one year, identify the prey species, determine dietary richness and diversity, and examine how proportions of all these vary with time (month/season). Some degree of variation between seasons would be expected because Melton (1975), Willis (1988), and Willis *et al.* (1992) found that termites were predated more in summer than winter. A certain amount of variation between individual aardvarks would also be expected and this would be tested for at the same time. Also, any selection between different castes of the

most important prey species were to be investigated and an estimate made of the numbers of ants and termites eaten per night and the calorific values of the main prey species;

- b) To investigate feeding patterns and behaviour with regard to such aspects as prey species selection and time spent feeding, and to examine how these vary between aardvarks and between seasons. The availability of two habituated aardvarks provided an ideal opportunity to study closely the feeding behaviour of the aardvark, an aspect never before possible. Comparisons could be made between the prey species (and their proportions) found in the faeces and those predated during observation;

## **Materials and methods**

### **Collection of faeces**

A minimum of 18 faecal samples were collected and stored each month, six from each tame aardvark, the rest from the other collared aardvarks and unknowns. This number was decided on because it was the estimate made for the minimum number of samples required to find all the prey species. The estimate was calculated by plotting the cumulative increase in new prey species for each sample against the corresponding increase in faecal sample size. The graph reached an asymptote when an increase in sample size yielded no further increases of new prey species. This point was the number of samples required to accurately sample all the prey species in the diet for a given period. The asymptotic graph is shown in Appendix II. As a precaution, however, it was decided to analyse between 20 and 24 samples per month.

Six samples were collected per month from each of the two tame aardvarks while they were being followed. Normally, only a small proportion of a complete faecal sample was randomly selected, as this was all that was required for analysis (see below for explanation). The faeces were collected in paper bags and dried in the sun. Samples were also collected from the other radio tagged aardvarks where possible, although this was more difficult due to their elusive behaviour. These samples were occasionally discovered fortuitously at night while tracking them from a distance, but were more commonly found by searching during the day in areas within their respective home ranges, especially where they had been known to be recently foraging. Burrow entrances were given priority when searching as these were known to be common sites where aardvarks defecated. Separate areas of the reserve were also searched fairly regularly to obtain fresh faecal samples from unknown aardvarks with the aim of increasing the sample size.

Only samples known to be deposited within 2-3 days were collected. It was possible to tell whether the age of the faeces were within these limits by both the appearance of the faecal excavation and the texture and smell of the pellets. Regular searching in well known areas also served to differentiate fresh deposits from older ones because fresh deposits would not have been present at previous searches.

### **Faecal analysis**

Once dried, faecal pellets were ready for analysis. A sample of approximately five to ten pellets, roughly 20g dry mass, were randomly selected, placed in water and soaked overnight. As aardvark faecal pellets vary in size and mass, the actual numbers used for analysis differed, depending on their size. A larger sample mass was not necessary because it had been found previously that approximately 15g of dry faecal pellets were sufficient to give representative results (Daniels, 1984). This was tested briefly during the present study, in which three 10g samples were randomly selected from one faecal deposit and analysed. The results agreed with those of Daniels (1984).

Once sufficiently softened by soaking, the pellets were carefully broken up in the water with a pestle and mortar, following Willis (1988). This freed the organic material from the soil, allowing it to float to the surface, leaving the heavier soil particles on the bottom. The organic matter in question consisted mostly of pieces of grass stem and seeds, as well as undigested insect parts such as heads, legs and other parts of the exoskeleton. Occasionally whole ants or termites made it through the aardvarks digestive system intact. The floated material was then filtered off using a fine sieve and knocked onto kitchen roll to dry off. Fresh water was added to the sample at least three times to extract as much of the organic material as possible. Once dry, the separated material was stored separately ready for sorting.

The organic matter was then placed on white paper and the individual ant and termite heads separated one by one. Approximately half the contents of every sample was sorted (about 10g of the 20g sample) so that roughly equivalent amounts of faeces were analysed. This was important for later analysis. The heads were extracted as they were reached on the paper so that there was no bias of finding larger or more visible species. Finally the heads were placed under a dissection microscope to categorise and count the species. Identification from heads alone was possible as they normally retained their shape and colour while going through the aardvark gut (personal observation, see also Calaby, in Willis 1988), even though they usually lost their antennae and sometimes their mandibles in the process. They remained distinctive enough to allow comparison with the heads of complete ants and termites collected

alive in the field and kept for reference. These complete specimens were identified either by Dr H. Robertson<sup>1</sup> or Dr R. Adam<sup>2</sup>.

### Species richness and diversity

Identification and enumeration of the prey species in the faeces of the aardvarks allowed for an estimation of the species richness and diversity of their diet. Two forms of richness were estimated, one of which was just the total number of prey species identified. The second was that of Margalef, which takes into account the numbers per prey species as well as the number of species themselves.

$$\text{Margalef Richness } d = (S-1) / \text{Log } (N)$$

where S is number of species, N is number of samples.

Diversity is rather more complex and there are a number of different methods available for its calculation. Authors have often suggested indices appropriate for their own studies which may not be considered a priori correct for general application, and this has led to a lack of uniformity in the calculation methods (Peet, 1974).

Simpson (1949) formulated one of the simplest measures of diversity that takes both the number of species and the distribution of those species (evenness) into account. It is “sensitive to the abundance only of the more plentiful species in a sample, and can therefore be regarded as a measure of dominance concentration,” Hill (1973). It gives relatively little weight to the rare species and more weight to the common species. Partly for this reason, partly because of its simplicity and partly because it allows comparison with the results of Willis (1988), Simpson’s index was chosen for the analysis of diversity of the faecal samples.

Simpson’s question was: What is the probability that two specimens picked at random in a community of infinite size will be the same species? For the purposes of this analysis, the slightly altered approach of Krebs (1994) was used: What is the probability of picking two specimens at random that are different species? If a particular species  $i$  is represented in the community by  $p_i$  (proportion of individuals), the probability of picking two of these at random is the joint probability  $p_i^2$ . If these probabilities are summed for all the  $i$  species in the community, one has Simpson’s diversity (D):

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<sup>1</sup> Robertson, Dr H. G., South African Museum, Cape Town

<sup>2</sup> Adam, Dr R. A., Free State Nature Conservation, Bloemfontein

The probability of picking two =  $1 - (\text{probability of picking two that are the same})$   
specimens that are different

$$\text{Simpson's index of diversity } D = \frac{1}{\sum_{i=1}^S (p_i)^2}$$

where  $p_i$  is the proportion of individuals of species  $i$  in the community and  $S$  is the number of species

Pielou's (1975) evenness ( $J$ ) was also calculated for individual replicates:

$$J = H' / \log S \quad (\text{where } H' \text{ is the Shannon diversity index})$$

### Caste proportions

Caste proportions occurring in the faeces were estimated for the two most important prey species. During the sorting of the faeces, *T. trinervoides* were categorised into soldiers and workers. Differentiation of the two was straight forward because the soldier heads were red in colour and had pointed snouts, whereas worker heads were a mix of creamy/yellow and brown and had biting mandibles (of no defensive value). Worker larvae were rarely found in the samples but when they occurred, were counted as workers because they were not easy to distinguish.

Among the Formicidae, not all species have a designated soldier caste. Instead, as is the case for *A. custodiens*, the size of the workers varies greatly and the larger individuals fill the roles of the soldiers. All workers are in fact able to bite, even the small ones, but larger workers have larger jaws and, therefore, a more formidable bite. The rest of the ant species found in the faeces were not considered for examination of caste proportions for a variety of reasons. *M. albopilosum* workers were all one size, *M. capensis*, although regular prey, were never found in large numbers in the faeces, and *D. helvolus* occurred too irregularly. The rest of the species occurred neither regularly or in large enough numbers to be viable.

Twenty faecal samples were picked randomly from four different aardvarks to represent two seasons (10 summer, 10 winter), and the *A. custodiens* heads within them separated from the other heads. An image analyser (Quantimet Cambridge Instruments, UK) was then used to quantify the different sizes of *A. custodiens* heads from within these samples. *A. custodiens* were also collected from their nests using an aspirator and the image analyser used to quantify their body sizes. These data were then directly comparable to their quantified head sizes from the faecal data.

## **Numbers of ants and termites eaten per night**

Nine dry faecal pellets from nine separate faecal deposits, including pellets from five different aardvarks, were analysed. Each pellet was weighed and broken up, then a random proportion, representing both outer and inner parts of the pellets separated, and the number of ant and termite heads counted in that portion. The remaining uncounted section was then re-weighed to estimate the mass of the sampled portion, and from this an estimate could be made of the number of heads per gram of faeces.

During observation periods that regularly spanned an entire nights foraging, the number of defecation's per night were recorded (along with the time intervals between consecutive defecation's) from which an average frequency could be calculated. The average dry mass of one complete faecal sample was also estimated for an "average" aardvark. This was calculated from a large number of complete samples collected from at least five different aardvarks. The number of ant and termite heads in an entire nights faecal deposits was then calculated in the following way:

The number of heads in 1g dry faeces multiplied by the average mass of an entire faecal deposit, multiplied by the average number of faecal deposits in one night.

This equation is for an average aardvark because it is calculated from the average number of heads in one gram of faeces, which may not be equal for different aardvarks and which varies all the time, and the average mass of a faecal deposit. Larger aardvarks probably deposit larger samples, as has found to be the case for ungulates (Coe, 1983; Putman, 1984), but they may also defecate less frequently, a factor which is unknown. It has been found that the mass of faecal deposits varies during the activity period, with the first samples being the heaviest (pers. obs). The equation makes the assumption that all aardvarks defecate the same number of times in one night (this could not be tested with only two habituated animals).

## **Determination of calorific values and moisture content of prey species**

Ant and termite species were collected from the study area with the aim of calculating the percentage moisture content and calorific values for each species. Samples were usually collected on different days from different nests and grouped together to form one sample, (guaranteeing population sampling). Collection usually took place mid to late afternoon, when many species were at least partially active. The ants and termites were collected either with an aspirator or with tweezers.

Once collected and separated from any soil and grass stems, the samples were weighed and stored frozen at approximately - 4°C. Those samples that were to be tested for percentage moisture content were placed in a drying oven between 60°C and 80°C until they reached a constant minimum mass. Percentage moisture content was then calculated as follows:

$$\frac{\text{Live mass} - \text{Dry mass}}{\text{Live mass}} \times 100 = \text{percentage moisture content} \quad (\text{Skinner, unpubl.})$$

All samples, whether dried initially or not, were stored frozen until determination of calorific values.

Calorific values were determined using a CP400 Mini Calorimeter. Before determination, all samples were oven dried between 60°C and 80°C. The CP400 Mini Calorimeter was able to calculate calorific values from samples as small as 0.1g, although sample masses of 0.3 to 0.4g were preferable. Most of the determinations were, therefore, carried out using sample masses between 0.2g and 0.4g. This meant that it was possible to carry out determinations in triplicate for most species, even those for which only very small amounts were originally collected.

### **Direct observations of feeding**

Detailed observations of feeding behaviour were obtained for aardvark M5 from January to December 1997, and for aardvark F4 from February to December 1997. It was possible to stand right next to these two animals while they foraged, without any apparent reaction, and it was assumed that they were behaving normally. They never ran away (which they were free to do) or showed any signs of trying to keep a distance from the observer, which all the unhabituated animals did when approached. Apart from when they were first approached in an evening, the two habituated aardvarks never showed any signs of acknowledgement or interest in the observer, unless they accidentally walked into him/her. One was so accustomed to observers that he occasionally used their legs as rubbing posts in the same way he had been observed to rub up against termite mounds and tree trunks.

Where possible, observations were made on some of the other radio tagged aardvarks when they were sighted, but these were always short lived (less than two minutes) and as soon as the animal in question became aware of the human presence, its behaviour changed from foraging to escape. These short observations never achieved any empirical feeding data but did indicate that these shy aardvarks foraged and fed in the same manner as the two tame aardvarks. This was evidence that, although the sample size for behavioural observations was only two animals, the two habituated animals were not

behaving aberrantly or differently from the rest of the aardvark population. In addition to this, two further aardvarks became habituated after the field work for the current thesis was completed, and these animals exhibited the same foraging and feeding behaviour as the other two, although there was variation in the proportion of time spent feeding on the different prey species (pers. obs.; Le Roche, pers. comm. and Lindsay, pers. comm.).

The two habituated aardvarks were regularly followed on foot at least five nights a week, sometimes for the full night (with a break), or sometimes for just one or two hours at different times of the night. Data were predominantly recorded on a dictaphone, but were at times also written down on data sheets. The following were recorded during every observation period:

- a) Time. This was recorded regularly, often at the beginning of a new feed, or at intervals of 10min if there was no activity or if the aardvark was engaged in a long feeding bout;
- b) Prey species identification. This was recorded at the site of the dig unless the species was unknown, in which case a sample was collected for closer examination;
- c) Feed bout length. Recorded with a stop watch. This was taken as the time from the very start of the digging activity to the end of the feed when the aardvark stopped inserting its snout into the dig. Each feeding bout was a discreet event which made this process straight forward. It was recognised that the recorded length of each feeding bout was an overestimate of the actual time spent taking in prey because it did not account for the handling time of digging into an ant nest or termite mound. However, as digging open the nests of the prey was an integral part of each individual feed, the digging time was deemed an essential part of the process and included in the feeding time. It also proved impractical to record only the periods of taking in prey (not including digging) while at the same time recording other data.

Whenever an aardvark predated a *T. trinervoides* mound the following observations were recorded:

- I) Feeding bout length;
- II) Mound size. Mounds were categorised by height: small <20cm, medium 20 - 40cm, and large >40cm. The height of a mound was used as an index for its population size because it has been found that the two measurements are highly correlated (Adam, 1993);
- III) Whether or not the mound had been previously predated (undug indicating a mound that showed no sign of previous excavation by an aardvark, and predug indicating a mound that had been previously excavated by an aardvark, however long before);

IV) Which side of the mound was opened up (North, South, etc.) (This was recorded mostly in August and September).

From July through October, *T. trinervoides* mounds predated by either of the two habituated aardvarks were marked with small cards, bearing the date and animal identification. Reuse of these mounds was also recorded on the cards whenever this occurred. This served to identify how often mounds were reused, the time between consecutive feeds, and whether both aardvarks used the same mounds.

### **Estimation of densities of termite mounds and prey activity patterns.**

Sampling grids of 100m x 100m were temporarily marked out at ten different sites within the study area. Two of these were placed on the flood plain, while the rest were set in the gently sloping areas away from the flood plain. The sites were picked randomly, but within the known ranges of aardvarks, especially the two habituated ones.

Within each grid the number of *T. trinervoides* mounds were quantified. Mounds were categorised by height (see methods for feeding observations above) and whether or not they had been excavated by an aardvark previously.

Prey activity patterns were also occasionally observed within the study area away from the sampling grids. Ant and termite ports were marked and the activity regularly plotted during the course of an afternoon and night to see when they became inactive. Temperatures were recorded concurrently at the site using a temperature logger (Tidbit™).

### **Statistical analyses**

Statistical techniques that are normally used for analysing behavioural data are designed primarily for drawing inferences about populations rather than individuals. It is more common to emphasise what members of a population have in common rather than show how they differ, and effects of individual differences are often ironed out (Martin & Bateson, 1995). In the case of the aardvark diet, where faecal analysis indirectly represents the feeding behaviour, a certain amount of individual variation would be expected. A pooled average of monthly diet for all possible aardvarks may end up with a result that represents no aardvark at all because pooled results include all prey species, while individual results often do not (individual aardvarks do not predate all possible prey species that are exploited by the aardvark population as a whole, pers. obs.). This may be the result of chance, prey species

occurrence, or it may represent preferences of individual aardvarks for specific prey species. Differences between individuals may be of considerable biological significance and cannot be dismissed as mere statistical noise (Martin & Bateson, 1995). With this in mind, most results were tested for variation between individual aardvarks as well as for variation in the specific area of interest.

Where possible, parametric statistical tests were preferred over non-parametric. Biological data, however, do not often meet certain assumptions made by parametric tests, namely that their distributions must be normal and their variances homogenous. Much of the data from the present study was no exception, and in some cases alternative tests were required. Transformation of data sometimes normalised it, allowing the use of parametric tests, so where possible this was carried out. When transformation was not successful, randomisation testing was carried out instead. The software used for the randomisation tests here came from Manly (1991), and were converted from FORTRAN into Q-basic.

Analyses of the temporal variation in prey species and their respective numerical contribution to the diet of the aardvarks was carried out using a multivariate technique comparing the similarity between faecal samples. The computer software package PRIMER was used to carry out these analyses.

Multivariate methods are characterised by the fact that they base their comparisons of two or more samples on the extent to which these samples share particular species at comparable levels of abundance. Either explicitly or implicitly, all multivariate techniques are founded on such *similarity coefficients*, calculated between every pair of samples (Clarke & Warwick, 1994). These then facilitate a *clustering* of samples into groups which are mutually similar, or an *ordination plot* in which, for example, the samples are “mapped” in such a way that the distances between pairs of samples reflect their relative dissimilarity of species compositions.

Hierarchical Agglomerative Clustering is a commonly used clustering technique, and is the one used in this thesis. It takes a similarity matrix as a starting point and successively fuses the samples into groups and the groups into larger clusters, starting with the highest mutual similarities then gradually lowering the similarity level at which groups are formed. The process ends with a single cluster containing all samples. The result is presented by a tree diagram or *dendrogram*, with one axis representing the full set of samples and the other defining a similarity level at which two samples or groups are considered to have fused (Clarke & Warwick, 1994).

There are several methods of ordination available, but only Non-Metric Multi-Dimensional Scaling (MDS) was used in this thesis. This was because it has several advantages over the other techniques, including making less assumptions about the data, and was recommended as probably the best one available (Clarke & Warwick, 1994). It maps the samples (in two dimensions in the present thesis) so that the placement of the samples reflects the similarity of their biological communities. In other words, distances between samples on the ordination plot attempt to match the corresponding dissimilarities in community structure: nearby points have very similar communities, samples which are far apart have few species in common or the same species at very different levels of abundance (Clarke & Warwick, 1994). If there are many samples to be compared and much variation between them, there may be a high level of “stress” or distortion to contend with, and this can make ordination diagrams in two dimensions very misleading (see Clarke & Warwick, 1994, for explanation). Apart from increasing the dimensionality of the ordination, high stress values can be lowered by reducing the sample size and removing outliers. Where stress had to be lowered for the present analysis, it is explained in the results.

Clustering and ordination are useful for demonstrating the similarities between communities in diagrammatic form, but are purely descriptive methods. A pre-requisite to interpreting community differences between sites (or times) should be a demonstration that there are statistically significant differences to interpret (Clarke & Warwick, 1994). Multivariate analysis of variance can be used to test for significance, but the assumptions of such a test would normally be violated by biological data, including the current data. Instead, a test was used which is built on a simple non-parametric permutation procedure, applied to a (rank) similarity matrix underlying the ordination or clustering of samples. This is termed analysis of similarity (ANOSIM). ANOSIM was carried out on the data representing the ant and termite community found in the faeces.

Because feeding times and prey species identification were recorded for every feed bout, average times spent feeding on the different prey species could be compared to examine whether the average feeding time for one particular prey species was significantly different from the average feeding times for other prey species. However, as the aardvarks fed consecutively with relatively short intervals between feeds, it was considered probable that there would be some level of autocorrelation between individual feed bouts (i.e. the length of one feed had an effect on the length on the next feed).

With this in mind, an autoregression model was fitted to the data to provide for any autocorrelation (the nature of the data was as a time series). Autocorrelation was investigated (up to the order 12), and evidence found for it at the third order. Dummy variables were created for all levels of all factors involved (e.g. one factor was prey species, and levels within this factor were the individual prey

species), then regression of all factors carried out (aardvark, season, time of night and prey species) taking into consideration the third order autocorrelation. Finally, 1df contrasts were performed in a pairwise fashion for all factors (e.g. comparing *A. custodiens* with every other prey species). The procedure was carried out by R. J. Grimbeek<sup>3</sup> using the SAS computer software package (SAS Institute Inc., SAS/ETS®)

For analysis of mound predation by the habituated aardvarks,  $\chi^2$  tests were carried out. By comparing the counts of termite mounds available in the sampling grids with the observations of feeding frequencies on mounds by the aardvarks, expected frequencies were calculated.

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## Results

### Faecal analysis - Prey species

A total of 23 different ant and termite species were recognised within the diet of the aardvarks of TdR for the period July 1996 to December 1997. Of these, 14 ants and two termites were identified to the level of genus or higher, while the remaining seven species could only be identified as belonging to the Family Formicidae. See Figure 15.

The list includes identifications made from direct observations as well as from the faecal analysis because two of the genera comprised species that were difficult to distinguish in the faeces. Separation of these similar species was straight forward in the field with live specimens but difficult in the faeces when only head capsules were available. The two genera were: *Anoplolepis* spp., comprising two species, *A. custodiens* and *A. steingroeveri*; and *Camponotus* spp., comprising *C. nasutus* and *C. sp. maculatus* gp. (*C. fulvopilosus*, the third prey species in this genus, was easily distinguishable from the first two, even in the faeces).

Due to the difficulty of differentiation, and, therefore, the chance of making inaccurate identifications, the two species of each genus were clumped together for the remaining faecal analysis. As will be seen later in the results and in the discussion, it can be assumed that the majority of the heads in the *Anoplolepis* category belong to *A. custodiens*.

Formicidae sp.1 and 2 were identified as male head capsules, so may conceivably have belonged to two of the other 14 genera already identified. However, there appeared to be no correlation between the occurrence of any of these 14 with either of the two male ants. The only ants occurring in all samples with either of the two were *Anoplolepis* spp. (mostly *A. custodiens*), but these were ruled out because males from this group were already identified. Furthermore, live specimens of Formicidae sp.1 and 2 were never found with any live specimens of the other identified species.

Six of the species listed in Figure 15 occurred five times or less in the total faecal samples and mostly only occurred in low numbers, ones or twos. They may have been ingested accidentally. They are indicated in Figure 15 by an asterisk (“\*”). For the purposes of the remaining faecal analysis they were all placed into one group: the “Minor species”.

For the complete dietary list of ants and termites in the faeces, sample by sample, see Appendix III.

Class: Hexapoda

Order: Hymenoptera

Family: Formicidae

Subfamily: Formicinae

*Anoplolepis custodiens* (F. Smith, 1858)  
*Anoplolepis steingroeveri* (Forel, 1894)  
*Camponotus fulvopilosus* (De Geer, 1778)  
*Camponotus* sp. *maculatus*-group  
*Camponotus nasutus* (Emery)

Subfamily: Myrmicinae

*Crematogaster* sp.  
*Messor capensis* (Mayr, 1862)  
*Monomorium albopilosum* (Emery, 1895)  
*Monomorium havilandi* (Forel, 1910)  
*Monomorium* sp. \*  
*Pheidole* sp.  
*Solenopsis punctaticeps* (Mayr)  
*Tetramorium* sp. \*

Subfamily: Dorylinae

*Dorylus helvolus* (Linnaeus)

Formicidae sp.1  
Formicidae sp.2  
Formicidae sp.3  
Formicidae sp.4 \*  
Formicidae sp.5 \*  
Formicidae sp.6 \*  
Formicidae sp.7 \*

Order: Isoptera

Family: Termitidae

*Trinervitermes trinervoides* (Sjostedt)

Family: Hodotermitidae

*Hodotermes mossambicus* (Hagen)

\* indicates species that occurred in less than five faecal samples and, therefore, placed in the group “Minor” for the remaining analyses.

**Figure 15.** The ant and termite diet of aardvarks on Tussen die Riviere, July 96-Dec 97

## Dietary proportions

Table 6 shows the overall average percentage occurrence of each prey species, calculated from all the faecal samples collected in 1997. Standard deviation, range and frequency of occurrence (the percentage of faecal samples within which a species was found) are also presented for each species. Importance Value (IV) and Relative Importance (RI) are presented for comparison with the results of Willis (1988).

**Table 6.** The contents of all faecal samples collected in 1997

|                          | Mean  | Std dev | Max   | Min | %          | Importance | Relative   |
|--------------------------|-------|---------|-------|-----|------------|------------|------------|
|                          | (%)   | (%)     | (%)   | (%) | occurrence | value      | importance |
| <i>Anoplolepis</i> spp.  | 69.87 | 25.17   | 100   | 0   | 99.62      | 69.6       | 1          |
| <i>T. trinervoides</i>   | 13.60 | 18.80   | 94.81 | 0   | 87.79      | 11.9       | 2          |
| <i>M. albopilosum</i>    | 8.28  | 13.51   | 92.21 | 0   | 84.73      | 7.02       | 3          |
| <i>D. helvolus</i>       | 2.72  | 11.14   | 90.25 | 0   | 22.14      | 0.60       | 6          |
| <i>H. mossambicus</i>    | 1.89  | 5.85    | 53.14 | 0   | 44.27      | 0.84       | 4          |
| <i>M. capensis</i>       | 1.08  | 3.22    | 34.75 | 0   | 56.87      | 0.61       | 5          |
| <i>Crematogaster</i> sp. | 0.69  | 4.06    | 50.42 | 0   | 12.21      | 0.08       | 7          |
| <i>S. punctaticeps</i>   | 0.53  | 3.38    | 34.21 | 0   | 7.63       | 0.04       | 9          |
| Formicidae sp.1          | 0.42  | 1.37    | 11.64 | 0   | 18.70      | 0.08       | 8          |
| Unknown                  | 0.21  | 1.81    | 27.73 | 0   | 10.31      | 0.02       | 12         |
| <i>Camponotus</i> spp.   | 0.18  | 0.54    | 5.45  | 0   | 20.61      | 0.04       | 10         |
| <i>C. fulvopilosus</i>   | 0.16  | 1.19    | 12.73 | 0   | 8.02       | 0.01       | 14         |
| <i>M.havilandi</i>       | 0.13  | 0.41    | 3.45  | 0   | 18.32      | 0.024      | 11         |
| Formicidae sp.3          | 0.12  | 0.50    | 4.08  | 0   | 11.07      | 0.013      | 13         |
| Formicidae sp.2          | 0.08  | 0.47    | 6.91  | 0   | 10.69      | 0.009      | 15         |
| <i>Pheidole</i> sp.      | 0.04  | 0.13    | 0.99  | 0   | 10.31      | 0.004      | 16         |

$$IV = \frac{\text{Mean (\%)} \times \% \text{ occurrence}}{100}$$

RI is a ranked index of IV used by Willis (1988), and the species with an RI of 1 was the one which had the highest importance value. An increasing numerical value of RI corresponds with decreasing importance.

It is clear that *Anoplolepis* spp. were by far the most important prey species in 1997, comprising an average of 69.87% of total prey numbers. They occurred in 99.62% of the samples (the most), corresponding to 262 out of a total of 263 samples. *Anoplolepis* spp. were, therefore, only absent from one sample. Their importance value of 69.6 was by far the highest.

The second and third most important prey species in terms of both average percentage of total prey numbers and frequency of occurrence were *T. trinervoides* and *M. albopilosum*. They occurred in 231 and 223 of the total 263 samples respectively. Along with *A. custodiens*, these two species made up a total of 91.75% of the total average prey numbers.

Only three other prey species individually comprised >1% of the total average prey numbers: *D. helvolus*, *H. mossambicus*, and *M. capensis*. Although both *H. mossambicus* and *M. capensis* occurred on average in lower numbers than *D. helvolus*, they both had a higher frequency of occurrence and, consequently, higher RI values than *D. helvolus*.

Overall the top six prey species above accounted for 97.44% of the total prey numbers in the faeces of 1997, leaving the remaining species a total of only 2.56%. Each of these averaged less than one percent of the total faecal contents and none occurred in more than 20% of the samples. They all played minor roles in the diet of the aardvarks of TdR during 1997.

### **Dietary variation with time**

The faecal samples were split up into months for examination of temporal variation within and between prey species. This was a somewhat subjective process in that a sample collected at the end of one month might have been deposited only two or three days before the next sample, which would then have been categorised as belonging to the next month. Monthly categories were considered more objective,

however, than seasonal categories which would have assumed variation to be caused by temperature or rainfall.

It was considered important to sample more than the minimum requirement of faeces per month, where possible, to ensure a high level of certainty that all possible species were counted. The minimum requirement decided on was 18 faecal samples (see Appendix II and methods). This was achieved for all the months of 1997 when the faeces were combined, except January. The average sample size per month for 1997 was 22, with January comprising 15 samples (the only month with less than 20 samples) and the rest comprising between 20 and 24 samples. The reason for the disparity in sample size was that some months proved more successful than others for locating faecal deposits of non-habituated aardvarks.

### Species richness and diversity

Figure 16 shows the monthly prey species richness (number of prey species) in the combined faeces of 1997.

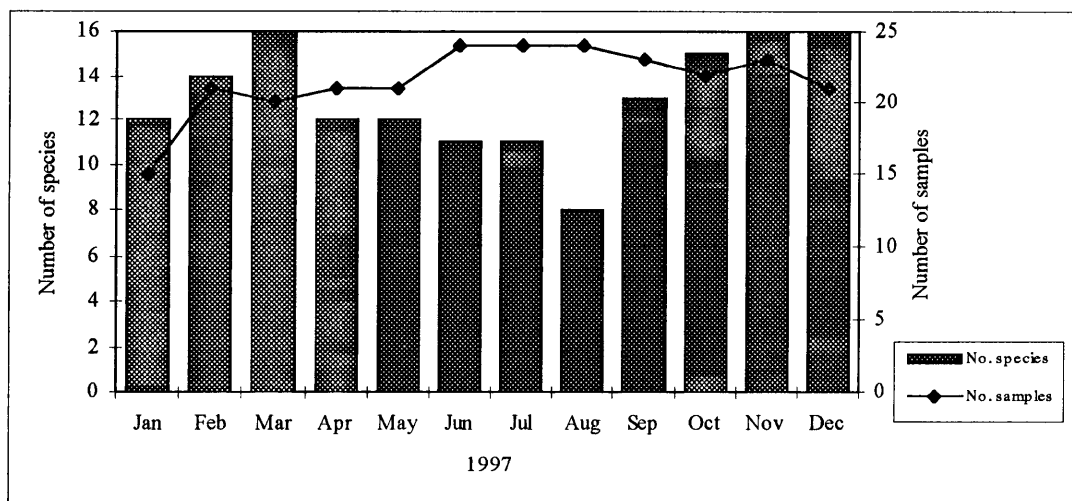


**Figure 16.** Monthly prey species richness and corresponding sample sizes for the combined faeces of 1997.

Due to the variation in sample size, species richness was not directly comparable between months. However, a general pattern was still identifiable when the number of samples per month were taken into

account. The highest species richness (16 species) occurred in the months of March, November and December, but corresponded with lower than average sample sizes. The lowest species richness occurred in the months of June, July and August (11, 11 and 8 respectively), corresponding with the largest sample sizes. The general pattern, therefore, appeared to be higher species richness in the summer months and lower species richness in the winter. January was somewhat ambiguous with a smaller sample size (15), which may have lowered its species richness.

The temporal variation in the prey species richness of the two habituated aardvarks is represented in Figure 17. Because the six samples per month for each animal were not enough to count all possible prey species, three months data were combined (January, February and March, etc.).

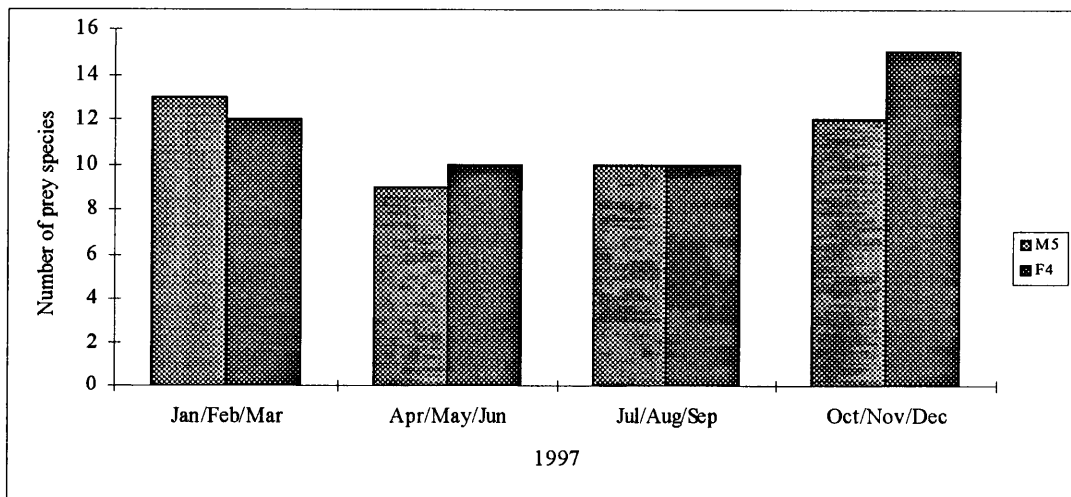


**Figure 17.** Prey species richness in the faeces of aardvarks M5 and F4, 1997. (All sample sizes = 18, except F4 Jan/Feb/Mar = 15 )

The highest species richness for aardvark M5 occurred in Jan/Feb/Mar, with 13 species, while the lowest occurred in Apr/May/Jun, with nine species. The corresponding highs and lows for aardvark F4 occurred respectively in Oct/Nov/Dec, with 15 species, and Apr/May/Jun and Jul/Aug/Sep, each with 10 species. Neither aardvark on its own predated as many ant and termite species as were predated by the combined aardvarks. The pattern of variation in species richness did, however, appear to uphold that of the combined faeces, where there was a decrease from summer to winter, followed by an increase into the next summer.

### Diversity

Diversity of prey species found in the faecal samples was calculated using Simpson’s diversity index. Average monthly diversity was calculated for the combined samples while diversity for the two habituated aardvarks was calculated in three month blocks. Results are shown in Table 7.

As the diversity index used was based on the probability of picking two specimens at random that were different species, the higher the calculated value, the higher the diversity. For the combined faeces the pattern of prey diversity was, therefore, similar to the pattern of species richness because there was a relatively high value in March, followed by a dip into the winter months, followed by an increase into summer. The highest diversity of 1997 was in November. Overall, however, there was a general increase from January to December. For the individual aardvarks, no real seasonal pattern was apparent except that the prey diversity of F4 increased continuously through the year.

**Table 7.** The diversity of prey species in the faeces of the combined aardvarks and aardvarks M5 and F4 individually, 1997. Simpson’s diversity index was used.

|           | Combined | A8    | A9    |
|-----------|----------|-------|-------|
| January   | 0.213    |       |       |
| February  | 0.328    | 0.343 | 0.163 |
| March     | 0.545    |       |       |
| April     | 0.301    |       |       |
| May       | 0.450    | 0.301 | 0.367 |
| June      | 0.397    |       |       |
| July      | 0.430    |       |       |
| August    | 0.525    | 0.464 | 0.603 |
| September | 0.549    |       |       |
| October   | 0.517    |       |       |
| November  | 0.633    | 0.409 | 0.632 |
| December  | 0.534    |       |       |

The indices of diversity and richness above were estimated using entire months or three months accumulation of species for the combined faeces and individual faeces respectively. Table 8 below represents average diversity indices for individual replicates, for both habituated aardvarks.

**Table 8.** More diversity indices for aardvarks M5 (a) and F4 (b). Represented are a different form of species richness (Margalef’s), which takes into account the number of individuals; Simpson’s diversity and Pielou’s evenness.

| a)  | Margalef<br>Richness | Simpson<br>index | Pielou<br>evenness |
|-----|----------------------|------------------|--------------------|
| JFM | 1.395 ± 0.585        | 0.241 ± 0.158    | 0.321 ± 0.148      |
| AMJ | 1.372 ± 0.470        | 0.281 ± 0.164    | 0.356 ± 0.153      |
| JAS | 1.320 ± 0.487        | 0.403 ± 0.166    | 0.520 ± 0.172      |
| OND | 1.953 ± 0.658        | 0.356 ± 0.195    | 0.410 ± 0.174      |

| b)  | Margalef<br>Richness | Simpson<br>index | Pielou<br>evenness |
|-----|----------------------|------------------|--------------------|
| JFM | 1.189 ± 0.777        | 0.159 ± 0.147    | 0.258 ± 0.197      |
| AMJ | 1.167 ± 0.483        | 0.297 ± 0.149    | 0.433 ± 0.245      |
| JAS | 1.345 ± 0.386        | 0.466 ± 0.163    | 0.563 ± 0.186      |
| OND | 2.569 ± 0.588        | 0.487 ± 0.180    | 0.486 ± 0.155      |

It is evident first (and this is the main reason for presenting the Table) that the average diversity (as given by the Simpson index) was lower for individual replicates than it was for accumulated replicates, as seen in Table 7. In general, individual faecal samples had low species richness and diversity, and this only increased when they were added together. However, the general pattern of changing diversity through the year for the individual replicates was similar to that of the accumulated samples (Table 7), except JFM for aardvark M5. The average evenness was highest for both aardvarks in JAS and lowest in JFM.

## Proportions of prey species

Figure 18 shows the monthly percentages of prey species for all the faecal samples collected between July 1996 and December 1997. Each month combines samples from the radio tagged aardvarks as well as from unknown aardvarks in other parts of the reserve, away from the main study area. The charts representing the early stages of the study, namely July through December 1996, do not include samples from the habituated animals, as these were not then part of the study. The charts for all months in 1997, however, do incorporate the habituated aardvark data.

The sample sizes for the months of September, October and November 1996 were small (three, two and four respectively) and, therefore, not necessarily representative of the aardvark population. They are included mainly for continuity. Sample sizes for July, August and December 1996, were 13, 19 and 9 respectively.

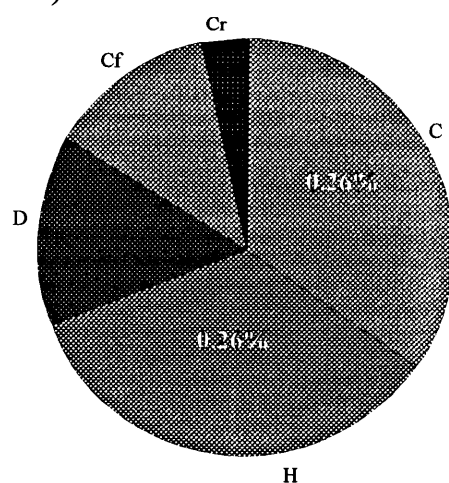
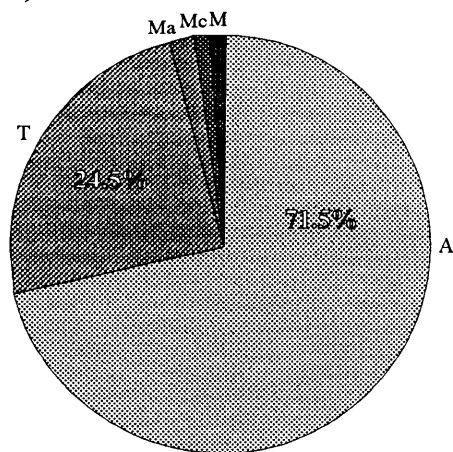
The first thing that is apparent from all months is that, on average, the Formicidae occurred in greater numbers in the faeces than the Isoptera. It should be noted here that this was not always true for every individual faecal sample, as can be seen from Table 6 where the maximum percentage occurrence of *T. trinervoides* in a single faecal sample was 94.81%. This indicates that in one sample at least termites were dominant over ants. The averaging of the samples by month cancelled out individual samples in which termites may have been more abundant. Appendix III presents the results of every faecal sample individually, and a number of examples can be found in which the Formicidae were not the dominant order.

*Anoplolepis* spp. were, on average, the most common ant species and, therefore, the most common prey species present in the faeces every month. In 1997, the month with the highest proportion of *Anoplolepis* spp. was January, with an average of 88.3%, while the lowest was November, with 58.3%. August 1996 showed the lowest overall proportions of *Anoplolepis* spp. with an average of 49.6%. August 1997 had the second lowest proportions for 1997 (61.2%).

The second and third most abundant prey species in the faeces of the aardvarks of TdR were *T. trinervoides* and *M. albopilosum*. The more important of the two in terms of an average percentage of the total alternated between months, but there was no apparent pattern to this. *T. trinervoides* was second most abundant 13 times during the 18 month period, while *M. albopilosum* was second most abundant 5 times.

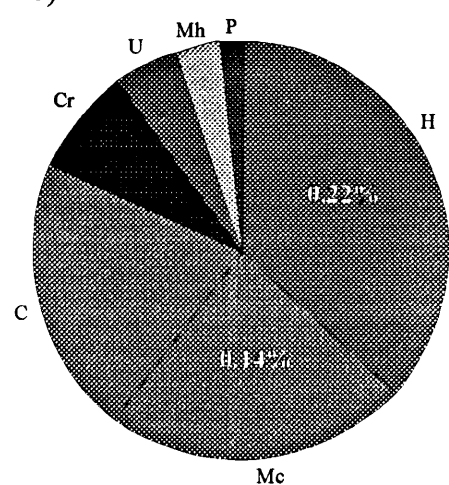
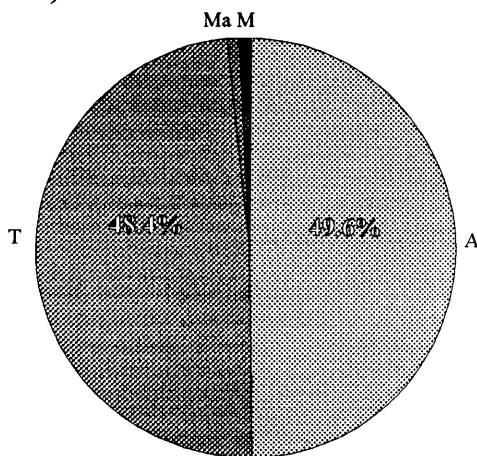
a)

July 96 b)



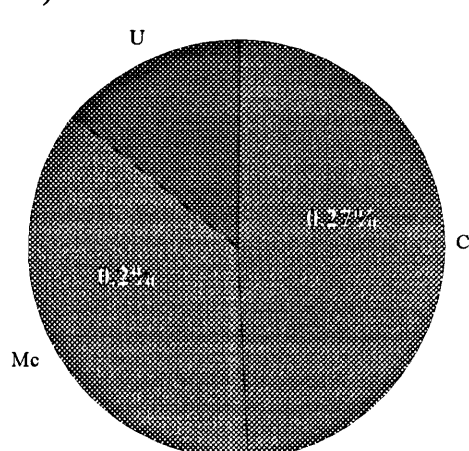
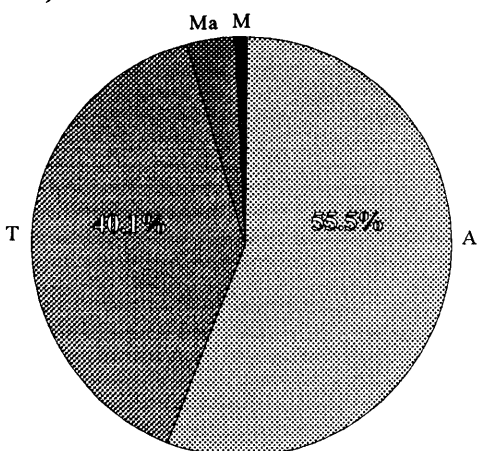
a)

August 96 b)



a)

September 96 b)



|                    |                     |                           |                      |
|--------------------|---------------------|---------------------------|----------------------|
| A=Anoplolepis spp. | T=T. trinervoides   | M=Minor species           | Ma=M. albopilosum    |
| Mh=M. havilandi    | Mc=M. capensis      | D=D. helvolus             | C=Camponotus sp.     |
| Cf=C. fulvopilosus | P=Pheidole sp.      | S=Solenopsis punctaticeps | Cr=Crematogaster sp. |
| F1=Formicidae sp.1 | F2=Formicidae sp. 2 | F3=Formicidae sp. 3       | U=Unidentified spp.  |
| H=H. mossambicus   |                     |                           |                      |

**Figure 18.** Monthly percentages of prey species in the faeces of the combined aardvarks of TdR, July to September 1996. a) Total sample: all prey species comprising >1% of a months diet (represented separately) plus all prey species comprising <1% (grouped into Minor species); b) all minor species comprising <1% of a months diet.

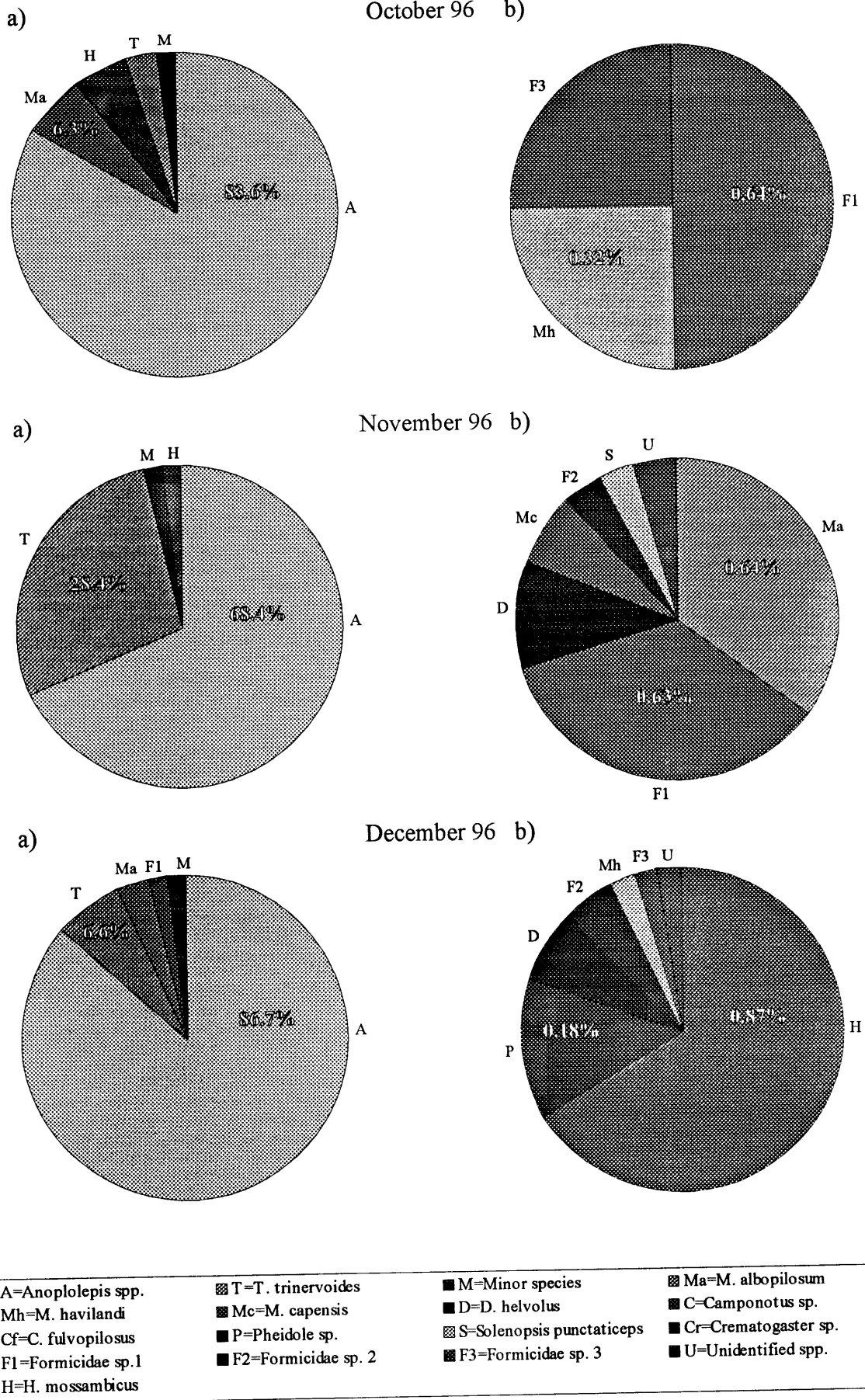


**Figure 18 (continued).** Monthly percentages of prey species in the faeces of the combined aardvarks of TdR, October to December 1996.

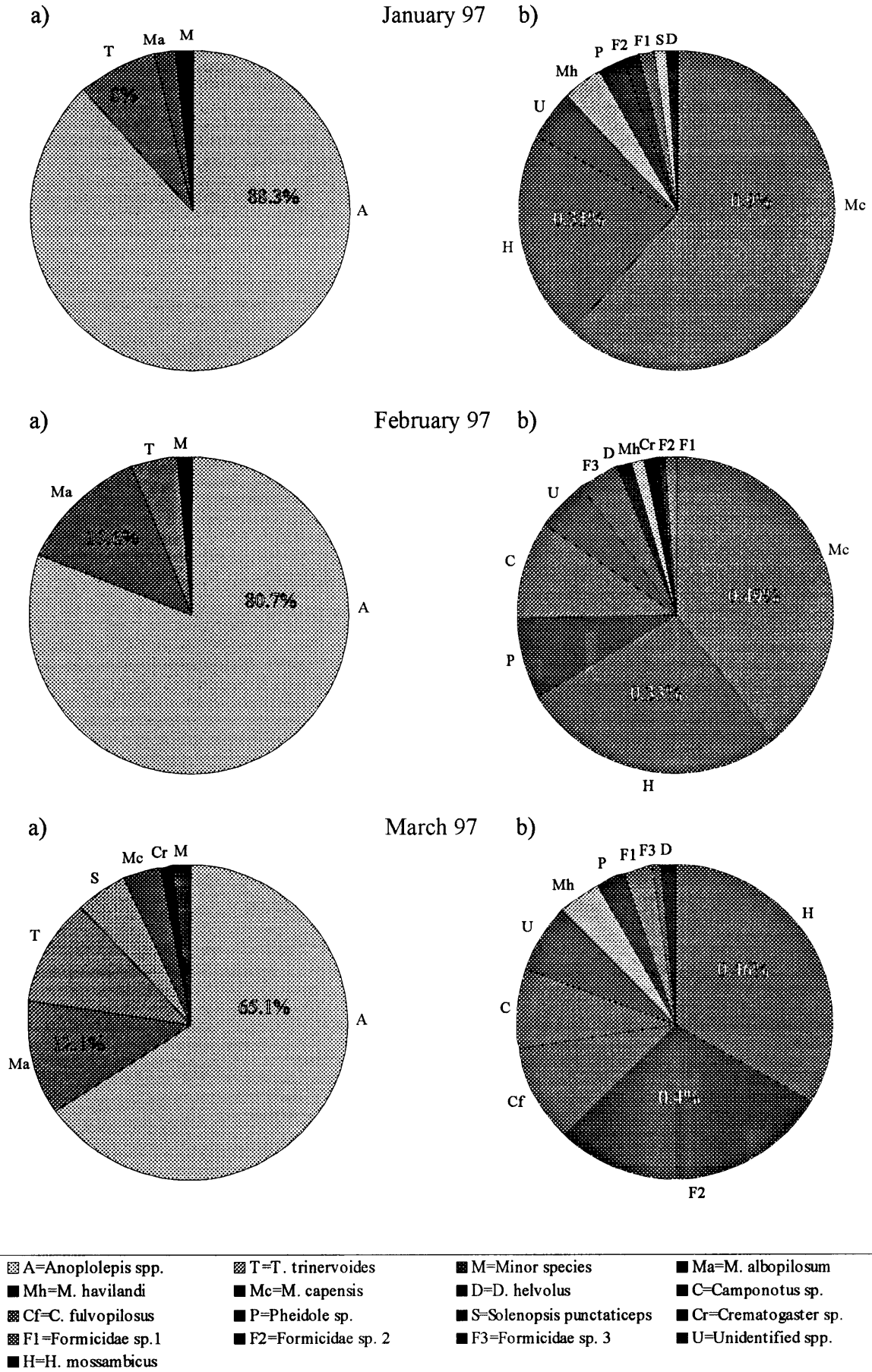


**Figure 18 (continued).** Monthly percentages of prey species in the faeces of the combined aardvarks of TdR, January to March 1997.

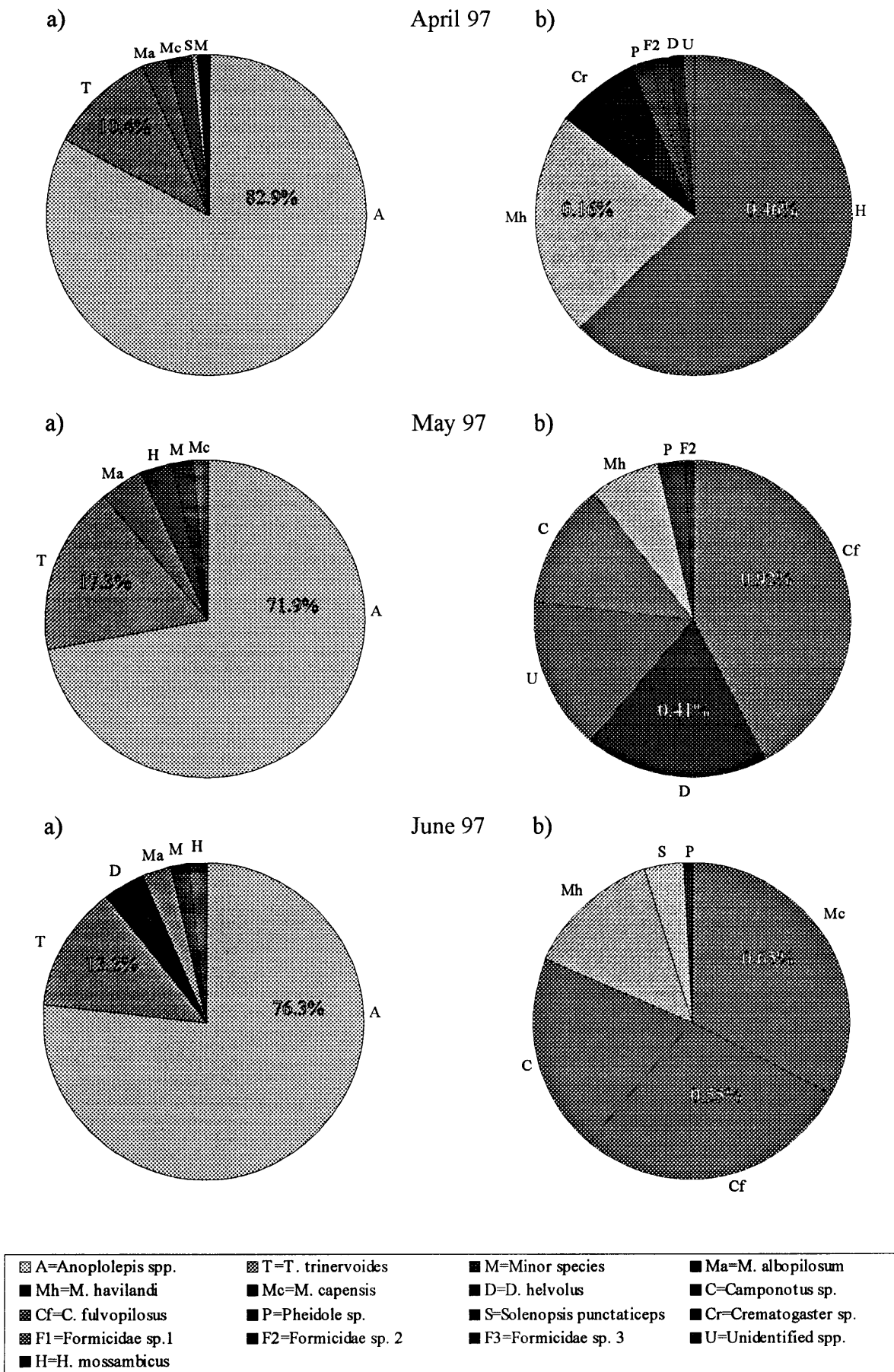


**Figure 18 (continued).** Monthly percentages of prey species in the faeces of the combined aardvarks of TdR, April to June 1997.

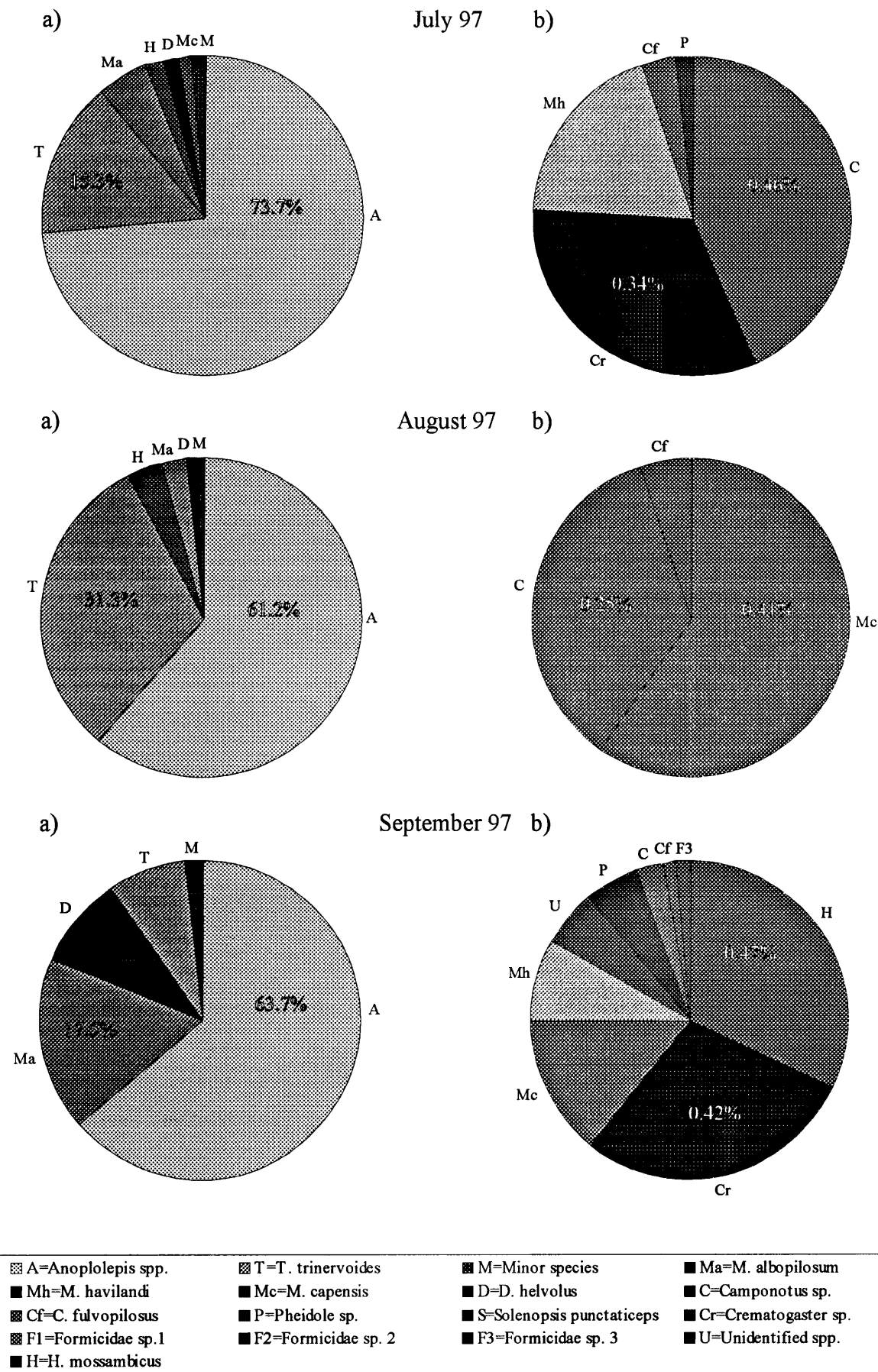


**Figure 18 (continued).** Monthly percentages of prey species in the faeces of the combined aardvarks of TdR, July to September 1997.

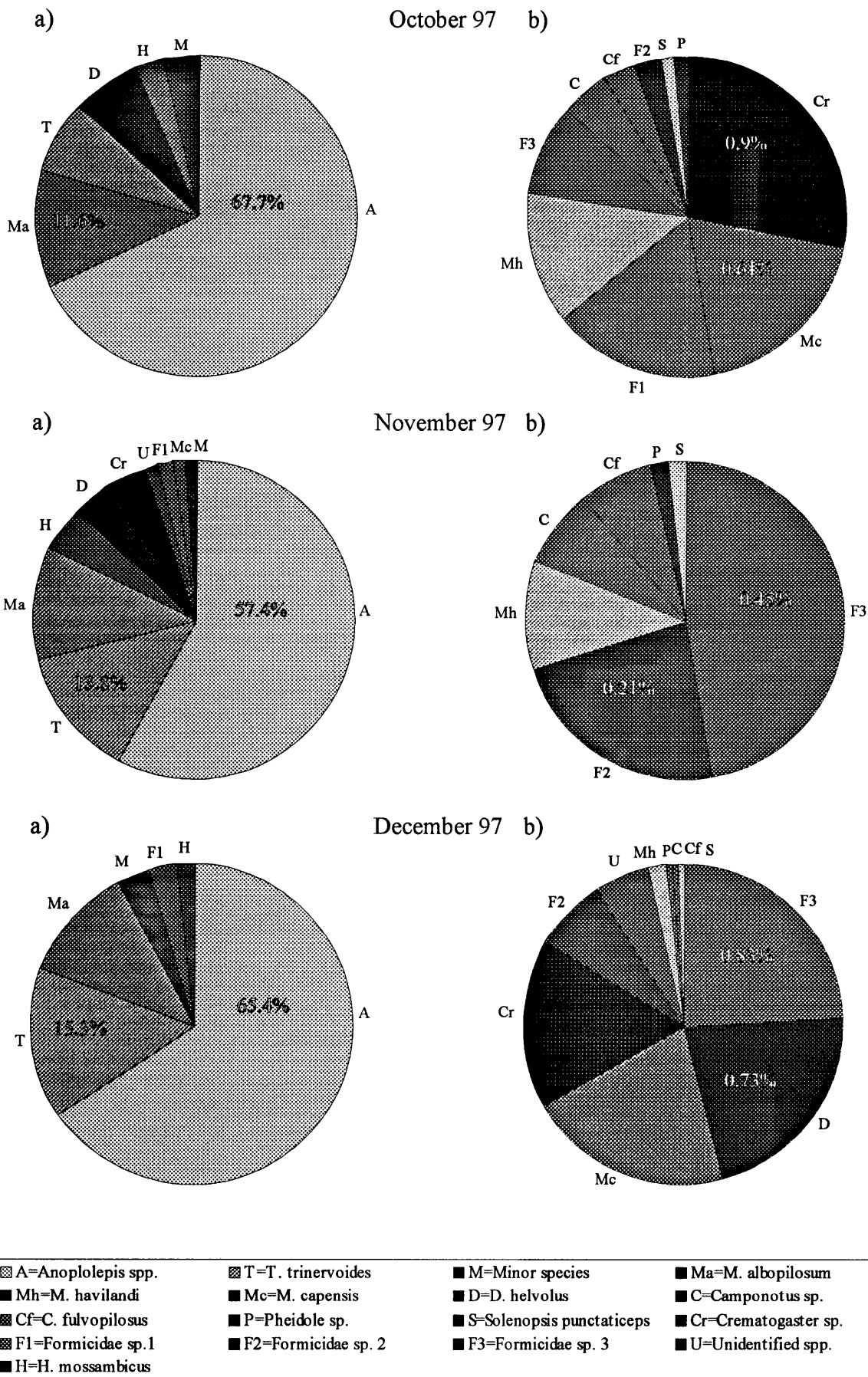


**Figure 18 (continued).** Monthly percentages of prey species in the faeces of the combined aardvarks of TdR, October to December 1997.

The highest proportions of *T. trinervoides* in 1997 occurred in August, with an average of 31.3%. For 1996, the highest proportions also occurred in August, with an average percentage of 48.4%. The lowest proportions of *T. trinervoides* in the faeces occurred in February 1997, with a value of 4.9% (October 1996 also had a very low percentage of *T. trinervoides*, but this month only comprised two samples).

The highest proportions of *M. albopilosum* in 1997 occurred in September, with an average of 17.5%. The lowest proportion was 2% in August which coincided with the *T. trinervoides* peak, while August 1996 had a proportion of 1.4% *M. albopilosum*.

Between July 1996 and December 1997 there were only five months in which one of *T. trinervoides* or *M. albopilosum* were not among the top three most abundant species in the faeces. These were: October 96, where *H. mossambicus* was third most abundant in place of *T. trinervoides*; November 96, where *H. mossambicus* was third in place of *M. albopilosum*; June 97, where *D. helvolus* was third in place of *M. albopilosum*; August 97, where *H. mossambicus* was the third in place of *M. albopilosum*, and; September 97, where *D. helvolus* was the third in place of *T. trinervoides*.

Apart from *H. mossambicus*, the remaining species did not regularly comprise >1% of the monthly totals in the faeces. *H. mossambicus* made up more than 1% of monthly prey species nine times, with a highest value of 4.5%, while *D. helvolus* and *M. capensis* did the same six times and five times respectively, with highest values of 9.4% and 3.8%. *S. punctaticeps* and *Crematogaster* sp. both topped 1% of monthly prey species twice.

The following species never comprised more than one percent of a complete months diet: *M. havilandi*, *Camponotus* spp., *C. fulvopilosus*, *Pheidole* sp., Formicidae sp.2, and Formicidae sp. 3.

Figures 19 and 20 show the monthly percentages of prey species in the faeces of aardvarks M5 and F4 respectively for 1997. Each month represents averages obtained from six faecal samples. The reason they are presented separately and individually from Figure 18 is to demonstrate the variation between aardvarks.

Formicidae were, on average, the dominant order in all months and for both aardvarks, with *A. custodiens*, on average, the most common species. The highest proportions of *A. custodiens* occurred in January 1997 for both aardvarks with averages of 93.4% and 99.3% for M5 and F4 respectively. The lowest proportions occurred in March for M5, with an average of 64%, and November for F4, with an

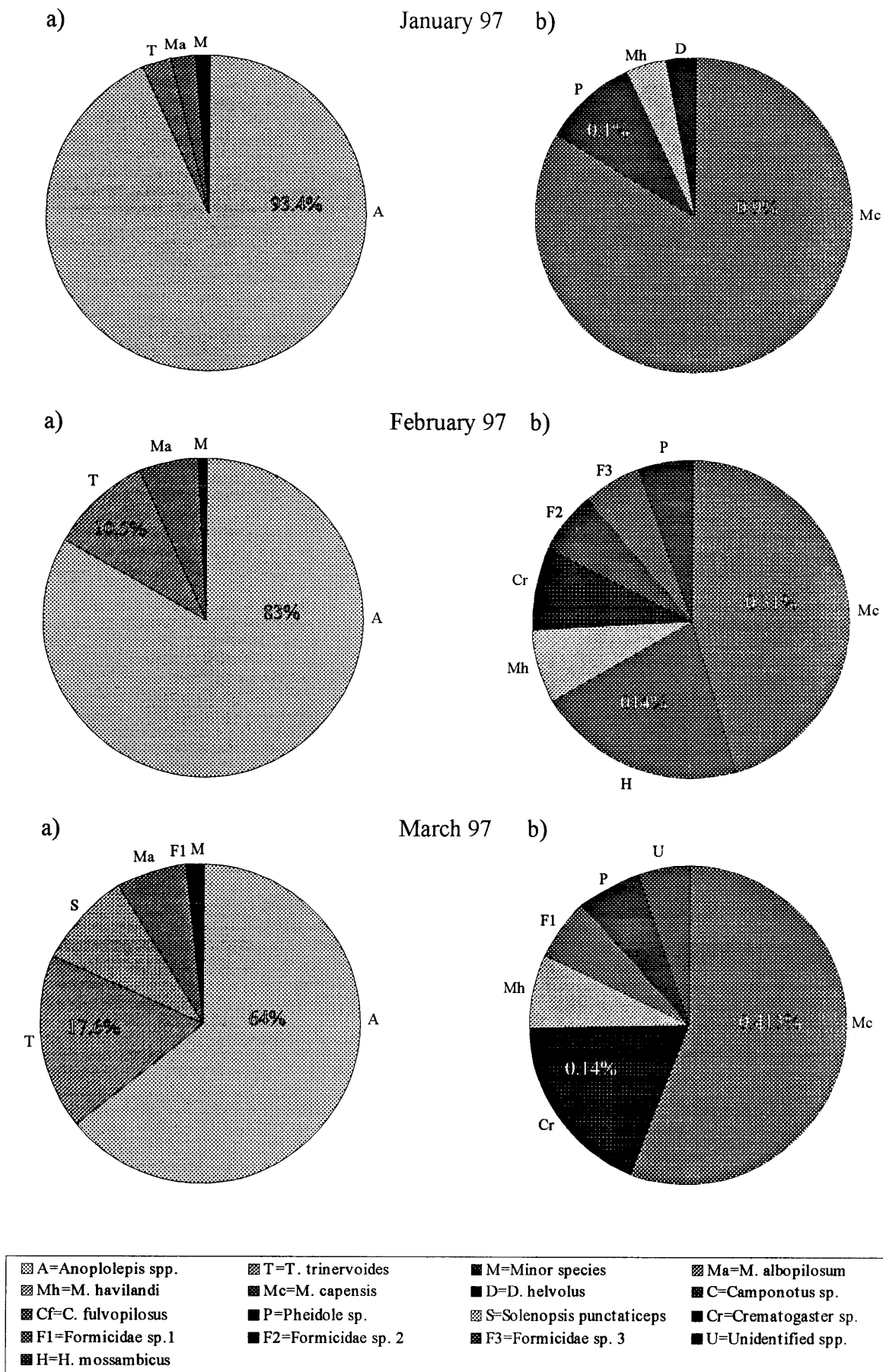


**Figure 19.** Monthly percentages of prey species in the faeces of aardvark M5, January to March 1997. a) Total sample: all prey species comprising >1% of a months diet (represented separately) plus all prey species comprising <1% (grouped into Minor species); b) all minor species comprising <1% of a months diet.

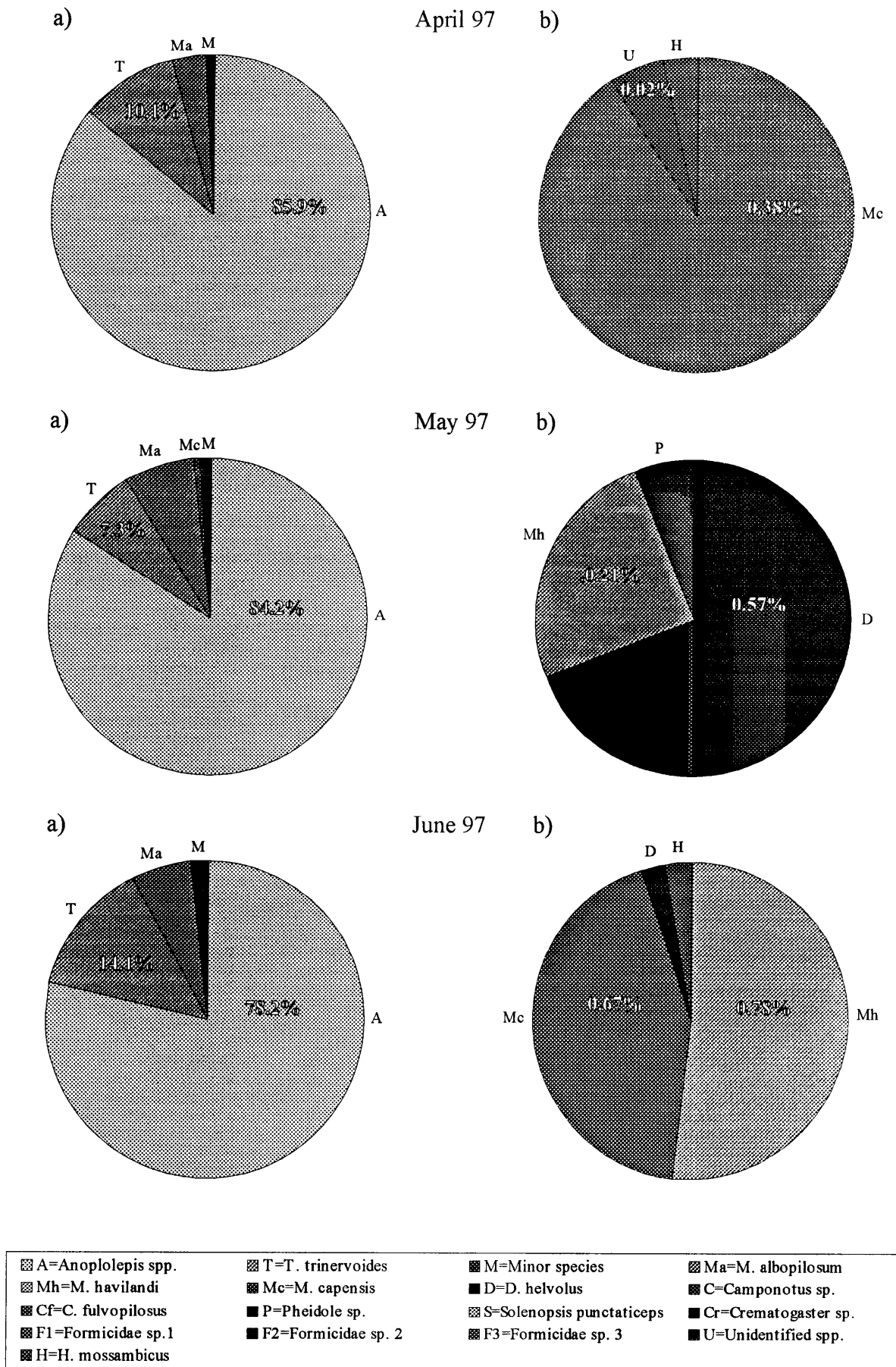


**Figure 19 (continued).** Monthly percentages of prey species in the faeces of aardvark M5, April to June 1997.

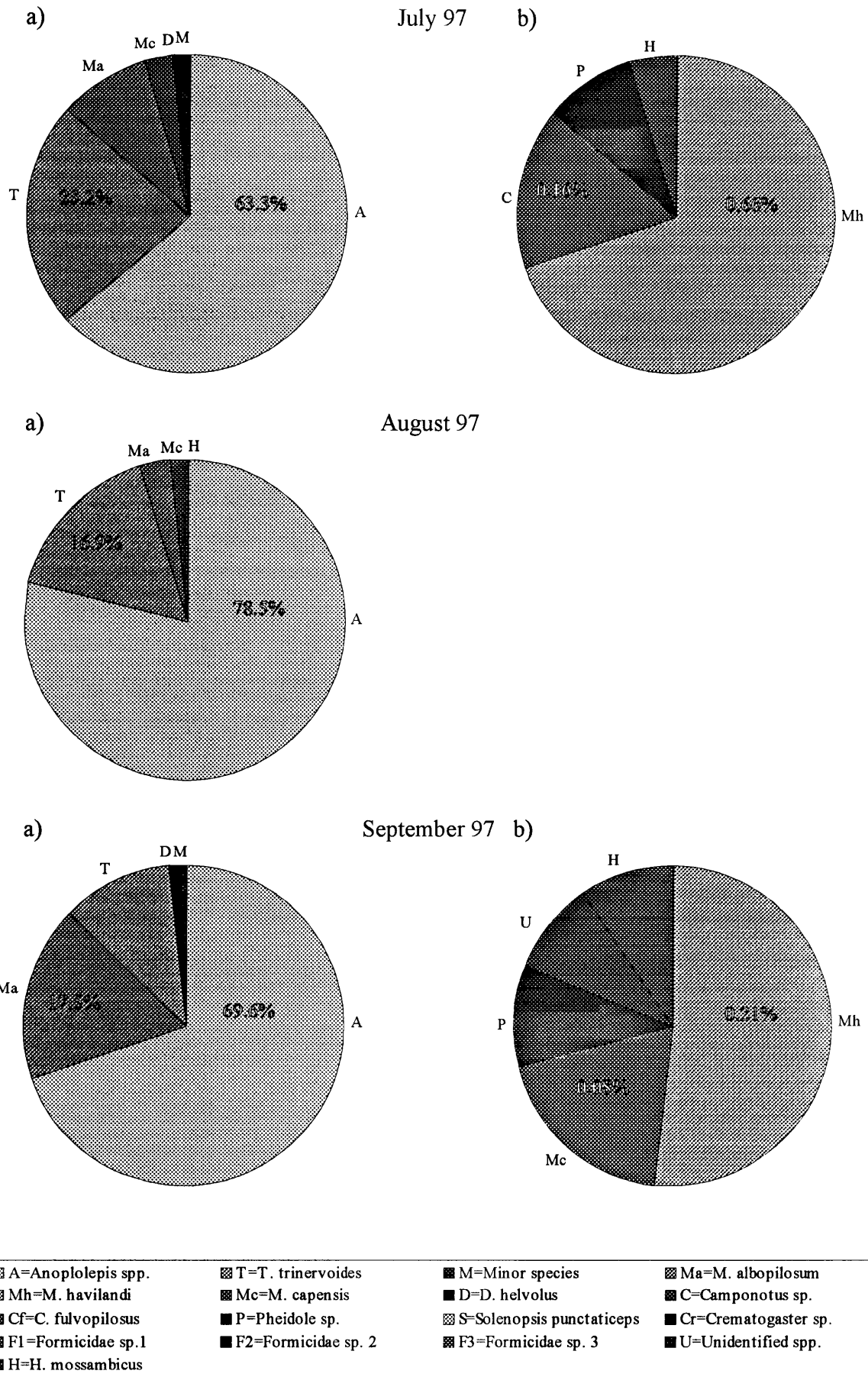


**Figure 19 (continued).** Monthly percentages of prey species in the faeces of aardvark M5, July to September 1997.

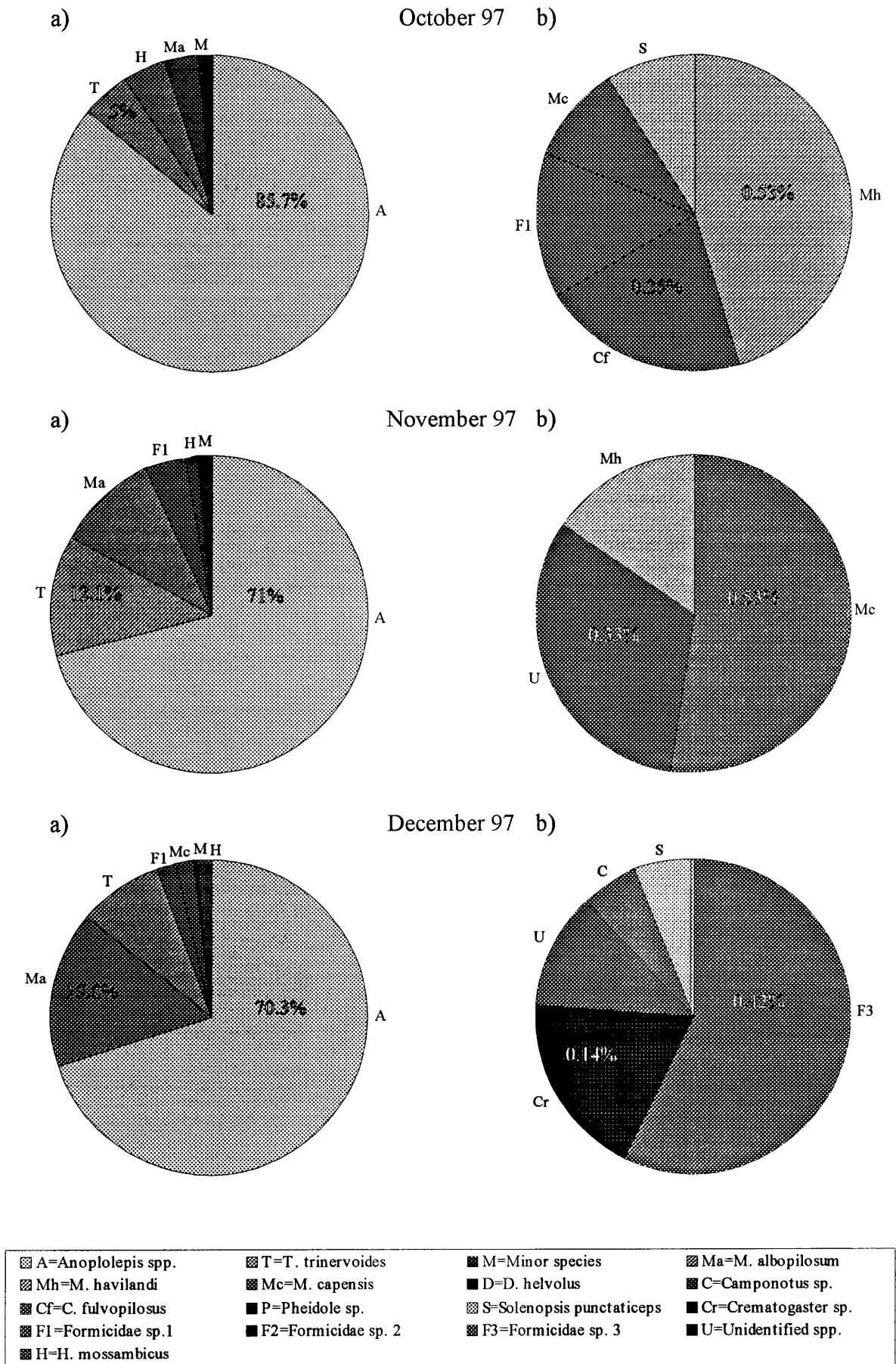


**Figure 19 (continued).** Monthly percentages of prey species in the faeces of aardvark M5, October to December 1997.

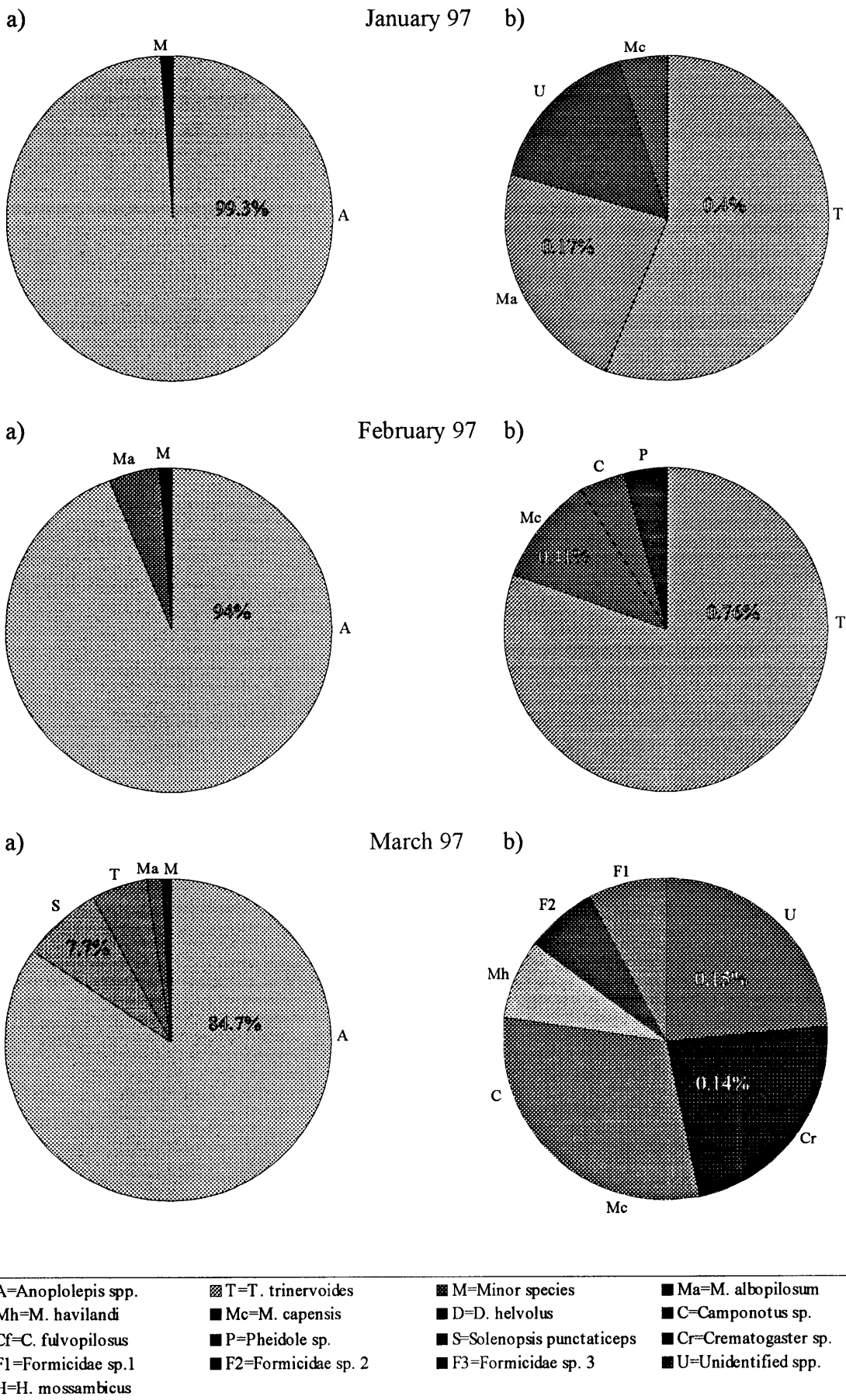


**Figure 20.** Monthly percentages of prey species in the faeces of aardvark F4, January to March 1997. a) Total sample: all prey species comprising >1% of a months diet (represented separately) plus all prey species comprising <1% (grouped into Minor species); b) all minor species comprising <1% of a months diet.

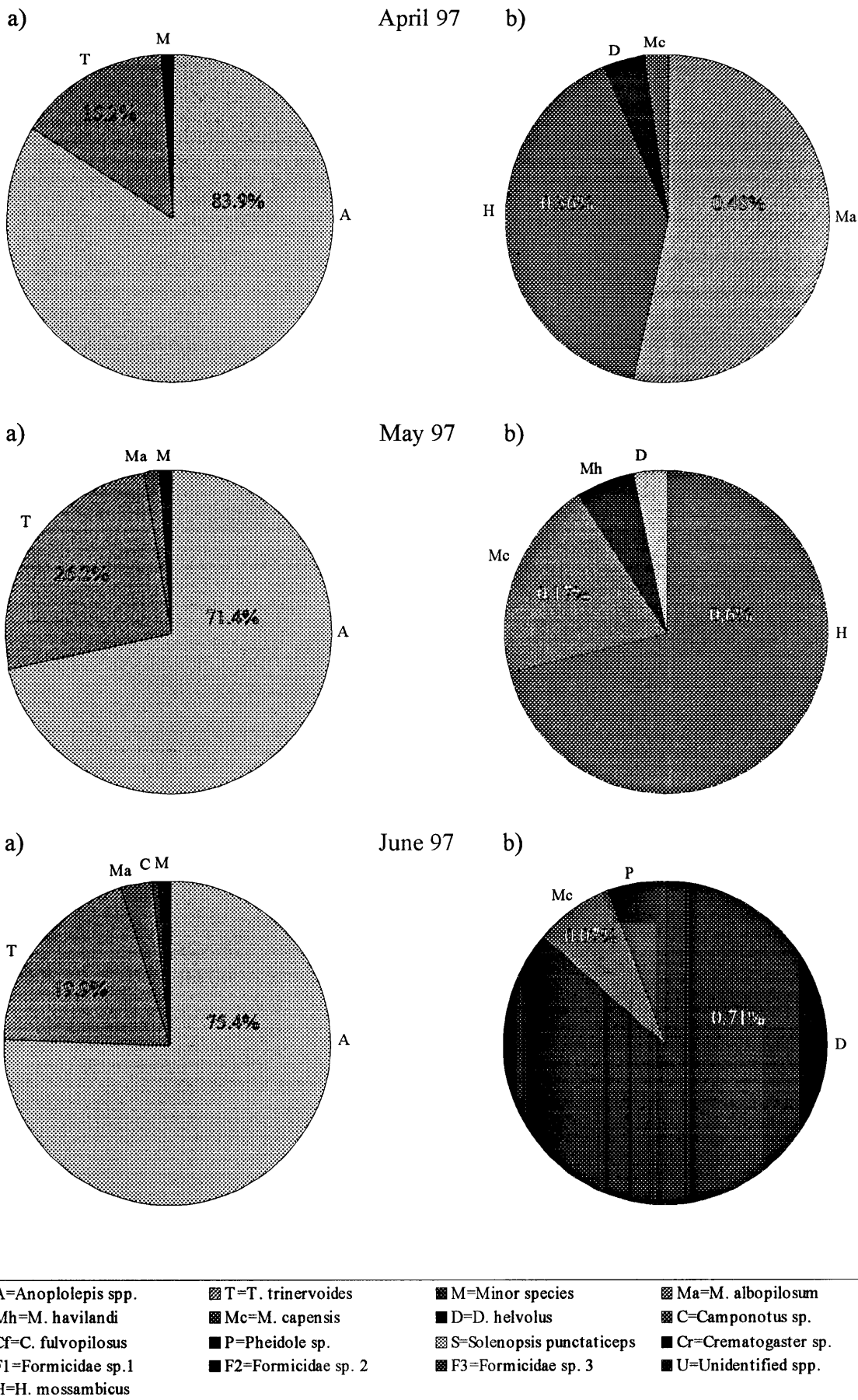


**Figure 20 (continued).** Monthly percentages of prey species in the faeces of aardvark F4, April to June 1997.

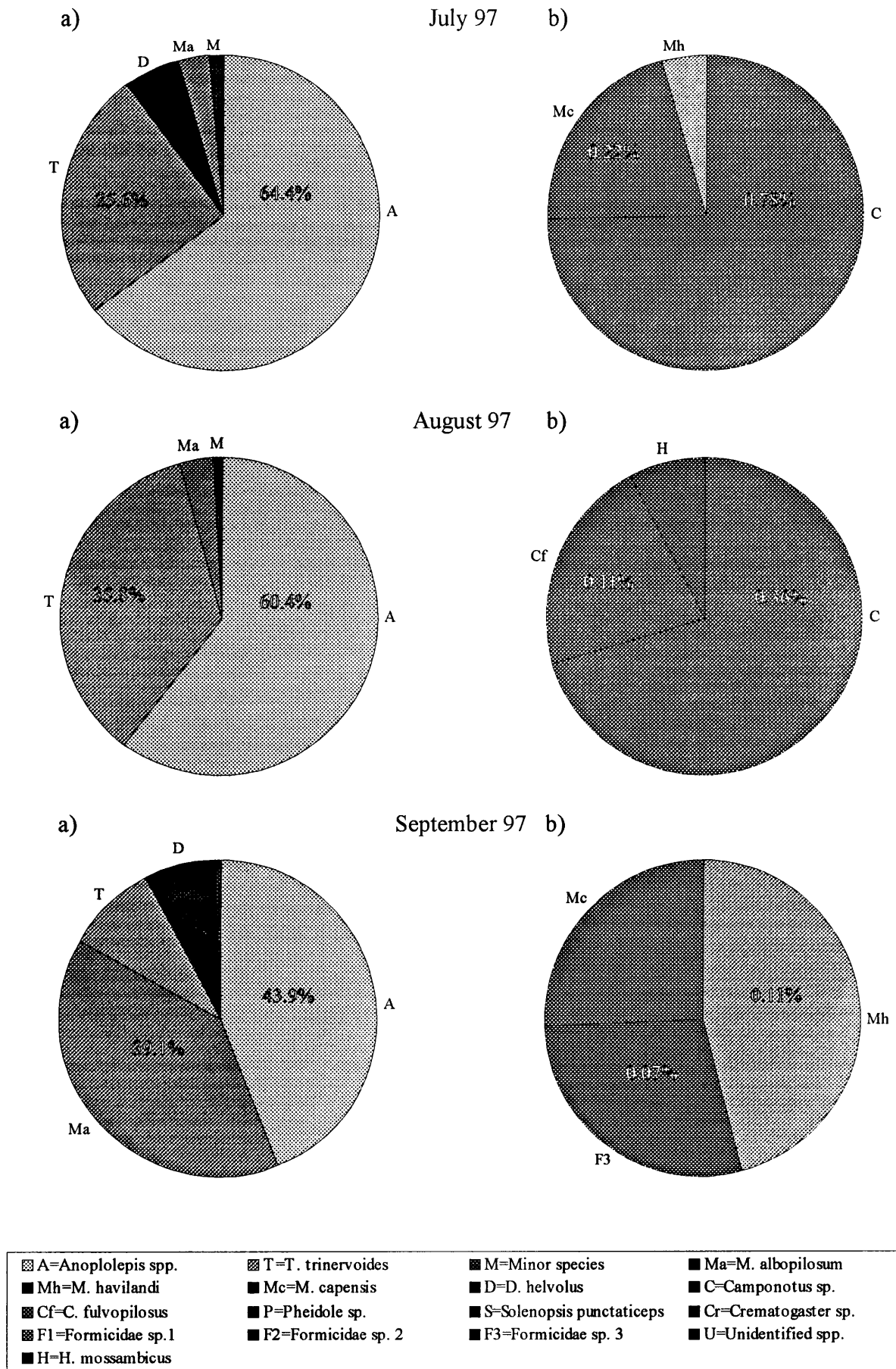


**Figure 20 (continued).** Monthly percentages of prey species in the faeces of aardvark F4, July to September 1997.

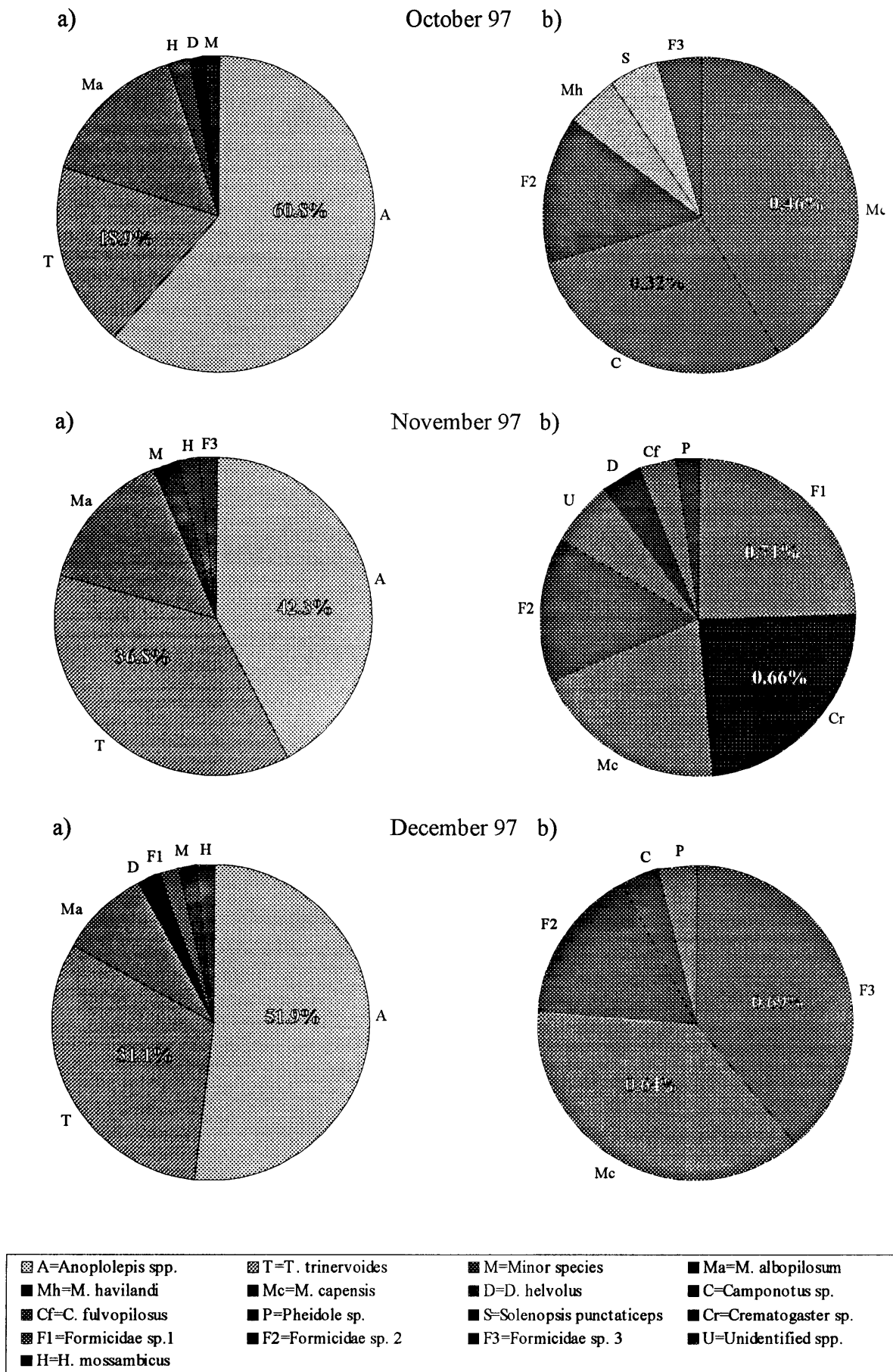


**Figure 20 (continued).** Monthly percentages of prey species in the faeces of aardvark F4, October to December 1997.

average of 42.3%. For aardvark M5, the proportions of *A. custodiens* fluctuated up and down with no apparent pattern of highs or lows to coincide with any season. *A. custodiens* numbers also fluctuated somewhat for aardvark F4 with no seasonal pattern, although there appeared to be a decreasing trend from January to December.

*T. trinervoides* and *M. albopilosum* were again the second and third most common prey species for both aardvarks, with *T. trinervoides* placed second 10 times in the faeces of M5 and nine times in the faeces of F4.

For each aardvark there were only two months in which a separate species entered the top three most abundant, and in all four cases *M. albopilosum* was displaced. Interestingly, *S. punctaticeps* displaced *M. albopilosum* in the faeces of both aardvarks in March 1997, and was in fact the second most important prey species for F4 at this time. In October 1997, *H. mossambicus* was the third most important species in the diet of M5, and in July *D. helvolus* was the third most important species in the diet of F4.

The prey species in common between M5 and F4 which never comprised more than 1% of a months diet were *M. havilandi*, *C. fulvopilosus*, *Pheidole* sp., and *Crematogaster* sp. In addition to these, *Camponotus* spp. and Formicidae sp.3 for aardvark M5, and *M. capensis*, Formicidae sp.1 and Formicidae sp.2 for aardvark F4 never comprised more than 1% of any months dietary intake.

### Analysis of similarity

Analysis of similarities were carried out to compare the “communities” of prey species in the faeces of aardvarks M5 and F4 at different times of the year. The two habituated aardvarks were tested separately because there were too many replicates for the results to be interpretable. The stress value (or distortion, see Clarke & Warwick, 1994) was too high for the information to be accurately represented on a two dimensional ordination plot, so comparing the aardvarks separately lowered the sample size and, therefore, the stress value.

After initially comparing each month with all the other months, it was decided to group the months by season instead and compare these. The seasons were: autumn (February-April 97), winter (May-July 97), spring (August-October 97), and summer (November 97-January 98). (Note that January 98 was not included in Figures 18 to 20.) Hierarchical agglomerative clustering, non-metric multidimensional

scaling, and analysis of similarities were all carried out for both aardvarks to look for similarities between seasons.

To reduce the stress further, some of the minor species were removed from the analysis. These were the ones which occurred infrequently in the replicates and never comprised more than five ant heads per sample (less than 2%). The species removed were *M. havilandi*, *Pheidole* sp., *C. fulvopilosus*, *Crematogaster* sp. and the Minor species. This was an acceptable form of data manipulation for the techniques used here, and was justified because the species removed contributed very little, often nothing to the prey community in the faeces. Anyway, the aim of the analysis of the community here was to investigate the contributions made by the more common species, not the rare species. The data were, therefore, left untransformed so that only the common species contributed to the similarities.

Figures 21 to 24 show the clustering and ordination for the faeces of aardvarks M5 and F4, while Tables 9 and 10 show the results of ANOSIM.

Both tests found evidence of significant differences between seasons on a global perspective, but pairwise comparisons were different for the two aardvarks. Aardvark M5 showed evidence of significant differences between autumn and summer, and between winter and summer. Aardvark F4 showed evidence of significant differences between autumn and winter, autumn and spring, and between winter and spring. Although 5% is the standard level at which significance is distinguished, the significance level between autumn and summer for aardvark F4 was only 6.3%. The significance level between autumn and winter for aardvark F4 was 4.8%, very close to 6.3%, and to make a distinction between them by stating one was significant while the other was not, is ridiculous. Therefore, the autumn and summer prey communities of aardvark F4 were different as well.

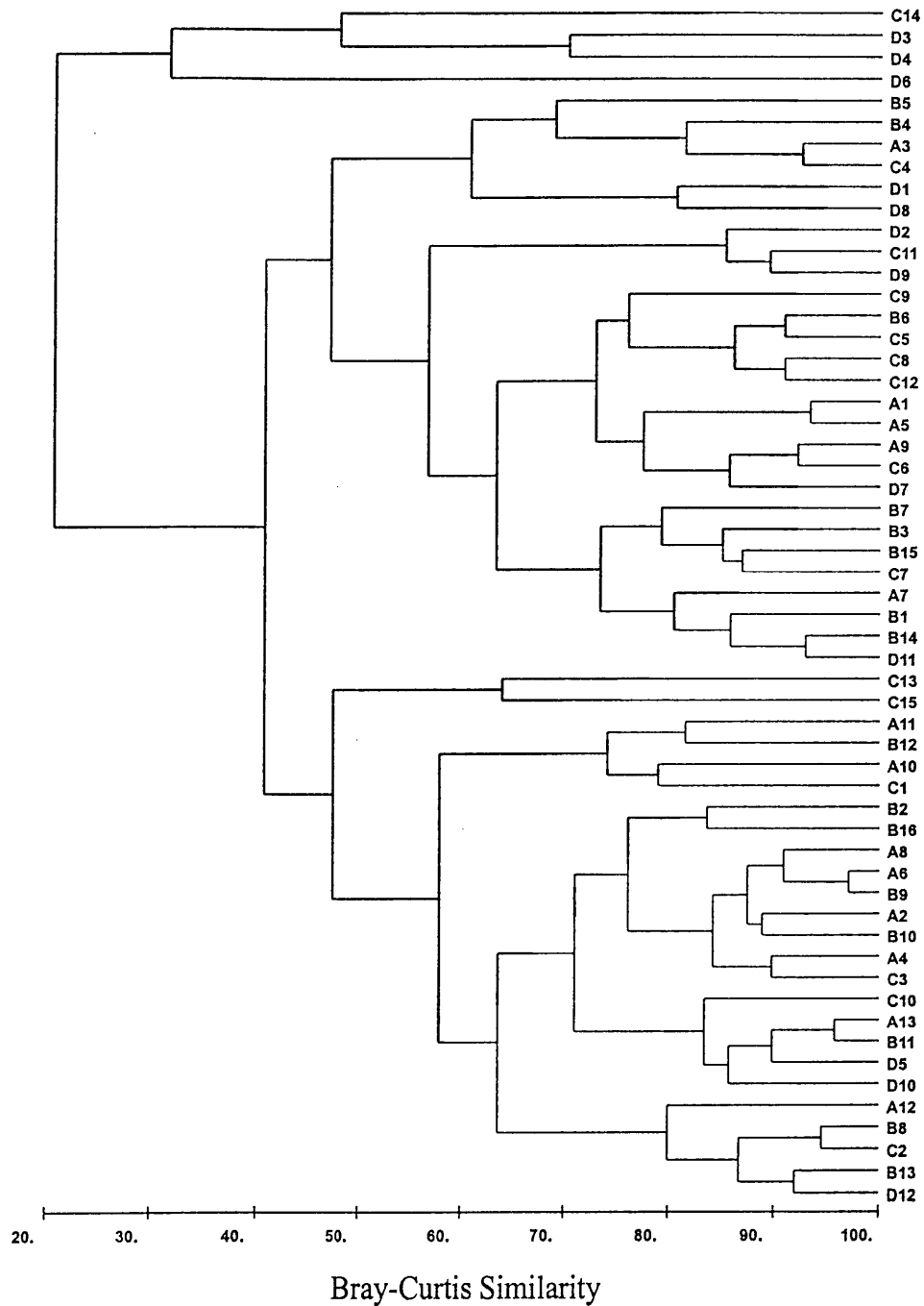


**Figure 21.** Hierarchical Agglomerative Clustering of replicate samples from four seasons for aardvark M5. A = Feb - Apr 97, B = May - Jul 97, C = Aug - Oct 97, D = Nov 97 - Jan 98. The number of replicates for each season was not the same after outlier removal.

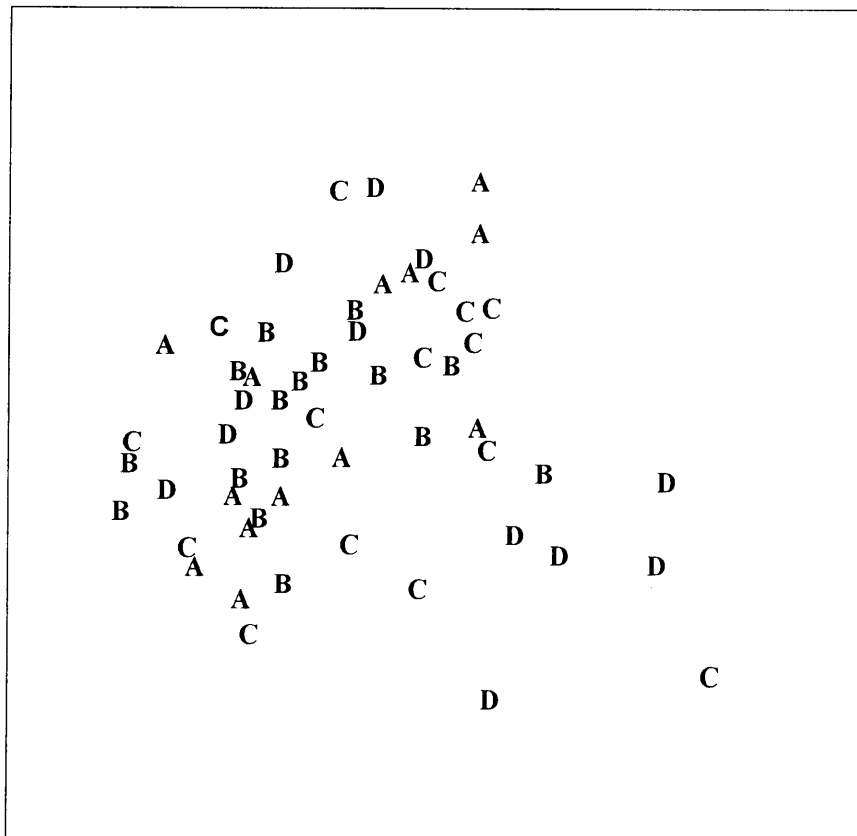


**Figure 22.** Non-metric Multi-Dimensional Scaling of replicate samples from four seasons for aardvark M5. A = Feb - Apr 97, B = May - Jul 97, C = Aug - Oct 97, D = Nov 97 - Jan 98. This ordination is based on the same similarity matrix used to construct the dendrogram of Figure 21. (Stress = 0.12)

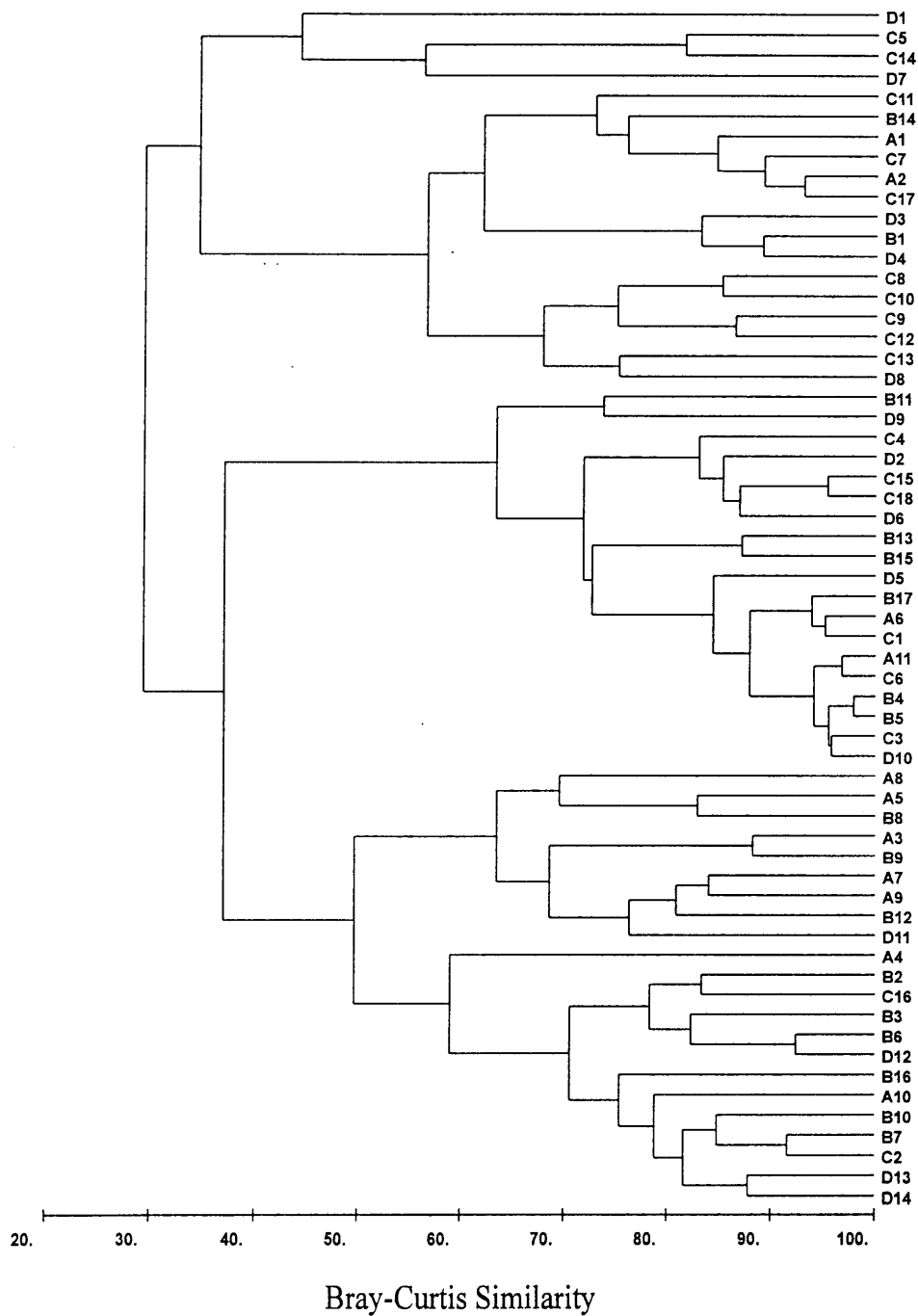


**Figure 23.** Hierarchical Agglomerative Clustering of replicate samples from four seasons for aardvark F4. A = Feb - Apr 97, B = May - Jul 97, C = Aug - Oct 97, D = Nov 97 - Jan 98. The number of replicates for each season was not the same after outlier removal.

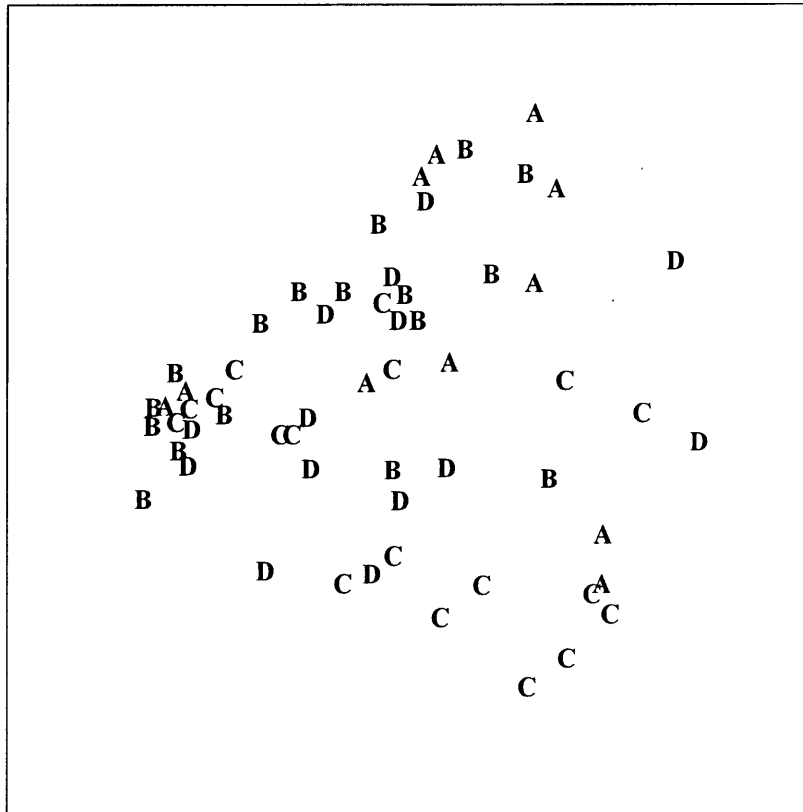


**Figure 24.** Non-metric Multi-Dimensional Scaling of replicate samples from four seasons for aardvark F4. A = Feb - Apr 97, B = May - Jul 97, C = Aug - Oct 97, D = Nov 97 - Jan 98. This ordination is based on the same similarity matrix used to construct the dendrogram of Figure 21. (Stress = 0.12)

**Table 9.** Analysis of similarity for aardvark M5. For pairwise tests, a = autumn, b = winter, c = spring, d = summer.

| Global test                                                          |                   |                     |                                |                    |
|----------------------------------------------------------------------|-------------------|---------------------|--------------------------------|--------------------|
| Sample statistic (Global R): 0.065                                   |                   |                     |                                |                    |
| Number of permutations: 5000                                         |                   |                     |                                |                    |
| Number of permuted statistics greater than or equal to global R: 139 |                   |                     |                                |                    |
| Significance level of sample statistic: 2.8%                         |                   |                     |                                |                    |
| Pairwise tests                                                       |                   |                     |                                |                    |
| Groups used                                                          | Statistical value | Number permutations | Number greater than stat value | Significance level |
| ( a , b )                                                            | -0.005            | 5000                | 2304                           | 46.1%              |
| ( a , c )                                                            | -0.03             | 5000                | 3494                           | 69.9%              |
| ( a , d )                                                            | 0.125             | 5000                | 201                            | 4.0%               |
| ( b , c )                                                            | 0.048             | 5000                | 615                            | 12.3%              |
| ( b , d )                                                            | 0.23              | 5000                | 23                             | 0.5%               |
| ( c , d )                                                            | 0.039             | 5000                | 964                            | 19.3%              |

**Table 10.** Analysis of similarity for aardvark F4. For pairwise tests, a = autumn, b = winter, c = spring, d = summer.

| Global test                                                         |                   |                     |                                |                    |
|---------------------------------------------------------------------|-------------------|---------------------|--------------------------------|--------------------|
| Sample statistic (Global R): 0.106                                  |                   |                     |                                |                    |
| Number of permutations: 5000                                        |                   |                     |                                |                    |
| Number of permuted statistics greater than or equal to global R: 26 |                   |                     |                                |                    |
| Significance level of sample statistic: 0.5%                        |                   |                     |                                |                    |
| Pairwise tests                                                      |                   |                     |                                |                    |
| Groups used                                                         | Statistical value | Number permutations | Number greater than stat value | Significance level |
| ( a , b )                                                           | 0.117             | 5000                | 238                            | 4.8%               |
| ( a , c )                                                           | 0.175             | 5000                | 104                            | 2.1%               |
| ( a , d )                                                           | 0.107             | 5000                | 314                            | 6.3%               |
| ( b , c )                                                           | 0.154             | 5000                | 24                             | 0.5%               |
| ( b , d )                                                           | 0.046             | 5000                | 731                            | 14.6%              |
| ( c , d )                                                           | 0.037             | 5000                | 918                            | 18.4%              |

Comparison of these ANOSIM results with the ordination plots makes the differences between seasons, where they occur, slightly more clear. The ordination plot for aardvark F4 (Figure 24) is the clearer of the two, and from this it can be seen that the spring community (C on the ordination plot) is generally separate from the autumn and winter communities (A and B on the ordination plot). The strongest evidence of differences between the communities from the ANOSIM was between winter (B) and spring (C.) and this is quite clear on the ordination plot.

Although the differences appear less obvious on the ordination plot for aardvark M5 (Figure 22), it is still possible to establish a separation between the summer community (D) and the autumn and winter communities (A and B). The strongest evidence for differences between the communities from the ANOSIM was between winter (B) and summer (D), as can be seen on the ordination plot.

However, although there was some separation between seasons, there was also a lot of variation within seasons for both aardvarks, as indicated by the spread on the ordination plot.

### **Proportions by Order**

So far the prey have been examined at the species level while the coarser level of Order has been generally ignored. Differences between the Formicidae and Isoptera might be considered more important in some biological respects because they are likely to be greater than differences within orders. Any patterns arising may prove more significant. Historically there has been more concern regarding the relative importance of ants to termites and how their proportions vary with time (especially with season), than the importance of individual species. Figures 25 to 27 represent the proportions of ants to termites in the diet of aardvarks of TdR.

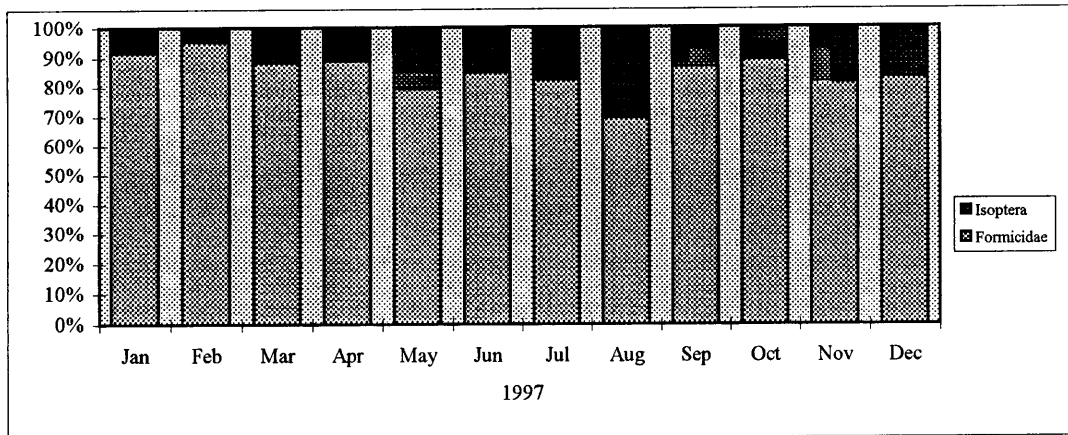


**Figure 25.** Monthly variation in proportions of Formicidae and Isoptera in the combined faeces of 1997.

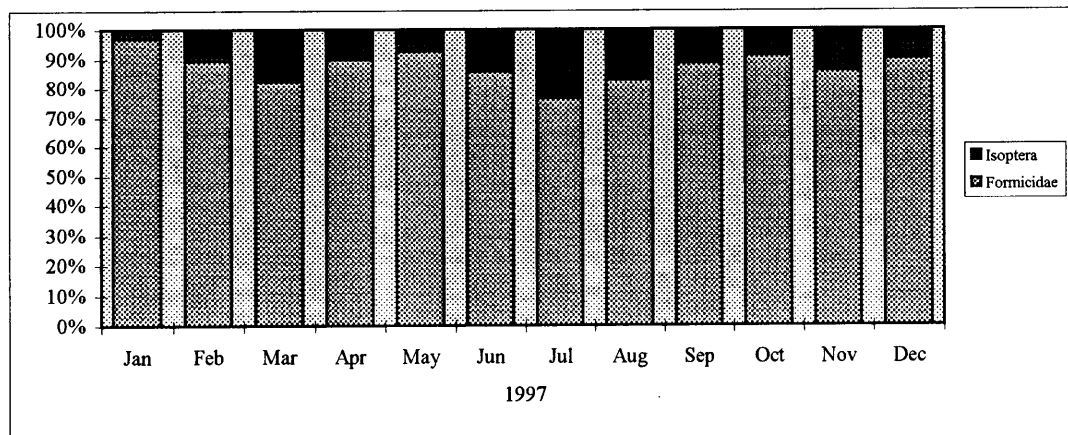


**Figure 26.** Monthly variation in proportions of Formicidae and Isoptera in the faeces of aardvark M5 for 1997.

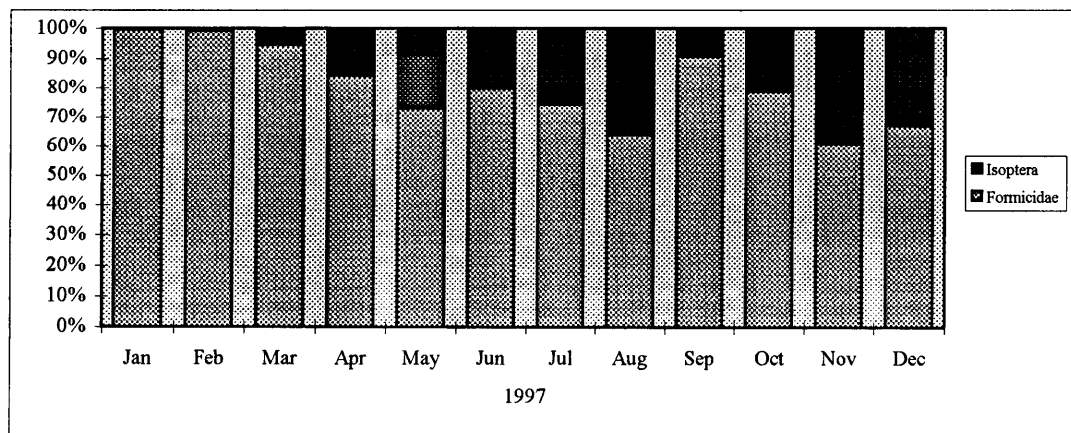


**Figure 27.** Monthly variation in proportions of Formicidae and Isoptera in the faeces of aardvark F4 for 1997.

The Formicidae were always, on average, more common in the faeces than the Isoptera, a fact that was also evident from Figures 18 to 20. When considering the order Formicidae as a single group in the combined faeces, the highest proportions of 1997 occurred in February, with an average percentage occurrence of 95.2%. This naturally corresponded with the lowest proportion of Isoptera, which when grouped together comprised 4.8%. The lowest proportions of Formicidae occurred in August, with an average percentage occurrence of 69.5%, and a corresponding Isoptera high of 30.5%. August 1996 comprised 51.4% Formicidae and 48.6% Isoptera. The general pattern through the year was a decreased proportion of Formicidae in the winter months, followed by an increase again into the summer, although not to the same level. The reverse pattern occurred in the Isoptera. A similar pattern was observed for aardvark M5, with the highest proportions of Formicidae occurring in January and December, and lowest occurring in July. No such pattern was obvious for aardvark F4, rather there was a general trend of reduced proportions of Formicidae through the year, with a partial increase in September and October.

### Caste proportions of Isoptera

Figure 28 shows the average monthly proportions of soldiers and workers in the combined faeces of 1997.

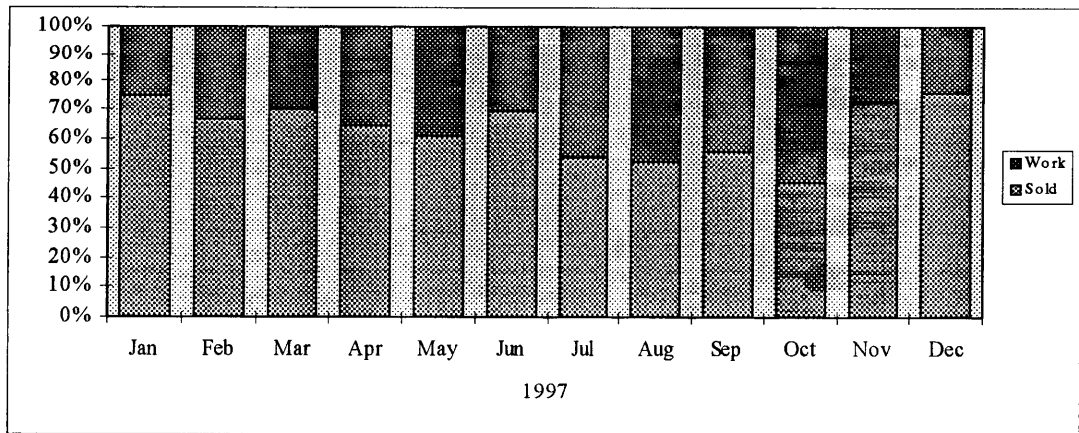


**Figure 28.** Monthly variation in the proportions of soldiers and workers in the combined faeces of 1997.

On average, soldiers of *T. trinervoides* occurred in greater proportions than workers in the faeces of aardvarks of TdR during 1997. January and December had the highest proportions of soldiers for the year, with 74.9% and 76.3% respectively, while August and October had the lowest, with 52.3% and 45.7% respectively. October was the only month in which workers occurred in greater proportions than soldiers. No apparent pattern was observed to correspond with season. Figures 29 and 30 represent the monthly proportions of soldiers and workers in the faeces of aardvarks M5 and F4 respectively. They are presented to show variation between animals.

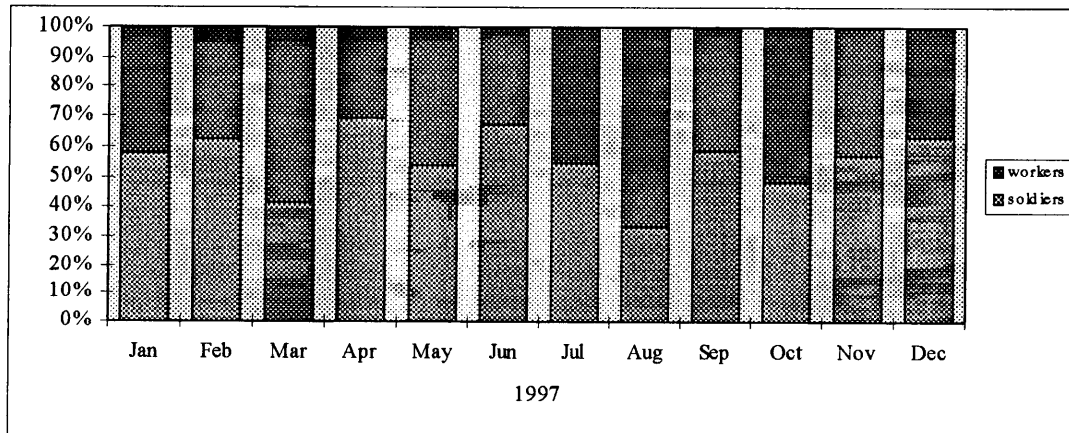


**Figure 29.** Monthly variation in the proportions of soldiers and workers in the faeces of aardvark M5.

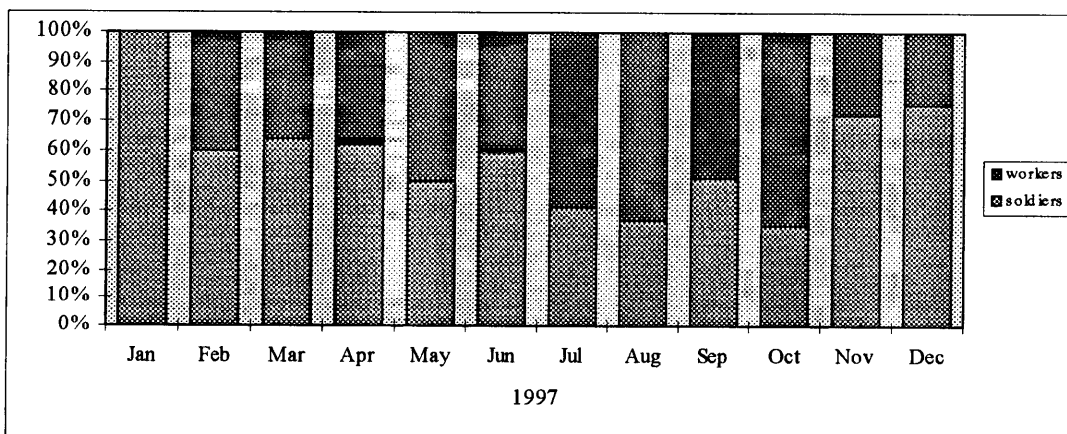


**Figure 30.** Monthly variation in the proportions of soldiers and workers in the faeces of aardvark F4.

As observed in the combined faeces, the proportions of the castes fluctuated throughout the year, and no apparent pattern was observed to correspond with season. On average soldiers occurred in greater proportions than workers for both aardvarks, although the difference between the castes were not as great as they were when all the faecal samples were combined.

Using the data from figures 29 and 30, variations in the proportions of soldiers and workers were tested statistically between months and aardvarks by randomisation with 3-way analysis of variance as the

test statistic. (the Cochran C test indicated that the variances were borderline homogenous so it was decided to use the distribution free test) Data was entered as actual numbers, not percentages. The results are shown in Table 11.

**Table 11.** Randomisation of monthly variation in numbers of soldier and worker castes of *T. trinervoides* in the faeces of aardvarks M5 and F4 for 1997.

| Randomization            |                                                                      |
|--------------------------|----------------------------------------------------------------------|
| Source of variation      | % of randomization mean squares<br>that exceed observed mean squares |
| Aardvark                 | 47.44                                                                |
| Month                    | 99.22                                                                |
| Caste                    | 0.16                                                                 |
| Aardvark x Month         | 99.06                                                                |
| Aardvark x Caste         | 86.82                                                                |
| Month x Caste            | 0.02                                                                 |
| Aardvark x Month x Caste | 29.02                                                                |

There was strong evidence of differences between the numbers of soldiers and workers, and strong evidence of an interaction between month and caste. This interaction means that the differences between castes were not the same for the different months.

To test whether the proportions of soldiers and workers in the faeces were the same as the proportions of the two castes available, the observed numbers were tested against the expected numbers. Expected values were calculated by multiplying the percentage of a caste available (from Adam, 1993) by the total number of soldiers and workers in the faeces. Table 12 shows both observed and expected numbers. (Expected percentages were 25% soldiers and 75% workers.)

**Table 12.** Observed and expected numbers of soldiers and workers in the faeces of aardvarks M5 and F4 combined.

|          | Soldiers | Workers |
|----------|----------|---------|
| Observed | 5325     | 5707    |
| Expected | 2758     | 8274    |

(Note that although soldiers occurred in greater proportions than workers in most months, total numbers of workers in the faeces were actually higher than numbers of soldiers.)

Applying Yates’ correction for continuity:

$$\chi^2 = 3184, \text{ df} = 1, \text{ p} < 0.001$$

Soldiers were found in the faeces in larger numbers than would have been expected from their availability, while workers were found in smaller numbers than would have been expected.

**Caste proportions in the Formicidae**

Results from the image analyser showed that the frequency patterns of different ant head sizes in the faeces were very similar for all aardvarks and all months, so they were combined in Figure 31. Nest results are shown in Figure 32.

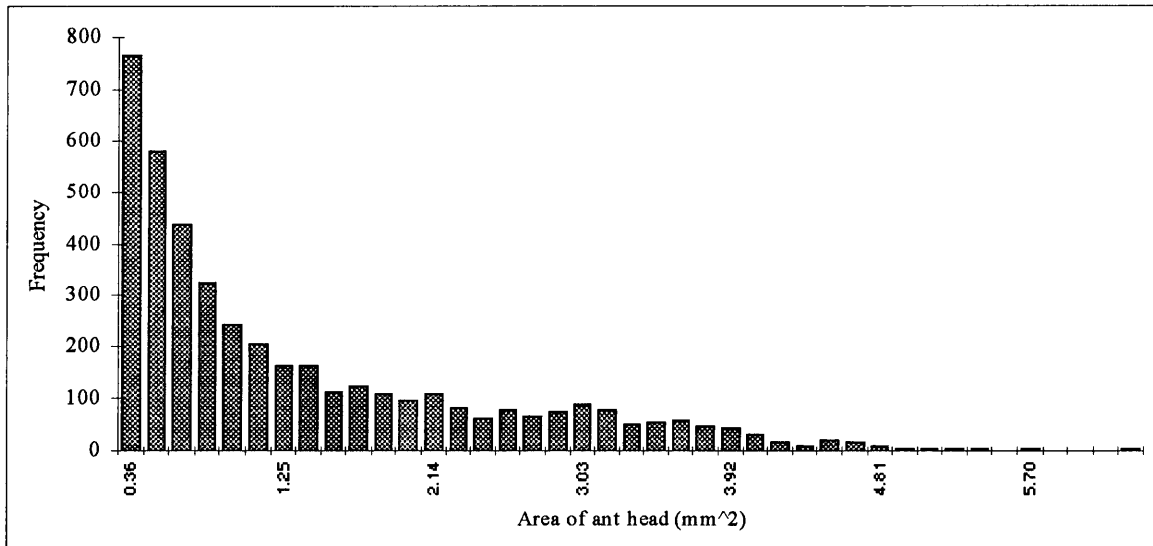


Figure 31. Range of sizes of *A. custodiens* heads from 20 faecal samples.

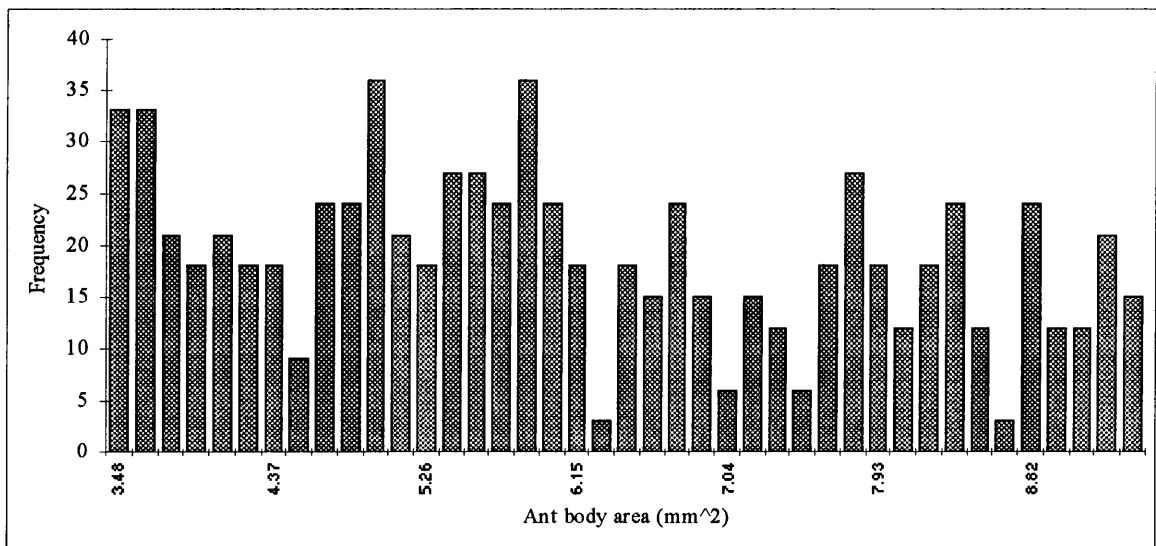


Figure 32. Range of sizes of *A. custodiens* (whole bodies) from nest collected ants.

Faecal results showed a very clear exponential decrease in frequency of heads with increased ant head size. Nest samples were different, showing large fluctuations in frequencies with increased ant size and greater numbers of large ants relative to small ants. Small ants were still more common than large ants in the nest samples.

### Number of ants and termites eaten per night

The average number of adult ant and termite heads per gram of faeces estimated from nine separate faecal pellets was 39.21 (Sd 17.56, min 16.5, max 72). Both Orders were counted at the same time and included in one value because they normally occurred together and it was impossible to separate them meaningfully.

The frequency of defecations by an aardvark in one night varied, apparently depending on the length of time the animal was active above ground (aside from the state of the its bowel movements which could not be known). Normally both habituated aardvarks defecated within the first ten minutes after emerging from their burrow at the beginning of their activity period, and this was often followed by a second defecation after another 15-30min. Thereafter the aardvarks defecated fairly regularly every 1.5 - 2h. The average number of defecations per night was six, with a range of four to seven.

The average dry mass of one faecal deposit calculated from 23 separate samples was 215g (Sd 85.5, min 34g, max 365g).

From the calculated factors above the number of ants and termites eaten per night could be estimated.

Number heads per gram x mass of 1 faecal sample x number defecations per night

$39.21 \times 215 \times 6 = 50\,581$  heads per night.

This is of course a very rough estimation (and is only applicable to adult castes of prey). Taking into account the possible variation in frequency of faecal deposition, the number of adult caste ants and termites eaten per night could vary between 40 000 and 60 000.

### Calorific values of prey species

The species collected from nests and mounds were: *A. custodiens*, *A. steingroeveri*, *M. capensis*, *M. albopilosum*, *D. helvolus*, *Camponotus* spp, *T. trinervoides* (soldiers, workers and alates separately) and *H. mossambicus*. Calorific values were determined in triplicate (occasionally duplicate if the sample mass was small) and the averages are presented in Table 13. The highest average calorific values of all the prey species tested occurred in the alates of *T. trinervoides*. The second highest, and

**Table 13.** Calorific values of some of the prey species of ants and termites from TdR. Standard deviations (Sd) are given where samples were tested in triplicate, and range (Rng) is given when samples were only tested in duplicate.

| Species                              | Month     | Calorific value<br>(MJ / kg) | Standard deviation<br>or Range |
|--------------------------------------|-----------|------------------------------|--------------------------------|
| <i>A. custodiens</i>                 | April     | 23.630                       | Rng 23.612-23.648              |
|                                      | July      | 20.587                       | Sd 0.705                       |
|                                      | September | 19.426                       | Sd 0.065                       |
|                                      | October   | 20.289                       | Sd 0.158                       |
|                                      | October   | 20.149                       | Sd 0.246                       |
|                                      | November  | 20.504                       | Sd 0.352                       |
|                                      | December  | 18.762                       | Sd 0                           |
|                                      | March     | 19.020                       | Rng 18.783-19.256              |
| <i>A. steingroeveri</i>              | October   | 26.014                       | Sd 0.519                       |
|                                      | November  | 23.404                       | Sd 0.685                       |
|                                      | November  | 19.692                       | Sd 0.816                       |
|                                      | December  | 18.695                       | Sd 0.633                       |
| <i>M. albopilosum</i>                | July      | 23.230                       | Rng 23.23-23.554               |
| <i>M. capensis</i>                   | May       | 20.629                       | Sd 0.436                       |
|                                      | November  | 19.532                       | Rng 19.396-19.667              |
| <i>D. helvolus</i>                   | May       | 21.793                       | Rng 21.77-21.816               |
| <i>T. trinervoides</i><br>(soldiers) | May       | 23.781                       | Sd 0.579                       |
|                                      | August    | 23.959                       | Rng 23.874-24.043              |
| <i>T. trinervoides</i><br>(workers)  | August    | 18.908                       | Sd 0.568                       |
|                                      | September | 18.847                       | Rng 18.329-19.365              |
|                                      | December  | 18.473                       | Rng 18.301-18.644              |
| <i>T. trinervoides</i><br>(alates)   | October   | 27.002                       | Sd 1.462                       |
| <i>H. mossambicus</i>                | May       | 19.390                       | Sd 0.314                       |
|                                      | July      | 18.999                       | Sd 0.174                       |

the only set with a similarly high value, was *A. steingroeveri* in October. This was much higher than the other monthly averages for *A. steingroeveri* and may have been the result of alates being mixed up with workers at this time (although it was mostly workers and the alates were of similar size to the larger workers).

Calorific values for *A. custodiens* fluctuated up and down slightly throughout 1997 without any apparent pattern, and because the value for July (winter) was very similar to that of November (summer) there was no cause to test for statistical differences between seasons. The difference between *A. custodiens* and *A. steingroeveri* was, however, tested statistically for the months of November and December (combined) using the T-test. Although an  $F_{\max}$  test indicated that the variances were not similar, the outcome of the test was insignificant ( $t = 0.698$ ,  $df = 10$ ,  $p = 0.49$ ) There was, therefore, no evidence of any differences between the two.

Calorific values within the three castes of *T. trinervoides* remained constant, even between months (for workers and soldiers at least, alates were only collected in one month), but calorific values between castes were very different. Workers had the lowest values per kilogram while alates had the highest. This variation was tested using a 1-way ANOVA for all three castes (the data was left untransformed: Cochran C test, p-level 0.83). (ANOVA:  $F = 132.1$ ,  $df = 2$ ,  $p < 0.0001$ ).

There was very strong evidence of variation in calorific values between the three castes of *T. trinervoides*. Post hoc tests indicated that all three castes differed from each other. In other words, soldiers had a higher calorific value per unit mass than workers, but a lower value per unit mass than alates.

Finally the differences between workers of the two termites species (*T. trinervoides* and *H. mossambicus*) were tested using the T-test. An  $F_{\max}$  test indicated that the differences between variances were not significant, so the data was left untransformed ( $T = -1.817$ ,  $df = 11$ ,  $p = 0.096$ ). There was no evidence of variation in calorific values between *T. trinervoides* workers and *H. mossambicus* workers.

### Percentage water content

The percentage water contents of five prey species are shown in Table 14. Most of the main species are represented. *M. albopilosum* was not tested because the ants were very small, making it very difficult to catch enough to measure water loss accurately. The water content of all five species shown were measured in duplicate and the results shown are averages.

**Table 14.** Percentage water content of five prey species.

| Prey species               | Water content (%) |
|----------------------------|-------------------|
| <i>A. custodiens</i>       | 70.6              |
| <i>A. steingroeveri</i>    | 64.3              |
| <i>M. capensis</i>         | 58.4              |
| <i>T. trinervoides</i> (w) | 77.2              |
| <i>H. mossambicus</i>      | 75                |

The two termites species had the highest percentage water contents, while *M. capensis* had the lowest. Statistical differences were not tested due to the low sample size.

### Energy consumption per night

From the estimates of numbers of adult ants and termites eaten per night, and the calorific values of the prey species, an estimate of the nightly energy consumption of an aardvark can be calculated.

Because there were fluctuations in the proportions of the main prey species in the diet, it was decided to use an average for the whole year. In Table 15 it was assumed that an aardvark consumed a total of 51 000 adult ants and termites per night, and this comprised 75% *A. custodiens*, 13% *T. trinervoides* soldiers, and 12% *T. trinervoides* workers. These two species were used because they were the most common in the diet, and the proportions of each were chosen as averages. Other species were not taken into account either because they did not occur frequently or because they were very small (as in the case of *M. albopilosum*). Estimated numbers of ants or termites per gram (dry mass), calculated during the present study, were: *A. custodiens* (minor, medium and major workers combined) 734/g; *T. trinervoides* soldiers 1089/g; and *T. trinervoides* workers 592/g. (These figures compared favourably with estimates made by Adam, 1993, for *T. trinervoides*: dry mass of 1 soldier = 0.93mg; dry mass of 1 worker = 1.65mg.)

**Table 15.** Estimated average energy consumption by an aardvark on Tussen-die-Riviere.

| Prey species                    | Numbers eaten<br>per night | Mass per night<br>(g) | Mean energy value<br>(MJ/kg) | Total energy<br>(kJ) |
|---------------------------------|----------------------------|-----------------------|------------------------------|----------------------|
| <i>A. custodiens</i>            | 38250                      | 52.1                  | 20.3                         | 1057.63              |
| <i>T. trinervoides</i> soldiers | 6630                       | 6.1                   | 23.87                        | 145.6                |
| <i>T. trinervoides</i> workers  | 6120                       | 10.3                  | 18.74                        | 193                  |
|                                 | 51000                      |                       |                              | 1396.23              |

Average nightly energy intake per aardvark was 1396.23 kJ. (Note that this was from estimated numbers of adult castes only, and does not include possible developmental stages or reproductives.)

## **Feeding observations**

Times of aardvark activity are discussed elsewhere in this thesis, but it is worth starting this section by noting that the foraging activities of the habituated aardvarks paralleled the patterns of their above ground activity. Aardvarks began foraging as soon as they were above ground and continued doing so until they returned to their burrows at the end of their activity period. Although they did occasionally stop for short periods of time while above ground, this was not a regular occurrence and was often the result of some type of disturbance, such as the presence of another animal nearby (aardvark or other mammal), which caused the animal to become vigilant. They also stopped to defecate every 1.5 to 2h, but the time used doing so was negligible. Generally, while above ground, the aardvarks were either searching for food or feeding. It is assumed that the aardvarks were inactive while in their burrows and did not feed during these periods, although of course this cannot be proven until direct observations are made.

Because activity patterns changed with the seasons, commencing and finishing earlier in winter than summer, foraging periods did the same. Feeding at 16h00 was common in July but never occurred in December. Likewise, foraging as late as 05h00 was not uncommon in December, but never took place in July. For discussion of these activity patterns, see chapter 5.

## **Aardvark foraging behaviour**

The following is a brief description of the foraging behaviour of the aardvark, as observed from the habituated animals during the course of the present study. Because aardvarks have not often been observed for extended periods in the wild, there has been some question as to how they locate their food. Of course, it has always been correctly assumed that smell is important, due to the anatomical and physiological adaptations of the aardvarks head, but hearing has also been considered to play a part because it is quite acute and is known to be important in other animals.

The anatomy of the aardvark skull indicates that its olfactory sense is very well developed. It is swollen in front of the eyes due to a layer of minutely convoluted bone which completely surrounds the large olfactory lobes. This bone is apparently covered with olfactory epithelium and served by olfactory receptors which are linked to the lobes. The surface area of olfactory receptors on both the lobes and bone combined is, therefore, very large (Kingdon, 1971). These physiological adaptations are consistent with an animal that uses its sense of smell to detect things at a very sensitive level, ideally in the case of

the aardvark to locate its small prey. Behavioural characteristics of aardvarks when foraging indicate that it is indeed smell that is used to locate ants.

As a result of its posture, the head of the aardvark is held fairly close to the ground at all times, even when not searching for food. A clear distinction, however, can be made between the position of the head and snout at times of active foraging and their positions at times of walking. When walking, the aardvarks head is held steady and clear of the ground, although it is not quite parallel with the surface, being slightly angled downwards. At times of foraging, the aardvark holds the end of its nose very much closer to the ground while at the same time making sweeping motions from side to side with its head, covering an area approximately 30cm wide. Sniffing sounds are often clearly audible at these times.

During this process the animal stops briefly many times, when it seems a potentially promising site has been located. It pushes the end of its snout flat on the surface, effectively getting its nose as close to the source as possible. The end of the nose is very soft, almost prehensile, and its entire surface appears to be sucked into contact with the ground. There is often no obvious opening, such as an ant port, at these sites, only flat earth, so whatever has been detected is hidden under the surface.

Close inspection of the soil in this way by the aardvark is often immediately followed by a light digging motion with one of its front feet, which effectively scratches open a shallow hollow. This scrape is then tested a second time by repeating the same flat nosed, pressing/sucking action with the snout. One of two things then happens. Either the aardvark digs down deeper because there is sufficient food below, or it moves on, presumably because the site is unsatisfactory. Often the aardvark tests many places in close proximity and in a short space of time before finding a suitable site.

This smelling action sucks up soil particles but these are prevented from entering the aardvarks lungs by dense hairs in the nostrils which are thought to act as a filter. 'The nose is a muscular swelling, capable of considerable movement, enclosing the two vertical slits of the nostrils. The septum between these nasal slits is equipped with a series of thick, fleshy processes (Skinner and Smithers, 1990) and it is possible that these bristles play a role in prey location as well, if they are sensitive to vibrations caused by the activities of subterranean ants, or to chemical stimuli such as formic acid released from the ants.

The hearing of the aardvark is also assumed to be very acute, and observations of wild animals supports this. Their hearing is much more sensitive than humans, and it was thought that it might also play an important role in prey location, as it is known to do with certain other mammal species, such as

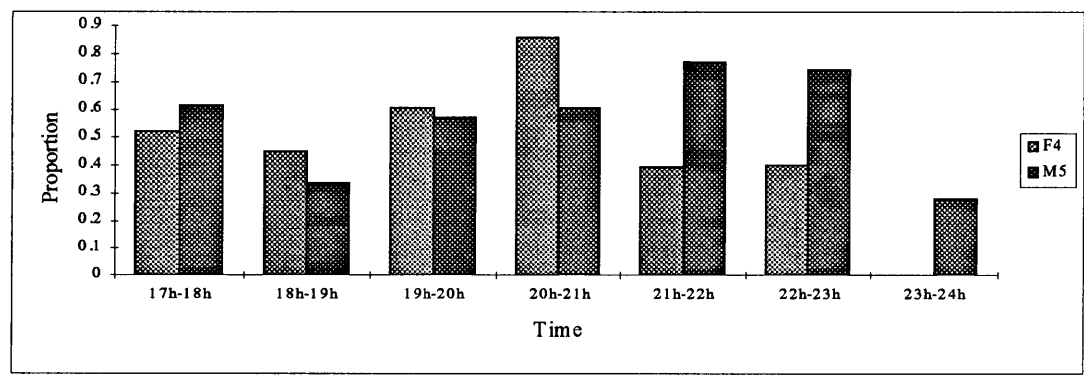
the bat-eared fox, *Otocyon megalotis* (Skinner and Smithers, 1990). However, the behaviour and posture of foraging aardvarks does not indicate that it plays any role whatsoever in the finding of ants. Whereas the aardvarks keep their snouts near or on the ground while foraging, the typical posture of their ears is directly up. Their ears are long and narrow, much like those of rabbits but unlike those of animals that use their hearing to locate food, such as the bat-eared fox. In addition, animals that use hearing to find food on the ground typically turn their face and ears parallel with the surface, towards the direction of their prey. Aardvarks do not do this. Instead the ears are held vertically and can be seen twitching to listen for sounds in the surroundings. Behaviourally speaking, the ears appear to be used mostly for predator avoidance.

### **The proportion of time aardvarks spend feeding during their activity periods - average time spent feeding per hour**

Figure 33 shows the variation in average proportions of time spent feeding during hourly time intervals for both aardvarks, for the months of May and September, 1997. The results were obtained in the following way: all the feed times recorded in a one hour period (e.g. May 2, 18h-19h) were summed and the result divided by the observation period length (one hour or less), to give a proportion. The same procedure was then performed on all the data (for different days) for the same time period (18h-19h) within that month. Averages were obtained for every time period (depending on aardvark activity patterns) and for months where sufficient data were available. Only two months are represented because all months were similar in the respect that they showed no pattern or trend. May and September represent early winter and early summer respectively.

The proportion of time spent feeding was sometimes greater in the early part of the night and sometimes greater later in the night. It often decreased, increased and then decreased again, or vice-versa, but there were no hourly periods during the course of a night when it was consistently higher or lower.

May



September

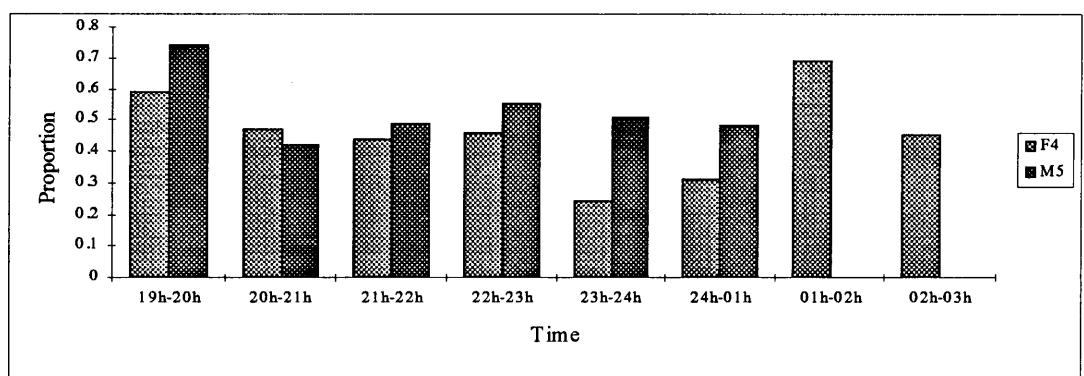


**Figure 33.** Variation in the proportion of time spent feeding per hour by aardvarks M5 and F4 in May and September 1997.

Testing for variation in proportions between time periods was difficult because sample sizes (number of replicates) were uneven between times of night, months and aardvarks. Due to a lack of statistically comparable data between the two aardvarks, only one animal was tested. A two way ANOVA was used to test for variation in proportions of hourly feeding times between two months, January and September, for aardvark M5. January and September were chosen because they had the most complete and comparable data sets. No data transformation was necessary (Cochran C-test:  $p = 0.295$ ). The results are shown in Table 16.

**Table 16.** Two way ANOVA of the proportions of times spent feeding during different hourly intervals for January and September 1997.

| 2-way ANOVA         |          |           |                |
|---------------------|----------|-----------|----------------|
| Source of Variation | <i>F</i> | <i>df</i> | <i>P-value</i> |
| Month               | 5.519    | 1         | 0.032          |
| Time of night       | 0.305    | 3         | 0.821          |
| Month x time        | 0.029    | 3         | 0.993          |

There was evidence for variation in the proportions of time spent feeding between January and September, but no evidence for variation between different times of night. There was also no evidence of an interaction, indicating that the differences between months were not different between the times of night. The average proportion of time spent feeding in September was greater than it was in January.

**Variation between months**

The data were then tested to see if there were any differences in the proportion of time spent feeding between months. Because there was no evidence of differences at different times of night, all the proportions in each month were clumped together, regardless of the time of night. However, the number of replicates were unequal between months, although not as seriously as the data for feeding proportions at different times of the night (see above), so the data were clumped. For each aardvark May, June and July (MJJ) were grouped as one period (cold months), and September, October and November (SON) were grouped as the second period (warm months). August was left out due to its intermediate temperatures. The results are represented in Table 17. Data transformation was unnecessary (Cochran-C test:  $p = 0.301$ ).

**Table 17.** Two way ANOVA of the proportion of time spent feeding for aardvarks M5 and F4 between seasons.

| 2-way ANOVA         |          |           |                |
|---------------------|----------|-----------|----------------|
| Source of Variation | <i>F</i> | <i>df</i> | <i>P-value</i> |
| Aardvark            | 0.004    | 1         | 0.951          |
| Month               | 9.492    | 1         | 0.003          |
| Interaction         | 0.259    | 1         | 0.612          |

There was strong evidence for variation in the proportion of time spent feeding between seasons (between MJJ and SON) but no evidence whatsoever of variation between aardvarks. There was also no evidence of an interaction, indicating that the differences between seasons were not different between the two aardvarks. The average proportion of time spent feeding was greater in the colder months (MJJ) than in the warmer months (SON) for both aardvarks.

**Prey species**

Fourteen ant and termite species were predated during observations by the habituated aardvarks within the study period. These were:

- Anoplolepis custodiens* (F. Smith, 1858)
- Anoplolepis steingroeveri* (Forel, 1894)
- Messor capensis* (Mayr, 1862)
- Monomorium albopilosum* (Emery, 1895)
- Monomorium havilandi* (Forel, 1910)
- Dorylus helvolus* (Linnaeus)
- Camponotus fulvopilosus* (De Geer, 1778)
- Camponotus nasutus* Emery
- Camponotus* sp.- *maculatus*-group.
- Crematogaster* sp.
- Solenopsis punctaticeps* Mayr
- Pheidole* sp.

*Trinervitermes trinervoides* (Sjostedt)

*Hodotermes mossambicus* (Hagen)

For a comparison of these species with the prey species found in their faeces and a more detailed account of their classification, see the results of the faecal analysis in Figure 15. For a complete monthly breakdown of prey species feed counts and summed feeding times see Appendix IV.

Table 18 shows the monthly diversity of prey species predated by aardvarks M5 and F4 during 1997. The Simpson index of diversity was used. Diversity fluctuated between months for both aardvarks with no apparent pattern. From appendix IV it can be seen that observation periods between aardvarks and between months were not of the same length. However, as diversity relies partly on the evenness of the prey species (in this case the percentage time spent feeding per species per month), it is less reliant on the number of species and, therefore, the sample period. To test for possible correlation between the diversity indices and observation periods per month (i.e. does an increased observation period necessarily lead to a greater diversity), a Spearman rank correlation coefficient was used. The results were as follows:

Aardvark M5:  $r = 0.361$  ( $n = 11$ ,  $p = 0.276$ ) No evidence of correlation

Aardvark F4:  $r = 0.219$  ( $n = 10$ ,  $p = 0.544$ ) No evidence of correlation

There was no evidence of a correlation between the total observation time length and diversity.

**Table 18.** Monthly prey species diversity of aardvarks M5 and F4 calculated from observations during 1997. Diversity index used was that of Simpsons.

|           | Simpsons diversity |       |
|-----------|--------------------|-------|
|           | M5                 | F4    |
| January   | 0.550              | -     |
| February  | 0.445              | -     |
| March     | 0.668              | 0.483 |
| April     | 0.668              | 0.547 |
| May       | 0.570              | 0.535 |
| June      | 0.408              | 0.574 |
| July      | 0.499              | 0.465 |
| August    | 0.536              | 0.633 |
| September | 0.639              | 0.610 |
| October   | 0.588              | 0.580 |
| November  | 0.698              | 0.499 |
| December  | -                  | 0.677 |

**Variation in prey species between months**

The monthly feed counts per prey species and the percentage of time spent feeding on each of these per month are shown in Figures 34 and 35. There are four months where only percentage of feed counts are represented because there were not sufficient data for percentage time spent feeding for these periods (February for aardvark M5, February, March and April for aardvark F4).

*A. custodiens* was the species predated most often by both aardvarks in all months except November for M5 and December for F4, and in all except the latter two cases it constituted 50% or more of feeds. For aardvark M5, June had the highest percentage of feeds on *A. custodiens* while November had the lowest. February had the second highest. For aardvark F4, February had the highest percentage of feeds on *A. custodiens* while December had the lowest. July had the second highest. For both aardvarks, the percentages of *A. custodiens* fluctuated throughout the year. M5 showed an increase from March to June followed by a decrease from July to November. F4 did not show this pattern but rather an increase

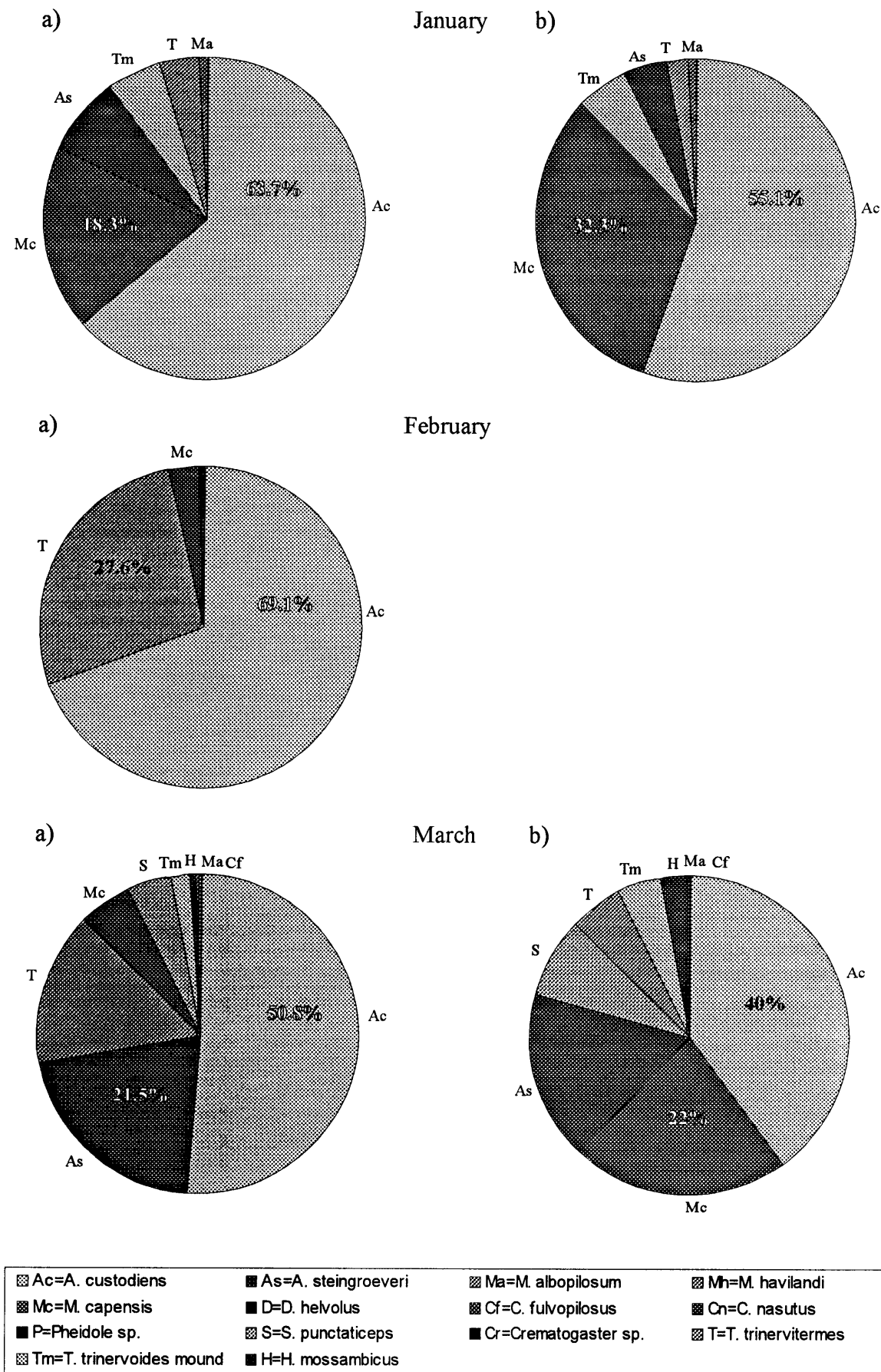


**Figure 34.** Feeding observations of aardvark M5, January to March 1997. a) Percentages of feeding counts per prey species; b) percentages of feeding times per prey species.

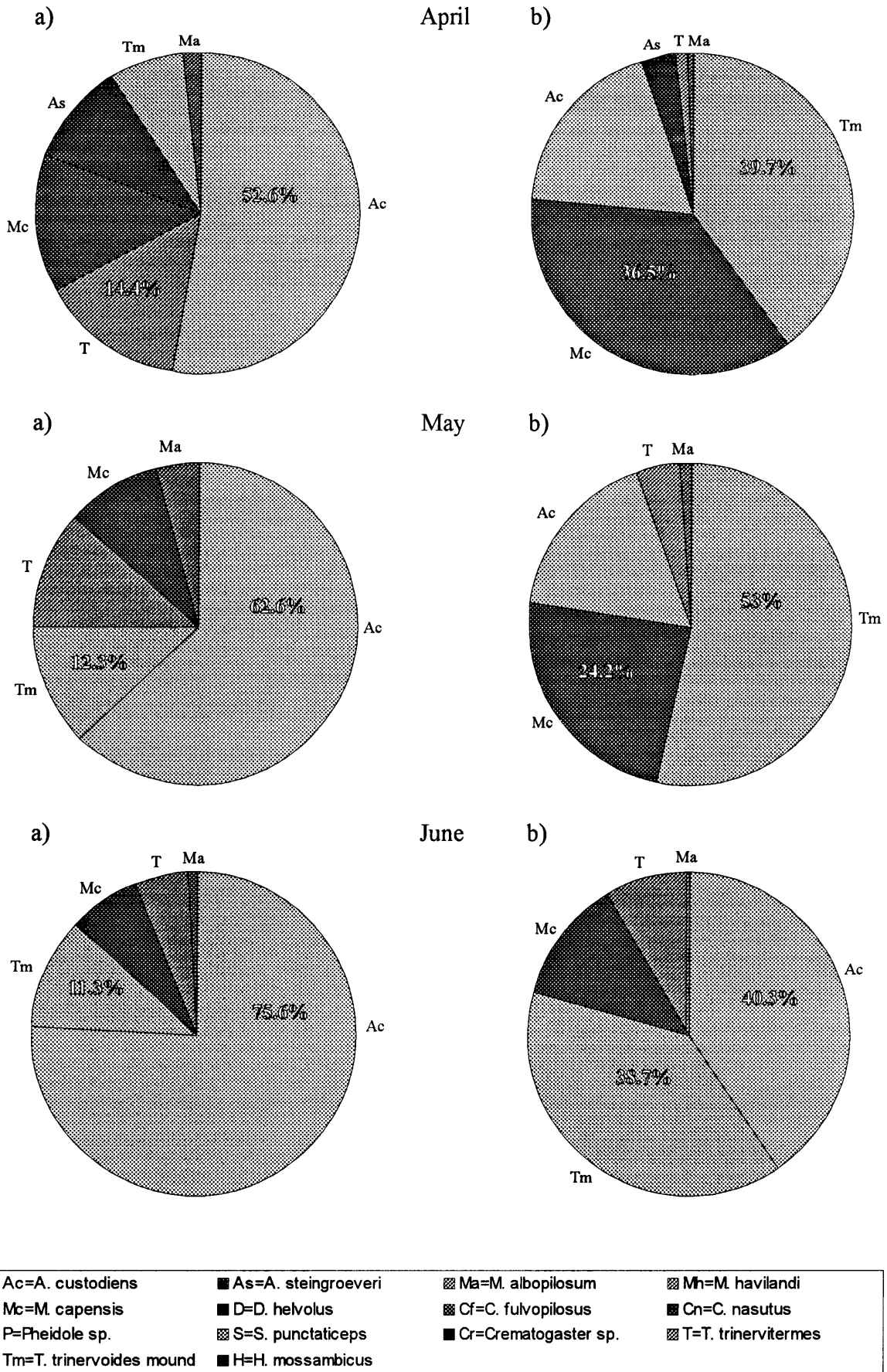


**Figure 34 (continued).** Feeding observations of aardvark M5, April to June 1997.

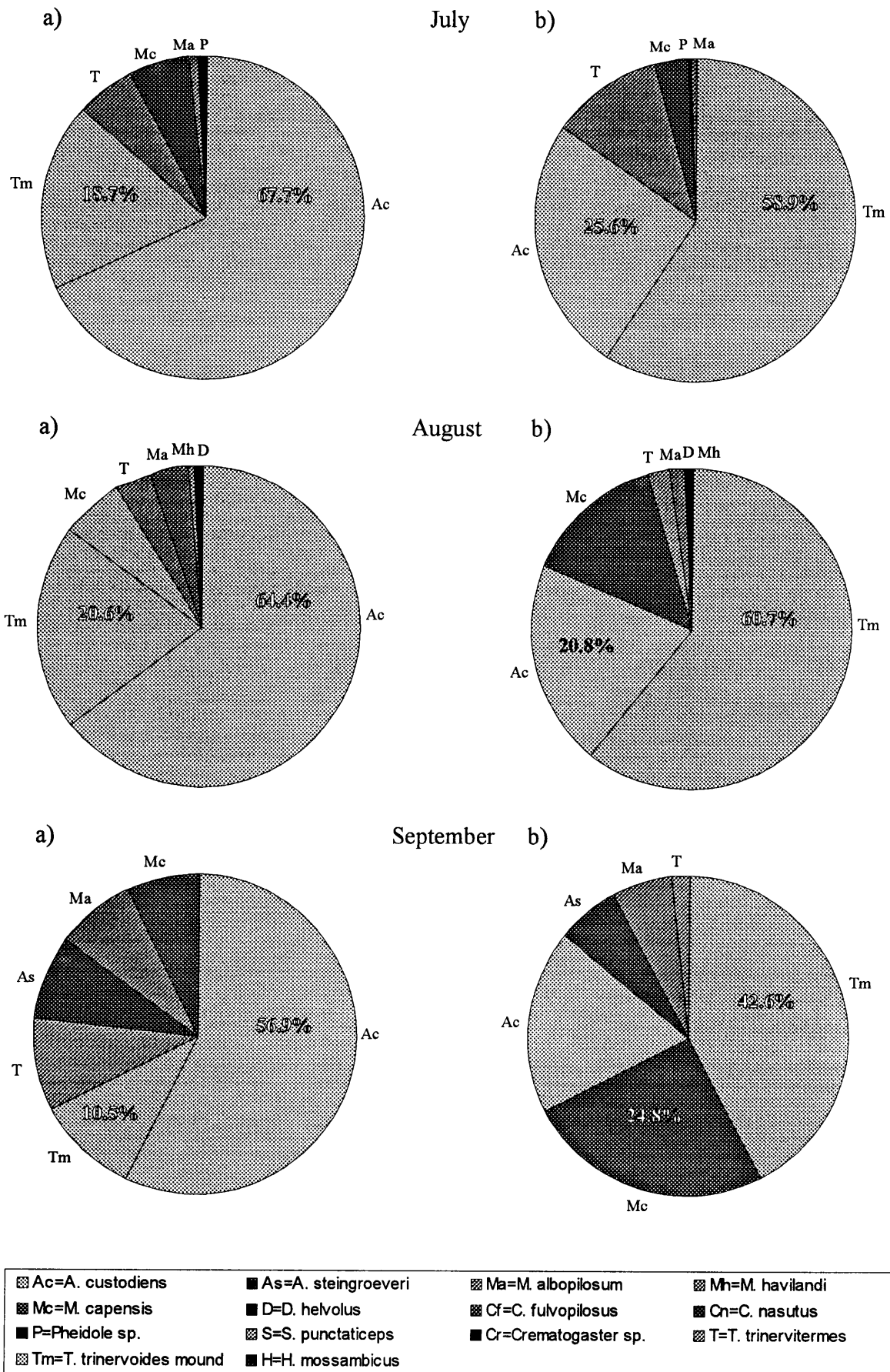


**Figure 34 (continued).** Feeding observations of aardvark M5, July to September 1997.

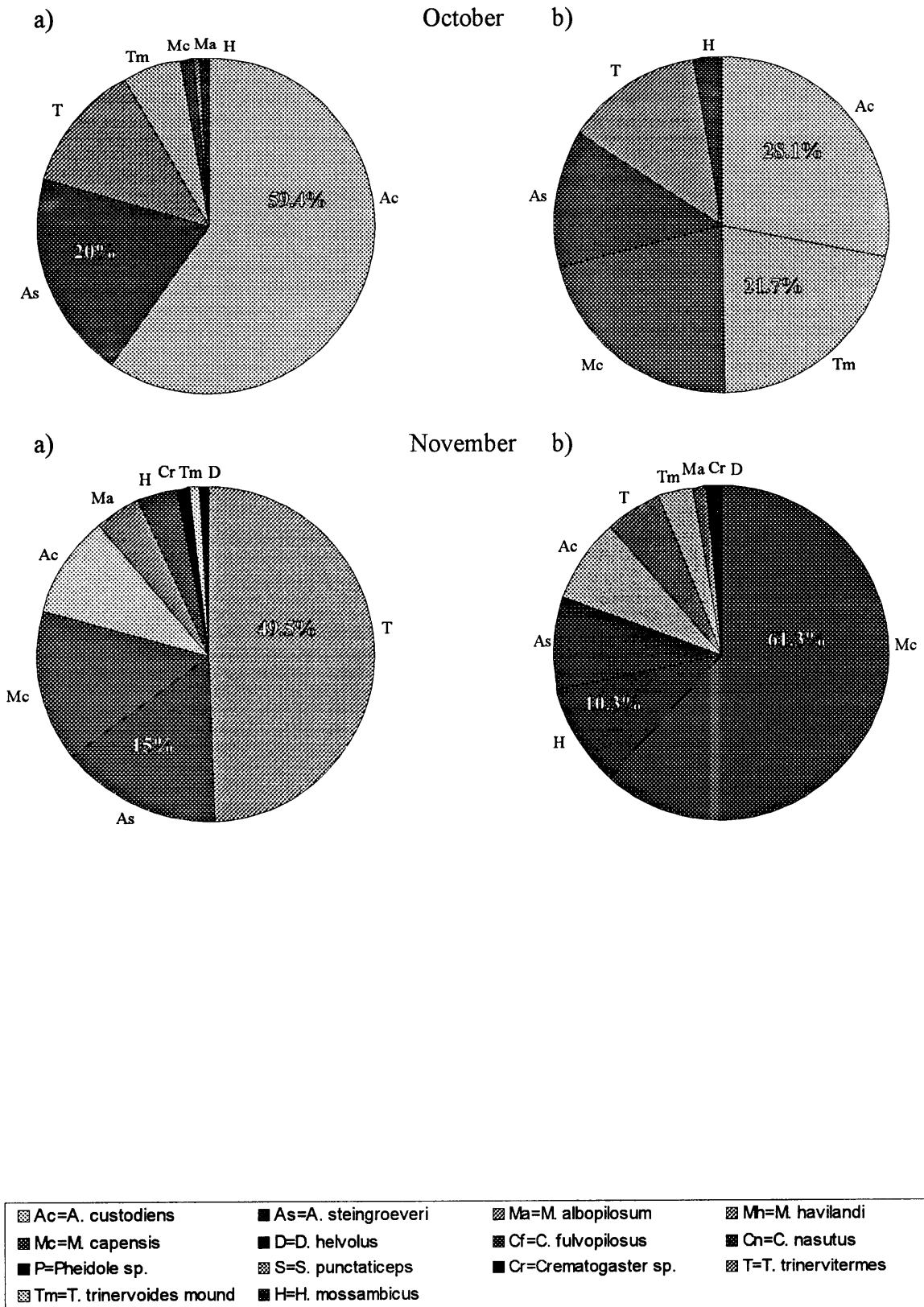
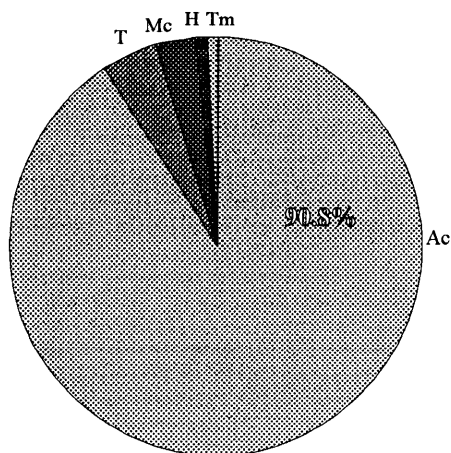
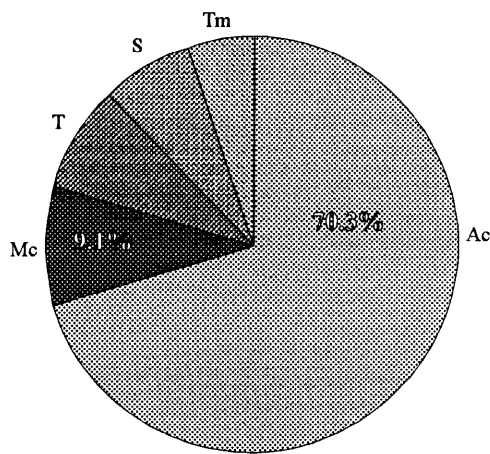


Figure 34 (continued). Feeding observations of aardvark M5, October to December 1997.

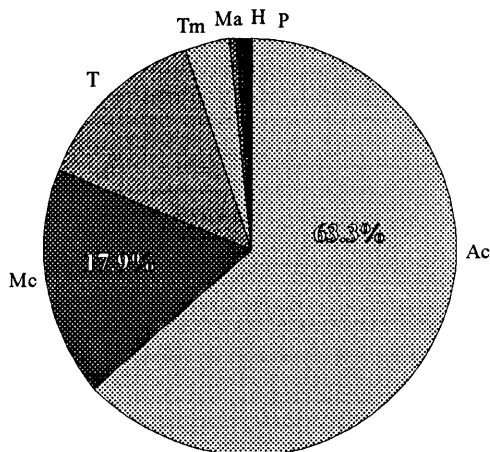
February



March



April



|                          |                     |                      |                     |
|--------------------------|---------------------|----------------------|---------------------|
| Ac=A. custodiens         | As=A. steingroeveri | Ma=M. albopilosum    | Mh=M. havilandi     |
| Mc=M. capensis           | D=D. helvolus       | Cf=C. fulvopilosus   | Cn=C. nasutus       |
| P=Pheidole sp.           | S=S. punctaticeps   | Cr=Crematogaster sp. | T=T. trinervitermes |
| Tm=T. trinervoides mound | H=H. mossambicus    |                      |                     |

**Figure 35.** Feeding observations of aardvark F4, February to April 1997 (percentage of feed counts only).

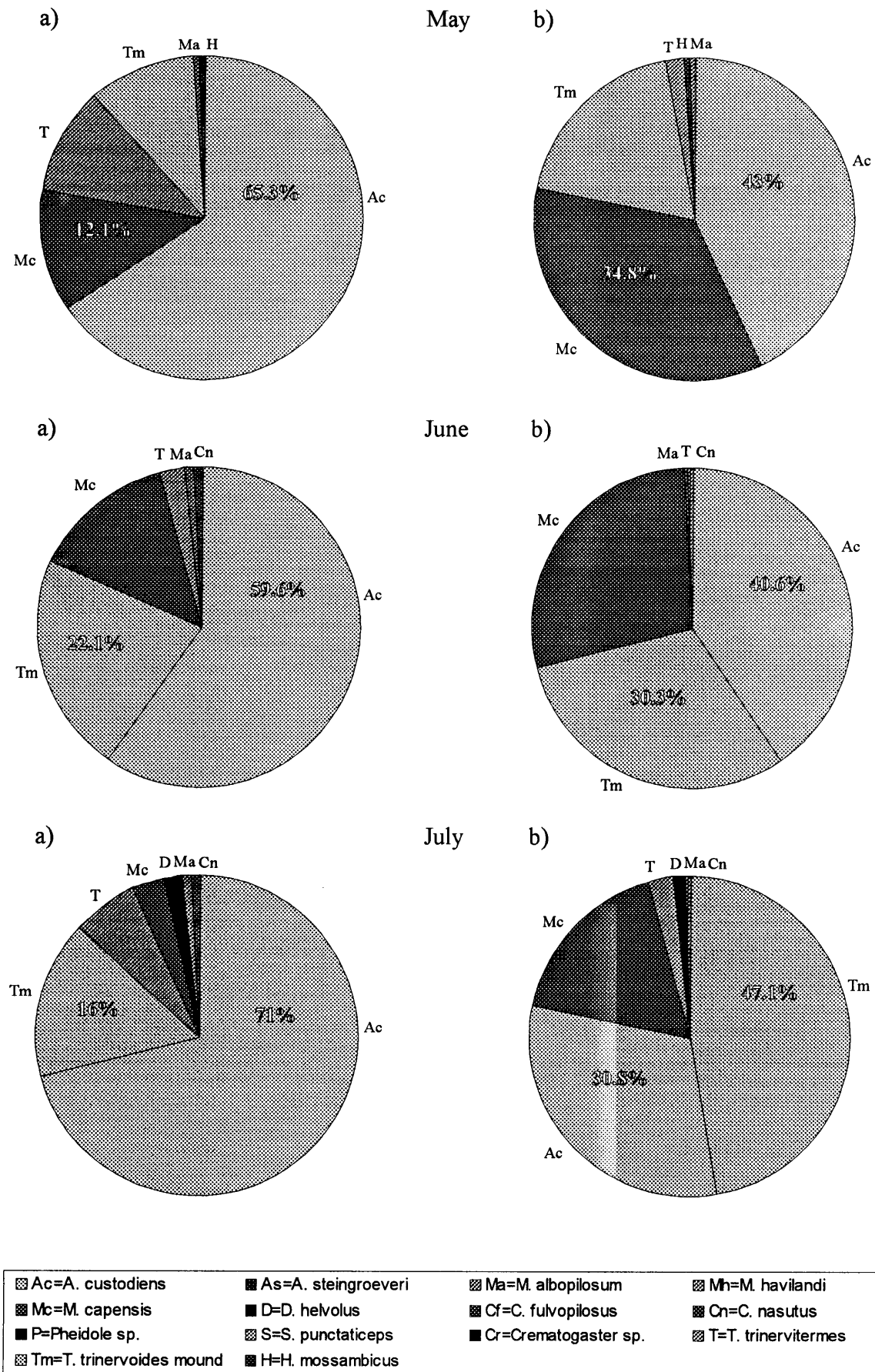


**Figure 35 (continued).** Feeding observations of aardvark F4, May to July 1997. a) Percentages of feeding counts per prey species; b) percentages of feeding times per prey species.

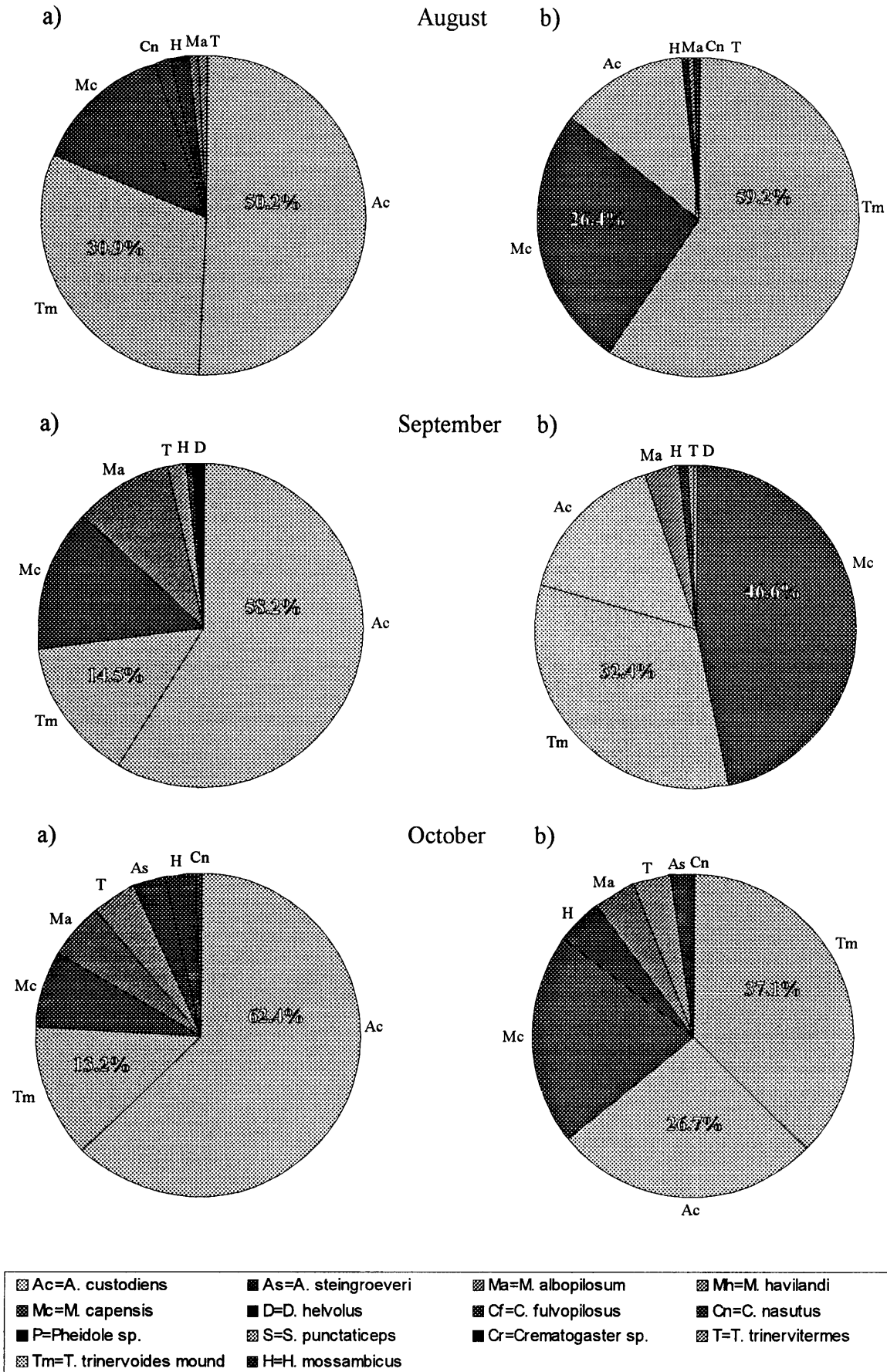


**Figure 35 (continued).** Feeding observations of aardvark F4, August to October 1997.

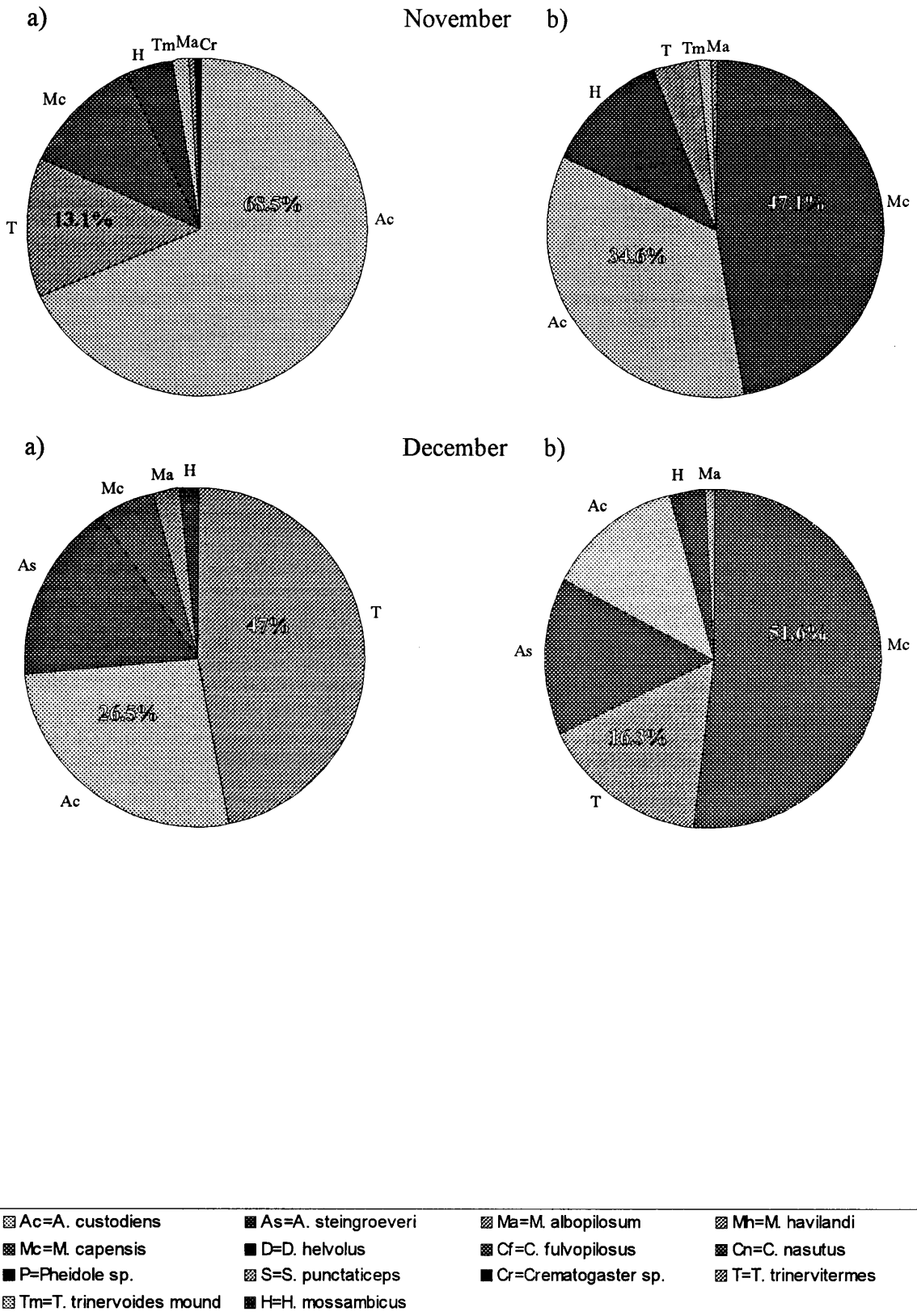


**Figure 35 (continued).** Feeding observations of aardvark F4, November and December 1997.

from August to November, the reverse to M5 for this period. Due to the relatively high percentages of *A. custodiens* in both seasons for both aardvarks, there appeared to be no seasonal differences.

*T. trinervoides* was the second most commonly predated species overall. In all months for both aardvarks *T. trinervoides* was second or third most commonly predated, either from ground digs (T) or mound digs (Tm). The exception to this was January for M5. *M. capensis* was third most commonly predated, occurring in the top three 15 times.

The Formicidae were predated more often than the Isoptera in all months except November for aardvark M5. In December, although F4 predated *T. trinervoides* more than any other species, the total percentage of feeds on termites was only 49.1%.

The pattern of percentage time spent feeding per species was somewhat different to the pattern just described for the number of feeding bouts per species. In every month for both aardvarks, the percentage of time spent feeding on *A. custodiens* was less than the percentage of actual feed counts. In other words the aardvarks appeared to spend relatively less time feeding on *A. custodiens* than the number of feeds would imply. The same pattern was true for *T. trinervoides* when examining the ground feeds. The percentage of time feeding on *T. trinervoides* from the ground was always less than the percentage of feed counts observed. June and July were exceptions to this pattern for aardvark M5.

The opposite was true, however, for both *T. trinervoides*, when predated from mounds, and *M. capensis*. For both these species the percentage time feeding was always greater than the percentage of feed counts observed, indicating that the aardvarks fed for longer on average on these species than the others. The only exceptions to this were January (Tm) and July (Mc), both for aardvark M5.

### **Variation in feeding times on *A. custodiens* between seasons**

Table 19 below shows the differences in feeding times on *A. custodiens* between the two habituated aardvarks and between summer and winter. The data were randomised using a 2-way ANOVA as the test statistic.

**Table 19.** Randomisation of feeding times on *A. custodiens* between aardvarks M5 and F4 and between summer and winter.

| Summary statistics |                                                                      |        |        |
|--------------------|----------------------------------------------------------------------|--------|--------|
|                    | Summer                                                               | A8     | A9     |
| Count              |                                                                      | 260    | 260    |
| Average            |                                                                      | 47.2   | 18.2   |
| Variance           |                                                                      | 1663.3 | 279.2  |
|                    | Winter                                                               |        |        |
| Count              |                                                                      | 260    | 260    |
| Average            |                                                                      | 39.5   | 66.3   |
| Variance           |                                                                      | 3015.2 | 3406.5 |
| Randomisation      |                                                                      |        |        |
|                    | % of randomization mean squares<br>that exceed observed mean squares |        |        |
| Season             |                                                                      |        | 0.1    |
| Aardvark           |                                                                      |        | 72.3   |
| Interaction        |                                                                      |        | 0.1    |

There was strong evidence of variation between seasons but no evidence of variation between the two aardvarks. There was also evidence of an interaction between the two, indicating that the differences between seasons were not the same for the aardvarks. This can be seen on examination of the summary statistics, which shows that the aardvarks showed reverse patterns of feeding times between summer and winter. M5 fed for longer on *A. custodiens* in summer than winter, but F4 fed for longer on *A. custodiens* in winter than in summer. The most significant difference between seasons was for F4, who’s average feeding time in winter was 66 seconds, while in summer it was only 18 seconds.

### Differences between the average feeding times on different species

Table 20 shows the average feeding times for the main prey species of aardvarks M5 and F4 and statistical differences between them. The statistical technique used to derive the p-values was described in the methods. Data were combined for both aardvarks.

**Table 20.** P-values for differences between the feeding lengths on the main prey species for aardvarks M5 and F4 (data combined)

| Prey species                | Prey species |       | <i>Ac</i> | <i>As</i> | <i>Mc</i> | <i>Ma</i> | <i>H</i> | <i>Tfp</i> | <i>Tm</i> | <i>Tam</i> |
|-----------------------------|--------------|-------|-----------|-----------|-----------|-----------|----------|------------|-----------|------------|
|                             | Mean         | Sd    |           |           |           |           |          |            |           |            |
| <i>A. custodiens</i>        | 49.4         | 60.4  | -         |           |           |           |          |            |           |            |
| <i>A. steingroeveri</i>     | 52.2         | 54.4  | 0.68      | -         |           |           |          |            |           |            |
| <i>M. capensis</i>          | 308.5        | 347.1 | 0.0001**  | 0.0001**  | -         |           |          |            |           |            |
| <i>M. albopilosum</i>       | 34           | 33.4  | 0.64      | 0.53      | 0.0001**  | -         |          |            |           |            |
| <i>H. mossambicus</i>       | 145.9        | 83.5  | 0.03*     | 0.19      | 0.005**   | 0.03*     | -        |            |           |            |
| <i>T. trinervoides (FP)</i> | 62.6         | 93.4  | 0.33      | 0.88      | 0.0001**  | 0.30      | 0.16     | -          |           |            |
| <i>T. trinervoides (M)</i>  | 265.3        | 277.5 | 0.0001**  | 0.0001**  | 0.10      | 0.0001**  | 0.04*    | 0.0001**   | -         |            |
| <i>T. trinervoides (AM)</i> | 93.6         | 100.4 | 0.09      | 0.42      | 0.0001**  | 0.09      | 0.54     | 0.39       | 0.0005**  | -          |

\* Statistically significant

\*\* Statistically highly significant

*Ac* = *A. custodiens*, *As* = *A. steingroeveri*, *Mc* = *M. capensis*, *Ma* = *M. albopilosum*, *H* = *H. mossambicus*,  
*Tfp* = *T. trinervoides* (from foraging ports), *Tm* = *T. trinervoides* (from mounds), *Tam* = *T. trinervoides* (from base of mound).

There were significant differences in average feeding times between many of the prey species, but the most important fact to take from these differences was that *M. capensis* and *T. trinervoides* predated from mounds were on average fed on for significantly longer than all the other species, while there was no evidence of a difference in the average feed time between them. There was no evidence of any difference in the average feeding times between *A. custodiens* and *A. steingroeveri*.

### Observed predation of *T. trinervoides* mounds

Table 21 represents the total number of *T. trinervoides* mounds predated by aardvarks M5 and F4 during all observations of 1997. The second column shows that the total observation times for each month and for each aardvark were not equal, so the results should not be interpreted as proportions. However, a similar pattern can be observed for both animals, and this was that the number of mounds predated increased in May, rose to a peak in July and August, and then declined again in October. F4 did not feed on any mounds in November, while in December neither she nor M5 fed on any mounds. (M5 did not feed on any mounds in December 1996 either, although this is not represented in the table).

Figure 36 shows the average monthly predation frequencies from *T. trinervoides* mounds by aardvarks M5 and F4, estimated from all observations of 1997. The results were obtained by dividing the number of observed mound feeds in a month by the total observation time (hours) for the same period. Note that the counts include only mounds that were fed upon properly, not mounds that were investigated, or even partially excavated, if the aardvark left without visibly feeding on the termites.

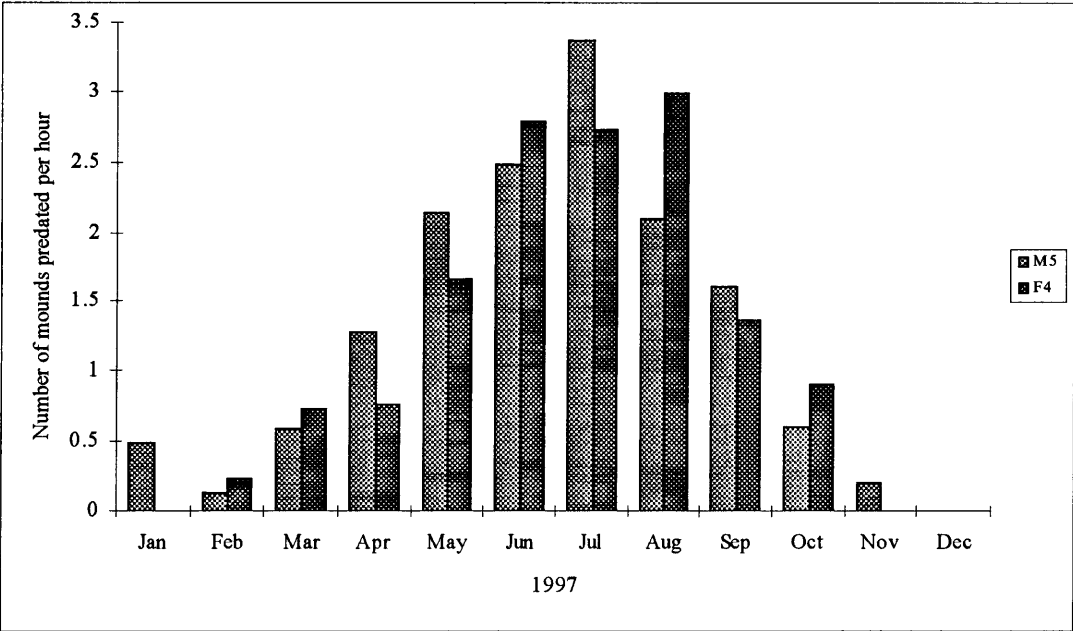


**Figure 36.** Average monthly feeding frequencies from *T. trinervoides* mounds by aardvarks M5 and F4 in1997.

**Table 21.** Predation of *T. trinervoides* mounds during 1997: a) aardvark M5; b) aardvark F4.

a)

| Month | Approx obs<br>time (hrs) | Predug | Large<br>Undug | Unknown | Predug | Medium<br>Undug | Unknown | Predug | Small<br>Undug | Unknown | Total |
|-------|--------------------------|--------|----------------|---------|--------|-----------------|---------|--------|----------------|---------|-------|
| Jan   | 35                       | 1      | 0              | 1       | 1      | 0               | 3       | 0      | 3              | 2       | 11    |
| Feb   | 52                       | 0      | 0              | 0       | 0      | 1               | 1       | 0      | 2              | 1       | 5     |
| Mar   | 37                       | 0      | 0              | 2       | 2      | 0               | 4       | 0      | 2              | 2       | 12    |
| Apr   | 40                       | 0      | 0              | 4       | 3      | 0               | 9       | 0      | 0              | 11      | 27    |
| May   | 20                       | 0      | 2              | 0       | 9      | 5               | 9       | 1      | 2              | 3       | 31    |
| Jun   | 12                       | 5      | 6              | 5       | 3      | 3               | 1       | 0      | 2              | 2       | 27    |
| Jul   | 12                       | 14     | 7              | 0       | 1      | 0               | 0       | 0      | 1              | 1       | 24    |
| Aug   | 15                       | 14     | 4              | 3       | 3      | 2               | 0       | 0      | 0              | 0       | 26    |
| Sep   | 35                       | 33     | 5              | 2       | 5      | 2               | 2       | 1      | 2              | 0       | 52    |
| Oct   | 33                       | 7      | 3              | 0       | 2      | 0               | 1       | 0      | 2              | 2       | 17    |
| Nov   | 20                       | 1      | 0              | 2       | 1      | 0               | 0       | 0      | 0              | 0       | 4     |
| Dec   | 14                       | 0      | 0              | 0       | 0      | 0               | 0       | 0      | 0              | 0       | 0     |
| Total | 325                      | 75     | 27             | 19      | 30     | 13              | 30      | 2      | 16             | 24      | 236   |

b)

| F4<br>Month | Approx obs<br>time (hrs) | Predug | Large<br>Undug | Unknown | Predug | Medium<br>Undug | Unknown | Predug | Small<br>Undug | Unknown | Total |
|-------------|--------------------------|--------|----------------|---------|--------|-----------------|---------|--------|----------------|---------|-------|
| Jan         | -                        | -      | -              | -       | -      | -               | -       | -      | -              | -       | -     |
| Feb         | 47                       | 0      | 0              | 0       | 0      | 0               | 0       | 0      | 1              | 1       | 2     |
| Mar         | 30                       | 0      | 0              | 0       | 0      | 0               | 1       | 0      | 0              | 2       | 3     |
| Apr         | 18                       | 0      | 0              | 0       | 2      | 1               | 3       | 0      | 1              | 1       | 8     |
| May         | 25                       | 0      | 0              | 0       | 8      | 6               | 6       | 4      | 4              | 6       | 34    |
| Jun         | 15                       | 10     | 6              | 1       | 12     | 5               | 2       | 0      | 2              | 1       | 39    |
| Jul         | 17                       | 24     | 8              | 4       | 1      | 0               | 1       | 0      | 1              | 0       | 39    |
| Aug         | 43                       | 101    | 12             | 5       | 5      | 2               | 0       | 0      | 1              | 0       | 126   |
| Sep         | 36                       | 33     | 2              | 3       | 6      | 2               | 1       | 1      | 1              | 0       | 49    |
| Oct         | 60                       | 47     | 1              | 3       | 0      | 1               | 1       | 0      | 0              | 0       | 53    |
| Nov         | 21                       | 0      | 0              | 0       | 0      | 0               | 0       | 0      | 0              | 0       | 0     |
| Dec         | 23                       | 0      | 0              | 0       | 0      | 0               | 0       | 0      | 0              | 0       | 0     |
| Total       | 335                      | 215    | 29             | 16      | 34     | 17              | 15      | 5      | 11             | 11      | 353   |

It is clear that for both animals there was an increase in mound predation frequency from February to July and August, followed by a decrease from August to December. Aardvark M5 showed a peak of mound feeding behaviour in July, while F4 showed the same peak in August. In 1997, therefore, *T. trinervoides* mounds were predated more frequently in winter than in summer by the two habituated aardvarks. This variation in predation frequencies was tested statistically by randomisation and the results shown in Table 22.

**Table 22.** Randomisation of predation frequencies from *T. trinervoides* mounds.

| Randomization       |                                                                      |
|---------------------|----------------------------------------------------------------------|
| Source of variation | % of randomization mean squares<br>that exceed observed mean squares |
| Aardvark            | 65.3                                                                 |
| Month               | 0.02                                                                 |
| Aardvark x Month    | 19.24                                                                |

There was strong evidence of variation between months, but no evidence of variation between aardvarks and no evidence of an interaction, indicating that the differences between months were not different for the aardvarks.

This increased feeding frequency from mounds during the winter months could have been compensated by a decreased average feeding time per bout, or in other words the two might have cancelled each other out, leaving no difference in overall feeding time per month. To check for this, the average monthly feeding bout lengths were calculated for each aardvark in 1997 and the results shown in Figure 37.

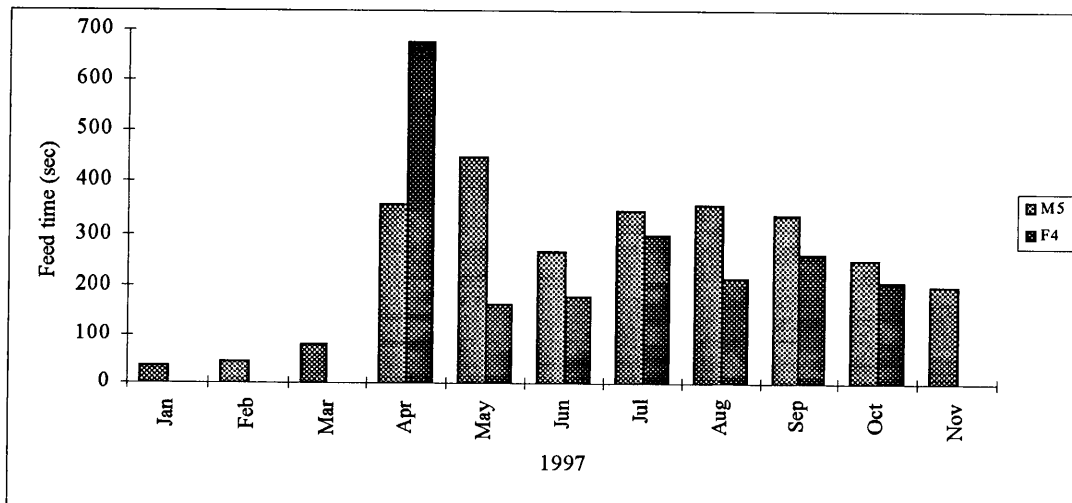


**Figure 37.** Average monthly feeding times from *T. trinervoides* mounds by aardvarks M5 and F4 in 1997.

For the months January, February, March and November 1997, no feeding times were represented for aardvark F4. This was because there were very few timed mound feeds for this animal during these periods. The variation in average feeding times was tested by randomisation and the results shown in Table 23.

**Table 23.** Randomisation of feeding times from *T. trinervoides* mounds.

| Randomization       |                                                                      |
|---------------------|----------------------------------------------------------------------|
| Source of variation | % of randomization mean squares<br>that exceed observed mean squares |
| Aardvark            | 9.7                                                                  |
| Month               | 0.02                                                                 |
| Aardvark x month    | 0.28                                                                 |

There was strong evidence of variation between months and strong evidence of an interaction, indicating that differences between months were not the same for the two aardvarks.

To investigate whether the differences in average feeding times between months as indicated by the randomisation test of Table 23 might have the effect of cancelling out the increased feeding frequency on mounds in winter found in Figure 36, the two were tested for correlation. The Spearman rank correlation coefficient was used to test this. Figures 38 and 39 show the relationship between feeding frequency and average feeding time. The amount of correlation is shown in each figure.

Aardvark M5:  $r = 0.50$  ( $N = 8$ , p-level 0.207) No evidence of a correlation

Aardvark F4:  $r = -0.357$  ( $N = 7$ , p-level 0.432) No evidence of a correlation

For both aardvarks there was no evidence of a correlation between feeding frequency and average feeding bout length on *T. trinervoides* mounds. Therefore, aardvarks M5 and F4 fed for longer from *T. trinervoides* mounds in winter than in summer.

Figure 40 represents the selection of mounds according to size and dig status (whether or not they were previously excavated by an aardvark). Data from both aardvarks were combined because they showed very similar patterns of selection. The months June through October are the only ones represented because they were the ones in which most of the mounds were predated and samples from other months were too small to give a reasonable representation.

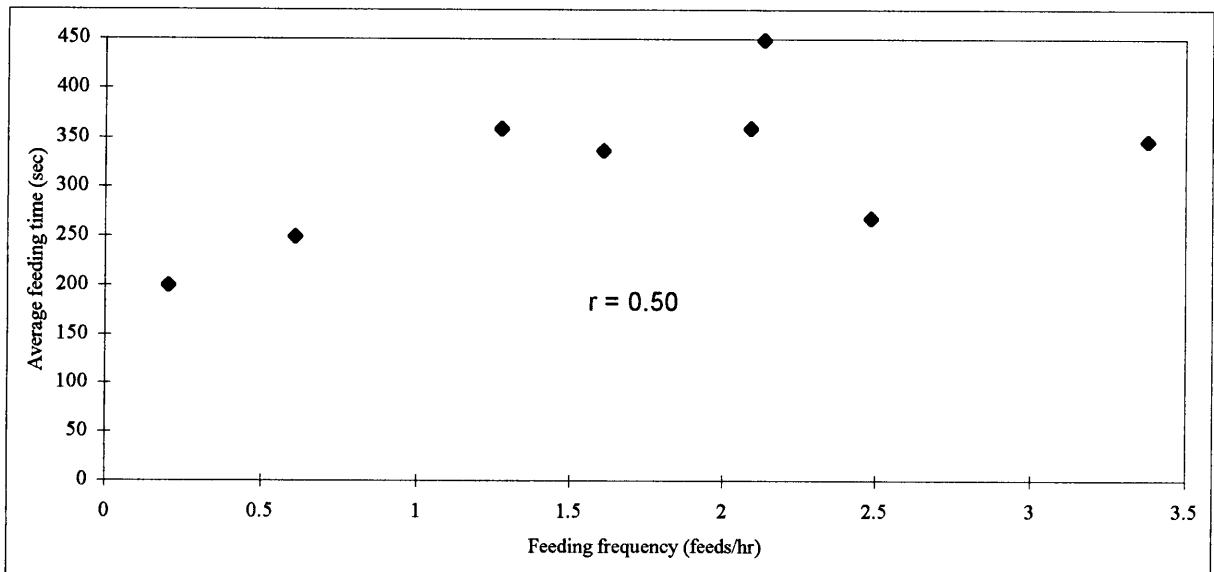


**Figure 38.** Aardvark M5 correlation of feeding frequency with average feeding bout length ( $r$  = Spearman rank correlation coefficient).

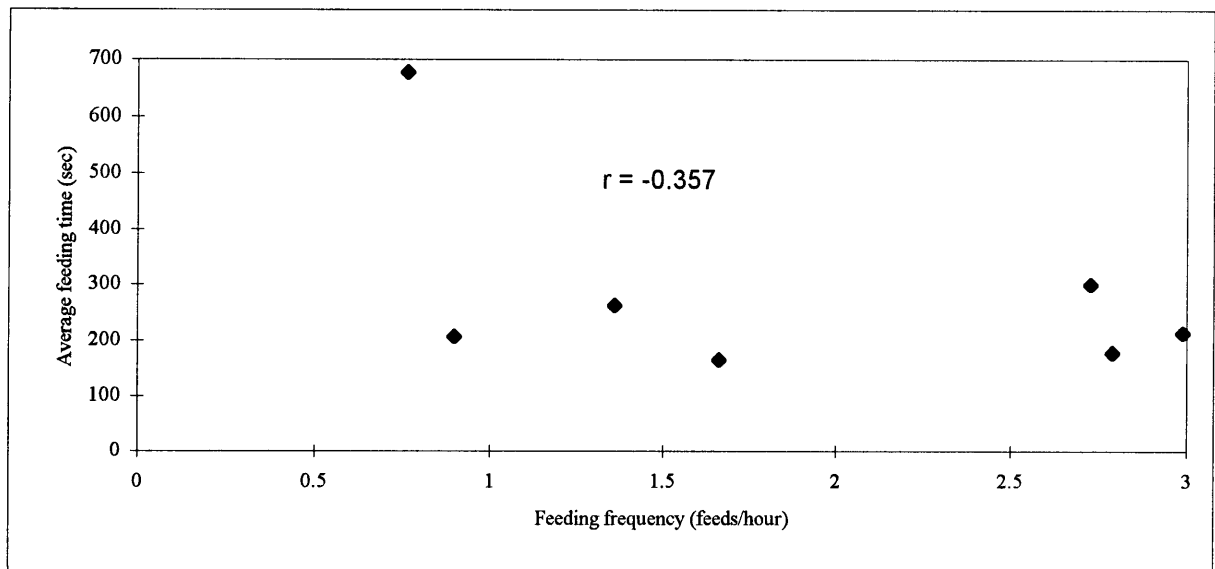


**Figure 39.** Aardvark F4 correlation of feeding frequency with average feeding bout length ( $r$  = Spearman rank correlation coefficient)

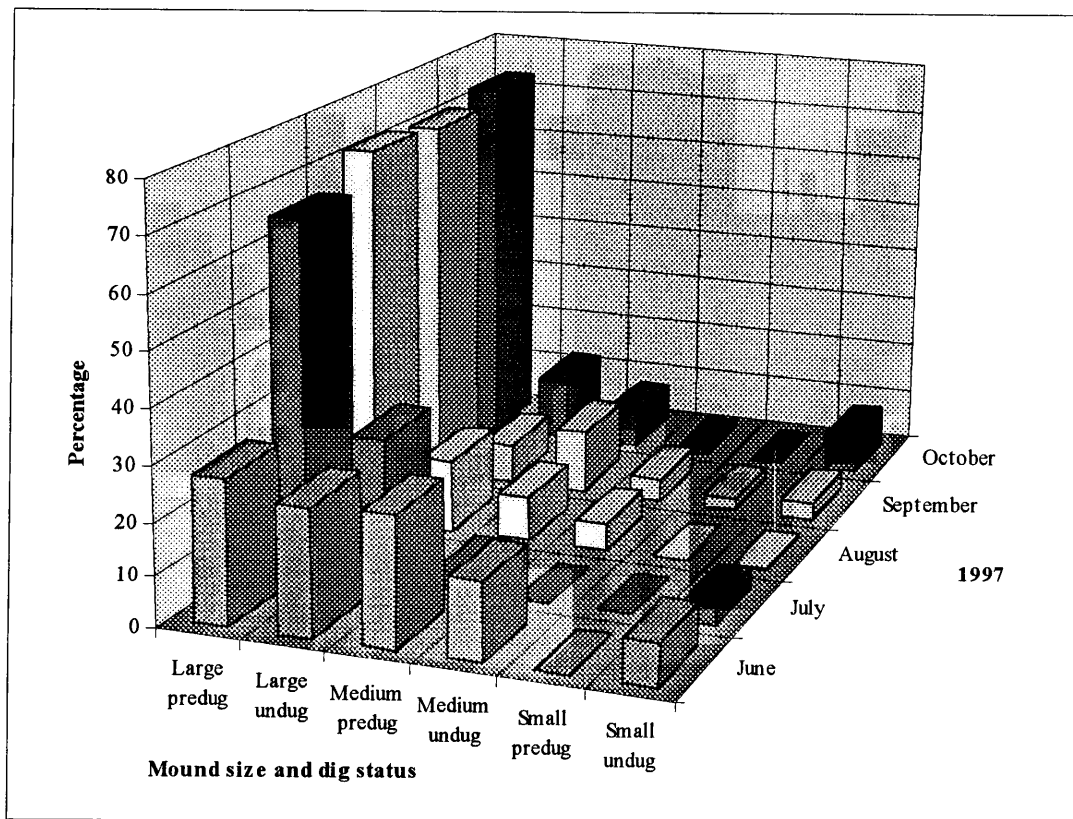


**Figure 40.** Utilisation of *T. trinervoides* mounds in 1997 by aardvarks M5 and F4, categorised by mound size and dig status.

Large mounds were always predated more often than medium mounds, except in June, where they were predated to a similar degree, and medium mounds were generally predated more often than small mounds. Large mounds that were already excavated prior to the observed feed were more commonly predated than large mounds showing no signs of previous excavation (except again in June, where this was less clear). Medium predug mounds also appear to have been predated more often than medium undug mounds, but the pattern was not as clear as that for large mounds. Small mounds show the reverse trend, where previously undug mounds were excavated more often than predug mounds.

#### Observed and expected predation frequencies of *T. trinervoides* mounds

Table 24 shows counts and percentages of the different categories of *T. trinervoides* mounds determined from the sample grids. It comprises the data from grids within M5's and F4's range and, therefore, represents the mound categories available to these aardvarks and the expected proportions in

which these mounds would be predated if the aardvarks had no selection preferences. There were more small mounds available than medium or large mounds, and more medium mounds available than large. In all mound size categories there were more undug mounds available than predug mounds.

**Table 24.** Counts and percentages of termite mounds from sampling grids.

|        | Small     |       | Medium    |       | Large     |       | Total     |      |
|--------|-----------|-------|-----------|-------|-----------|-------|-----------|------|
|        | frequency | %     | frequency | %     | frequency | %     | frequency | %    |
| Undug  | 222       | 39.22 | 139       | 24.56 | 68        | 12.02 | 429       | 75.8 |
| Predug | 23        | 4.06  | 61        | 10.78 | 53        | 9.36  | 137       | 24.2 |
| Total  | 245       | 43.28 | 200       | 35.34 | 121       | 21.38 | 566       | 100  |

Table 25 shows the observed counts of predation on the different mound categories by aardvarks M5 and F4.

**Table 25.** Counts and percentages of termite mounds predated by aardvarks M5 and F4 during 1997.

|        | Small     |       | Medium    |       | Large     |       | Total     |       |
|--------|-----------|-------|-----------|-------|-----------|-------|-----------|-------|
|        | frequency | %     | frequency | %     | frequency | %     | frequency | %     |
| M5     |           |       |           |       |           |       |           |       |
| Undug  | 19        | 11.18 | 15        | 8.82  | 27        | 15.88 | 61        | 35.88 |
| Predug | 2         | 1.18  | 30        | 17.65 | 77        | 45.29 | 109       | 64.12 |
| Total  | 21        | 12.36 | 45        | 26.47 | 104       | 61.17 | 170       | 100   |
| F4     |           |       |           |       |           |       |           |       |
| Undug  | 13        | 4.1   | 19        | 5.99  | 29        | 9.15  | 61        | 19.24 |
| Predug | 6         | 1.89  | 34        | 10.73 | 216       | 68.14 | 256       | 80.76 |
| Total  | 19        | 5.99  | 53        | 16.72 | 245       | 77.29 | 317       | 100   |

The questions to be answered from the data in Tables 24 and 25 were: How do the frequencies of different sized mounds predated by aardvarks compare to the different sizes of mounds available?, and; how do the frequencies of undug and predug mounds predated compare to those available?

Table 26 shows the observed and expected frequencies of predation on different sized mounds by aardvarks M5 and F4. Expected predation frequencies for each mound size and each aardvark were calculated by multiplying the proportion of mounds available in a particular size category (sampling grid results, Table 24) by the total number of mounds predated by one of the aardvarks (observed predation frequencies, Table 25). For example, the expected frequency of large mounds predated by aardvark M5 = 0.2138 x 170 = 36.3.

If there had been observations from a larger number of aardvarks, the predation results would have been clumped and analysed in one  $\chi^2$  test to avoid multiple p-values. However, as only two aardvarks were available for such observations, and individual behaviour can be considered important (grouping all aardvarks might not represent any one aardvark) it was decided to test the aardvarks separately. To correct for the potential *type I* error when carrying out the same test more than once, that is rejecting the null hypothesis when it is actually true, the p-value (significance level) can be lowered (although this may lead to a *type II* error, which is not rejecting the null hypothesis when it is false). From the results below it can be seen that the differences between the observed and expected frequencies were so great that there was in fact no chance of attaining a false result.

**Table 26.** Observed and expected predation frequencies of different sized *T. trinervoides* mounds for aardvarks M5 (a) and F4 (b).

| a)       | Small | Medium | Large | b)       | Small | Medium | Large |
|----------|-------|--------|-------|----------|-------|--------|-------|
| Observed | 21    | 45     | 104   | Observed | 19    | 53     | 245   |
| Expected | 73.6  | 60.1   | 36.3  | Expected | 137.2 | 112    | 67.8  |

The  $\chi^2$  test was used to analyse the frequencies.

$$\begin{aligned}
 \text{Aardvark M5: } \chi^2 \text{ (2df)} &= 37.6 \text{ (small)} + 3.8 \text{ (medium)} + 126.3 \text{ (large)} \\
 &= 167.7 \text{ (highly significant)}
 \end{aligned}$$

$$\begin{aligned} \text{Aardvark F4: } \chi^2 \text{ (2df)} &= 101.8 \text{ (small)} + 31.1 \text{ (medium)} + 463.1 \text{ (large)} \\ &= 596 \text{ (highly significant)} \end{aligned}$$

The critical value for 2 df, at  $p = 0.01$  is 9.21.

Results were highly significant for both aardvarks for all sizes of mound, except medium mounds predated by aardvark M5. From Table 26 it can be inferred that large mounds were predated more often than would have been expected from their availability, while small mounds were predated less often than would have been expected. Aardvark F4 predated medium mounds less often than would have been expected from their availability, but there is no clear evidence whether aardvark M5 predated medium mounds more or less often than would have been expected.

Table 27 shows the observed and expected frequencies of predation on undug and predug mounds by aardvarks M5 and F4. Expected frequencies were estimated by multiplying the proportions of mounds available in either category (undug or predug, see Table 24) by the total number of mounds predated by one of the aardvarks (Table 25). For example, the expected frequency of undug mounds predated by aardvark M5 =  $0.758 \times 170 = 128.86$ . Again, the aardvarks were tested separately with the same reasoning.

**Table 27.** Observed and expected predation frequencies of undug and predug *T. trinervoides* mounds for aardvarks M5 (a) and F4 (b).

|    |          |       |        |    |          |       |        |
|----|----------|-------|--------|----|----------|-------|--------|
| a) |          | Undug | Predug | b) |          | Undug | Predug |
|    | Observed | 61    | 109    |    | Observed | 61    | 256    |
|    | Expected | 128.9 | 41.1   |    | Expected | 240.3 | 76.7   |

$\chi^2$  values were calculated using Yates’ correction for continuity (subtraction of 0.5 from the numerator of the  $\chi^2$  equation) because there was only one degree of freedom.

$$\begin{aligned} \text{Aardvark M5: } \chi^2 \text{ (1df)} &= 36.3 \text{ (undug)} + 110.5 \text{ (predug)} \\ &= 146.8 \text{ (highly significant)} \end{aligned}$$

$$\begin{aligned} \text{Aardvark F4: } \chi^2 \text{ (1df)} &= 134.5 \text{ (undug)} + 416.8 \text{ (predug)} \\ &= 551.3 \text{ (highly significant)} \end{aligned}$$

The critical value for 1df, at p=0.01 is 6.63

Results were highly significant for undug and predug mounds for both aardvarks. From Table 27 the same trend can be inferred for both aardvarks. Predug mounds were predated more often than would be expected from their availability, while undug mounds were predated less often than expected.

**Observed feeding times on *T. trinervoides* mounds**

Figure 41 shows the average (mean) times spent feeding on the three different sizes of *T. trinervoides* mounds by the two habituated aardvarks. Error bars represent one standard deviation.

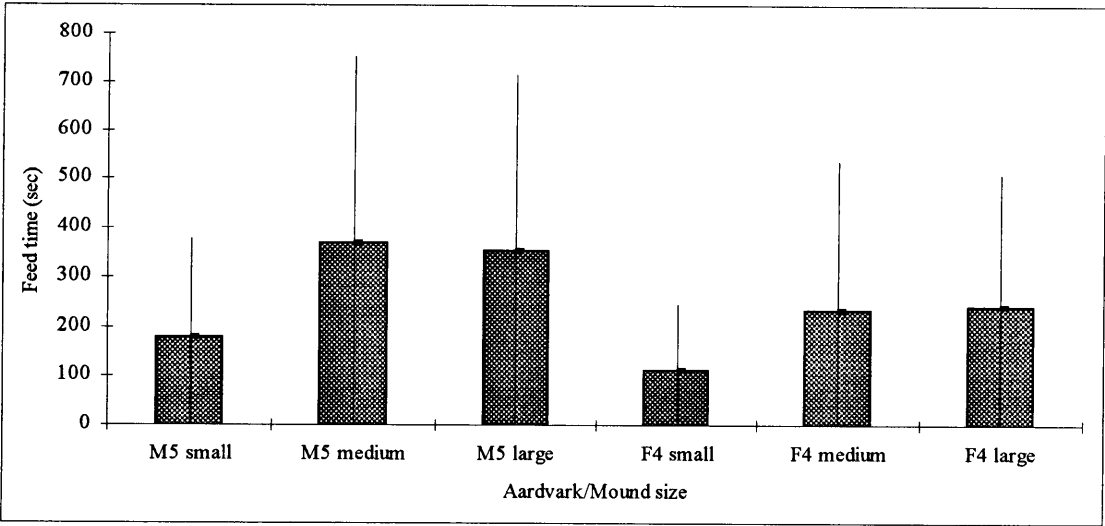


**Figure 41.** Variation in feeding times on *T. trinervoides* mounds relative to mound size.

Aardvark M5, on average, fed for the longest time on medium sized mounds and the shortest time on small mounds. Aardvark F4 also spent the least time on small mounds, but fed for the longest average time on large mounds. For both aardvarks and all mound size categories there was a large amount of

variation in feeding times and all size categories included zero feeding time at some point (in other words they dug open a mound but didn’t feed).

To test whether these observed differences in feeding times between different sized mounds were significant a 2-way ANOVA was carried out, with the data Log<sub>10</sub> transformed. Not all the data used in Figure 41 were entered in the test because the numbers of feeds were not spread evenly between different sized mounds (values were selected randomly.) Results are shown in Table 28.

**Table 28.** Two-way ANOVA of feeding times between aardvarks for different mound sizes.

| 2-way ANOVA           |          |           |                |
|-----------------------|----------|-----------|----------------|
| Source of Variation   | <i>F</i> | <i>df</i> | <i>P-value</i> |
| Aardvark              | 3.10225  | 1         | 0.07915        |
| Mound size            | 12.5074  | 2         | 5.9E-06        |
| Aardvark x mound size | 0.49759  | 2         | 0.60847        |

There was strong evidence of variation in feeding times between the different sizes of mound, but no real evidence of variation in feeding times between aardvarks. There was also no evidence of an interaction between aardvarks and mound size indicating that the differences between size categories were not different between aardvarks.

Examination of Figure 41 indicates that the greatest difference between feeding times were between small and medium mounds for aardvark M5 and between small and large mounds for aardvark F4. Small mounds were predated for significantly shorter time periods than the other sizes of mound.

Figure 42 shows the variation in feeding times between undug and predug mounds.

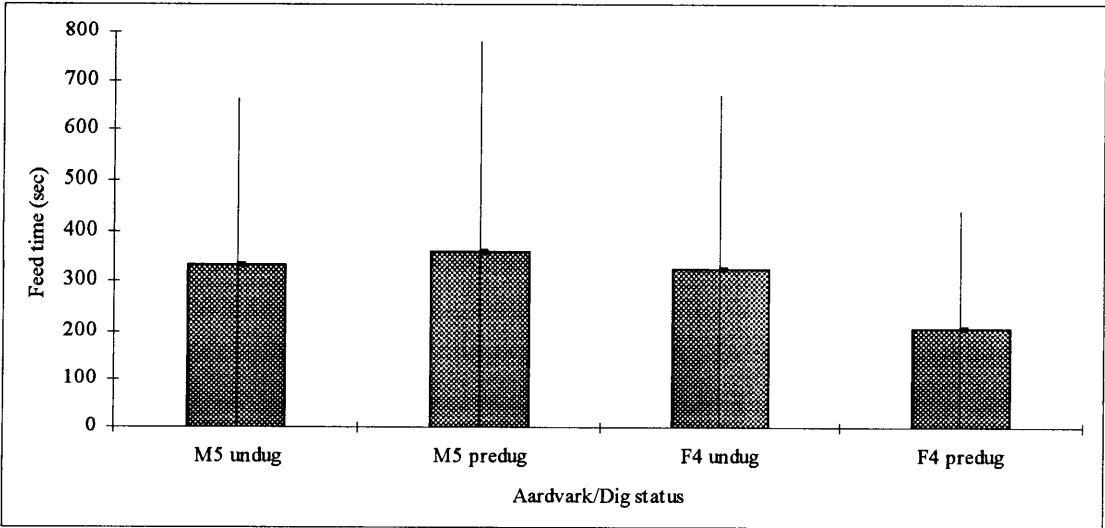


**Figure 42.** Variation in feeding times on *T. trinervoides* mounds relative to dig status.

Again there was a large amount of variation in feeding times and occasionally both undug and predug mounds were excavated but not fed on. M5 fed for longer on predug mounds, while F4 fed for longer on undug mounds. The data were tested using for variation using a 2-way ANOVA, the data being Log<sub>10</sub> transformed because they had variances greater than the mean. The results, shown in Table 29, indicated that neither M5 nor F4 showed any significant differences between the length of average feeding bouts on undug and predug mounds.

**Table 29.** Two way ANOVA of feeding times between undug and predug *T. trinervoides* mounds for aardvarks M5 and F4.

| 2 way ANOVA           |          |           |                |
|-----------------------|----------|-----------|----------------|
| Source of Variation   | <i>F</i> | <i>df</i> | <i>P-value</i> |
| Aardvark              | 0.94046  | 1         | 0.33338        |
| Dig status            | 0.21974  | 1         | 0.63977        |
| Aardvark x dig status | 3.1115   | 1         | 0.07933        |

**The orientation of aardvark diggings in *T. trinervoides* mounds**

The orientation of the digs were categorised into eight sections: 0 - 45°(N - NE), 45 - 90° (NE - E), 90 - 135° (E - SE), 135 - 180° (SE - S), 180 - 225° (S - SW), 225 - 270° (SW - W), 270 - 315° (W - NW), and 315 - 360° (NW - N).

The observed and expected frequencies for the orientation of digs into *T. trinervoides* mounds by aardvarks M5 and F4 are shown in Table 30. (Note that the total number of mounds for which a dig orientation was recorded was not the same as that for all predated mounds during observations, as in Table 21, because the orientations were only recorded from July to September.)

**Table 30.** Observed and expected frequencies of orientation of digs into *T. trinervoides* mounds, August and September 1997.

| Orientation | Observed frequencies | Expected frequencies |
|-------------|----------------------|----------------------|
| 0-45        | 22                   | 37.75                |
| 45-90       | 9                    | 37.75                |
| 90-135      | 14                   | 37.75                |
| 135-180     | 61                   | 37.75                |
| 180-225     | 163                  | 37.75                |
| 225-270     | 10                   | 37.75                |
| 270-315     | 16                   | 37.75                |
| 315-360     | 7                    | 37.75                |

The expected frequencies were calculated with the assumption that if digging was random, every side of the mound would have an equal probability of being excavated. Hence, in a large sample, each side would be dug the same number of times. In this case there were eight orientation categories to be equally divided between 302 termite mounds.

$\chi^2$  (7df) = 531.27 (highly significant)

The critical value for 7 df, at  $p = 0.01$  is 18.48.

All the orientation values were significant, and all except two were lower than expected. The bearings of  $135 - 180^\circ$  and  $180 - 225^\circ$  were the only ones greater than expected. The latter was also the orientation most significantly different with a  $\chi^2$  value of 415.56. This result indicates that the sampled mounds were excavated significantly more on their south sides than on other sides, and this could not have occurred by chance.

**The re-use of *T. trinervoides* mounds**

All mounds that were at least partially excavated through August and September were marked and the feeding times recorded (as normal). Mounds that were briefly investigated (sniffed in passing) were not often marked due to time constraints. Obviously, the two aardvarks were not followed continuously throughout the whole two month period, so some predated mounds would not have been marked, while the predation of some already marked mounds would have been missed. It was unlikely that any unknown aardvark, other than M5 or F4, could have predated any of the marked mounds during the period because none were ever seen before or during the period. Table 31 shows the average feeding times on mounds with respect to the number of days since they had been previously predated.

**Table 31.** The average feeding times on reused mounds after specified time periods.

| Number of nights since previous feed |        |        |        |        |        |        |        |        |       |
|--------------------------------------|--------|--------|--------|--------|--------|--------|--------|--------|-------|
|                                      | 1      | 2      | 3      | 4      | 5      | 6~10   | 11~15  | 16~20  | 20+   |
| Mean (sec)                           | 124.07 | 72.6   | 119.29 | 10.8   | 205    | 149.12 | 349.29 | 64.286 | 83.75 |
| SD                                   | 154.59 | 131.76 | 161.82 | 5.0695 | 215.02 | 146.22 | 591.47 | 156.93 | 123.9 |

The longest average feeding times took place 11-15 days after a previous feed and five days after a previous feed. The average feed time after one night was longer than that for five of the other time periods of longer duration. A Spearman rank correlation coefficient was used to examine the relationship between the length of the feed and the time lapsed since the previous feed.

$r = 0.05$  ( $N = 9$ ,  $p$ -level 0.898)

There was no evidence whatsoever of a correlation between the length of a feed and the number of days since the previous feed.

The data used in Table 31 were log transformed for one-way analysis of variance (Cochran C test value 0.16). There was no evidence for variation in feeding times between mounds that had been re-predated after different periods of time (ANOVA:  $F = 1.14$ ,  $df = 8$ ,  $p = 0.35$ ).

## Discussion

### Faecal analysis - Species identified

The number of prey species found in the faeces of the aardvarks during the present study (23) were more than found by Willis (1988) and Willis *et al.* (1992), who also examined aardvark prey species from their faeces at TdR, but only identified 14 species. This is explained by the fact that the earlier study sampled a great deal less faecal samples than the present one, and as would be expected, the more samples examined, the greater the chances of finding rarely eaten species. This was shown to be true in appendix II, where a minimum of 18 samples in one period was required to find most prey species, including many of the rarer ones. Willis sampled ten faecal deposits in March and ten in July 1988 to compare seasonal variation. As discussed in appendix II, if a larger number of samples had been examined in the present study, it is probable that further species would have been found, but for each new species, relatively more samples would have had to be examined. There was a trade off between spending more time sorting faeces and finding new prey species, but when those species probably had little or no biological significance, saving time was preferable. It is appropriate to indicate, as was done in appendix II, that even with a total of over 270 faecal samples examined, the number of prey species identified was barely higher than the number found in three of the individual months (March, November and December), when all faeces were combined.

The list of prey species compiled by Willis (1988) was as follows: Formicidae:- *Aenictus eugenii*, *Anoplolepis custodiens*, *Camponotus* sp., *Crematogaster* sp., *Dorylus helvolus*, *Messor capensis*, *Monomorium albopilosum*, *M. havilandi*, *Monomorium* sp., *Pheidole* sp., *Solenopsis* sp., and *Tetramorium* sp; Isoptera:- *Hodotermes mossambicus* and *Trinervitermes trinervoides*.

Considering the ten year lapse between the present study and that by Willis (1988), and the difference in the study site within TdR (Willis' study area was in a different part of the reserve to that of the present, in an area known as Groenvlei), it is remarkable how similar the prey species were between the two. Of the species identified to genus level or higher in the present study, and these were mostly the important ones in terms of occurrence, the only differences were that three species of *Camponotus* were found instead of one, two species of *Anoplolepis* were found instead of one, and no *Aenictus eugenii* were identified while Willis found it well represented in one sample. It is possible that *A. steingroeveri* was present in the faeces of the 1988 study, but that distinction was not made between it and *A. custodiens* because of their similarities when only heads are available (remembering that the two were

not distinguished in the faecal analysis of the present study either). With regard to the two species of termites occurring on TdR, the two studies concurred on the fact that both were represented in the diet.

Taking into consideration the minor differences between the two studies mentioned above, which can probably be accounted for by the difference in faecal sample size, it appears that the close similarities found regarding the prey species indicates that aardvarks all over TdR feed on similar species and that their selection has not changed over the course of a decade.

Comparing the prey species in the faeces of the present study with those predated during observations indicates that there were no species predated that did not subsequently come through in the faeces at some point. This means that it was unlikely that any species were missed out entirely from the faecal analysis due to being completely digested by the aardvark (although the proportions of different species or castes in the faeces may not have accurately represented those originally ingested - discussed later).

There were some species found in the faeces that were never seen to be predated by the habituated aardvarks during observations, but these were mostly those that only occurred in low numbers in the faeces. The probability of them being predated at these times was low. These species were *Monomorium* sp., *Tetramorium* sp. and all the unidentified Formicidae species (1 to 7). The Formicidae species 1 to 3 were not “Minor” species in the faeces like the others mentioned, but for some unknown reason were never observed to be predated. This may indicate, for species 1 and 2 at least (which were identified as male head capsules), that they were actually species already identified and were, therefore, predated during observation without it being realised. This factor remains to be tested.

Other references to the diet of aardvarks in southern Africa where empirical data were collected come from Smithers (1971, 1983), Smithers & Wilson (1971) and Melton & Daniels (1986). With regard to the prey species identified by these studies, which included examination of stomach contents by the first three and faecal analysis by the last, there was some agreement with the two studies carried out at TdR (including the present) but also some differences. These differences are probably explained by the differences in geographical situation between the study areas, which naturally has a large impact on the distribution of ant and termite species. Smithers (1971, 1983) determined the diet of aardvarks in Botswana and Zimbabwe, while Melton & Daniels (1986) examined faeces from Natal, South Africa. Many ant and termite species occurring in Botswana, Zimbabwe and even Natal do not occur in the southern Free State, and vice versa. The further north one goes, the more tropical the climate becomes and the more ant and termite species occur (Coatan & Sheasby, 1975; Hölldobler & Wilson, 1994). An

example of this concept can be provided by comparison with the number of ant and termite species pitfall trapped by Swart (1996) at Sabi Sand Wildtuin while studying pangolin (*Manis temminckii*) and the number of ant and termite species trapped at TdR by Willis (1988). Fifty five species were collected at Sabi Sand compared to 36 at TdR.

Formicid ants were identified as the principal components of three aardvark stomach contents in Botswana (Smithers, 1971), while termites were only found in trace quantities. Eight stomach contents from Zimbabwe (Smithers & Wilson, 1979) showed similar species composition to the three stomach contents above, and included *Dorylus* sp. and *A. custodiens*. Four consisted entirely of ants, another three contained ants in varying proportions, and four contained termites (one of which must have been entirely termites). A further 20 aardvark stomach contents were examined in Zimbabwe (Smithers, 1983), of which 15 contained ants and 13 contained termites. The list of species were as follows: Formicidae:- *Camponotus* sp., *Dorylus* sp., *Alaopone* sp., *Crematogaster* sp., *Typhlophone* sp., and *Anoplolepis custodiens*; Isoptera:- *Macrotermes falciger*, *Odontotermes badius*, *Odontotermes* sp., *Trinervitermes rhodesiensis*, *T. rapulum*, *Allodotermes tenax*, *Hodotermes mossambicus*, and *Pseudacanthotermes militaris*.

Melton & Daniels (1986) examined faeces from the Umgeni Valley Nature Reserve, Natal, and found that ants were the predominant prey species, with *Dorylus* sp. being the most important. Other ant species were unidentified. Termite species identified were *Odontotermes* sp., *Hodotermes mossambicus* and *Trinervitermes trinervoides*. This species composition was put together with only five faecal samples, however, which could potentially have come from one aardvark and hence not have been representative of the population.

The differences alluded to above between the studies at TdR and those further north are more clear when the termite prey species are considered. Interestingly, most of the studies found *Trinervitermes* spp. and *H. mossambicus* in the aardvarks diet, so when available these two species were commonly eaten, but the northern studies also identified at least four genera of Isoptera not in the diet of aardvarks at TdR. The reason for the absence of these termite genera in the diet of aardvarks at TdR was geographical; they don't occur in the southern Free State. In terms of the ants, there were overlaps in the genera predated between all the studies, such as *Anoplolepis* spp., *Dorylus* spp. and *Camponotus* spp. *A. custodiens* was mentioned in all of them.

## Species contributions

In the present study, the overall contribution made by the Formicidae in the diet of aardvarks was much greater than that made by the Isoptera. In particular, *Anoplolepis* spp. stood out clearly above the rest as the predominant prey species of aardvarks at TdR, in all months of the study (July 1996 to December 1997). This is in agreement with the results of Willis (1988) who found *A. custodiens* to be the most common prey species in the faeces, both in summer and winter. Willis (1988) presented a Table of faecal contents similar to that of Table 6 in the results section of this chapter, showing frequency of occurrence of prey species, proportions of prey species, and importance values of each prey species. In fact, the importance values and relative importance of prey species in Table 6 of the present thesis were calculated specifically for comparison with the results of Willis (1988).

Willis (1988) found that *A. custodiens* were present in all faecal samples, making up an average of 43.95% of the dietary items. It had by far the highest importance value (43.95, calculated in the same way as that of the present thesis) and was, therefore, the most important species in the faeces. From Table 6 it can be seen that *Anoplolepis* spp. were only absent in one of 263 faecal samples from 1997, so their frequency occurrence was virtually the same as that found by Willis (1988). The average percentage of 69.87% was considerably higher than found by Willis (1988), but this was probably due, in part, to the inclusion by Willis of *A. eugenii*, which comprised 11.45% of the overall percentages, but came from only one sample. This undoubtedly skewed the results. Also, Willis included items in his calculation not included in Table 6, such as seeds and fly pupae.

The remaining faecal contents presented by Willis (1988) were slightly different from those of the present thesis with respect to the order of importance of other prey species. What were similar, however, were the low average proportions and importance values of these other species relative to *A. custodiens*.

The biggest difference was probably *H. mossambicus*, which Willis found to be second most important, but which was only fourth most important in the present study. The difference in its importance value between the two studies was quite considerable. Also different was the percentage occurrence because the 1988 study found *H. mossambicus* in every faecal deposit, whereas the present one found it in only 44% of 1997 samples. During the feeding observations *H. mossambicus* was not often predated by either of the two habituated aardvarks, and certainly not every night. There were some months when it was not eaten at all. In 1998, after the field work for the present study was completed, the two habituated aardvarks apparently made more regular excavations for *H. mossambicus* during March and

April than had previously been observed (Le Roch, pers. comm.), although probably not significantly so. Also, one of the aardvarks habituated in 1998 switched from feeding on predominantly *M. capensis* in July 98 to predominantly *H. mossambicus* in November 98, at least during observational periods (Lindsey, pers. comm.). It is, therefore, possible that common species such as *H. mossambicus*, which were not regularly predated in comparison to *A. custodiens*, but that did make up part of the aardvarks diet quite often, were at times predated frequently enough to be found in most faecal samples. This could have been the case in the 1988 study. Alternatively, the aardvarks responsible for the faeces analysed in the 1988 study may simply have had a greater preference for *H. mossambicus* than those of the present study. A third possibility is that *H. mossambicus* was more available in 1988 than 1997, as a result of higher numbers in the veld. It has been established that during wet periods *H. mossambicus* populations are low, while during dry periods populations increase dramatically (Hewitt *et al.*, 1990). However, during the first half of 1988 TdR had higher than average rainfall (Willis, 1988), and higher rainfall than during the period of the present study. This appears to be the opposite of the required rainfall pattern, because higher rainfall in 1988 should have meant lower numbers of *H. mossambicus*. As the previous years rainfall (1987) was not presented, it is possible that it was a drier year, leading to higher numbers of *H. mossambicus*.

*T. trinervoides* was second most important in the present study compared to third in 1988, when it was relegated by *H. mossambicus*. The average proportions of total numbers was very similar between the two studies (13.8% in 1988, 13.6% present) but the percentage occurrence was considerably different (30% in 1988, 87.8% present).

*M. albopilosum* was third most important in the present study, compared to sixth in 1988. Willis found *M. albopilosum* to occur in only 55% of faecal samples and comprise an average of 1.86% of prey items. The present study located it in 85% of samples, with an average of 8.28% of prey items.

There was also some disagreement between the two studies regarding the placement of the rest of the prey species in order of importance, but this can probably be considered of little relevance due to their lower occurrence and low average percentages of total numbers. Interestingly, *M. capensis* was found by both studies to be fifth most important in the faeces, with Willis (1988) finding it in 70% of samples with a mean of 2.6%, compared to 57% of samples in the present study and a mean of 1.1%.

The contrast between the two studies regarding the differential contributions made by the individual prey species could be explained by a combination of factors. First, the time lapse between studies, although not altering the actual prey species themselves significantly, could have played a role in

modifying the degree to which the different species were predated. It would be expected that ant and termite populations would vary to some degree in size and abundance through time (e.g. *A. custodiens* populations in citrus orchards at Letaba, Steyn, 1954), in relation to environmental variables that have either beneficial or negative effects on their numbers.

One such variable could be rainfall. The mean monthly rainfall during the course of the 1988 study was higher than the average calculated from 1968 - 1987, and in fact the month of February 1988 had the highest rainfall for the whole period. During 1996 and 1997 the mean monthly rainfall was lower than average for most months, except November/December 1996 and March 1997 (see Figure 3). Therefore, the rainfall during the study period of 1996 - 1997 was probably lower than that of the 1988 study. Unfortunately, very little is documented about the community ecology of most ant and termite species in southern Africa and how they are altered by environmental conditions or any other potential influencing factors, but it is probable that large differences in rainfall patterns would have some impact on the densities of ant communities, and even the survival of some colonies. Ant and termite species would probably have differential survivorship at different levels of rainfall, and this would influence the extent to which they could be predated. A greater knowledge of environmental affects on the survivorship of ant communities might give clues for the differences between the two studies.

A second factor that could have contributed to the differences between the two studies was the separate sites in which the research was conducted. The main focus of the present research was on the south-west side of the reserve in a loop of the Orange River. The 1988 study concentrated around an area on the Caledon River side of the reserve (Groenvlei), which is separated from the aforementioned area by the high central ridge of sedimentary rock. There are, however, two factors that possibly reduce the importance of the separate sites as a cause of the disparity. First, the ant communities sampled by Willis (1988) at Groenvlei were similar to those around the present site in 1997, at least in terms of species present. From quadrat data, personal observations and pitfall trapping data collected by Lindsey (pers. comm.) in 1998, it appears that ant species occurring in the present study area were similar to those found by Willis, and that they occurred in similar proportions, at least for the more dominant species. Secondly, the combined faecal data of Figure 18 of the present thesis included faeces collected from the Groenvlei area, and sites elsewhere along the Caledon River, and so incorporated some of the potential differences between areas into the results. Bearing these factors in mind, it is still probable that there were some differences between the communities, and these could have had an impact on the foraging behaviour of the aardvarks.

A third possible cause of the differences between studies were inevitable random processes, which were more likely to occur as a result of the fairly low sample sizes analysed by Willis (1988) and Willis *et al.* (1992). As already discussed, the lower the sample size, the more chance of missing out rarer prey species and the greater the chance of an abnormally large percentage of one species in a single sample skewing the data.

### **The limitations of faecal analysis**

One potential inaccuracy in the estimates of numbers and proportions of different prey species eaten by aardvarks which needs to be considered before any genuine conclusions can be drawn from faecal results is the differential digestibility of these prey species. Analyses of faeces can normally only give an approximate indication of dietary composition; differential digestibility of different food stuffs will result in absolute proportions of residues in the faeces which may differ considerably from the proportions in which the food stuffs were actually ingested (Putman, 1984).

A basic assumption when determining an animal's diet by frequency of occurrence in faeces is that each occurrence of a prey species in different faeces represents different prey individuals (Bowland & Bowland, 1991). Bowland & Bowland (1991) found in the serval (*Felis serval*) and black backed jackal (*Canis mesomelas*) that such an assumption may be questionable and may result in an over-estimation of prey when sequentially passed faeces are collected. An important difference, however, between predators such as the above, which eat relatively large prey such as mice, and a predator like the aardvark, is that analysis of the carnivores scats looks for separate parts of single animals (such as teeth), so there is a chance of assigning faecal items to different prey individuals when they in fact belong to the same animal. There was no chance of this occurring in the analysis of aardvark faeces because individual ant heads were counted, and as no ant had more than one head, an over-estimation was not possible.

Another potential cause of inaccuracy arises with differential particle size, especially in the analysis of plant material eaten by herbivores. Analyses based on fragment counts score plant cuticle fragments of different sizes equally, when the proportion by volume in ingested food stuffs is not equivalent. Again, this does not affect counting of ant heads, where one head represents one ant.

Few food stuffs have constant digestibility or persistence rates, and the digestibility of a particular species may vary according to the constituents of the rest of the diet with which it is mixed (Putman, 1984). As insects, ants and termites have a cuticle which functions in support, muscle attachment,

permeability barriers and protection (Rockstein, 1978). This cuticle forms the exoskeleton and is a complex secretion from differentiated epidermal cells of ectodermal origin. It is composed of a complex glycoprotein formed from the binding of chitin with protein. Chitin is the major component of the cuticle and is a very strong, lightweight material. The composition of the cuticle varies between insect taxa and between different developmental stages within species.

The heads of adult worker ants have a thick sclerotised cuticle that is not digested by the aardvarks (see below) but their developmental stages do not have this resistance. The outer coats of insect eggs (the chorion) do not generally contain chitin (Hinton, 1981) and as a result are less resistant to chemical or mechanical attack such as they are exposed to in the digestive system of aardvarks. Larvae are soft with a transparent chitinous integument that is very thin and easily ruptured and are also less resistant to chemical attack than adult workers. Neither eggs nor larvae were ever found in the faecal samples of the aardvarks and it can, therefore, be assumed that they were virtually always totally digested. Formicidae pupae were the only developmental stages of ants to ever make it through into the faeces, but they were only ever found in low numbers. At certain times of the year these pupae were a common site in the excavated nests of ants on TdR and must have been ingested to some extent (discussed later). They must, therefore, also be predominantly digested by the aardvarks, but not as entirely as the eggs and larvae.

Personal observations during faecal analysis indicated that adult Formicidae heads appeared to come through without being digested. For there to be differential digestibility of heads amongst the adults it would be expected that heads would come through in the faeces at different levels of digestion. In other words there would be a gradation in the thickness of the heads, with the more digested ones being thinner and more delicate than less digested heads. This did not appear to be the case. Virtually all adult ant heads were still hard during faecal analysis. It was assumed, therefore, that all the heads of adult Formicidae ants eaten by the aardvarks came through in the faeces, give or take a small number, so long as they were not damaged mechanically in the process, such as by chewing. The exception to this was *M. capensis* which was regularly chewed by the aardvarks, and will be discussed later. This assumption that all heads came through in the faeces was not made for the eggs, larvae and pupae, for the reasons given above.

The heads of all castes of *T. trinervoides* were more delicate than Formicidae heads and probably more easily digestible as well. Friend (1982) suggested that ants have heavier exoskeletons and are more difficult to digest than softer bodied termites. Even so, differential digestibility does not necessarily mean that some termite heads (adults) were completely digested by the aardvarks, but rather that adult

ant heads may have been more resistant to digestion than adult termite heads. The heads of adult sterile *T. trinervoides* are sclerotised (as are those of ants, to a greater degree) and, therefore, resistant to the chemical attrition of an animals digestive system. It is considered unlikely that they would be digested while passing through the gut of the aardvark (Adam, pers. comm.), so long as they are not damaged before being swallowed. Because the aardvarks were never observed chewing when feeding on *T. trinervoides* it was assumed that virtually all heads of adult castes came through in the faeces. As with the ants, this assumption was not made for the larval stages of termites because larvae are not sclerotised. *T. trinervoides* larvae were in fact rarely found in the faeces.

The heads of adult *H. mossambicus* are much harder and more heavily sclerotised than those of *T. trinervoides*, so it was assumed that they came through completely in the faeces

### **The difference between the faecal proportions of species and the observed proportions**

The most obvious method available for assessment of differential digestion is to establish constant relationships between ingesta and egesta in feeding trials (Putman, 1984). Such trials are difficult to conduct because they require captive animals, and as mentioned above were not, but the observations of feeding behaviour carried out during the course of this study allowed some comparison of the proportions between observed predation and faecal results.

Comparison of the prey species proportions in the faeces of aardvarks M5 and F4 (Figures 19 and 20) with the proportions predated under observation (Figures 34 and 35) immediately indicates a disparity. For the most important prey species, none of the Figures agreed. Either a species was represented in the faeces in greater proportions than it was observed to be fed on, or it was under-represented relative to the number of feeds observed. In most months *Anoplolepis* spp. and *M. albopilosum* were present in the faeces in greater proportions than they were observed to be fed on, often as much as 15 to 20% in the case of the former. The reverse was true for both *M. capensis* and *T. trinervoides*, which were apparently under-represented in the faeces relative to the amount of observed feeds on them. The disparity becomes greater when the proportion feeding time is considered for each of these species (see Figures 34 and 35). The proportion of time spent feeding on *A. custodiens* was lower than the proportion of its feed counts, while the proportions of time spent feeding on both *M. capensis* and *T. trinervoides* were greater than the proportion of their feed counts.

Appendix V shows comparisons between monthly percentage occurrence in the faeces and monthly percentage of time spent feeding for the two main prey species, *A. custodiens* and *T. trinervoides*, for

both habituated aardvarks. The disparity mentioned above is easier to visualise in this form than by cross reference of Figures 19, 20, 34 and 35, but these diagrams will be discussed later.

Whether the proportions of a prey species in the faeces were greater or less than the proportions of that same species in the observed feeds, there was still general agreement that an increased proportion of that species in the faeces correlated with an increased proportion in the observed feeds.

Two possible explanations for these differences were differential digestibility (as above) or differential rates of intake. If differential digestibility was a factor, *Anoplolepis* spp. and *M. albopilosum* would have been less easily digested than *M. capensis* and *T. trinervoides*. If the second factor was important it would mean that *Anoplolepis* spp. and *M. albopilosum* were eaten more quickly than *M. capensis* and *T. trinervoides*. Unfortunately, neither possibility was tested during the study, and neither would be easy to test, but from knowledge of the ecology of the prey species gained during the study, certain hypotheses can be considered.

The behaviour of the different prey species should have some effect on their potential rate of intake by the aardvarks because they have differing nesting habits, activity patterns and defensive responses. Species that are densely packed in their nests and that are easily accessible, such as being close to the surface, should be extracted at a greater rate than species that are less densely packed and live deeper. Also, it might be expected that species that swarm to the sight of the attack in defence of the nest make themselves more accessible, thereby increasing the rate of intake.

Personal observations from the excavation of a number of ant nests while collecting ants for calorific analysis, and from predatory digs made by the aardvarks while foraging, indicated that density might have played a role in the rate of uptake of the three ant species. Both *Anoplolepis* spp. and *M. albopilosum* were found in dense congregations when dug out of their nests, whereas *M. capensis* was not. The relatively low numbers of *M. capensis* in the faeces compared to the observed feeding times may, therefore, have been partly the result of lower densities of ants reducing the intake rate.

*T. trinervoides* on the other hand were found in very high densities, particularly when inside a mound, so aardvarks would have been expected to have high rates of intake when feeding on them. *T. trinervoides* were, however, under-represented in the faeces relative to the proportion of observed feeds. This indicates that something other than intake rate was responsible for the apparent under-representation of *T. trinervoides* in the faeces, or that even though the termites were densely packed in the mounds, there was a confounding factor that lowered the intake rate.

*Anoplolepis* spp. dig depths varied from light scratches at the ground which simply opened up ant ports, to digs as deep as 50cm. The average depth was approximately 10cm (pers. obs). Steyn (1954) described the nest architecture of *A. custodiens*. Nests usually had several exits, with extensive horizontal tunnels and irregular vestibules made within the first 5cm from the surface. From one of these vestibules a single vertical tunnel usually led to the first queen cell. Successive queen cells were linked by vertical tunnels. The average depth of the lowest queen cell was 45cm. The shallow digs made by the aardvarks probably extracted *A. custodiens* from tunnels and vestibules near the surface, while successively deeper digs were reaching the queen cells further below.

*M. albopilosum* were on average extracted from digs of 10.5cm depth, but there was less variation than with *Anoplolepis* spp. Nothing is documented on their nesting habits but they were never deeper than 20cm.

*M. capensis* digs were the shallowest of the three ants, with an average of 6cm, and were rarely extracted from digs deeper than 15cm. *M. capensis* is a granivorous ant (Dean & Yeaton, 1993; Milton & Dean, 1993; Vorster *et al*, 1992) which stores seeds inside nests. Seed storage is confined to cells within the mounds of organic material which sits on top of nests, while workers, larvae and alates are found in the subterranean galleries and passages. No reference was found concerning the depths of these subterranean tunnels, but nest-mounds (the epigeous build up of seed husks and other detritus above the nest chambers) were found to average 1022mm in length, 680mm width, and 186mm height.

There was not a great difference between the required dig depths for the three ant species just discussed so it appears unlikely that depth related accessibility was a factor influencing handling times. Apart from when the aardvarks dug deeper than average holes for *A. custodiens* (up to 50cm), the initial digging time to reach the ants was similar (and quick).

Where there was a difference in the digging time for *M. capensis* was in the way it was extracted compared to the other two ant species. *A. custodiens* and *M. albopilosum* predations were normally discreet events such that the aardvark made one excavation only. In the case of *Anoplolepis* spp. the aardvarks often dug intermittently between feeding, but these extra digs either deepened or extended the original holes. In the case of *M. capensis*, the aardvarks regularly made lots of separate scratches at the ground in close proximity, often covering areas of 1-2m diameter over a period of 30 minutes or more. This pattern of feeding many times in a small area on *M. capensis* fits in with the nest architecture of the ant, of which the dimensions are given above.

An added factor that may partially explain the low numbers of *M. capensis* in the faeces is the fact that aardvarks spent time chewing them. All four habituated aardvarks (including the two not used in the present study), chewed when feeding on *M. capensis* but they did not often chew on other species. The animals often spent longer chewing than taking in ants at these times, and often an aardvark had a cheek visibly full of food. Such a chewing action could crush the ants to a point where they are more easily digested and less likely to come through the digestive system in a recognisable form. It also would have served to increase the handling time. The feeding pattern was dig, take in ants, chew... dig, take in ants, chew... etc.

The digging time for extraction of *T. trinervoides* depended on whether they were dug out of epigeous mounds or from shallow scrapes in the soil surface away from the mounds. The former generally required a greater initial effort because the outer layers of mounds were very hard, while the latter was probably the easiest form of food dig available to the aardvarks relative to the other ant species. When *T. trinervoides* forage on the surface away from mounds they get to their foraging sites by moving through tunnels approximately 2.5cm under the surface of the ground (Adam, 1993) and are, therefore, always easily accessible. Digging them up at these times only requires shallow holes. When the termites are on the surface the aardvarks do occasionally lick them directly off the ground, but this is not as common as digging them out of the tunnels. Two possible reasons for this are that the termites are more concentrated when in the tunnels than when on the surface, and that the aardvarks tongue is not adapted to “lapping” up small prey when spread out on the ground, such as is the tongue of the aardwolf (*Proteles cristatus*). The aardvarks tongue is instead adapted for insertion into the narrow tunnels of ant and termite nests. As mentioned earlier, digging into a mound took longer than other food digs because of the hard outer layers, but the inner structure of the mounds were much softer (Adam, 1993; pers. obs.) and once inside the going was easier and thousands of termites were readily accessible. Adam (1993) reported numbers of *T. trinervoides* of over 880 000 in large mounds, and as they were not as fast moving as ants in general, and could only move to other parts of the mound to escape, were virtually sitting targets for the aardvark.

An added factor to confound the digging time into a mound was whether or not the aardvark dug the mound for the first time, or whether it dug in the hole of an already excavated mound. Digging open a mound for the first time naturally took longer because the outer layers had to be excavated first.

The third possible factor influencing intake rate was the defence behaviour of the different prey species. *Anoplolepis* spp. workers emerged from their tunnel systems in large numbers when under attack from an aardvark (pers. obs) although this was reduced in the colder months when the lower temperatures

inhibited their freedom of movement. While they were in the tunnels nearer the surface such defensive behaviour probably increased the intake rate of the aardvarks, but when on the surface they were effectively no longer available for predation because the aardvarks did not often take ants from there. Steyn (1954) reported that adult workers remained in the tunnel systems during the cold months, so were still accessible but not swarming to the site of attack.

*M. albopilosum* appeared to rush out of their nests as well, but as they were smaller and had smaller nests it was difficult to tell what their behaviour was. When their nests were opened up it often appeared as though the whole core was exposed because hundreds of tiny ants were on the surface. *M. capensis* were rarely observed around the site of the dig while the aardvark was feeding and were often only identified after the animal had moved away. Even then they were visible only in very low numbers. Swarming the site of the breach was, therefore, not the behavioural reaction of this ant species and as their defence appears to be very poor anyway (the largest individuals cannot penetrate human skin) it is apparent why this is so.

The reaction of *T. trinervoides* to predation is dependent on the caste, because soldiers move to the site of attack while workers move away from it, further into the mound (Adam, pers. comm.; pers. obs). Should the aardvark be seeking soldiers as a food source this situation would be ideal, and in fact soldiers were often represented in the faeces more than workers. This may, however, have been the result of the soldiers being in the way rather than a selection, so if the workers were more sought after, the handling time may have been increased because the aardvark had to chase them. Often when feeding in a mound the aardvarks intermittently dug away more of the internal structure to chase after termites, specifically workers.

To summarise the possible causes of variation in intake rate of the four main prey species, *A. custodiens* and *M. albopilosum* occurred in relatively dense congregations, had good depth related accessibility, and swarmed to the surface in defence, all of which indicated quick gathering times for the aardvark. These factors may help explain why they occurred in higher proportions in the faeces than in the feeding observations. *M. capensis* occurred in relatively low densities, did not swarm to the surface in defence and were chewed. It had a slower handling time which appeared to be correlated to lower proportions in the faeces than in the feeding observations. *T. trinervoides* took longer to get to when inside mounds, but once the aardvark had broken in, the densities of termites were very high (and there were many more available than any of the ants from their nests). When extracted away from mounds, *T. trinervoides* were easily accessible. The low proportions of *T. trinervoides* in the faeces compared to the feeding observations cannot be explained by long gathering times.

## Species richness and diversity

The variation in overall dietary species richness with time was demonstrated in Figures 16 and 17. Both indicated that the number of species predated by aardvarks was lower in winter than summer. The average species richness (Margalef) per replicate calculated for the seasons (Table 8) did not indicate such a clear winter summer distinction, but rather a general increase through 1997 for both habituated aardvarks. This does not necessarily indicate a contradiction, however, it just shows the difference in the way the data were used to calculate the two indices. The first calculated overall species richness in a cumulative way, so that any new species in a month or season increased the richness value, regardless of which replicate it was. The second calculated richness for each replicate individually, so any new species for a month or season could only contribute to the richness of its specific replicate. In other words, rare prey species increased the richness when it was accumulated over a season, but did not do so when restrained to a single sample. The reason for this was that individual replicates implicitly had low richness relative to the overall seasonal values, because no individual faecal sample had more than six or seven species, and most were confined to five or less.

It therefore appears that when considering any given time period of short duration there was no seasonal trend in prey species richness, but when the diet for longer periods, such as months or seasons, were compared, there was a seasonal trend - prey species richness was higher in summer than winter. This increased richness in summer must have been the result of predation on more of the rarer species.

Regarding the average species richness, although there was no apparent trend, there was a rise in richness in summer (NDJ) for both aardvarks. This does not fit in with any trend but rather indicates a change in the aardvarks feeding behaviour not associated with a cycling external source. The cause of this is unknown.

The observation results of species richness' were not comparable between months because the monthly hours of observation were unequal and, unlike the faecal data, the months with the longest observation periods were not those with the lowest species richness, so there was no negative correlation. Instead there appeared to be a positive correlation between the total observation time and species richness, so no legitimate conclusions could be drawn.

A pattern for the variation in prey diversity was harder to determine. With the combined faecal data it appeared that the winter months had a lower prey diversity than the summer months, similar to that of overall species richness. This was in agreement with the results of Willis (1988) and Daniels (1984)

who found greater prey diversity in aardvark faeces during the wet season (summer) than during the dry. However, examination of the faeces from the two habituated aardvarks separately showed no such seasonal trend. In fact the average diversity in Table 8 indicated that aardvark F4 showed a continual increase in prey diversity throughout the year.

Two possible explanations for such a unidirectional change in prey diversity with time, aside from seasonal changes in the ant community, might be that the aardvark changed its feeding preferences which led to it feeding on more prey species (or on the same species more evenly), or that the animal changed the area in which it foraged and, therefore, the ant communities to which it was exposed. Feeding preferences were not investigated in this study, so this slightly anthropomorphic idea is an unknown factor, but it was known that aardvark F4 shifted the main area of her home range during the study, so this may have been a partial cause of the apparent alteration in the diversity of her diet.

Table 8 also shows evenness of the prey species in the faeces of both aardvarks and indicates that in each case it increased from January to September, then decreased slightly in summer, although not to the low levels of the previous autumn. July to September had the highest levels of evenness in the prey species indicating a better spread of prey species in the faeces. This was probably the result of the high predation rate of *T. trinervoides* mounds at the time, lowering the dominance of *Anoplolepis* spp.

### Dietary variation in time

The diet of the aardvarks of TdR as established by the faecal analysis, was separated into monthly percentages to examine variation with time (see Figures 18 to 20). It was considered probable *a priori* to this that there would be changes in the composition of the diet with time, and that these changes might be somehow correlated with the seasons. The faeces in the present study were grouped initially by month rather than season because months were considered more objective than seasons and because there were sufficient data to do so. Grouping by season would have presumed at the outset that any variation must be caused by it and might have missed more subtle or gradual differences that shorter intervals could highlight. Figures 18 to 20 show immediately that there were considerable differences in the proportions of prey species between months, even consecutive ones, and that there were differences in species composition as well.

The two dominant species in all months faeces were *Anoplolepis* spp. and *T. trinervoides* (*A. custodiens* and *T. trinervoides* were also dominant in the feeding observations). Two main points can be drawn from examination of the monthly variation. First, by comparing the monthly variation of

*Anoplolepis* spp. in all three Figures (18 to 20) it is apparent that they were not identical. The two most similar data sets were from aardvark M5 and the combined data of all aardvarks. Both fluctuated down then up, three times and four times respectively, with high and low values occurring in both warm and cold months, but not necessarily at the same time. In the same vein, *T. trinervoides* fluctuated with the reverse pattern, again with high and low values in both warm and cold months, but no apparent trend. The percentages of *Anoplolepis* and *T. trinervoides* in the faeces of aardvark F4 did not follow any patterns exhibited by the two just described, instead there was a general trend of decreasing *Anoplolepis* and increasing *T. trinervoides* through 1997, with a couple of minor reversals in June and October. There was, therefore, quite a lot of variation between the different aardvarks.

Secondly, from the fluctuation (or lack of it) just described, it appears that there was no trend in the variation of percentages of either species. Because there were highs and lows in months coinciding with both warm and cold months, no seasonal trend could justifiably be identified, at least not from the monthly separation. This was in contrast to the findings of both Melton (1975) and Willis (1988) who found that ants were predated more often in winter than summer, and termites predated more often in summer than winter. It is possible, therefore, in the case of the 1988 study, that the differences found between seasonal proportions of both prey Orders were due to chance, and that the variation demonstrated could have in fact been reversed had slightly different months been selected to collect the faeces.

In addition to this, although no apparent trend was discernible, percentages of *T. trinervoides* were generally high in the colder months and had their highest peaks in the months of August, July and September for the combined data, aardvark M5 and aardvark F4 respectively. As July and August are both cold months, this result was the reverse to that found by Melton (1975) and Willis (1988), as described above. This will be discussed in more detail later.

As would be expected, the patterns of fluctuation in the Formicidae, as shown in Figures 25 to 27, were similar to those for the two dominant species just discussed. In the combined faeces and the faeces of M5, levels of termites were generally higher in the winter months of 1997, although there was a certain level of fluctuation. Termites in the faeces of F4 were also high in the winter months, but continued at high levels into the summer, except for a reversal in September. High levels of termite predation in the winter months is the opposite to what was found by Melton (1975) and Willis (1988), as discussed above.

After the main two prey species, the third most important was *M. albopilosum*. It occurred in about 85% of all faecal samples at an average of just over 8% of total heads. As with the previous prey species, *M. albopilosum* numbers fluctuated in the faeces through the year, but there did appear to be a general high level around September. Both aardvarks M5 and F4 had their highest levels of *M. albopilosum* in September, as did the combined aardvarks. The exception was September 1996 which did not have a high level. The trend was clearest in Aardvark F4, where percentages of *M. albopilosum* were always well below 10% but then suddenly increased to 39% in September. Levels were then generally higher for the rest of the year before decreasing again at the beginning of 1998 (this last point can be seen by examining appendix III). Similar but less pronounced trends occurred in the combined faeces and those of M5. Examination of Figures 34 and 35 for the feeding observations agrees with the faecal results. Both aardvarks M5 and F4 showed a marked increase in predation of *M. albopilosum* in September 1997.

This common pattern for different aardvarks must indicate some ecological factor in the life cycle of *M. albopilosum* which cannot be answered by this thesis. Were the ecology of this ant species better understood the answer would probably be found. From observations of feeding during September there were often pupae visible in the nests of *M. albopilosum* after the aardvark had left the site. An increase in pupae production at this time might form an improved food source for the aardvark and might, therefore, be the cause of the increased predation of *M. albopilosum*. Also, if the occurrence of pupae in the nests coincided with high levels of eggs and larvae, as it did with one of the peaks of egg production in *A. custodiens* at Letaba (Steyn, 1954) (see below) this would have been an added incentive to predate the species at this time. Unfortunately, these developmental stages of ants rarely appeared in faecal samples as discussed above, so whether the aardvarks were eating a lot of them in September is not known. Also, it was just not possible to see whether these stages were being eaten during observations because all that could be observed were the prey species in the nest (it was not possible to observe the ants being taken into the aardvarks mouth).

What was apparent was that many pupae extracted from the nests fell onto the ground at the site of the dig and were not ingested by the aardvarks (hence the observation of pupae at the food digs). Sometimes entire caches were found untouched after the aardvarks had stopped feeding, just centimetres away from the dig site in the same ant nest. This might indicate that the aardvarks were not preferentially selecting pupae when they were available (similar observations were made for *A. custodiens* and *A. steingroeveri* when pupae were observed). It is, however, also possible that although pupae were apparently discarded when available, this may have been by accident, and those left uneaten may have been a small proportion of those ingested. This would be similar to the feeds on ants and

termites at most other times because some prey were always left uneaten at dig sites after the aardvarks finished feeding.

Of the rest of the prey species, only two fluctuated to a degree in which a trend could be ascertained. Formicidae species 1 (actually a male ant) was virtually absent from all months in 1997 before October, at which time it started to appear in the faeces. November and December faeces had the highest levels of this species in all the faeces, after which the numbers dropped again to nothing. From appendix III it can be seen that the December 1996 faeces of M5 and October and November 96 faeces of other aardvarks also had elevated levels of Formicidae sp.1, indicating a cycle that occurred in two consecutive years and not just 1997. As pointed out in the results section, Formicidae sp. 1 was only identified as the head of a male ant, so could theoretically have belonged to one of the other identified species. Regardless of which species it was, October to December was obviously the period of the year in which these male ants occurred, and at this time the aardvarks preyed on them. Because these male ants were unidentified and never observed in the field, feeding observations could not back up the faecal results.

*S. punctaticeps* was virtually absent from the faeces of aardvarks M5 and F4 for all months except March, at which time there was a very distinct increase. This pattern was not observed in the faeces of the other aardvarks, in fact only one replicate contained a substantial number of *S. punctaticeps* heads, and this occurred in April 97. This was close to March, so could naturally be incorporated into this period. The reason for the lack of samples from other aardvarks with *S. punctaticeps* is unknown, but possibly had something to do with the distribution of this prey species in other areas of the reserve. Again, the reason for the upsurge in predation of this species probably had something to do with its life cycle, and in fact most of the faecal samples in March had the heads of queens alongside workers, often in quite large numbers. The time around March may have been the period in which *S. punctaticeps* produced queens, and as queens generally have high calorific and nutritive values relative to workers they would be of more value to predate than workers alone. Alternatively, it is possible that *S. punctaticeps* were unusually close to the surface at this time as a result of the flying of queens, and were, therefore, more likely to be located by the aardvarks. After March and April, *S. punctaticeps* disappeared from the faeces. Feeding observations were in agreement with the faecal results, because both aardvarks M5 and F4 were observed to feed on *S. punctaticeps* at different localities only during March 1997, and queens were visible in the nests after the excavations were completed.

It is interesting to find trends in the feeding habits of the aardvark as above, and to postulate possible reasons for their occurrence, but as the three latter prey species above did not play significant roles in

the diet of the aardvarks of TdR it may not be particularly relevant to do so. Such trends predominantly reflect the life cycles of the ants rather than the ecology of the predator. The same can be said of the two prey species that were most important in the diet of aardvarks of TdR during the study period, *A. custodiens* and *T. trinervoides*, except that they were more significant because they formed the staple part of the diet. Fortunately, of all the prey species recorded, these two (along with *H. mossambicus*) have been the most studied and are the best understood ecologically. What follows is a brief examination of the life histories of the two prey species and a comparison of these with their observed fluctuations in the diets of the aardvarks of TdR.

Figure 43 illustrates the life cycle of *A. custodiens* as determined by Steyn (1954) at Letaba in the NE Lowveld of South Africa. Forty eight nests were excavated every month from June 1948 to June 1949 and the different developmental stages counted. Note that each monthly figure is the total count for the month, i.e. 48 nests, not the count for one nest. It should be realised that the study was carried out at a warmer site than the present project, so ant numbers may have been higher, particularly in winter, and that the majority of the study was conducted inside a citrus estate, not the same habitat as TdR. The author did, however, make comparisons between the orchards and open veld, which was beneficial to the present study. Figure 43 does not include ant workers because that required killing the nest with insecticide, which the author did not want. This was done separately instead.

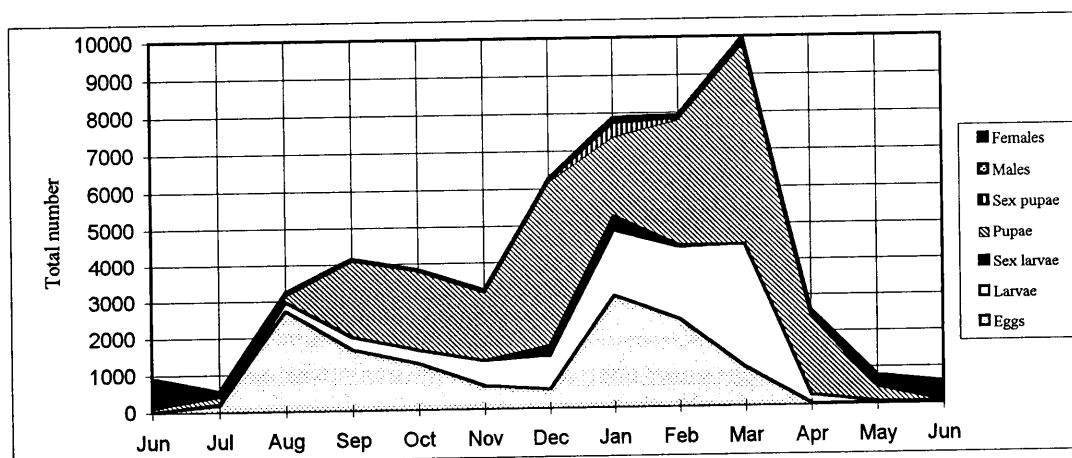


**Figure 43.** Summary of monthly excavations of 48 *A. custodiens* nests at Letaba, 1948/49, from Steyn (1954).

The following conclusions can be drawn from Steyns results:

Numbers of all the developmental stages were lowest in winter (May-July), with a few pupae and females existing alone. January to March had the highest levels in total (peak in March).

Egg production had two peaks in August and January, and in both cases the high levels lasted three months.

Levels of larvae and pupae increased from August to March, then decreased through the winter. The sexual larvae and pupae only occurred from November to February/March.

Female ants were most numerous in winter.

From separate but comparable nests, Steyn (1954) counted the number of adult workers. Results below were averages from 12 nests in each month.

May 1949: 716 workers

June 1949: 653 workers

July 1949: 576 workers

Steyn (1954) reported a second decrease in adult worker numbers in the nests during the late summer months.

The duration of egg, larval and pupal stages were found to be temperature dependent, with higher temperatures (up to a point) lowering the developmental time. For minor worker production the duration of the egg stage was 10-18 days, while for the larval and pupal stages it was 16-25 days and 33-40 days respectively. Medium and major worker development took slightly longer, but not more than a few days for each stage. Therefore, minor adult sterile workers would have started to emerge within 80 days after the onset of egg production, which started in July/August at Letaba, and would have continued to emerge for 80 days after the cessation of egg production in March. Numbers of adult worker sterile caste would, therefore, have continued to decline at the end of the winter (from an average of 576 workers per nest in July, see above), due to natural mortality (with no recruitment), until approximately early October, at which time they would have started to increase again. Numbers of adult sterile workers should have been at their lowest in August and September.

For the purposes of this study, the life cycle of *A. custodiens* at TdR is assumed to parallel the life cycle of *A. custodiens* at Letaba because the two sites share similar seasonal variation and timing. However, the two sites have locally different temperature ranges and rainfall patterns, with TdR being drier and much colder in winter, and this probably delays the onset of egg, larvae and pupae production at TdR and shifts the timing of reproduction along by a few weeks. As the life cycle of *A. custodiens* has only been studied at Letaba, the exact effect of climatic variation on the start and duration of the life cycle is unknown, but it is likely that the high levels of larvae and pupae found at Letaba in the summer months also occur at TdR, although the duration of the cycle is probably shortened at one or both ends.

The colder average temperatures of TdR should slow down the developmental rate of the eggs, larvae and pupae (as discussed above), and added to the expected later onset of egg production (again as a result of lower temperatures), adult sterile workers probably emerge later at TdR than at Letaba. The lowest levels of adult sterile workers at TdR are assumed to occur between September and October.

If aardvarks fed preferentially on adult sterile workers and did not seek the developing stages for additional nutrition, the time of year when they would have been most successful would obviously have been when there were the most adult sterile workers available. This should have been between December and March at TdR. If aardvarks sort out the developing stages of *A. custodiens* when available, the best time to do so would also have been from December to March, thus overlapping with the best time for adult sterile workers. It appears, therefore, that the best time of year to feed on *A. custodiens* would be early summer to autumn.

It would be difficult to tell whether this was the case because the aardvarks would have continued to feed on adult sterile workers regardless of whether the ants were more or less available. A reduced level in the faeces may simply indicate less ants per nest, not a reduction in their selection. Also, as discussed earlier, eggs and other developmental stages are more easily digested because they have not got the same sclerotised cuticle of adults, and as a result were rarely found in the faeces. Their absence in the faeces, therefore, does not necessarily indicate that they were not eaten.

Pupae were the only developmental stage found in the faeces, and when they occurred they were always in low numbers. They were found mostly from October to January in both 1996 and 1997, with a very small number in February 1997 as well. High levels of pupae coincide with high levels of eggs and larvae, so it is possible that during the time the aardvarks were feeding on pupae they were also taking

advantage of higher levels of eggs and larvae. Feeding trials or analysis of stomach contents would be the only way to investigate whether or not aardvarks fed on the developing stages of *A. custodiens*.

Comparison of the life cycle of *A. custodiens* with appendix V, which show the monthly proportions of *Anoplolepis* spp. from both the faeces and feeding observation times, does not give any clue as to whether or not there was any relationship between ant numbers available (adult or developing) and the feeding behaviour of the aardvarks. There was a lot of monthly fluctuation in the numbers of worker heads found in the faeces and in the proportion of time spent feeding between months, but there was little agreement between the two aardvarks for this variation. Values for M5 were both high and low in both warm and cold months, while those for F4 decreased fairly continuously throughout 1997 (this was discussed earlier). Comparison of the life cycle of *A. custodiens* with the combined faecal data would not be useful in this situation because monthly percentages would be averages from many animals and may not reflect the behaviour of any one aardvark.

At the time when the numbers of developmental stages of *A. custodiens* should have been at their lowest (in winter), the levels of observed predation on their nests by the aardvarks were also low, but not at their lowest. The levels of *A. custodiens* in the faeces of M5 were intermediate at this time, except in July, while the levels in the faeces of F4 continuously decreased through the period, but never increased again in the summer as would have been expected if correlated with numbers of developing ants. No conclusions can be drawn from these results.

Whether or not the eggs, larvae and pupae were important constituents in the diet of the aardvarks on TdR during 1997, their reduced numbers in the winter months did not appear to force the aardvarks to stop feeding on *A. custodiens*.

This might indicate that the aardvarks did not alter their feeding on *A. custodiens* according to the presence or absence of other developmental stages within the nests, but that when these developmental stages occurred in higher numbers, the aardvarks diet was improved as a result of gaining eggs, larvae and pupae as well as adult workers. The aardvarks calorific and nutritional intake would have, therefore, been improved during the summer months, not because they fed more often on *A. custodiens* but because when they did so they also got the added bonus of the developing ants. The quality of individual feeds would have been greater rather than the quantity, assuming the aardvarks made use of the developing ants when they were available (it is known that they must have at least ingested pupae, because these were found in the faeces in low numbers). What may be of importance here is the result

that the two habituated aardvarks spent more time per hour feeding in winter than in summer, and this may have been the result of not just a decreased activity period, but also a poorer quality of diet.

If the aardvarks made use of the increased levels of developing *A. custodiens* when they occurred, they might have been expected to feed for longer on average so as to have enough time to ingest as many as possible. The average feeding lengths on *A. custodiens* by the two habituated aardvarks were tested to investigate whether more time was spent feeding in summer to allow for greater intake of these developing ants. The results (Table 19) were conflicting, with aardvark M5 feeding for longer in summer but F4 feeding for longer in winter. In fact the most significant difference between seasonal feeding times was for F4. No conclusion could be drawn regarding whether or not the aardvarks fed for longer when eggs, larvae and pupae were in abundance.

Steyn (1954) found that most major and medium workers hibernated during the winter months, and that the vertical tunnels of the nests were densely packed with these ants at this time. During winter some workers act as repletes which function as living containers of stored provisions and Steyn (1954) found that 50% of the hibernating ants had white fat-filled abdomens in July. Many of the ants studied at Letaba were different from those of TdR in that they foraged in citrus orchards and were able to make use of greater amounts of honeydew from insects on the fruit trees. Colonies outside the orchards were found to predate many more insects and consequently had markedly higher percentages of majors and mediums. The colonies at TdR can be expected to have been more similar to the colonies outside the orchards at Letaba, and, therefore, have greater proportions of major and medium workers hibernating in the tunnels. If a percentage of these workers acted as repletes in the same way as they did at Letaba, they may have formed an improved food source for the aardvarks in the winter months.

Calorific values of *A. custodiens* in Table 13 showed some variation through the year but were not high or low for any particular season. July 1997 had the second highest values, possibly as a result of some fat-filled repletes, but the highest calorific values occurred in April 1997. For some unknown reason this month's values were considerably higher than the rest. Both aardvarks showed high percentages of *A. custodiens* in the faeces of April, but there were other months with similarly high percentages which did not have high calorific values. The percentage of time spent feeding on *A. custodiens* from observations was not high in April. There did not appear, therefore, to be a correlation between higher calorific values and higher predation rates.

*T. trinervoides* are significantly different from *A. custodiens* as a potential prey species for aardvarks in many ways. First, they nest in mounds (except in the first three years of their colony foundation,

Adam, 1993) which grow in size with colony age and which are very hard structures under dry conditions. Breaking into these mounds requires a great deal more effort and time than opening up an *A. custodiens* nest (pers. obs.), but once inside the reward might be considered much greater if numbers are important. *T. trinervoides* colonies vary from 10 000 adult sterile caste in small mounds, to over 880 000 adult steriles in large mounds (Adam, 1993). Establishing colonies which have not yet constructed an epigeous mound obviously have lower numbers of termites. These numbers are vastly superior to colonies of *A. custodiens* which consist of less than 1000 adult sterile workers.

The behaviour of the two prey species is considerably different as well. *T. trinervoides* is predominantly a nocturnal forager, although in winter they may forage in the late afternoon (Adam, 1993), while *A. custodiens* is predominantly a diurnal species (Steyn, 1954; Swart, 1996). *A. custodiens* has been found active above ground after dark at TdR in warmer months (pers. obs.) but even then activity ceases within a few hours of sunset. Surface activity of *T. trinervoides* virtually ceases in the winter months (Adam, 1993; Anderson, 1994), except for occasional and limited foraging in the late afternoon, so at these times the termites are confined to their mounds. In warmer months parties of workers and soldiers move away from their mounds in shallow tunnels and go above ground to harvest grass. At these times they can be predated easily from shallow digs or licked directly off the surface, but they can also still be extracted from the mounds. In winter they can only be predated from their mounds.

Populations of adult sterile caste *T. trinervoides* do not decrease significantly in winter months (Adam, 1993) as they appear to do in *A. custodiens* (Steyn, 1954), possibly as a result of warmer and more humid living conditions within their mounds. Temperature variation is reduced within the mounds and in underground nests of *A. custodiens*, but the greater numbers of termites keep temperatures and humidities higher. The temperature in the centre of the mound is always higher than average temperatures in the rest of the mound, and in winter the difference is 4 to 7°C (Adam, 1993). The variation in average temperatures in the centre and bottom of the mound is also less than the variation in other parts of the mound. Because the eggs and larvae are located in the centre and bottom of the mound (Adam, 1993), and as the adults migrate to these parts in the colder months, they have an improved chance of survival.

The numbers of *T. trinervoides* larvae within mounds have not been accurately determined because the technique used by Adam (1993) to count adult sterile castes precluded the counting of larvae at the same time (this was due to the soft cuticles of the larvae which could not withstand the process used to count the adult castes). However, it has been estimated that the larvae comprise approximately one

third of the population of a *T. trinervoides* mound (Adam, pers. comm.), which would mean significant numbers even within medium mounds. It appears that the numbers of these larvae do not decrease to the same extent in winter as the larvae of *A. custodiens* do (and presumably other ant species), so they are still available to the aardvarks, although they probably are reduced slightly (Adam, pers. comm.). The *T. trinervoides* population within a mound are under food stress during the winter because they do not forage and have to survive on food stores, so in severe years this may have a more significant effect on the population.

*T. trinervoides* alate production begins in March, with the appearance of the first alate instars (Adam, 1993). After this various alate instars may be found in a mound with up to three different instars in the same mound at the same time. By October all the alates have reached the adult stage and are ready to fly. *T. trinervoides* alates are, therefore, present in their mounds for eight months of the year. Alate numbers per colony are small relative to the numbers of workers and soldiers, but there are still very large numbers in excess of 27 000 in large mounds (Adam, 1993). These alates are 12, 20 and 57 times more expensive to produce than major workers, major soldiers and minor soldiers respectively and consequently are worth much more to any predator in terms of calorific value than the adult sterile castes (termite for termite).

The production of alates is the only aspect of the annual cycle of *T. trinervoides* that changes significantly enough within the year to possibly cause differential predation by aardvarks at different times of the year. Numbers of the other castes remain fairly constant and are, therefore, equally available at any time within a particular colony. Because adult alates have a very high energy content relative to adult sterile castes, the period when they occur could be considered a very good time for aardvarks to be feeding on *T. trinervoides* mounds.

From Figure 36 it is evident that *T. trinervoides* mounds were predated more frequently per unit time by the two habituated aardvarks in the winter of 1997 than in the summer. The predation rate started to increase in March, reached a peak in July and August, and then declined again until November, when mound predation ceased entirely. This cycle was repeated in 1998, with both aardvarks feeding from mounds in the cold months and ceasing to do so in November (Lindsey, pers. comm.). The increase in mound predation in March appeared to coincide with the onset of alate production, although the larval alates at this stage would have still been very small and of no greater value as an energy source than other larvae (Adam, pers. comm.). The alate larvae are known to overtake the other larval castes in size only in their third instar (Adam, 1993), which occurs sometime around July/August. This means that up until then they are of no greater value to a foraging aardvark than the rest of the larvae.

The peak time when the two aardvarks fed from mounds (July/August) was only the beginning of the period when *T. trinervoides* alates were really worth exploiting due to their relatively very high calorific values. The best time for aardvarks to exploit the alates might have been expected to be September and October, when all the alates would have been fully developed and rich in energy. This did not appear to be the case, although both aardvarks were still predating mounds during this time in both 1997 and 1998. Observations made in October 1997 while collecting *T. trinervoides* for calorific analysis revealed that winged (adult) alates were present in mounds in large numbers at this time and, therefore, the lowered predation from mounds could not be explained by earlier development of the alates. During observations of feeding, winged alates were observed in mounds in October, but even at this late stage there were still alates that were soft bodied (white in colour) and in which wings were not fully formed. These were, however, considerably larger than the rest of the castes and would have had greater calorific values.

If the aardvarks selected positively for the high energy contents of alates, they would have been expected to eat them at their most valuable stage. Why the aardvarks did not do this, or did not exploit them to the highest degree when they were most available, could have two explanations. First, the aardvarks may not have selected for alates at all, in which case the predation from mounds during winter would have a cause other than the occurrence of alates. The second, and more likely reason, is that the aardvarks did exploit the growing alate larvae at a time when they (the aardvarks) were under relatively high nutritional stress (May to August), but when this stress was reduced in spring the aardvarks were no longer as reliant on *T. trinervoides* alates and, therefore, predated them to a lesser degree. The reason for such food stress in winter would be the low numbers of *A. custodiens*, particularly the developmental stages (but also adult workers), from May to August, as has already been discussed. In September the numbers of developmental stages of the ants should have increased and this would have reduced the nutritional stress on the aardvarks.

Unfortunately, it was not possible to tell whether the alates were in fact exploited by the aardvarks at the times of high predation frequencies, because the alates remained soft bodied until after August (Adam, 1993) and as such would not have come through in the faeces. As mentioned above, some non-sclerotised alates were observed in mounds even in early October, and such prey would leave no evidence due to complete digestion. Therefore, although the elevated mound predation by aardvarks in winter coincided with the production of alates, there was no evidence that the aardvarks actually ate them, so the causal relationship between alates and mound feeding remains hypothetical.

Regardless of whether or not the aardvarks fed on alates and larvae when feeding from *T. trinervoides* mounds in winter, they would have to have ingested an increased number of adult sterile caste at the same time due to the aardvarks method of “bulk” feeding. Inserting the long wet tongue into an ant or termite nest is not selective enough to pick up only a specific caste because any prey item that gets in the way adheres to the tongue and must be ingested. Of course, if the aardvarks were selecting adult sterile caste, they would have appeared in the faeces in elevated levels anyway.

The results of the faecal analysis agree partially with the expected increase in *T. trinervoides* adult sterile castes in the diet of the aardvarks with increased mound predation, in that there was an increase in the numbers of heads in the faeces from January to July/August 1997 (for the combined faeces and both individual habituated aardvarks). However, with the reduction of mound predation after August, there should have been a corresponding reduction in the number of *T. trinervoides* heads in the faeces. This was not really the case. Although there was a partial reduction in numbers in the combined faeces and those of aardvark M5, the expected reverse pattern was not as clear. In the case of aardvark F4, a decrease in numbers of *T. trinervoides* heads did not occur at all after August. Instead the percentages remained at winter levels until the end of the year.

Feeding observations (Figure 34 and 35) indicated that the reason for this was that the two habituated aardvarks switched from feeding from mounds in winter to feeding from subterranean tunnels away from mounds in summer. So, even though mound predation virtually ceased by the end of October, the aardvarks were still eating *T. trinervoides*, just from a different source. Figures 34 and 35 also indicated that feeding on *T. trinervoides* from their subterranean tunnels away from mounds was higher from February to April 1997 than it was from June to August, when the termites were inactive, and this would have kept the levels in the faeces up. Although this was true for aardvark F4, levels of predation of *T. trinervoides* away from mounds were not as high in the first part of 1997 as they were in the last part, and this was reflected in the faeces. The reason for this was unknown, but may have been an individual factor specific to that aardvark.

The increase in predation of mounds in winter and, therefore, *T. trinervoides*, does not agree with the previous studies by Melton (1975) and Willis (1988) which indicated that termites were taken more often in the wet season (summer) than in the dry. The explanation given by the authors of the two studies with regard to the decreased intake of termites in winter was that in the colder months the termites became quiescent and moved to the lower parts of their mounds or nests, thus becoming less available. This appears a plausible reason and it is certainly true that *T. trinervoides* becomes inactive in winter (Adam, 1993) and remain in their mounds. However, it could be argued that the confining of

termites to their nests or mounds when it is too cold for them to forage actually makes them more accessible because they are then concentrated in one place.

The energy expenditure of digging into a mound might be worth while due to the large numbers of prey encountered within the confines of the mound. Digging open a few mounds with a pick axe in the middle of winter at night during the course of the present study revealed that *T. trinervoides* were still available within the upper reaches of the mounds, albeit in apparently reduced densities. Further digging deeper into the centre of these mounds provided evidence that in fact these termites were not so hard to locate, and certainly within the digging capabilities of aardvarks. Also, observations of the aardvarks feeding in mounds indicated that they often dug into the centre, below the ground level, where the *T. trinervoides* were located in their greatest densities (Adam, 1993). The termites congregate in the centre because it is the warmest part of the mound, as discussed above. Larval *T. trinervoides*, including the developing alates, are also concentrated in the centre of mounds below ground level (Adam, 1993).

Figure 40 shows that large *T. trinervoides* mounds were predated more often than medium sized mounds, which in turn were predated more often than small mounds. This is the reverse pattern of the mounds available, as revealed by the grid counts (Table 24). Small mounds were more common than medium mounds, which were more abundant than large mounds. The decreasing proportion of mounds with a general increase in size, as indicated by the sampling grids, was expected, because life tables of *T. trinervoides* follow the same pattern (Adam, 1993). Many of the few *T. trinervoides* colonies that survive long enough to successfully construct a small mound (a colony has to be approximately three years old before it can do this, Adam, 1993), don't live long enough to increase in size to any great extent. There will always be more small mounds than large.

The  $\chi^2$  results from Table 26 back up the results of Figure 40, indicating that large mounds were predated more often than would have been expected from their availability while small mounds were predated less often than would have been expected from their availability. It is, therefore, apparent that the two habituated aardvarks preferentially selected large mounds over small ones.

One possible explanation for this selection could be that large mounds had more termites than smaller mounds. Adam (1993) showed that the size of the *T. trinervoides* population within a mound increased extremely rapidly with a corresponding increase in size of mound. From a height of 30 to 50cm, the termite population size within increased exponentially. Larger mounds formed a bigger resource and the aardvarks could spend more time feeding in them without depleting termite numbers to the extent that

densities became low, thus reducing the intake rate. However, even small mounds had termites populations of just under 10 000 adult sterile caste (Adam, 1993) which would be the basis of a substantial meal if combined with others.

A second possible explanation for preferential selection of larger mounds was the relative proportions of soldier castes within different sized mounds. A larger proportion of soldiers within one of the size categories might be expected to have a negative effect on the selection of a mound by an aardvark. Adam (1993) found that the proportions of workers within mounds increased significantly with an increase in mound size, meaning that the number of soldiers decreased. This was as a result of a significant decrease in minor soldiers (smaller soldiers), not major soldiers, which actually increased slightly with mound size (although not significantly). Small mounds had a greater proportion of minor soldiers relative to major soldiers than large mounds, probably because minor soldiers were less energetically costly to produce (this is an important consideration for small colonies, which cannot reproduce as quickly as large colonies and have to balance colony protection with growth). The fact that small mounds had a higher proportion of soldiers than large mounds was not unexpected because defence is especially critical in small colonies, which cannot withstand severe losses in numbers as well as larger colonies can. In terms of the ratio of soldiers to workers, therefore, small mounds had a better defence than large mounds. However, the fact still remains that large mounds, with their superior numbers still had the greatest defence, simply because they could deploy more soldiers overall, and this should have been a greater deterrent.

A third possible explanation, and one that is probably the most important, is the fact that only mounds over 30cm high produce alates (Adam, 1993). Twenty eight percent of mounds in the size class 31 to 40cm produce alates, while alates emerge from 83% of mounds between 41 to 50cm. All mounds of height greater than 51cm produce alates. In the present study mounds were considered large when over 40cm high, so it can be assumed that 83% or more contained alates. Selection of large mounds by the aardvarks, therefore, meant selection of mounds with alates. Medium mounds were taken as being between 20 and 40cm high, so less than 28% would have contained alates. As the exact height of mounds were not measured, it is not possible to assess the potential contribution made by the occurrence of alates to the predation of medium mounds.

As discussed above, there was no evidence that the aardvarks fed on *T. trinervoides* alates when they were available, because they were not found in the faeces, but this selection of larger mounds, the ones that produce by far the most alates, is further evidence (albeit circumstantial) that aardvarks were selecting *T. trinervoides* alates in the winter months.

Figure 40 also indicates that large mounds were more commonly predated if they had been excavated at least once previously. This did not follow the pattern of available mounds, in which large undug mounds were more common than large predug mounds. This is an indication, at least for the two focal animals, that large predug mounds were preferentially selected over large mounds that were previously undug. As will be seen, the reuse of *T. trinervoides* mounds as a source of food by aardvarks, be it on consecutive nights or weeks apart, indicates that the termite populations within are not exterminated by the predators excavations.

$\chi^2$  results from Table 27 indicated that predug mounds were positively selected for, while undug mounds were negatively selected. The most plausible explanation for this was the relative ease in which they were re-excavated to reach the termites compared to the difficulty of digging open the hard outer layers of a mound from scratch. Personal observations of the excavations made by the two focal aardvarks on *T. trinervoides* mounds indicated a longer time period from the start of the dig to the start of the feed when a previously undug mound was excavated than when a predug mound was predated. This would mean that there was a greater expenditure of energy when feeding on previously undug mounds.

The aardvarks are, however, capable of digging open previously undug mounds even in what appeared to be the hardest of conditions. This behaviour would be expected to occur anyway, simply because all mounds die at some stage (the maximum life expectancy of *T. trinervoides* colonies is 34 years, Adam, 1993), and once this has occurred the only mounds left to predate are undug. In terms of energy efficient foraging, it might be expected that the greater the cost of attaining food, the greater should its energy return be. It is not worth spending much time and energy on a resource with insufficient return. It might therefore be expected that the aardvarks would spend longer feeding in mounds that cost them more in terms of energy to dig into, such as previously undug mounds, than mounds that were relatively easy to excavate, namely predug mounds.

Figure 42 shows the relative time spent feeding on both undug and predug mounds. The results were conflicting, with aardvark M5 spending more time feeding on average in predug mounds, and F4 feeding for longer in previously undug mounds. Aardvark M5, therefore, did the opposite to what was expected. As the ANOVA found no evidence for differences in feeding bout length on either undug or predug mounds for both animals, the hypothesis that undug mounds would be fed on for longer was not upheld. There were in fact a number of occasions when an aardvark was observed to dig into a mound that had not previously been excavated, reach a position where feeding would normally have commenced, but then proceed to reverse out and leave the mound without feeding. These excavations

sometimes took as long as three minutes, and the aardvarks must have expended considerable energy in the process, but why the animal would not attempt to regain some of the lost energy by feeding is unknown. (The possible explanation that the animal dug in but was dissatisfied with the contents, for reasons such as a lack of alates, appears unlikely because observations indicated that the mounds on which this behaviour occurred were often large and should have contained large numbers of termites, including alates.)

Figure 40 also indicates that small undug mounds were predated more often than small predug mounds. This was the reverse pattern of predation on large mounds. The reason for this was probably that when a small mound was excavated, there was often nothing left of the epigeal portion (although the colony may have survived underground) and it would no longer be recognised as a mound. Small mounds would not have contained any alates or many larvae, so predation on these, as would be the case for predation on *T. trinervoides* away from mounds, would have been mainly for adult sterile castes (workers and soldiers).

### **Dietary variation between seasons**

The differences in the amount of predation on the different prey species, specifically the most important ones, have been discussed above in relation to monthly variation, and it has been attempted to relate these differences to changes within the life cycles of the main prey species. A second analysis was carried out to investigate the temporal variation in predation of these prey species using the same data, but with the prey species from the faecal results treated as communities rather than individuals. Analyses of similarities were carried out to investigate whether the ant communities within the faeces differed seasonally. Naturally, if the ant communities within the faeces differed seasonally, then the ant communities predated by the aardvarks differed seasonally. As mentioned in the methods, the prey community data was not transformed so that only seasonal differences between the dominant prey species were analysed, not the minor species.

The results of the ANOSIM (Tables 9 and 10) are difficult to interpret. Although there was evidence of differences between seasonal faecal communities, these differences occurred between different seasons for the two aardvarks. For aardvark M5, the summer faecal communities differed from the spring and winter communities, but for aardvark F4 these seasonal communities did not differ (although autumn/summer were borderline). Aardvark F4 showed differences between autumn and winter and autumn and spring, while aardvark M5 showed no evidence at all for differences between these seasons.

Differences between seasonal communities in the faeces and, therefore, between the ant and termite communities predated by the aardvarks, could theoretically be accredited directly to the changes in ant and termite communities resulting from seasonal climatic variation. From the discussion above it was apparent that there were in fact differences between seasons within populations of the two main prey species, *A. custodiens* and *T. trinervoides*. Willis (1988) and Willis *et al.* (1992) found differences in the ant and termite communities between summer and winter, based on pitfall trapping data. Although the communities were not analysed statistically, he found that the communities possessed a complex temporal distribution, with the communities exhibiting pronounced seasonality in abundance, species richness, composition and diel patterns of foraging activity. Species richness and abundance were higher in summer than in winter, with a general reduction in activity over winter and an increase as conditions became warmer.

However, the seasonal differences in faecal prey communities did not occur between equivalent seasons for the different aardvarks, so it might be erroneous to conclude that it was differences in the ant and termite communities, caused by seasonal weather patterns, that caused the differences to occur between the aardvarks faecal prey communities. Ant and termite communities need to be investigated further before conclusions can be drawn regarding the relationship between the ant community variation and aardvark prey community variation.

### **Caste proportions of *T. trinervoides***

On average, the faeces analysed from 1997 contained a greater proportion of adult soldier caste *T. trinervoides* than adult worker caste. This was found to be the case for the combined results and for both habituated animals. In the combined faeces only one month contained more workers than soldiers, in the faeces of aardvark M5, three months comprised higher proportions of workers, and in the faeces of F4, five months contained more workers. In all three cases, October was one of the months that contained higher proportions of workers. The varying proportions fluctuated throughout 1997 but it would be difficult to demonstrate a trend. If there was any pattern at all, it was that worker proportions were higher in winter than in summer.

The main difference between *T. trinervoides* predations in summer and winter was that the aardvarks fed mostly from mounds in winter and from shallow digs away from mounds in summer (as discussed above). Adam (1993) found that there were differences in caste proportions between foraging parties (those predated from shallow digs away from mounds) and mound populations. Foraging parties consisted of  $58 \pm 8\%$  major workers,  $14 \pm 5\%$  major soldiers and  $28 \pm 10\%$  minor soldiers. Mound

populations consisted of  $75 \pm 8\%$  major workers,  $9 \pm 3\%$  major soldiers and  $16 \pm 7\%$  minor soldiers. Foraging parties, therefore, had 17% fewer workers than mound populations.

Because aardvarks cannot select between soldiers and workers when they are mixed together and, therefore, ingest whichever their tongues come into contact with, it might be expected that when feeding from mounds they would ingest higher proportions of workers than when feeding on foraging parties, simply because mounds have higher proportions of workers. In winter, the soldier/worker ratio should be lower (less soldiers) than summer because the aardvarks feed predominantly from mounds, where there are proportionately less soldiers. Although the pattern was not clear, it could be argued that this was true: the months in the middle of the year were the ones with the higher proportions of workers. (The pattern was clearest for the combined faeces.)

One problem with this explanation was that the October faeces contained high proportions of soldiers (the highest in 1997 for both the combined faeces and aardvark M5) while observations indicated that the frequency of predation from mounds declined at this time (see Figure 36). However, observations of feeding times (Figures 34 and 35) indicated that times spent feeding from mounds was still high in October, relative to feeding on *T. trinervoides* away from mounds, and then dropped off suddenly in November. This was the case for both aardvarks, and compares favourably with Figures 18 to 20, which show that after October the proportions of workers in the faeces decreased. This was most distinct for aardvark F4. In November and December, both aardvarks preyed on *T. trinervoides* from their foraging ports away from mounds, and would have been exposed to lower proportions of workers. Worker proportions in their faeces during these two months were lower.

Although it appears that proportions of workers in the faeces were higher in winter than in summer, coinciding with the period when aardvarks would have encountered relatively more workers, there was still the fact that soldiers generally outnumbered workers in the faeces. In mounds, soldiers only comprise 25% of the adult sterile population, while in foraging parties they comprise 42% (Adam, 1993). It was shown that aardvarks preyed on soldiers to a greater level than would have been expected, while preying on workers to a lesser degree than would have been expected.

Assuming that there was no differential digestibility between the two castes (as discussed above), the cause of this discrepancy can probably be explained by the behaviour of the different castes. When the colony (mound or foraging party) was under attack, the soldiers moved to the site of the breach while the workers moved away, either further into the mound or into the foraging tunnels (pers. obs.; Adam, pers. comm.) Such behaviour meant that within seconds of commencing feeding on *T. trinervoides*, the

aardvarks were exposed to higher proportions of soldiers and lower proportions of workers than would be found in a colony under normal, undisturbed circumstances. If the aardvark only made one dig at the beginning of the feeding bout and did not dig again, after a short period (seconds) only soldiers would have been encountered and ingested. Soldiers would probably have been even more predominant in the faeces in this case. The aardvarks, however, generally dug intermittently at regular intervals when feeding on mounds (pers. obs.) which indicates that they may have been chasing after the workers as they moved deeper into the mound. The resulting proportions of castes ingested by the aardvarks would have been intermediate between the undisturbed proportions (75W:25S) and disturbed proportions (predominantly soldiers).

Soldier *T. trinervoides* produce sticky terpenoids in the enlarged frontal glands of their head capsules (Prestwich, 1983; Braekman *et al.*, 1984), which predators of this termite, or other nasute genera, must contend with. The aardwolf (*Proteles cristatus*), is another mammal in southern Africa known to eat members of the genus *Trinervitermes*, and Richardson (1987b) suggests that it is the phylogeny of the aardwolf that equips it with the ability to tolerate these chemicals. It is proposed that the hyaenids, of which the aardwolf is one, were derived from civet-like viverrids (Savage, 1978), and the African civet, *Civettictis civetta*, is able to tolerate poisonous food stuffs such as millipedes. According to Richardson (1987b) and Anderson (1994) the aardwolf's specialisation towards feeding primarily on *Trinervitermes* spp. would have proceeded simultaneously with selection for the ability to tolerate the terpenes. This specialisation supposedly enabled the aardwolf to invade a trophic niche which was almost entirely devoid of competitors.

Anderson (1994) suggests that aardvarks occasionally dig into *T. trinervoides* mounds but feed on the more palatable larvae and worker termites, while Richardson (1994) states that *Trinervitermes* only occurs infrequently in the diets of aardvarks. Aardwolves have been found to ingest between 220 000 (Williams *et al.*, 1997) and 310 000 (Richardson, 1987a) termites per night, so it appears that aardvarks eat *T. trinervoides* in considerably lower quantities than aardwolves. However, aardvarks clearly do not predate *T. trinervoides* infrequently, as evidenced by observed predation on mounds and foraging tunnels, and by termite heads in the faeces, so must be capable of dealing with the noxious compounds in the soldiers heads. As discussed in the main introduction, aardvarks are thought to be most closely related to the paenungulates, which are predominantly herbivores, so ancestry is unlikely to play a role in their tolerance of the terpenes. The explanation for this tolerance is unknown.

### Caste proportions of *A. custodiens*

According to Steyn (1954), *A. custodiens* has three polymorphic worker castes, with all transitions in size occurring between minor, medium and major workers. From the numbers of pupae in excavated nests, it was found that the percentages of the three adult worker castes would have been 61.6% minors, 33.7% mediums, and 4.7% majors. This was, however, for *A. custodiens* in the citrus orchards at Letaba, and Steyn (1954) stated that colonies outside orchards had markedly higher percentages of majors and mediums. The reason given for this was the absence of pure stands of trees with honeydew producing soft scale, aphids and mealybugs which were primarily the responsibility of minor workers. Major and larger medium workers rarely frequented the citrus trees to gather honeydew, but rather caught insects, and outside orchards insects became more important in the diet. Therefore, at TdR *A. custodiens* should be more reliant on insect prey rather than honeydew (and they were observed predating termites and other small insects regularly during the present study), so proportions of major soldiers should be higher than the 4.7% found in the orchards at Letaba.

The image analyser results for body sizes of nest caught *A. custodiens* were different from the results for faecal ant heads in that there was no exponential distribution in size, and major workers occurred in much higher proportions relative to minor workers than they did in the faecal results. There were still, however, more minor and medium workers than major workers. From Steyn's results (1954) it can be assumed that at TdR major workers occurred in greater proportions than found at Letaba (4.7%), but how much greater is unknown. The results from the image analyser should be treated with caution because it is not known what proportion of the complete nests sampled were represented, as whole nests were not captured. Because the aspirator form of collection could only collect the ants from the tops of the ant tunnels and the surface, the technique would have missed any ants remaining in the lower reaches. If, for example, minor workers were more prone to avoiding defensive behaviour (there was no evidence for this), then they might have been under-represented by the sampling.

Allometric growth in ants causes the size of their heads to increase disproportionately with increasing body size, with major workers having proportionately larger heads than minor workers of the same species (Sudd & Franks, 1987). Although not as extreme as in some species, this is the case for *A. custodiens* (pers. obs.). Because whole bodies of nest caught ants were analysed for size, while only heads of faecal ants were analysed, the relative difference between the smallest and largest body sizes would have been less than the difference between the smallest and largest head sizes. This would have affected the image analyser results for nest caught ants, with the appearance of more larger workers

relative to smaller workers than actually occurred. This factor suggests that there were probably more minor workers relative to major workers in the nest caught ants than the image analyser indicated.

It is difficult to determine whether the aardvarks preyed on minor workers of *A. custodiens* to a greater degree than would have been expected from their availability, but they certainly did not preferentially select major workers. If the defensive attributes of major workers acted as a deterrent to the aardvarks, then the aardvarks might have been expected to select for minor or medium workers. Major workers certainly had greater biting ability than minors, and were capable of producing greater quantities of formic acid, but such defences rarely appeared to cause the aardvarks much distress (pers. obs.). It is unlikely that the aardvarks avoided major workers.

On the other hand, larger ants have higher nutritional and water contents than smaller ants by virtue of their size, so smaller ants need to be eaten in much larger quantities for the same input. Logically, larger ants would provide greater return for effort, which would mean improved energy availability for the aardvarks or less time required for feeding. However, whatever the reasoning, aardvarks did not select larger workers over smaller ones. As discussed previously, it would be very difficult for an aardvark to be selective when feeding on such small prey items when they occur in dense aggregations, so they probably just take what comes to them.

### Numbers of prey eaten

The average number of ants and termites eaten per night, per aardvark was found to be 50581. Two things must be remembered about this figure. First, it was an average calculation, so there would be variation linked to the time spent foraging. In the warmer months, the aardvarks spent more time active above ground, so they had longer to forage and should have preyed on more prey nests. However, it appeared that in the colder months the aardvarks spent more time feeding per hour, so there was a degree of cancellation between foraging period and feeding intensity (although how much is unknown). There should also be some variation between individual aardvarks, depending on such factors as body size, sex and reproductive status.

Secondly, the number 50 581 only accounts for the adult ant and termite heads found in the faeces, and does not take into consideration the possibility of a higher digestibility of eggs, larvae and pupae. As discussed above, no developing stages of ants or termites were ever found in the faeces (except for a small number of pupae), but if ingested when available, these items might have increased the numbers of prey substantially. No genuine estimation can be made of the numbers of developing stages ingested

by the aardvarks without carrying out feeding trials or examining stomach contents, but it is possible that they were eaten in large numbers. The peak number of such developmental stages in one nest of *A. custodiens* would have been approximately 200 at the end of summer (calculated from numbers given by Steyn, 1954, for 48 nests at Letaba), while the number of adult worker caste in these same nests would have been over 600 (except at the end of winter). Thus the developing stages probably comprised approximately one quarter of the nest population at their maximum numbers. In winter, although adult worker numbers dropped, numbers of developing ants were very low, so would not have contributed to the diet.

If the aardvarks did make use of these developing stages of *A. custodiens*, it would be expected that there would have been a differential rate of intake relative to the adult workers due to the fact that the latter are mobile, while the developing stages are not. However, whether developing stages were predated more than the adult workers relative to their proportions is unknown. Assuming that they were predated at the same level, they would have increased the number of prey items by one quarter.

With an average of 38 250 adult worker *A. custodiens* eaten per night, predation of eggs, larvae and pupae at the same time might have increased this to 47 800. This, as stated earlier, was a peak value, and would have been lower in most months, especially winter, when the developing stages would not have added to the total prey at all.

With respect to *T. trinervoides*, larvae could have made a substantial contribution to the diet during the time when aardvarks were feeding from mounds. When feeding occurred at foraging ports away from mounds, it can be safely assumed that larvae did not contribute to the diet at all because they do not move out of the mound with adult sterile castes (Adam, 1993). As has been discussed earlier, mound predation started in March and continued through until October. In the other months mound predation was very limited. The numbers of larvae within a mound have not been counted, but it is estimated that they contribute one third of a mounds population (Adam, pers. comm.). What is known about the larvae is that they live in the middle of the mound just below ground level, and numbers in winter do not decrease significantly as they do in *A. custodiens*. When aardvarks predated *T. trinervoides* mounds they normally dug right into the centre and slightly downwards (as much as 30cm, pers. obs.), which meant they were feeding where the larvae were situated. As the larvae *T. trinervoides* never made it through the digestive tract of the aardvark, it can not be estimated to what degree the aardvarks predated them, but the fact that the feeding occurred at the site where larvae were found indicates that it is probable that they were eaten at the same time as the adult steriles.

If the contribution made by *T. trinervoides* larvae was equal to their proportions in the mounds, then they would have increased the numbers of *T. trinervoides* eaten by one third, to a number of 17 000. It seems probable that the contributions made by larvae were greater than their relative proportions suggest because the aardvarks regularly fed where they occurred, but again, due to their high digestibility, this can not be known. *T. trinervoides* alates also occurred in the mounds between March and October, as discussed, and as they do not become sclerotised until August, they do not appear in the faeces because their heads are completely digested. Numbers of alates in large mounds may reach 27 000, so potentially they could have contributed significantly to the numbers of extra termites per night.

An increase in numbers of prey eaten per night would have increased the energy consumption of the aardvarks. Although the energy contents of eggs, larvae and pupae of *A. custodiens* were unknown, as was the energy content of *T. trinervoides* larvae, it can be assumed that the increase in energy intake with a one third increase in prey items would have been quite substantial. Added to this is the fact that *T. trinervoides* alates have a very high energy content when they start to get larger than normal larvae, and would provide a substantial boost to the energy intake of the aardvarks. Adam (1993) found that alates were 12, 20 and 57 times more expensive to produce than major workers, major soldiers and minor soldiers respectively and were, therefore, that many more times valuable as an energy source to the aardvarks.

If developmental and alate stages of *A. custodiens* and *T. trinervoides* did improve the diet of the aardvarks of TdR, it is probably of importance that they did so at different times of the year. Eggs, larvae and pupae of *A. custodiens* occurred in summer and at this time the aardvarks could have supplemented their diets with them. In winter, when these numbers were low, the aardvarks could have made up for the lower energy intake from *A. custodiens* by supplementing their diet with *T. trinervoides* from mounds, where there were plenty of larvae and alates in mounds over 30cm high.

It is known that the aardwolf is under dietary stress in winter due to a lack of surface activity of its predominant food, *T. trinervoides* (Anderson, 1994). The aardvark, unlike the aardwolf, is capable of digging open termite mounds where there are large numbers of termites, including the highly energetic alates, and so may not be under the same food stress as the aardwolf. However, the estimation of daily energy intake for the aardvark calculated in this study falls well below that of the aardwolf. The aardwolf has an estimated field metabolic rate of 2891.2 kJ/d (Williams *et al.*, 1997), which is significantly greater than the estimate of daily energy intake for aardvarks (1396.23 kJ/d), calculated during this study. The aardwolf's field metabolic rate was calculated using the doubly labelled water

technique and was the energy consumption for an aardwolf in summer, weighing 7768g (winter estimates were lower).

Considering that an adult aardvark weighs five times more than an aardwolf, it appears that the estimate for aardvarks in the present study is far too low. The extra energy that eggs, larvae and pupae would add to the aardvarks diet should increase the energy intake of the aardvark, but it would not be enough. The average nightly energy intake estimated in the present study for an average aardvark on TdR should, therefore, be treated with caution until field metabolic rates can be calculated, perhaps using the doubly labelled water technique.

McNab (1979, 1984, 1986) found that insectivorous mammals, and mammals that use burrows, have low metabolic rates relative to other mammals of similar size but differing feeding and living habits. The aardvark is both a burrowing and insect eating mammal, so might be expected to have a low metabolic rate compared to other mammals of similar size. This remains to be tested, particularly in the field, and would make for very interesting research in the future.

In conclusion the present study confirms the more recent findings that aardvarks feed predominantly on ants, while termites play a secondary role. No other dietary items were located in the faeces except very occasional Coleoptera larvae which were undoubtedly ingested accidentally. No confirmation of the theory that aardvarks eat the geocarpic cucumber, *Cucumis humifructus*, could be made because the plant does not occur at TdR. Termites were found to be more important in winter than summer, contrasting with the findings of two previous studies which found them more important in summer. The predation from *T. trinervoides* mounds in winter during the present study was a clear indication of increased feeding on termites in winter, although it is possible that predation on termites foraging at the surface, which takes place in summer, could significantly increase in certain years. The considerable variation in numbers of different prey species eaten during the year, often with little or no apparent pattern, may imply that erroneous conclusions would be inferred if strict rules be applied to an aardvarks diet. As the two main prey species were the most common at TdR, it is probable that aardvarks eat the most available species (although ant size, which is related to calorific values and water contents, may be important as well), so in other areas of Africa, where *A. custodiens* and *T. trinervoides* do not occur, aardvarks feed on different species. The greater “choice” of ants and termites further north in east Africa probably allows the aardvark a considerably more diverse diet.

## SUMMARY

The aim of the present study was to examine aspects of the ecology of the aardvark, *Orycteropus afer*, including activity patterns, home ranges, burrow utilisation and diet.

Aardvarks were found to emerge from their burrows earlier in winter than in summer, which in some animals involved becoming active regularly in the afternoon, a considerable move away from strict nocturnal behaviour. Many aardvarks remained nocturnal, however, and emergence from holes normally occurred just after night fall, which varied with season. In January aardvarks did not become active until after 20h30, while in July they were regularly active just after 18h00. Activity periods were generally shorter in winter, with the two habituated aardvarks foraging for an average of five hours in June. Activity periods were longest in March for the habituated animals, with an average of eight hours, although they were known to be active for up to nine hours. Burrow re-entry times were also earlier in winter than summer, with animals regularly ceasing surface activities before midnight. Activity cessation may have been controlled by temperature in the coldest months, when the aardvarks generally became inactive at temperatures of 2 to 4°C, but in the months leading up to winter, they became inactive hours before dawn, at temperatures of 7.5 to 10°C, considerably above the minimum tolerance they exhibited in winter. Inactivity of ants and termites did not apparently control burrow re-entry times because aardvarks were predominantly active when their prey were inactive, even in summer.

Home range estimates varied from 133.1ha to 301.7ha for 95% MCP, and from 147.3ha to 384.4ha for 90% adaptive kernel. No differences were apparent between sexes, while aardvark age (using mass as an index) did not seem to be very important (of the two females for which estimates were made, the younger individual had the larger range). It is probable that very young aardvarks maintain a smaller home range than adults. Fifty percent adaptive kernel estimates varied between 40.5ha and 92.4ha. The aardvarks spent 50% of their time in approximately 1/4 to 1/3 of their entire home range. Three of the aardvarks demonstrated a bivariate distribution in their home ranges at the 50% adaptive kernel level, which may have been resource related. One of the females carried out a noticeable shift in her home range, the reasons for which were unknown. There was considerable overlap in the home ranges of the aardvarks, including male-male, male-female and female-female overlap.

Two separate methods indicated that aardvarks travelled between 2.11km and 4.39km per night, at an average foraging speed of approximately 548.4m per hour. They often travelled in a loop, never traversing their whole home range in one night, and they regularly ended up at the burrow from which they started. Burrows were reused on consecutive days for an average of 4.9 to 8.6 days ( $n = 3$ ), with a

maximum of 38 consecutive days by the habituated female. There was no statistical evidence of a difference between two males and one female for the average time spent using a single burrow, although the maximum for the female was 15 days longer than that for the males. Aardvarks rarely returned to a burrow once they had stopped using it, and they were never observed digging new burrows during the study, although this must have occurred at times. Burrows were located in all areas of the aardvarks home ranges and were never shared with other aardvarks. Burrow temperatures at a depth of 2m were considerably buffered from air temperatures, thus sheltering the aardvarks from night time winter temperatures that often fell below freezing before sunrise, and from summer daytime temperatures that regularly exceeded 30°C.

Twenty one species of ant and two species of termite were found in the faeces of aardvarks during the study period. Of these, the five most important in terms of overall numbers and percentage occurrence were *Anoplolepis custodiens*, *Trinervitermes trinervoides*, *Monomorium albopilosum*, *Hodotermes mossambicus* and *Messor capensis*. Considerable monthly variation occurred in the percentage contributions made by the different prey species, but ants always occurred in greater proportions on average than termites. *A. custodiens* was the most numerous species on average in all months. Prey species richness was higher in summer than winter, but prey diversity showed no clear trend. No clear patterns were identified from the faecal results, except that certain species such as *M. albopilosum* and *Solenopsis punctaticeps* occurred more at times when their reproductives were available. This was related more to the ecology of the ants than to the ecology of the aardvarks. Seasonal differences were found in the faecal prey communities of the two habituated aardvarks, but these differences were not the same for the two animals. One aardvark exhibited differences between summer and autumn, and summer and winter prey communities, while the other exhibited differences between autumn and winter, autumn and spring, and winter and spring communities. If the seasonal variation in prey species had occurred as a result of variations in the prey communities themselves, then prey community differences should have occurred between the same seasons for the two aardvarks, assuming the ants and termites were affected by season. This was not the case.

Soldier caste *T. trinervoides* occurred in greater proportions in the faeces than worker caste, and in higher numbers than would have been expected from their proportions within wild populations. Workers were predated less than expected from their available proportions. The probable reason for this was that soldiers were predisposed to predation as a result of moving to the sites of aardvark attack to defend the colony, while workers moved away from the sites of attack to escape. It is unlikely that aardvarks could select between soldiers and workers when they were mixed together, but by repeatedly digging after the workers the aardvarks increased the proportions eaten. Workers occurred in the faeces

more in winter than summer, probably because aardvarks predated *T. trinervoides* from mounds in winter where worker proportions were highest, while predating the same species from foraging parties away from mounds in summer, where worker proportions were lower.

Aardvarks did not predate major workers of *A. custodiens* more than would have been expected from their availability, but it could not be determined whether medium or minor caste were predated more than would have been expected from their availability. As a result of greater body size, individual major workers would have had higher calorific and water contents than individual minor workers, thus making them a better food resource, but major workers also had better biting defences as a potential deterrent. From the faecal caste proportions of both *T. trinervoides* and *A. custodiens* it appears that aardvarks ingested whatever they found available in a nest, although they may have improved their chances of eating worker termites by digging after them in mounds.

The average number of adult caste ants and termites eaten per night was estimated at 50 581. This figure did not account for the possibility of additional eggs, larvae and pupae, which were not generally found in the faeces due to them being almost entirely digested. It is highly probable that these developmental stages were ingested, but to what degree was unknown. Using the calorific values of prey species determined during the study, the estimated energy intake of an aardvark for an average night was 1396.23kJ (again remembering that this only included adult sterile caste prey and assumed that all adult sterile caste came through the digestive tract of the aardvarks in an identifiable state).

Aardvarks foraged the whole time they were active above ground, without stopping for rest periods. Feeding intensity (or the length of time spent feeding per hour) was not higher at any particular time of night, but was higher in winter than summer. Feeding observations did not identify any new prey species that the faecal analysis had not already found, but there were nine minor species in the faeces not predated during observations. *A. custodiens* was the prey species most commonly predated, but not always the species on which the aardvarks spent most time feeding. This was because there were significant differences between the average feeding times for different species. Feeds on *T. trinervoides* from mounds, and on *M. capensis*, were significantly longer than feeds on any other prey species, including *A. custodiens*.

Predation from *T. trinervoides* mounds increased in March, reached a peak in July and August, then decreased until November, when it stopped almost completely. There were a number of possible reasons for winter predation from mounds, including that the termites formed a concentrated food source at the time because they were not foraging away from the mounds, alates were present in the

mounds, and ant numbers were at their lowest in winter (especially developmental stages of these ants) so the termites formed a supplementary food source while the ant numbers were depressed. Large mounds were predated more than would have been expected from their availability. This could have been because they formed a larger food resource and because alates were only produced in mounds over 30cm height. Mounds that had previously been excavated by an aardvark were more commonly predated than mounds that had not previously been excavated. The reason for this was probably that they required less time and energy to open up.

## REFERENCES

- Acocks, J. P. H. 1975. Veld types of South Africa (2nd edn.). *Mem. Bot. Surv. Sth. Afr.* No. 42.
- Adam, R. A. 1993. Aspects of the biology of the harvester termite *Trinervitermes trinervoides* (Sjostedt) (Isoptera:Termitidae). Ph.D. Thesis, University of the Orange Free State.
- Anderson, M. D. 1994. The influence of seasonality and quality of diet on the metabolism of the aardwolf, *Proteles cristatus* (Sparrman 1783). M.Sc. Thesis, University of Pretoria.
- Arnold, G. 1915-1926. A monograph of the Formicidae of South Africa. *Annals of the South African Museum*, **14**: 1-766; **23**: 191-295.
- Bowland, J. M. & Bowland, A. E. 1991. Differential passage rates of prey components through the gut of serval *Felis serval* and black-backed jackal *Canis mesomelas*. *Koedoe* **34**: 37-39.
- Botha, B. J. V., Grobler, N. J., & Geringer, G. J. 1971. Geologie van die Wildplaas Tussen die Riviere, Bethulie, O.V.S. Unpublished internal report No. 1/9/B5, Free State Provincial Government.
- Braekman, J. C., Daloze, D., Dupont, A., Pasteels, J. M. & Josens, G. 1984. Diterpene composition of defence secretion of four West African *Trinervitermes* soldiers. *Chem. Ecol.* **10**: 1363-1370.
- Clarke, K. R. & Warwick, R. M. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory. Bourne Press Limited, Bournemouth, UK.
- Coatan, W. G. H. & Sheasby, J. L. 1975. National Survey of the Isoptera of Southern Africa, 10. The genus *Hodotermes*, Hagen (Hodotermitidae). *Cimbebasia* **3**: 105-138.

- Coe, M. J. & Carr, R. D. 1983. The relationship between large ungulate body weight and faecal pellet weight. *Afr. J. Ecol.* **21**: 165-174.
- Cresswell, W. J. & Smith, G. C. 1992. The effects of temporally autocorrelated data on home range analysis. In: *Wildlife Telemetry: remote monitoring and tracking of animals* (Eds. I. Priede and S. Swift), pp. 272-284. Ellis Harward, Chichester.
- Daniels, C. 1984. Some aspects of habitat utilisation and feeding ecology of the aardvark *Orycteropus afer*. B.Sc. (Hons) Thesis, University of Natal, Pietermaritzburg.
- Dean, W. R. J. & Yeaton, R. I. 1993. The effects of harvester ant *Messor capensis* nest-mounds on the physical and chemical properties of soils in the southern Karoo, South Africa. *J. Arid Environ.* **25**: 249-260.
- 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. *Hoppe-Seyler's Z. Physiol. Chemie.* **364**: 1585-1595.
- De Jong, W. W., Zweers, A., & Goodman, M. 1981. Relationship of aardvark to elephants, hyraxes and sea cows from  $\alpha$ -crystallin sequences. *Nature.* **292**: 538-540.
- 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.
- FitzSimons, F. W. 1919. *The natural history of South Africa*. Longmans Green, London.
- Fowler, J. & Cohen, L. 1992. *Practical statistics for field biology*. John Wiley and Sons, Chichester.
- Friend, T. 1982. The numbat-an endangered specialist. *Austr. Nat. Hist.* **20**: 339-342.

- Harris, S., Cresswell, W. J., Forde, P. G., Trehella, W. J., Woollard, T. & Wray, S. 1990. Home range analysis using radio tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* **20**: 97-123.
- Hediger, H. & Verschuren, J. 1948. Observations sur la psychologie animale. Fascicule 1. Exploration des Parcs Nationaux du Congo Belge. Bruxelles, Inst. Parcs Nat. Congo Belge.
- 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.
- Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**: 427-432.
- Hinton, H. E. 1981. *Biology of insect eggs (Vol. 1)*. Pergamom Press, New York.
- Hoffman, T. 1996. Eastern Mixed Nama Karoo. In: Low, A. B. and Rebelo, A. G. (Eds.) *Vegetation of South Africa, Lesotho and Swaziland*. Dept Environmental Affairs and Tourism, Pretoria.
- Hölldobler, B. & Wilson, E. O. 1994. *Journey to the ants*. Harvard University Press, Cambridge.
- Hollmann, J. & Myburgh, S. 1995. Aardvark and cucumber: a remarkable relationship. *Veld and Flora*. Dec 95. 108-109.
- Hollmann, J. 1996. A fruitful affair. *BBC Wildlife*. November. 28-30.
- Kingdon, J. 1971. *East African Mammals, An Atlas of Evolution in Africa*. Vol. 1. Academic Press, London. 378-387.

Krebs, C. J. 1994. *Ecology: The Experimental Analysis of Distribution and Abundance* (4th edn.). HarperCollins, New York.

Lavergne, A., Douzery, E., Stichler, T., Catzeflis, F. M., & Springer, M. S. 1996. Interordinal mammalian relationships: evidence for paenungulate monophyly is provided by complete mitochondrial 12S rRNA sequences. *Mole. Phylogen. Evol.* **6**: 245-258.

Louw, J. F. 1968. Die ekologie van die malmier *Anoplolepis custodiens* (Sm.)(Formicidae) in die sentrale Oranje Vrystaat. Die Bogrondse aktiwitietspeil van die werkers. *J. Entomol. Soc. Sth. Afr.* **31**: 241-248.

Lubin, Y. D. & Montgomery, G. G. 1981. Defences of Nasutitermes termites (Isoptera:Termitidae) against Tamandua anteaters (Edentata, Myrmecophagidae). *Biotropica* **13**: 66-76.

Madsen, O., Deen, P. M. T., Pesole, G., Saccone, C. & de Jong, W. W. 1997. Molecular evolution of mammalian aquaporin-2: further evidence that elephant shrew and aardvark join the paenungulate clade. *Mol. Biol. Evol.* **14**: 363-371.

Magurran, A. E. 1988. *Ecological Diversity and Its Measurement*. Croon Helm, London.

Manly, B. F. J. 1991. *Randomisation and Monte Carlo methods in biology*. Chapman and Hall, London.

Martin, P. & Bateson, P. 1993. *Measuring behaviour: an introductory guide*. (2nd edn.) Cambridge University Press, Cambridge.

McNab, B. K. 1979. The influence of body size on the energetics and distribution of fossorial and burrowing mammals. *Ecology* **60**: 1010-1021.

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

- McNab, B. K. 1986. The influence of food habits on the energetics of eutherian mammals. *Ecological Monographs* **56**: 1-19.
- Meester, J. 1971. Order Tubulidentata. In: Meester, J. and Setzer, H. W., (Eds.) *The mammals of Africa: and identification manual*. **10**: 1-2. Smithsonian Institution Press, Washington D.C.
- Meester, J. A. J., Rautenbach, I. L., Dippenaar, N. J., & Baker, L. M. 1986. Classification of Southern African Mammals. *Transvaal. Museum. Monogr.* **5**: 182.
- Meeuse, A. D. J. 1958. A possible case of interdependence between a mammal and a higher plant. *Arch. Neerl. Zool.* **13**: 314-318.
- Meeuse, A. D. J. 1962. The Cucurbitaceae of southern Africa. *Bothalia* **8**: 1-111.
- Melton, D. A. 1975. The aardvark at night. *Animals* **16**: 108-110.
- Melton, D. A. 1976. The biology of aardvark (Tubulidentata-Orycteropodidae). *Mammal Rev.* **6**: 75-88.
- Melton, D. A. 1984. The elusive aardvark. *Natal Wildlife* **25**: 9.
- Melton, D. A. & Daniels, C. 1986. A note on the ecology of the aardvark, *Orycteropus afer*. *S. Af. J. Wildl. Res.* **16**: 112-114.
- Milton, S. J. & Dean, W. R. J. 1993. Selection of seeds by harvester ants (*Messor capensis*) in relation to condition of arid rangeland. *J. Arid Environ.* **24**: 63-74.
- Mitchell, P. C. 1905. On the intestinal tract of mammals. *Trans. Zool. Soc. Lond.* **17**: 437-536.
- Mitchell, P. C. 1916. Further observations on the intestinal tract of mammals. *Proc. Zool. Soc. Lond.* 1916: 183-251.

Mitchell, B. L. 1965. An unexpected association between a plant and an insectivorous animal. *Puku* **3**: 178.

Mitchell, J. D., Hewitt, P. H. & van der Linde, de K. 1993. Critical thermal limits and temperature tolerance in the harvester termite *Hodotermes mossambicus* (Hagen). *J. Insect. Physiol.* **39**: 523-528.

Nel, J. A. J. 1978. Notes on the food and foraging behaviour of the bat-eared fox, *Otocyon megalotis*. *Bull. Carnegie. Mus. Nat. Hist.* **6**: 132-137.

Nel, J. J. C. & Hewitt, P. H. 1978. Swarming in the harvester termite *Hodotermes mossambicus* (Hagen). *J. ent. Soc. Sth. Afr.* **41**: 195-198.

Pages, E. 1970. Sur l'ecologie et les adaptations de l'orycterope et des pangolins sympatrique du Gabon. *Biol. Gabon.* **6**: 27-92.

Patterson, B. 1975. The fossil aardvarks (Mammalia: Tubulidentata). *Bull. Mus. Comp. Zool.* **147**: 185-237.

Patterson, M. 1978. Pholidota and Tubulidentata. Ch 12 in *Evolution of African Mammals* (Eds. Maglio, V. J., and Cooke, H. B. S.) pp268-278. Harvard University Press, Cambridge.

Peet, R. K. 1974. The measurement of species diversity. *Ann. Rev. Ecol. Syst.* **5**: 285-307.

Peet, R. K. 1975. Relative diversity indices. *Ecology* **56**: 496-498.

Pielou, E. C. 1975. *Ecological diversity*. John Wiley and Sons, New York.

Porter, C. A., Goodman, M., & Stanhope, M. J. 1996. Evidence on mammalian phylogeny from sequences of exon 28 of the von Willebrand Factor gene. *Mol. Phylogen. Evol.* **5**: 89-101.

Prestwich, G. D. 1983. The chemical defences of termites. *Sci. Am.* **249**: 68-76.

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

Putman, R. J. 1984. Facts from faeces. *Mammal Rev.* **14**: 79-97.

Redford, K. H. 1983. Mammalian myrmecophagy: feeding, foraging and food preference. Ph.D. Thesis, Harvard University.

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

Richardson, P. R. K. 1987*a*. Food consumption and seasonal variation in the diet of the aardwolf. *Z. Saeugetierk.* **52**: 307-325.

Richardson, P. R. K. 1987*b*. Aardwolf: the most highly specialised myrmecophagous mammal? *Sth. Afr. J. Sci.* **83**: 405-410.

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

Rockstein, M. 1978. *Biochemistry of insects*. Academic Press, New York.

Rooney, S. M., Wolfe, A. & Hayden, T. J. 1998. Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. *Mammal Rev.* **26**: 89-98.

Savage, R. J. G. 1978. Carnivora. In *Evolution of African Mammals*: 249-267. (Eds.) V. J. Maglio and H. B. S. Cooke. Harvard University Press, Cambridge.

Shortridge, G. C. 1934. *The mammals of South West Africa*. Vols I & II. Heinemann, London.

Shoshani, J., Goldman, C. A., & Thewissen, J. G. M. 1988. *Orycteropus afer*. *Mammalian Species* No. 300: 1-8. (American Society of Mammalogists)

Simpson, E. H. 1949. Measurement of diversity. *Nature* **163**: 688.

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

Skinner, J. D. & Smithers, R. H. N. 1990. *The mammals of the southern African subregion* (2nd edn.). University of Pretoria, Pretoria.

Smithers, R. H. N. 1971. The Mammals of Botswana. *Mus. Mem. Natl. Mus. Monum. Rhod.* **4**:188-199.

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

Smithers, R. H. N. 1986. South African Red Data Book - terrestrial mammals. South African National Scientific Programmes Report 125. Council for Scientific and Industrial Research, Pretoria.

Smithers, R. H. N., & Wilson, V. J. 1979. Check list and Atlas of the Mammals of Zimbabwe Rhodesia. *Museum Memoir* No. 9.

Sokal, R. R. & Rohlf, F. J. 1995. *Biometry: the principles and practice of statistics in biological research* (3rd edn.). Freeman, New York.

Sonntag, C. F. 1925. A monograph of *Orycteropus afer*. 1. Anatomy except the nervous system, sense organs and hair. *Proc. Zool. Soc. Lond.* 1925, 331-438.

Springer, M. S., Cleven, G. C., Madsen, O., de Jong, W. W., Waddell, V. G., Amrine, H. M. & Stanhope, M. J. 1997. Endemic African mammals shake the phylogenetic tree. *Nature* **388**: 61-64.

Stanhope, M. J., Smith, M. R., Waddell, V. G., Porter, C. A., Shivje, M. S. & Goodman, M. 1996. Mammalian evolution and the Interphotoreceptor Retinoid Binding Protein (IRBP) gene: convincing evidence for several superordinal clades. *J. Mol. Evol.* **43**: 83-92.

Stanhope, M. J., Madsen, O., Waddell, V. G., Cleven, G. C., de Jong, W. W., & Springer, M. S. 1998. Highly congruent molecular support for a diverse Superordinal clade of endemic African mammals. *Mol. Phylogen. Evol.* **9**: 501-508.

Steyn, J. J. 1954. The pugnacious ant (*Anoplolepis custodiens* Smith) and its relation to the control of citrus scales at Letaba. *Memoirs Entomol. Soc. Sth. Afr.* No.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 temminckii*, in the Sabi Sand Wildtuin. M.Sc. Thesis, University of Pretoria.

Swihart, R. K. & Slade, N. A. 1985. Testing for independence of observations in animal movements. *Ecology* **66**: 1176-1184.

Underwood, A. J. 1997. *Experiments in ecology*. Cambridge University Press, Cambridge.

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.

Verschuren, J. 1948. Exploration du Parc National de la Garamba. Ecologie et biologie des grands mammaféres. Bruxelles: Institute des Parcs Nationaux du Congo Belge.

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

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

Vorster, H., Hewitt, P. H. & van der Westhuizen, M. C. 1994. The effect of seed foraging and utilisation by the granivorous ant *Messor capensis* (Mayr) (Hymenoptera: Formacidae) on the grassveld composition of the central Orange Free State. *Afr. Entomol.* **2**: 175-179.

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

Williams, J. B., Anderson, M. D., & Richardson, P. R. K. 1997. Seasonal differences in field metabolism, water requirements, and foraging behaviour of free-living aardwolves. *Ecology* **78**: 2588-2602.

Willis, C. K. 1988. Relative importance of ants and termites in the feeding ecology of the aardvark, *Orycteropus afer* Pallas. B.Sc. (Hon) Thesis, University of Pretoria.

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.

Worton, B. J. 1989. Kernal methods for estimating the utilisation distribution in home range studies. *Ecology* **70**: 164-168.

**Appendix I.** Home range asymptotes and sample size. Graphs showing the number of positional fixes needed to obtain asymptotic home range estimates for aardvarks (a) M5, (b) F4, (c) M4, (d) F2

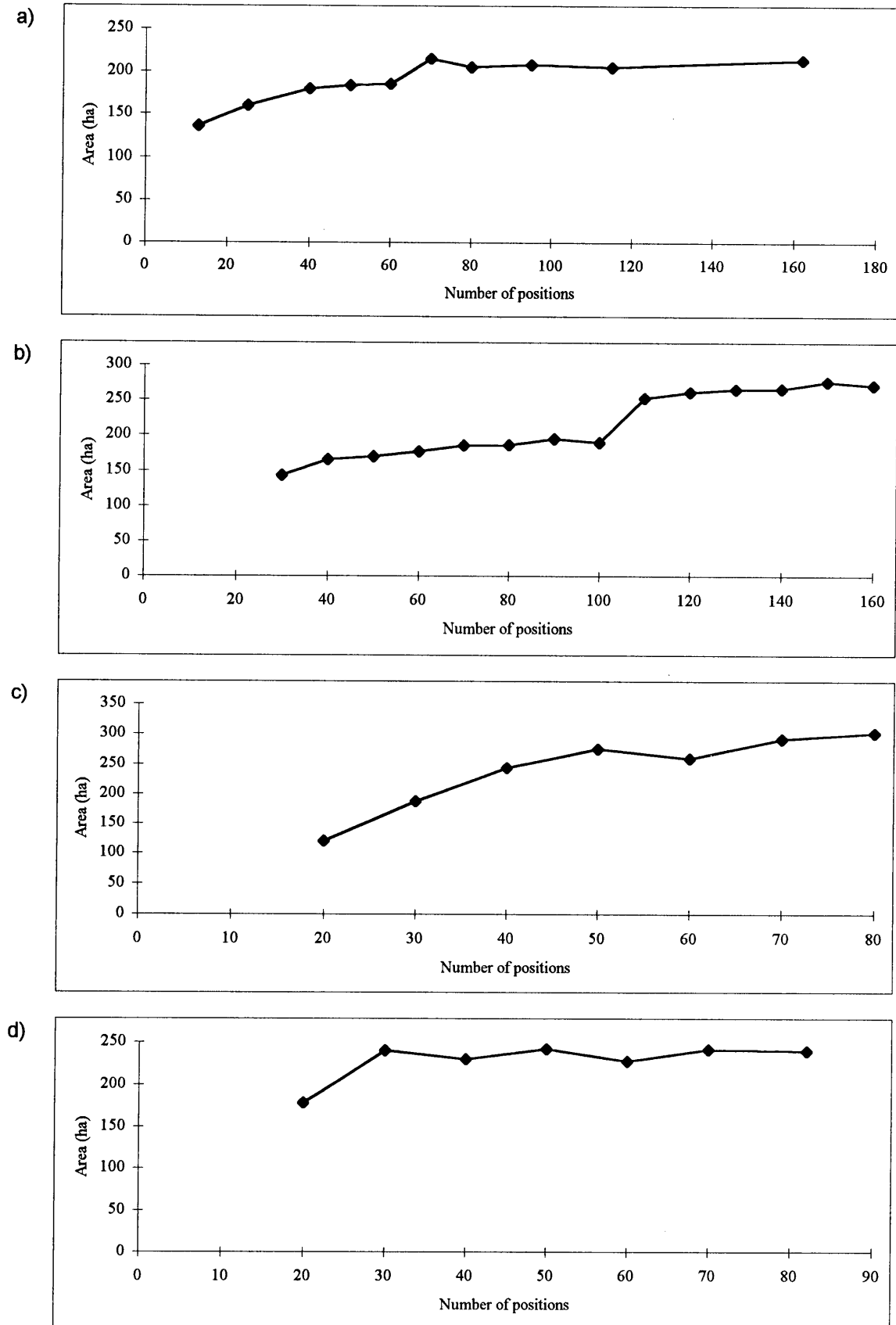


**Figure 44.** Home range asymptotes and sample size.

## Appendix II

It was recognised that categorising faecal samples by months effectively reduced each sample size and may consequently have had an effect on the number of species encountered per month. The lower the sample size, the less chance of finding all possible prey species, especially those that have a very low frequency of occurrence. For this reason the number of faecal samples required to sample all the more regular prey species was examined.

Figure 45 plots the cumulative increase in prey species numbers with the corresponding increase in faecal sample size. Each data point represents the number of prey species encountered for the given sample size in one month. Six months from 1997 were included in the analysis and in some cases one point represents more than one month where there was an overlap. An asymptote was reached when any increase in sample size yielded no further increase in new prey species. This point was the number of samples required to accurately sample all the prey species in the diet for a given period.

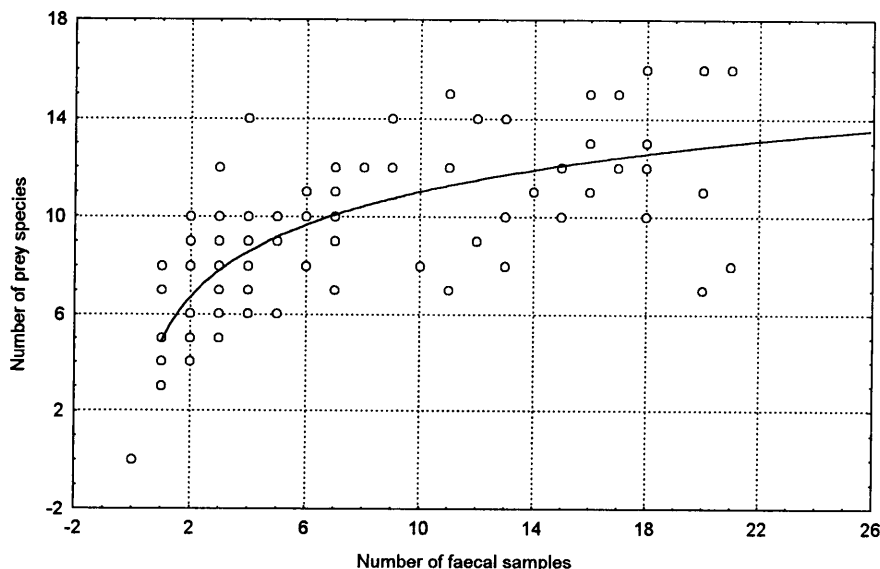


**Figure 45.** Cumulative prey species numbers with increasing sample size.

Figure 45 counts the Minor species as one group, not individually, for reasons of infrequent occurrence as pointed out earlier, and does not, therefore, represent the number of faecal samples required to

identify every single prey species. However, as these Minor species occurred so infrequently, it was assumed that they were of relatively little importance and were left as one group.

Although it is probable that infinitely increasing the sample size would increase the prey species numbers, there is a finite number of ant species on TdR and, therefore, there has to be an upper limit to the potential number of prey species. Also, any new species not encountered in the present analysis would not be expected to occur as frequently as any of the Minor species already counted (they would in fact be expected to occur less frequently), and need not then be considered important. Also, trying to increase the sample size to include all possible prey species would be impractical.

It is worth pointing out as well that the total number of prey species encountered in the faeces from July 1996 to December 1997, comprising over 270 samples, was no greater than that encountered in the individual months of March, November and December, so long as the Minor species were grouped as one.

Examination of Figure 45 indicates that approximately 18 samples were the minimum requirement for locating all prey species. If separate slopes were to be drawn for each of the six months used, variation in their gradients and asymptotes would be apparent as a result of some months reaching their maximum species richness in less samples than others. Also, the total number of species was higher in some months than others. The line of best fit in Figure 45 was plotted as an average instead of for specific months, so did not quite reach an asymptote, but it can be seen from the individual data points that all species were counted by the 18<sup>th</sup> sample, whether it was a month with high species richness or low species richness.

### Appendix III

**Table 32.** Prey species numbers in aardvark faeces

| M5       |       |     |    |    |    |    |        |    |   |    |    |    |     |    |    |   |          |
|----------|-------|-----|----|----|----|----|--------|----|---|----|----|----|-----|----|----|---|----------|
| Date     | Total | A   | Ma | Mh | Mc | D  | C spp. | Cf | P | F1 | F2 | F3 | S   | Cr | T  | H | Other    |
| 11/13/96 | 402   | 350 | 1  | 0  | 1  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 49 | 1 | 0        |
| 12/04/96 | 327   | 312 | 8  | 0  | 0  | 0  | 0      | 0  | 0 | 7  | 0  | 0  | 0   | 0  | 0  | 0 | 0        |
| 12/05/96 | 240   | 223 | 8  | 0  | 0  | 0  | 0      | 0  | 1 | 7  | 0  | 0  | 0   | 0  | 1  | 0 | 0        |
| 12/05/96 | 348   | 318 | 13 | 0  | 0  | 0  | 0      | 0  | 1 | 15 | 0  | 0  | 0   | 0  | 1  | 0 | 0        |
| 12/07/96 | 185   | 115 | 14 | 0  | 0  | 0  | 0      | 0  | 1 | 3  | 0  | 0  | 0   | 0  | 52 | 0 | 0        |
| 12/07/96 | 331   | 309 | 0  | 0  | 0  | 0  | 0      | 0  | 2 | 9  | 0  | 0  | 0   | 0  | 11 | 0 | 0        |
| 12/08/96 | 288   | 272 | 8  | 0  | 0  | 1  | 0      | 0  | 0 | 7  | 0  | 0  | 0   | 0  | 0  | 0 | 1?,1 Col |
| 01/16/97 | 977   | 922 | 50 | 0  | 3  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 2  | 0 | 0        |
| 01/17/97 | 535   | 490 | 24 | 0  | 7  | 1  | 0      | 0  | 2 | 0  | 0  | 0  | 0   | 0  | 11 | 0 | 0        |
| ?/01/97  | 617   | 600 | 0  | 0  | 7  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 10 | 0 | 0        |
| ?/01/97  | 404   | 360 | 1  | 0  | 1  | 0  | 0      | 0  | 1 | 0  | 0  | 0  | 0   | 0  | 41 | 0 | 0        |
| 01/28/97 | 372   | 349 | 13 | 1  | 7  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 2  | 0 | 0        |
| 01/30/97 | 367   | 346 | 9  | 0  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 10 | 0 | 0        |
| 02/02/97 | 329   | 286 | 42 | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 1  | 0 | 0        |
| 02/03/97 | 426   | 346 | 15 | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 65 | 0 | 0        |
| 02/12/97 | 675   | 640 | 18 | 0  | 3  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 14 | 0 | 0        |
| 02/19/97 | 464   | 355 | 13 | 0  | 2  | 0  | 0      | 0  | 1 | 0  | 0  | 0  | 0   | 0  | 89 | 4 | 0        |
| 02/20/97 | 384   | 336 | 41 | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 1  | 1  | 0   | 0  | 5  | 0 | 0        |
| 02/26/97 | 301   | 214 | 8  | 1  | 3  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 1  | 74 | 0 | 0        |
| 02/07/97 | 180   | 82  | 0  | 0  | 0  | 98 | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 0  | 0 | 0        |
| 02/10/97 | 296   | 238 | 53 | 0  | 1  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 4  | 0 | 0        |
| 02/13/97 | 338   | 288 | 29 | 0  | 0  | 8  | 0      | 0  | 1 | 0  | 0  | 0  | 0   | 0  | 2  | 8 | 2        |
| 02/16/97 | 253   | 244 | 7  | 0  | 1  | 0  | 1      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 0  | 0 | 0        |
| 02/17/97 | 173   | 136 | 20 | 1  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 9  | 7 | 0        |
| 02/18/97 | 201   | 180 | 14 | 1  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 3  | 3 | 0        |
| 03/02/97 | 304   | 143 | 29 | 1  | 4  | 0  | 0      | 0  | 0 | 0  | 21 | 0  | 104 | 0  | 2  | 0 | 0        |
| 03/03/97 | 344   | 253 | 50 | 0  | 4  | 0  | 0      | 0  | 1 | 1  | 0  | 0  | 13  | 0  | 22 | 0 | 0        |
| 03/05/97 | 117   | 110 | 1  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 1  | 0  | 4   | 1  | 0  | 0 | 0        |
| 03/11/97 | 77    | 0   | 4  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 73 | 0 | 0        |
| 03/12/97 | 206   | 165 | 5  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 36  | 0  | 0  | 0 | 0        |
| ?/03/97  | 443   | 373 | 53 | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0   | 0  | 16 | 0 | 1?       |

| Date     | Total | A    | Ma  | Mh | Mc | D  | C spp. | Cf | P | F1 | F2 | F3 | S | Cr | T   | H | Other |
|----------|-------|------|-----|----|----|----|--------|----|---|----|----|----|---|----|-----|---|-------|
| 04/07/97 | 354   | 284  | 22  | 0  | 3  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 45  | 0 | 0     |
| 04/14/97 | 1164  | 1110 | 0   | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 53  | 1 | 0     |
| 04/17/97 | 328   | 318  | 3   | 0  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 5   | 0 | 0     |
| 04/20/97 | 378   | 358  | 4   | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 16  | 0 | 0     |
| 04/29/97 | 692   | 441  | 54  | 0  | 5  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 191 | 0 | 1?    |
| 04/30/97 | 937   | 789  | 52  | 0  | 1  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 95  | 0 | 0     |
| 05/01/97 | 415   | 342  | 35  | 1  | 6  | 1  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 30  | 0 | 0     |
| 05/04/97 | 649   | 520  | 39  | 0  | 7  | 14 | 0      | 0  | 2 | 0  | 0  | 0  | 0 | 0  | 67  | 0 | 0     |
| 05/08/97 | 389   | 281  | 49  | 1  | 5  | 4  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 48  | 1 | 0     |
| 05/20/97 | 215   | 208  | 3   | 0  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 2   | 0 | 0     |
| 05/27/97 | 220   | 175  | 20  | 0  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 23  | 0 | 0     |
| 05/29/97 | 405   | 381  | 11  | 3  | 1  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 9   | 0 | 0     |
| 06/02/97 | 347   | 336  | 6   | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 5   | 0 | 0     |
| 06/03/97 | 346   | 300  | 29  | 0  | 1  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 16  | 0 | 0     |
| 06/11/97 | 426   | 269  | 71  | 13 | 6  | 1  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 65  | 1 | 0     |
| 06/13/97 | 602   | 413  | 12  | 7  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 168 | 0 | 0     |
| 06/17/97 | 411   | 324  | 9   | 2  | 4  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 72  | 0 | 0     |
| 06/27/97 | 405   | 305  | 24  | 0  | 4  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 72  | 0 | 0     |
| 07/01/97 | 344   | 181  | 56  | 2  | 6  | 0  | 2      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 97  | 0 | 0     |
| 07/16/97 | 285   | 188  | 56  | 2  | 9  | 0  | 1      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 29  | 0 | 0     |
| 07/17/97 | 370   | 247  | 43  | 10 | 10 | 0  | 0      | 0  | 2 | 0  | 0  | 0  | 0 | 0  | 57  | 1 | 0     |
| 07/18/97 | 330   | 206  | 17  | 0  | 7  | 21 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 79  | 0 | 0     |
| 07/29/97 | 386   | 315  | 4   | 0  | 16 | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 51  | 0 | 0     |
| 07/30/97 | 306   | 155  | 4   | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 147 | 0 | 0     |
| 08/03/97 | 281   | 265  | 2   | 0  | 10 | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 2   | 2 | 0     |
| 08/05/97 | 467   | 413  | 8   | 0  | 8  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 38  | 0 | 0     |
| 08/07/97 | 305   | 109  | 16  | 0  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 178 | 0 | 0     |
| 08/15/97 | 333   | 245  | 1   | 0  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 85  | 0 | 0     |
| 08/20/97 | 358   | 326  | 15  | 0  | 4  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 13  | 0 | 0     |
| 08/21/97 | 440   | 387  | 32  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 21  | 0 | 0     |
| 09/02/97 | 343   | 284  | 46  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 13  | 0 | 0     |
| 09/12/97 | 422   | 328  | 34  | 0  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 56  | 1 | 1?    |
| 09/16/97 | 325   | 280  | 34  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 11  | 0 | 0     |
| 09/17/97 | 196   | 137  | 28  | 0  | 0  | 16 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 15  | 0 | 0     |
| 09/21/97 | 316   | 125  | 86  | 4  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 101 | 0 | 0     |
| 09/25/97 | 339   | 209  | 108 | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 22  | 0 | 0     |

# Appendix III

| Date     | Total | A   | Ma  | Mh | Mc | D | C spp. | Cf | P | F1 | F2 | F3 | S | Cr | T   | H  | Other |
|----------|-------|-----|-----|----|----|---|--------|----|---|----|----|----|---|----|-----|----|-------|
| 09/16/97 | 351   | 290 | 51  | 0  | 2  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 8   | 0  | 0     |
| 09/16/97 | 390   | 312 | 67  | 0  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 10  | 0  | 0     |
| 09/16/97 | 371   | 334 | 25  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 12  | 0  | 0     |
| 09/16/97 | 327   | 290 | 30  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 7   | 0  | 0     |
| 09/16/97 | 359   | 320 | 320 | 0  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 6   | 0  | 0     |
| 10/05/97 | 150   | 133 | 15  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0   | 2  | 0     |
| 10/08/97 | 307   | 299 | 0   | 0  | 0  | 0 | 0      | 1  | 0 | 0  | 0  | 0  | 0 | 0  | 4   | 3  | 0     |
| 10/15/97 | 289   | 246 | 32  | 2  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 8   | 0  | 0     |
| 10/20/97 | 376   | 265 | 5   | 4  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 61  | 41 | 0     |
| 10/27/97 | 340   | 329 | 2   | 0  | 0  | 0 | 0      | 4  | 0 | 1  | 0  | 0  | 1 | 0  | 3   | 0  | 0     |
| 10/31/97 | 280   | 213 | 11  | 4  | 1  | 0 | 0      | 0  | 0 | 2  | 0  | 0  | 1 | 0  | 25  | 23 | 0     |
| 11/06/97 | 161   | 132 | 7   | 1  | 1  | 0 | 0      | 0  | 0 | 5  | 0  | 0  | 0 | 0  | 9   | 4  | 2?    |
| 11/14/97 | 332   | 163 | 108 | 1  | 2  | 0 | 0      | 0  | 0 | 5  | 0  | 0  | 0 | 0  | 48  | 4  | 1?    |
| 11/19/97 | 310   | 295 | 5   | 0  | 2  | 0 | 0      | 0  | 0 | 5  | 0  | 0  | 0 | 0  | 3   | 0  | 0     |
| 11/21/97 | 314   | 292 | 8   | 0  | 0  | 0 | 0      | 0  | 0 | 11 | 0  | 0  | 0 | 0  | 3   | 0  | 0     |
| 11/26/97 | 228   | 71  | 42  | 0  | 2  | 0 | 0      | 0  | 0 | 8  | 0  | 0  | 0 | 0  | 101 | 3  | 1?    |
| 11/27/97 | 232   | 175 | 3   | 0  | 1  | 0 | 0      | 0  | 0 | 27 | 0  | 0  | 0 | 0  | 15  | 11 | 0     |
| 12/01/97 | 400   | 315 | 56  | 0  | 0  | 0 | 0      | 0  | 0 | 10 | 0  | 0  | 1 | 0  | 15  | 2  | 1?    |
| 12/03/97 | 252   | 217 | 10  | 0  | 0  | 0 | 0      | 0  | 0 | 7  | 0  | 0  | 0 | 0  | 13  | 5  | 0     |
| 12/04/97 | 231   | 152 | 57  | 0  | 0  | 0 | 0      | 0  | 0 | 13 | 0  | 0  | 0 | 0  | 1   | 8  | 0     |
| 12/09/97 | 360   | 221 | 100 | 0  | 5  | 0 | 0      | 0  | 0 | 6  | 0  | 9  | 0 | 3  | 15  | 1  | 0     |
| 12/29/97 | 360   | 220 | 25  | 0  | 11 | 0 | 0      | 1  | 0 | 0  | 0  | 0  | 0 | 0  | 102 | 0  | 1?    |
| 12/30/97 | 284   | 195 | 50  | 0  | 7  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 32  | 0  | 0     |
| 01/06/98 | 282   | 133 | 10  | 0  | 3  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 134 | 2  | 0     |
| 01/10/98 | 332   | 290 | 0   | 2  | 3  | 0 | 0      | 0  | 0 | 1  | 0  | 0  | 1 | 0  | 34  | 1  | 0     |
| 03/16/98 | 333   | 280 | 1   | 0  | 49 | 1 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0   | 1  | 1?    |
| 03/19/98 | 287   | 256 | 10  | 0  | 11 | 1 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 9   | 0  | 0     |

# Appendix III

| Date     | Total | A    | Ma | Mh | Mc | D  | C spp. | Cf | P | F1 | F2 | F3 | S  | Cr | T   | H  | U         |
|----------|-------|------|----|----|----|----|--------|----|---|----|----|----|----|----|-----|----|-----------|
| F4       |       |      |    |    |    |    |        |    |   |    |    |    |    |    |     |    |           |
| 01/27/97 | 288   | 286  | 1  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 1   | 0  | 0         |
| 01/29/97 | 287   | 285  | 0  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 1   | 0  | 1?        |
| 01/30/97 | 2024  | 2009 | 3  | 0  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 10  | 0  | 0         |
| 02/04/97 | 508   | 441  | 57 | 0  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 8   | 0  | 0         |
| 02/08/97 | 639   | 557  | 75 | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 7   | 0  | 0         |
| 02/12/97 | 407   | 402  | 0  | 0  | 1  | 0  | 1      | 0  | 1 | 0  | 0  | 0  | 0  | 0  | 2   | 0  | 0         |
| 02/14/97 | 275   | 260  | 14 | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 1  | 0  | 0  | 0  | 0   | 0  | 0         |
| 02/16/97 | 248   | 245  | 3  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0         |
| 02/17/97 | 352   | 343  | 4  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 5   | 0  | 0         |
| 03/02/97 | 346   | 309  | 13 | 0  | 1  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 1  | 1  | 18  | 0  | 2 Tet, 1? |
| 03/04/97 | 155   | 146  | 1  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 1  | 0  | 7   | 0  | 0         |
| 03/05/97 | 253   | 210  | 0  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 43 | 0  | 0   | 0  | 0         |
| 03/09/97 | 262   | 212  | 0  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 41 | 0  | 9   | 0  | 0         |
| 03/16/97 | 357   | 238  | 16 | 1  | 0  | 0  | 1      | 0  | 0 | 0  | 1  | 0  | 45 | 1  | 54  | 0  | 0         |
| 03/23/97 | 367   | 346  | 4  | 0  | 1  | 0  | 1      | 0  | 0 | 1  | 0  | 0  | 0  | 1  | 13  | 0  | 0         |
| 04/07/97 | 523   | 388  | 0  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 134 | 1  | 0         |
| 04/11/97 | 346   | 322  | 0  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 21  | 3  | 0         |
| 04/13/97 | 223   | 209  | 0  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 12  | 2  | 0         |
| 04/16/97 | 309   | 283  | 1  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 25  | 0  | 0         |
| 04/24/97 | 864   | 800  | 22 | 0  | 1  | 2  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 37  | 2  | 0         |
| 04/30/97 | 377   | 216  | 0  | 2  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 157 | 0  | 0         |
| 05/01/97 | 321   | 312  | 1  | 0  | 0  | 1  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 7   | 0  | 0         |
| 05/05/97 | 663   | 535  | 54 | 1  | 3  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 68  | 2  | 0         |
| 05/21/97 | 526   | 461  | 5  | 0  | 1  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 49  | 10 | 0         |
| 05/23/97 | 363   | 282  | 0  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 76  | 5  | 0         |
| 05/27/97 | 282   | 115  | 0  | 0  | 1  | 0  | 0      | 0  | 0 | 0  | 1  | 0  | 0  | 0  | 165 | 0  | 0         |
| 05/28/97 | 307   | 136  | 0  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 171 | 0  | 0         |
| 06/02/97 | 375   | 311  | 1  | 0  | 0  | 0  | 2      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 59  | 2  | 0         |
| 06/03/97 | 215   | 161  | 12 | 0  | 0  | 1  | 1      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 40  | 0  | 0         |
| 06/04/97 | 190   | 169  | 3  | 0  | 0  | 0  | 3      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 15  | 0  | 0         |
| 06/08/97 | 250   | 215  | 11 | 0  | 1  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 23  | 0  | 0         |
| 06/16/97 | 372   | 309  | 8  | 0  | 0  | 5  | 9      | 0  | 1 | 0  | 0  | 0  | 0  | 0  | 40  | 0  | 0         |
| 06/27/97 | 444   | 160  | 9  | 0  | 0  | 11 | 10     | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 254 | 0  | 0         |

### Appendix III

| Date     | Total | A   | Ma  | Mh | Mc | D  | C spp. | Cf | P | F1 | F2 | F3 | S | Cr | T   | H  | U |
|----------|-------|-----|-----|----|----|----|--------|----|---|----|----|----|---|----|-----|----|---|
| 07/01/97 | 253   | 231 | 0   | 0  | 1  | 0  | 2      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 19  | 0  | 0 |
| 07/02/97 | 379   | 198 | 1   | 0  | 2  | 41 | 3      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 134 | 0  | 0 |
| 07/04/97 | 354   | 270 | 54  | 1  | 0  | 3  | 7      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 19  | 0  | 0 |
| 07/16/97 | 252   | 91  | 1   | 0  | 0  | 53 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 107 | 0  | 0 |
| 07/24/97 | 311   | 272 | 2   | 0  | 0  | 3  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 34  | 0  | 0 |
| 07/28/97 | 265   | 114 | 10  | 0  | 1  | 0  | 3      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 137 | 0  | 0 |
| 08/03/97 | 229   | 95  | 6   | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 128 | 0  | 0 |
| 08/04/97 | 419   | 366 | 9   | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 44  | 0  | 0 |
| 08/10/97 | 442   | 260 | 5   | 0  | 0  | 0  | 6      | 3  | 0 | 0  | 0  | 0  | 0 | 0  | 167 | 1  | 0 |
| 08/15/97 | 273   | 166 | 3   | 0  | 0  | 0  | 1      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 103 | 0  | 0 |
| 08/20/97 | 245   | 211 | 26  | 0  | 0  | 0  | 1      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 7   | 0  | 0 |
| 08/24/97 | 215   | 59  | 5   | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 151 | 0  | 0 |
| 09/12/97 | 282   | 211 | 67  | 1  | 1  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 2   | 0  | 0 |
| 09/22/97 | 242   | 74  | 135 | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 33  | 0  | 0 |
| 09/23/97 | 259   | 90  | 113 | 0  | 0  | 48 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 8   | 0  | 0 |
| 09/23/97 | 347   | 150 | 122 | 1  | 0  | 1  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 73  | 0  | 0 |
| 09/24/97 | 353   | 239 | 89  | 0  | 0  | 21 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 4   | 0  | 0 |
| 09/29/97 | 254   | 32  | 130 | 0  | 0  | 51 | 0      | 0  | 0 | 0  | 0  | 1  | 0 | 0  | 40  | 0  | 0 |
| 10/06/97 | 336   | 59  | 118 | 0  | 3  | 30 | 1      | 0  | 0 | 0  | 1  | 1  | 0 | 0  | 95  | 28 | 0 |
| 10/08/97 | 286   | 239 | 29  | 0  | 0  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 16  | 2  | 0 |
| 10/12/97 | 475   | 338 | 25  | 0  | 4  | 0  | 1      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 107 | 0  | 0 |
| 10/19/97 | 291   | 211 | 19  | 1  | 1  | 0  | 0      | 0  | 0 | 0  | 1  | 0  | 1 | 0  | 52  | 5  | 0 |
| 10/26/97 | 284   | 194 | 75  | 0  | 1  | 2  | 3      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 5   | 4  | 0 |
| 10/27/97 | 299   | 155 | 25  | 0  | 1  | 0  | 1      | 0  | 0 | 0  | 1  | 0  | 0 | 0  | 112 | 4  | 0 |
| 11/02/97 | 279   | 263 | 8   | 0  | 0  | 1  | 0      | 0  | 0 | 0  | 1  | 0  | 0 | 0  | 5   | 1  | 0 |
| 11/14/97 | 142   | 14  | 21  | 0  | 0  | 0  | 0      | 0  | 0 | 1  | 0  | 1  | 0 | 4  | 91  | 10 | 0 |
| 11/14/97 | 166   | 49  | 56  | 0  | 2  | 0  | 0      | 1  | 0 | 0  | 0  | 4  | 0 | 0  | 46  | 8  | 0 |
| 11/24/97 | 339   | 188 | 67  | 0  | 1  | 0  | 0      | 0  | 0 | 5  | 4  | 3  | 0 | 4  | 67  | 0  | 0 |
| 11/27/97 | 250   | 36  | 12  | 0  | 2  | 1  | 0      | 0  | 1 | 3  | 1  | 2  | 0 | 0  | 192 | 0  | 0 |
| 11/28/97 | 328   | 167 | 36  | 0  | 4  | 0  | 0      | 0  | 0 | 3  | 2  | 10 | 0 | 0  | 101 | 5  | 0 |
| 12/01/97 | 265   | 209 | 22  | 0  | 3  | 0  | 1      | 0  | 0 | 24 | 0  | 1  | 0 | 0  | 4   | 1  | 0 |
| 12/08/97 | 402   | 171 | 69  | 0  | 0  | 56 | 0      | 0  | 0 | 4  | 6  | 6  | 0 | 0  | 70  | 20 | 0 |
| 12/09/97 | 390   | 69  | 94  | 0  | 1  | 1  | 0      | 0  | 0 | 2  | 1  | 7  | 0 | 0  | 213 | 2  | 0 |
| 12/19/97 | 209   | 31  | 8   | 0  | 1  | 1  | 0      | 0  | 0 | 1  | 0  | 1  | 0 | 0  | 165 | 1  | 0 |
| 12/27/97 | 281   | 244 | 2   | 0  | 2  | 0  | 0      | 0  | 0 | 3  | 0  | 0  | 0 | 0  | 26  | 4  | 0 |
| 12/29/97 | 233   | 164 | 5   | 0  | 3  | 0  | 0      | 0  | 1 | 0  | 0  | 0  | 0 | 0  | 58  | 2  | 0 |

# Appendix III

| Date                 | Total | A    | Ma | Mh | Mc | D | C spp. | Cf | P | F1 | F2 | F3 | S | Cr | T    | H  | U  |
|----------------------|-------|------|----|----|----|---|--------|----|---|----|----|----|---|----|------|----|----|
| 01/07/98             | 231   | 174  | 7  | 0  | 7  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 1 | 0  | 39   | 2  | 1? |
| 01/09/98             | 256   | 189  | 11 | 0  | 6  | 0 | 0      | 0  | 0 | 0  | 1  | 0  | 0 | 0  | 42   | 7  | 0  |
| 03/06/98             | 91    | 19   | 17 | 0  | 13 | 0 | 2      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 38   | 2  | 0  |
| Other Aardvarks 1996 |       |      |    |    |    |   |        |    |   |    |    |    |   |    |      |    |    |
| Jul-96               | 608   | 166  | 3  | 0  | 0  | 0 | 10     | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 427  | 2  | 0  |
| Jul-96               | 676   | 213  | 1  | 0  | 1  | 1 | 2      | 8  | 0 | 0  | 0  | 0  | 0 | 0  | 450  | 0  | 0  |
| Jul-96               | 415   | 262  | 28 | 0  | 2  | 0 | 5      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 116  | 2  | 0  |
| Jul-96               | 419   | 261  | 28 | 0  | 2  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 128  | 0  | 0  |
| Jul-96               | 803   | 800  | 2  | 0  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0    | 0  | 0  |
| Jul-96               | 2423  | 578  | 13 | 0  | 9  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 1822 | 1  | 0  |
| Jul-96               | 357   | 348  | 2  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0    | 7  | 0  |
| Jul-96               | 2053  | 2000 | 0  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 53   | 0  | 0  |
| Jul-96               | 705   | 600  | 45 | 0  | 7  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 53   | 0  | 0  |
| Jul-96               | 15    | 8    | 0  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 4    | 3  | 0  |
| Jul-96               | 371   | 341  | 0  | 0  | 24 | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 5    | 1  | 0  |
| Jul-96               | 337   | 308  | 0  | 0  | 13 | 4 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 1  | 11   | 0  | 0  |
| Jul-96               | 291   | 254  | 0  | 0  | 11 | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 26   | 0  | 0  |
| Aug-96               | 1264  | 1250 | 0  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 4    | 10 | 0  |
| Aug-96               | 415   | 127  | 1  | 0  | 1  | 0 | 0      | 0  | 1 | 0  | 0  | 0  | 0 | 0  | 285  | 0  | 0  |
| Aug-96               | 488   | 37   | 2  | 0  | 3  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 446  | 0  | 0  |
| Aug-96               | 402   | 377  | 0  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 25   | 0  | 0  |
| Aug-96               | 1014  | 208  | 2  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 804  | 0  | 0  |
| Aug-96               | 341   | 60   | 0  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 281  | 0  | 0  |
| Aug-96               | 1276  | 349  | 0  | 0  | 0  | 0 | 1      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 926  | 0  | 0  |
| Aug-96               | 1421  | 154  | 0  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 1262 | 5  | 0  |
| Aug-96               | 346   | 297  | 3  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 44   | 2  | 0  |
| Aug-96               | 1218  | 715  | 73 | 0  | 12 | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 418  | 0  | 0  |
| Aug-96               | 550   | 179  | 0  | 0  | 0  | 0 | 1      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 370  | 0  | 0  |
| Aug-96               | 554   | 298  | 12 | 1  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 2  | 240  | 0  | 0  |
| Aug-96               | 587   | 222  | 25 | 0  | 1  | 0 | 2      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 337  | 0  | 0  |
| Aug-96               | 361   | 181  | 25 | 1  | 2  | 0 | 7      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 138  | 5  | 2? |
| Aug-96               | 409   | 247  | 2  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 160  | 0  | 0  |
| Aug-96               | 722   | 118  | 2  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 602  | 0  | 0  |
| Aug-96               | 616   | 596  | 4  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 16   | 0  | 0  |
| Aug-96               | 297   | 287  | 6  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 1    | 3  | 0  |
| Aug-96               | 373   | 174  | 5  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 2  | 192  | 0  | 0  |

### Appendix III

| Date                 | Total | A   | Ma  | Mh | Mc | D | C spp. | Cf | P | F1 | F2 | F3 | S  | Cr  | T   | H  | U            |
|----------------------|-------|-----|-----|----|----|---|--------|----|---|----|----|----|----|-----|-----|----|--------------|
| Sep-96               | 482   | 123 | 26  | 0  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 332 | 0  | 0            |
| Sep-96               | 512   | 245 | 0   | 0  | 2  | 0 | 3      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 262 | 0  | 0            |
| Sep-96               | 429   | 400 | 26  | 0  | 0  | 0 | 1      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 1   | 0  | 1?           |
| Oct-96               | 157   | 134 | 8   | 1  | 0  | 0 | 0      | 0  | 0 | 2  | 0  | 1  | 0  | 0   | 7   | 4  | 0            |
| Oct-96               | 422   | 345 | 32  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 10  | 35 | 0            |
| Nov-96               | 376   | 366 | 0   | 0  | 0  | 3 | 0      | 0  | 0 | 3  | 0  | 0  | 0  | 0   | 0   | 4  | 0            |
| Nov-96               | 174   | 0   | 0   | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 172 | 2  | 1 Col, 1 Dip |
| Nov-96               | 347   | 310 | 8   | 0  | 1  | 0 | 0      | 0  | 0 | 6  | 1  | 0  | 1  | 0   | 9   | 10 | 1?           |
| Other Aardvarks 1997 |       |     |     |    |    |   |        |    |   |    |    |    |    |     |     |    |              |
| Jan-97               | 327   | 304 | 20  | 0  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 2   | 0  | 0            |
| Jan-97               | 670   | 600 | 2   | 0  | 2  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 66  | 0  | 0            |
| Feb-97               | 208   | 159 | 4   | 0  | 2  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 1  | 0   | 39  | 1  | 2?           |
| Feb-97               | 757   | 738 | 10  | 0  | 2  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 7   | 0  | 0            |
| Feb-97               | 429   | 406 | 16  | 0  | 0  | 0 | 0      | 0  | 2 | 1  | 0  | 0  | 0  | 0   | 0   | 4  | 0            |
| Feb-97               | 430   | 415 | 11  | 0  | 1  | 0 | 1      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 2   | 0  | 0            |
| Feb-97               | 228   | 199 | 25  | 0  | 1  | 0 | 0      | 0  | 1 | 0  | 0  | 0  | 0  | 0   | 2   | 0  | 0            |
| Feb-97               | 279   | 237 | 33  | 0  | 0  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 4   | 5  | 0            |
| Feb-97               | 285   | 256 | 19  | 0  | 1  | 1 | 1      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 7   | 0  | 0            |
| Feb-97               | 245   | 9   | 218 | 0  | 7  | 0 | 3      | 0  | 1 | 0  | 0  | 1  | 0  | 0   | 3   | 3  | 0            |
| Feb-97               | 231   | 5   | 213 | 0  | 6  | 0 | 1      | 0  | 1 | 0  | 0  | 1  | 0  | 0   | 0   | 4  | 0            |
| Mar-97               | 442   | 24  | 249 | 0  | 24 | 0 | 3      | 1  | 0 | 1  | 0  | 0  | 0  | 2   | 135 | 3  | 0            |
| Mar-97               | 381   | 90  | 245 | 0  | 18 | 0 | 2      | 10 | 2 | 0  | 0  | 0  | 0  | 3   | 10  | 0  | 1?           |
| Mar-97               | 386   | 0   | 259 | 0  | 23 | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 100 | 4   | 0  | 0            |
| Mar-97               | 213   | 142 | 0   | 0  | 65 | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 1   | 5  | 0            |
| Mar-97               | 141   | 83  | 0   | 0  | 49 | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 1   | 8  | 0            |
| Mar-97               | 215   | 144 | 6   | 0  | 3  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 54  | 8  | 0            |
| Mar-97               | 252   | 228 | 2   | 0  | 3  | 0 | 1      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 17  | 0  | 1?           |
| Mar-97               | 317   | 232 | 4   | 2  | 31 | 0 | 0      | 0  | 0 | 0  | 0  | 1  | 0  | 0   | 40  | 7  | 0            |
| Apr-97               | 165   | 152 | 8   | 0  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 4   | 0  | 0            |
| Apr-97               | 212   | 206 | 4   | 0  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 0   | 1  | 0            |
| Apr-97               | 209   | 113 | 18  | 4  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 71  | 2  | 0            |
| Apr-97               | 176   | 168 | 3   | 0  | 2  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 3   | 0  | 0            |
| Apr-97               | 293   | 281 | 5   | 0  | 2  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 3   | 0   | 2  | 0            |
| Apr-97               | 316   | 133 | 31  | 0  | 0  | 0 | 0      | 0  | 1 | 0  | 1  | 0  | 92 | 0   | 58  | 0  | 0            |
| Apr-97               | 119   | 115 | 3   | 0  | 1  | 0 | 0      | 0  | 0 | 0  | 0  | 0  | 0  | 0   | 0   | 0  | 0            |

### Appendix III

| Date   | Total | A   | Ma | Mh | Mc | D   | C spp. | Cf | P | F1 | F2 | F3 | S | Cr | T   | H  | U  |
|--------|-------|-----|----|----|----|-----|--------|----|---|----|----|----|---|----|-----|----|----|
| Apr-97 | 267   | 230 | 2  | 0  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 1  | 33  | 0  | 0  |
| Apr-97 | 307   | 265 | 9  | 5  | 4  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 24  | 0  | 0  |
| May-97 | 330   | 6   | 1  | 1  | 2  | 16  | 1      | 0  | 1 | 0  | 1  | 0  | 0 | 0  | 301 | 0  | 0  |
| May-97 | 55    | 30  | 0  | 0  | 3  | 0   | 3      | 7  | 0 | 0  | 0  | 0  | 0 | 0  | 3   | 5  | 4? |
| May-97 | 45    | 21  | 0  | 0  | 2  | 0   | 0      | 3  | 0 | 0  | 0  | 0  | 0 | 0  | 0   | 19 | 0  |
| May-97 | 128   | 71  | 31 | 0  | 0  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 12  | 14 | 0  |
| May-97 | 338   | 253 | 20 | 3  | 3  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 59  | 0  | 0  |
| May-97 | 148   | 144 | 1  | 0  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 2   | 0  | 0  |
| May-97 | 232   | 202 | 14 | 0  | 4  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 12  | 0  | 0  |
| May-97 | 145   | 122 | 0  | 0  | 2  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 21  | 0  | 0  |
| May-97 | 156   | 115 | 3  | 1  | 0  | 0   | 0      | 0  | 1 | 0  | 0  | 0  | 0 | 0  | 29  | 7  | 0  |
| Jun-97 | 318   | 20  | 3  | 0  | 2  | 287 | 0      | 0  | 0 | 0  | 0  | 0  | 6 | 0  | 0   | 0  | 0  |
| Jun-97 | 344   | 310 | 7  | 1  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 25  | 0  | 0  |
| Jun-97 | 275   | 205 | 15 | 0  | 7  | 2   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 46  | 0  | 0  |
| Jun-97 | 390   | 223 | 5  | 0  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 161 | 0  | 0  |
| Jun-97 | 300   | 283 | 0  | 0  | 0  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 13  | 4  | 0  |
| Jun-97 | 166   | 113 | 0  | 0  | 0  | 0   | 0      | 21 | 0 | 0  | 0  | 0  | 0 | 0  | 2   | 30 | 0  |
| Jun-97 | 295   | 256 | 10 | 0  | 0  | 0   | 6      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 12  | 11 | 0  |
| Jun-97 | 257   | 206 | 3  | 0  | 7  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 27  | 14 | 0  |
| Jun-97 | 356   | 326 | 1  | 0  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 23  | 5  | 0  |
| Jun-97 | 240   | 225 | 0  | 0  | 8  | 6   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0   | 1  | 0  |
| Jun-97 | 252   | 228 | 0  | 3  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 18  | 2  | 0  |
| Jun-97 | 208   | 143 | 21 | 0  | 0  | 4   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 10  | 30 | 0  |
| Jul-97 | 114   | 70  | 27 | 1  | 4  | 0   | 3      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 8   | 1  | 0  |
| Jul-97 | 250   | 232 | 4  | 0  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0   | 13 | 0  |
| Jul-97 | 90    | 90  | 0  | 0  | 0  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0   | 0  | 0  |
| Jul-97 | 143   | 106 | 4  | 0  | 1  | 0   | 2      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 23  | 7  | 0  |
| Jul-97 | 197   | 164 | 27 | 0  | 0  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 1   | 5  | 0  |
| Jul-97 | 256   | 207 | 17 | 0  | 0  | 0   | 1      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 10  | 21 | 0  |
| Jul-97 | 184   | 155 | 25 | 0  | 2  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0   | 2  | 0  |
| Jul-97 | 312   | 275 | 8  | 1  | 0  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 27  | 1  | 0  |
| Jul-97 | 303   | 271 | 2  | 0  | 8  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 22  | 0  | 0  |
| Jul-97 | 282   | 238 | 5  | 0  | 4  | 0   | 1      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 10  | 24 | 0  |
| Jul-97 | 275   | 229 | 1  | 1  | 1  | 3   | 5      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 34  | 1  | 0  |
| Jul-97 | 396   | 201 | 2  | 0  | 4  | 0   | 3      | 4  | 0 | 0  | 0  | 0  | 0 | 37 | 145 | 0  | 0  |

### Appendix III

| Date   | Total | A   | Ma | Mh | Mc | D   | C spp. | Cf | P | F1 | F2 | F3 | S | Cr | T   | H   | U  |
|--------|-------|-----|----|----|----|-----|--------|----|---|----|----|----|---|----|-----|-----|----|
| Aug-97 | 302   | 297 | 2  | 0  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 1   | 1   | 0  |
| Aug-97 | 263   | 62  | 3  | 0  | 0  | 98  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 98  | 2   | 0  |
| Aug-97 | 330   | 236 | 0  | 0  | 0  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 94  | 0   | 0  |
| Aug-97 | 212   | 143 | 0  | 0  | 2  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 67  | 0   | 0  |
| Aug-97 | 419   | 321 | 0  | 0  | 4  | 0   | 0      | 1  | 0 | 0  | 0  | 0  | 0 | 0  | 93  | 0   | 0  |
| Aug-97 | 277   | 204 | 0  | 0  | 0  | 0   | 6      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 67  | 0   | 0  |
| Aug-97 | 376   | 154 | 25 | 0  | 0  | 1   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 196 | 0   | 0  |
| Aug-97 | 560   | 50  | 0  | 0  | 0  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 510 | 0   | 0  |
| Aug-97 | 203   | 182 | 0  | 0  | 0  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 5   | 16  | 0  |
| Aug-97 | 294   | 90  | 0  | 0  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 98  | 105 | 0  |
| Aug-97 | 244   | 215 | 12 | 0  | 0  | 0   | 3      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 3   | 11  | 0  |
| Aug-97 | 341   | 196 | 3  | 0  | 1  | 0   | 3      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0   | 138 | 0  |
| Sep-97 | 258   | 167 | 17 | 1  | 0  | 59  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 6   | 8   | 0  |
| Sep-97 | 274   | 206 | 27 | 1  | 0  | 25  | 0      | 0  | 1 | 0  | 0  | 0  | 0 | 0  | 4   | 10  | 0  |
| Sep-97 | 419   | 50  | 2  | 0  | 0  | 366 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0   | 0   | 1? |
| Sep-97 | 417   | 309 | 17 | 0  | 0  | 1   | 2      | 0  | 0 | 0  | 0  | 0  | 0 | 21 | 63  | 3   | 1? |
| Sep-97 | 170   | 144 | 13 | 0  | 2  | 0   | 1      | 1  | 0 | 0  | 0  | 0  | 0 | 1  | 1   | 7   | 0  |
| Sep-97 | 349   | 89  | 4  | 0  | 1  | 254 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 0   | 1   | 0  |
| Sep-97 | 202   | 40  | 48 | 0  | 1  | 0   | 0      | 0  | 2 | 0  | 0  | 0  | 0 | 10 | 96  | 1   | 4? |
| Sep-97 | 405   | 380 | 7  | 0  | 6  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 3  | 9   | 0   | 0  |
| Sep-97 | 298   | 263 | 25 | 0  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 8   | 1   | 0  |
| Sep-97 | 337   | 55  | 0  | 0  | 2  | 0   | 1      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 277 | 2   | 0  |
| Sep-97 | 399   | 274 | 52 | 1  | 0  | 29  | 0      | 0  | 1 | 0  | 0  | 0  | 0 | 0  | 42  | 0   | 0  |
| Oct-97 | 29    | 5   | 17 | 1  | 0  | 0   | 0      | 0  | 0 | 0  | 0  | 1  | 0 | 5  | 0   | 0   | 0  |
| Oct-97 | 122   | 107 | 3  | 0  | 0  | 0   | 0      | 0  | 1 | 0  | 0  | 1  | 0 | 1  | 0   | 9   | 0  |
| Oct-97 | 540   | 261 | 13 | 1  | 0  | 211 | 2      | 0  | 0 | 0  | 0  | 1  | 0 | 0  | 0   | 51  | 0  |
| Oct-97 | 227   | 162 | 16 | 0  | 0  | 32  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 6   | 11  | 0  |
| Oct-97 | 264   | 186 | 60 | 0  | 12 | 0   | 0      | 0  | 0 | 0  | 2  | 4  | 0 | 0  | 0   | 0   | 0  |
| Oct-97 | 385   | 54  | 32 | 0  | 0  | 282 | 0      | 3  | 0 | 0  | 1  | 0  | 0 | 0  | 1   | 12  | 0  |
| Oct-97 | 255   | 201 | 5  | 0  | 0  | 17  | 2      | 0  | 0 | 4  | 0  | 0  | 0 | 0  | 0   | 26  | 0  |
| Oct-97 | 293   | 170 | 91 | 6  | 1  | 0   | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 0  | 25  | 0   | 0  |
| Oct-97 | 196   | 167 | 3  | 0  | 0  | 0   | 1      | 0  | 0 | 4  | 0  | 0  | 0 | 0  | 16  | 5   | 0  |
| Oct-97 | 177   | 140 | 1  | 0  | 9  | 0   | 0      | 0  | 0 | 13 | 0  | 0  | 0 | 3  | 10  | 1   | 0  |
| Nov-97 | 281   | 222 | 0  | 0  | 0  | 43  | 1      | 1  | 0 | 1  | 0  | 0  | 0 | 0  | 4   | 9   | 0  |
| Nov-97 | 207   | 94  | 2  | 0  | 0  | 0   | 0      | 0  | 0 | 1  | 0  | 0  | 0 | 0  | 0   | 110 | 0  |
| Nov-97 | 99    | 78  | 10 | 0  | 5  | 0   | 0      | 0  | 0 | 0  | 0  | 1  | 0 | 5  | 0   | 0   | 0  |
| Nov-97 | 170   | 146 | 5  | 0  | 3  | 6   | 0      | 0  | 0 | 1  | 1  | 0  | 0 | 0  | 4   | 4   | 0  |
| Nov-97 | 176   | 155 | 12 | 2  | 4  | 0   | 0      | 0  | 0 | 2  | 0  | 0  | 0 | 0  | 0   | 0   | 1? |

| Date   | Total | A   | Ma | Mh | Mc | D  | C spp. | Cf | P | F1 | F2 | F3 | S | Cr  | T   | H  | U       |
|--------|-------|-----|----|----|----|----|--------|----|---|----|----|----|---|-----|-----|----|---------|
| Nov-97 | 109   | 57  | 32 | 0  | 8  | 1  | 0      | 0  | 0 | 0  | 0  | 1  | 0 | 6   | 0   | 4  | 0       |
| Nov-97 | 238   | 34  | 5  | 0  | 0  | 4  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 120 | 7   | 0  | 66?, 2? |
| Nov-97 | 209   | 69  | 12 | 0  | 0  | 63 | 0      | 0  | 0 | 2  | 0  | 1  | 0 | 49  | 2   | 0  | 9?, 2?  |
| Nov-97 | 249   | 236 | 1  | 0  | 3  | 0  | 1      | 0  | 0 | 0  | 0  | 0  | 0 | 2   | 3   | 3  | 0       |
| Nov-97 | 330   | 125 | 82 | 1  | 9  | 36 | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 9   | 48  | 20 | 0       |
| Nov-97 | 296   | 93  | 76 | 0  | 0  | 88 | 3      | 2  | 0 | 1  | 0  | 0  | 1 | 0   | 0   | 32 | 0       |
| Dec-97 | 234   | 184 | 8  | 1  | 2  | 0  | 0      | 0  | 0 | 0  | 0  | 0  | 0 | 26  | 1   | 2  | 2?, 8?  |
| Dec-97 | 319   | 174 | 91 | 0  | 1  | 0  | 0      | 0  | 0 | 8  | 3  | 13 | 0 | 0   | 27  | 2  | 0       |
| Dec-97 | 464   | 247 | 59 | 1  | 5  | 0  | 0      | 0  | 0 | 34 | 1  | 0  | 0 | 0   | 114 | 3  | 0       |
| Dec-97 | 488   | 351 | 55 | 0  | 3  | 0  | 0      | 0  | 0 | 30 | 0  | 10 | 0 | 0   | 39  | 0  | 0       |
| Dec-97 | 208   | 176 | 0  | 0  | 1  | 0  | 0      | 0  | 0 | 20 | 0  | 0  | 0 | 0   | 9   | 2  | 0       |
| Dec-97 | 139   | 73  | 37 | 0  | 1  | 0  | 0      | 0  | 0 | 8  | 1  | 6  | 0 | 0   | 7   | 6  | 0       |
| Dec-97 | 346   | 310 | 1  | 0  | 0  | 2  | 0      | 0  | 0 | 6  | 0  | 0  | 0 | 0   | 0   | 26 | 1 Tet   |
| Dec-97 | 200   | 134 | 12 | 0  | 0  | 0  | 0      | 0  | 0 | 2  | 0  | 0  | 0 | 0   | 52  | 0  | 0       |
| Dec-97 | 302   | 267 | 9  | 1  | 0  | 0  | 0      | 0  | 0 | 7  | 2  | 1  | 0 | 0   | 12  | 3  | 0       |

# Appendix IV.

**Table 33. (a) Total feeding observations for aardvark M5 in 1997**

| Obs time            |       |                  | Ac    | As   | Mc    | Ma   | D   | Cf | Cr | S  | Mh | P  | T    | Tm    | H    | Grand tot |
|---------------------|-------|------------------|-------|------|-------|------|-----|----|----|----|----|----|------|-------|------|-----------|
| Dec                 | 6hrs  | Species count    | 155   | 0    | 0     | 2    | 0   | 0  | 0  | 0  | 0  | 0  | 3    | 0     | 0    | 160       |
|                     |       | Sum of feed time | 7917  | 0    | 0     | 43   | 0   | 0  | 0  | 0  | 0  | 0  | 20   | 0     | 0    | 7980      |
| Jan                 | 14hrs | Species count    | 205   | 6    | 59    | 2    | 0   | 0  | 0  | 0  | 0  | 0  | 13   | 17    | 0    | 302       |
|                     |       | Sum of feed time | 8782  | 740  | 5158  | 75   | 0   | 0  | 0  | 0  | 0  | 0  | 350  | 845   | 0    | 15950     |
| Feb                 | 22hrs | Species count    | 640   | 0    | 28    | 0    | 0   | 0  | 0  | 0  | 0  | 0  | 256  | 1     | 1    | 926       |
|                     |       | Sum of feed time |       |      |       |      |     |    |    |    |    |    |      |       |      |           |
| Mar                 | 28hrs | Species count    | 402   | 170  | 41    | 1    | 0   | 1  | 0  | 35 | 0  | 0  | 121  | 16    | 5    | 792       |
|                     |       | Sum of feed time |       |      |       |      |     |    |    |    |    |    |      |       |      |           |
| Apr                 | 22hrs | Species count    | 223   | 45   | 57    | 8    | 0   | 0  | 0  | 0  | 0  | 0  | 61   | 30    | 0    | 424       |
|                     |       | Sum of feed time | 6660  | 1335 | 12980 | 100  | 0   | 0  | 0  | 0  | 0  | 0  | 360  | 14120 | 0    | 35555     |
| May                 | 14hrs | Species count    | 152   | 0    | 23    | 10   | 0   | 0  | 0  | 0  | 0  | 0  | 28   | 30    | 0    | 243       |
|                     |       | Sum of feed time | 4758  | 0    | 6555  | 242  | 0   | 0  | 0  | 0  | 0  | 0  | 1164 | 14322 | 0    | 27041     |
| Jun                 | 6hrs  | Species count    | 121   | 0    | 11    | 1    | 0   | 0  | 0  | 0  | 0  | 0  | 9    | 18    | 0    | 160       |
|                     |       | Sum of feed time | 4533  | 0    | 1430  | 3    | 0   | 0  | 0  | 0  | 0  | 0  | 930  | 4358  | 0    | 11254     |
| Jul                 | 9hrs  | Species count    | 105   | 0    | 9     | 2    | 0   | 0  | 0  | 0  | 0  | 1  | 9    | 29    | 0    | 155       |
|                     |       | Sum of feed time | 4311  | 0    | 570   | 40   | 0   | 0  | 0  | 0  | 0  | 70 | 1921 | 9900  | 0    | 16812     |
| Aug                 | 10hrs | Species count    | 103   | 0    | 10    | 6    | 1   | 0  | 0  | 0  | 1  | 0  | 6    | 33    | 0    | 160       |
|                     |       | Sum of feed time | 3766  | 0    | 2535  | 310  | 90  | 0  | 0  | 0  | 5  | 0  | 413  | 10990 | 0    | 18109     |
| Sep                 | 11hrs | Species count    | 141   | 21   | 17    | 20   | 0   | 0  | 0  | 0  | 0  | 0  | 23   | 26    | 0    | 248       |
|                     |       | Sum of feed time | 3319  | 1140 | 4445  | 1000 | 0   | 0  | 0  | 0  | 0  | 0  | 368  | 7628  | 0    | 17900     |
| Oct                 | 5hrs  | Species count    | 95    | 32   | 2     | 1    | 0   | 0  | 0  | 0  | 0  | 0  | 20   | 9     | 1    | 160       |
|                     |       | Sum of feed time | 2326  | 1109 | 1740  | 5    | 0   | 0  | 0  | 0  | 0  | 0  | 1093 | 1795  | 210  | 8278      |
| Nov                 | 12hrs | Species count    | 21    | 32   | 31    | 10   | 1   | 0  | 2  | 0  | 0  | 0  | 106  | 3     | 8    | 214       |
|                     |       | Sum of feed time | 1221  | 1292 | 9032  | 205  | 105 | 0  | 60 | 0  | 0  | 0  | 823  | 483   | 1510 | 14731     |
| Total species count |       |                  | 2363  | 306  | 288   | 63   | 2   | 1  | 2  | 35 | 1  | 1  | 655  | 212   | 15   | 3944      |
| Total Feed time     |       |                  | 47593 | 5616 | 44445 | 2023 | 195 |    | 60 |    | 5  | 70 | 7442 | 64441 | 1720 | 173610    |

Ac=*A. custodiens* As=*A. steingroeveri* Mc=*M. capensis* Ma=*M. albopilosum* D=*D. helvolus* Cf=*C. fulvopilosus* Cn=*C. nasutus*  
Cr=*Crematogaster* sp. S=*S. punctaticeps* Mh=*M. havilandi* P=*Pheidole* sp. T=*T. trinervoides* Tm=*T. trinervoides* mounds H=*H. mossambicu*

Note: the hours observations in this appendix are not the same as the hours observations for the *T. trinervoides* mounds.

# Appendix IV (continued).

**Table 33 (continued). (b) Total feeding observations for aardvark F4 in 1997**

| 1997                | Obs. time |                  | Ac    | As   | Mc    | Ma   | D   | Cn | Cr | S  | P | T    | Tm    | H    | Grand Tot |
|---------------------|-----------|------------------|-------|------|-------|------|-----|----|----|----|---|------|-------|------|-----------|
| Feb                 | 4hrs      | Species count    | 138   | 0    | 4     | 0    | 0   | 0  | 0  | 0  | 0 | 7    | 1     | 2    | 152       |
|                     |           | Sum of feed time |       |      |       |      |     |    |    |    |   |      |       |      |           |
| Mar                 | 11hrs     | Species count    | 208   | 0    | 27    | 0    | 0   | 0  | 0  | 21 | 0 | 25   | 15    | 0    | 296       |
|                     |           | Sum of feed time |       |      |       |      |     |    |    |    |   |      |       |      |           |
| Apr                 | 29hrs     | Species count    | 272   | 0    | 77    | 3    | 0   | 0  | 0  | 0  | 1 | 60   | 15    | 2    | 429       |
|                     |           | Sum of feed time |       |      |       |      |     |    |    |    |   |      |       |      |           |
| May                 | 19hrs     | Species count    | 226   | 0    | 42    | 2    | 0   | 0  | 0  | 0  | 0 | 38   | 37    | 1    | 346       |
|                     |           | Sum of feed time | 14851 | 0    | 12027 | 60   | 0   | 0  | 0  | 0  | 0 | 685  | 6756  | 180  | 34559     |
| Jun                 | 15hrs     | Species count    | 127   | 0    | 31    | 3    | 0   | 1  | 0  | 0  | 0 | 4    | 47    | 0    | 213       |
|                     |           | Sum of feed time | 11063 | 0    | 7741  | 120  | 0   | 5  | 0  | 0  | 0 | 55   | 8253  | 0    | 27237     |
| Jul                 | 14hrs     | Species count    | 213   | 0    | 10    | 3    | 5   | 2  | 0  | 0  | 0 | 19   | 48    | 0    | 300       |
|                     |           | Sum of feed time | 10768 | 0    | 6360  | 105  | 372 | 6  | 0  | 0  | 0 | 846  | 16453 | 0    | 34910     |
| Aug                 | 21hrs     | Species count    | 164   | 0    | 46    | 4    | 0   | 5  | 0  | 0  | 0 | 2    | 101   | 5    | 327       |
|                     |           | Sum of feed time | 4482  | 0    | 9012  | 185  | 0   | 36 | 0  | 0  | 0 | 18   | 20216 | 225  | 34174     |
| Sep                 | 21hrs     | Species count    | 209   | 0    | 51    | 35   | 3   | 0  | 0  | 0  | 0 | 5    | 52    | 4    | 359       |
|                     |           | Sum of feed time | 5945  | 0    | 17388 | 1239 | 15  | 0  | 0  | 0  | 0 | 167  | 12081 | 450  | 37285     |
| Oct                 | 23hrs     | Species count    | 350   | 20   | 43    | 31   | 0   | 1  | 0  | 0  | 0 | 25   | 74    | 17   | 561       |
|                     |           | Sum of feed time | 6820  | 600  | 5394  | 1077 | 0   | 2  | 0  | 0  | 0 | 865  | 9478  | 1288 | 25524     |
| Nov                 | 10hrs     | Species count    | 215   | 0    | 36    | 2    | 0   | 0  | 1  | 0  | 0 | 41   | 5     | 14   | 314       |
|                     |           | Sum of feed time | 4081  | 0    | 5551  | 35   | 0   | 0  | 30 | 0  | 0 | 452  | 192   | 1441 | 11782     |
| Dec                 | 6hrs      | Species count    | 62    | 39   | 13    | 5    | 0   | 0  | 0  | 0  | 0 | 110  | 0     | 5    | 234       |
|                     |           | Sum of feed time | 1251  | 1335 | 3662  | 1140 | 0   | 0  | 0  | 0  | 0 | 1497 | 0     | 306  | 9191      |
| Total species count |           |                  | 2184  | 59   | 380   | 88   | 8   | 9  | 1  | 21 | 1 | 336  | 395   | 50   | 3532      |
| Total Feed time     |           |                  | 59261 | 1935 | 67135 | 3961 | 387 | 49 | 30 |    |   | 4585 | 73429 | 3890 | 214662    |

**Appendix V.** Comparisons between faecal results and observed feeding times for *Anoplolepis* spp. and *T. trinervitermes*.

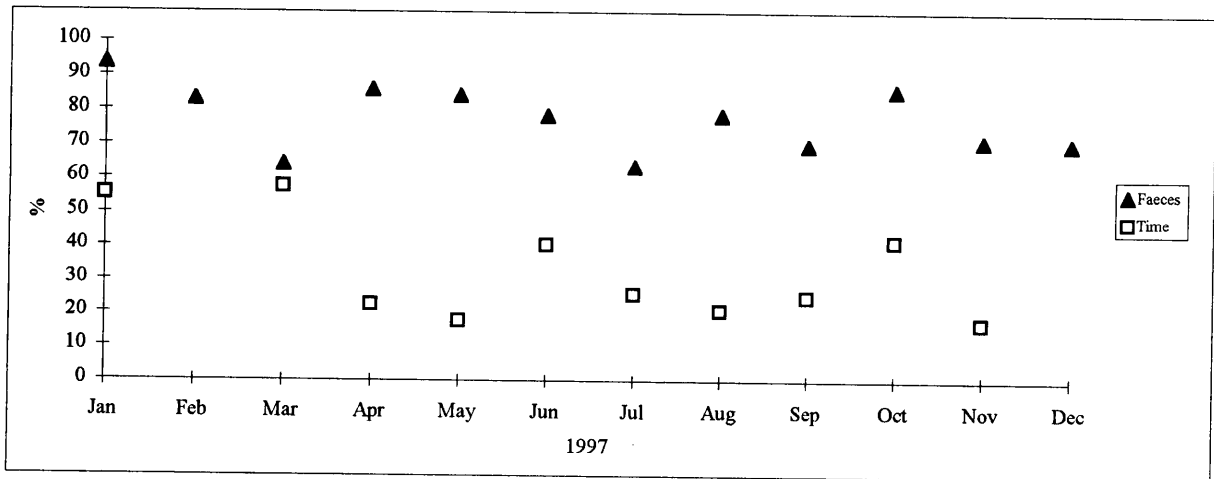


**Figure 46.** Comparison between the average monthly proportions of *Anoplolepis* spp. in the faeces of aardvark M5 with the monthly proportion of time spent feeding on *Anoplolepis* spp. during observation

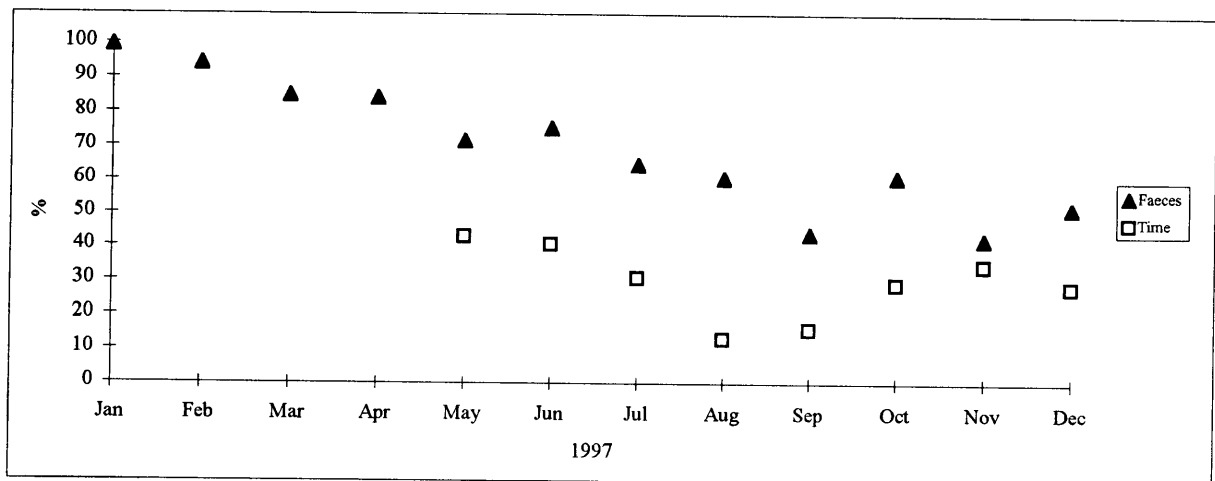


**Figure 47.** Comparison between the average monthly proportions of *Anoplolepis* spp. in the faeces of aardvark F4 with the monthly proportion of time spent feeding on *Anoplolepis* spp. during observation

Appendix V (continued).

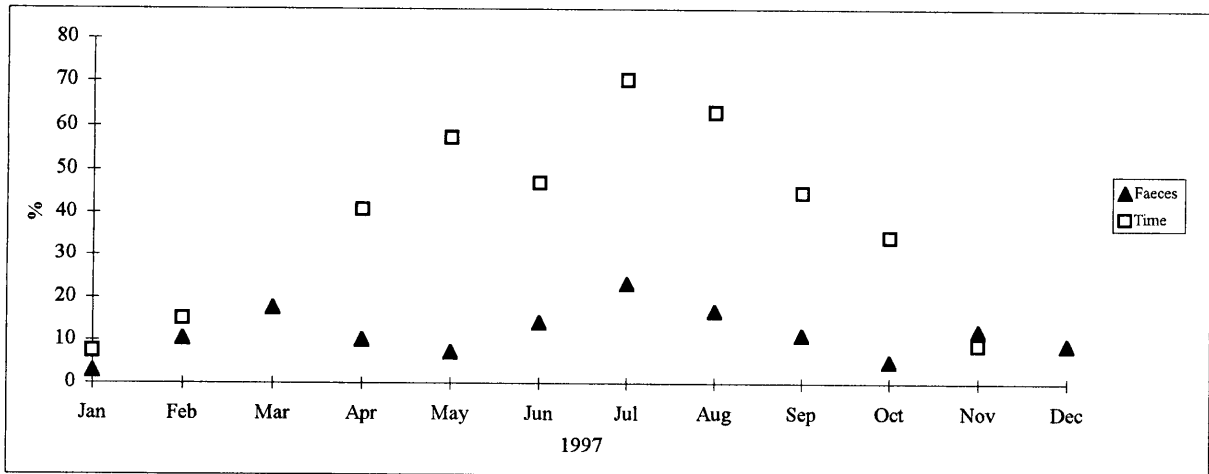


**Figure 48.** Comparison between the average monthly proportions of *T. trinervoides* in the faeces of aardvark M5 with the monthly proportion of time spent feeding on *T. trinervoides* (both from mound feeds and ground feeds) during observations.

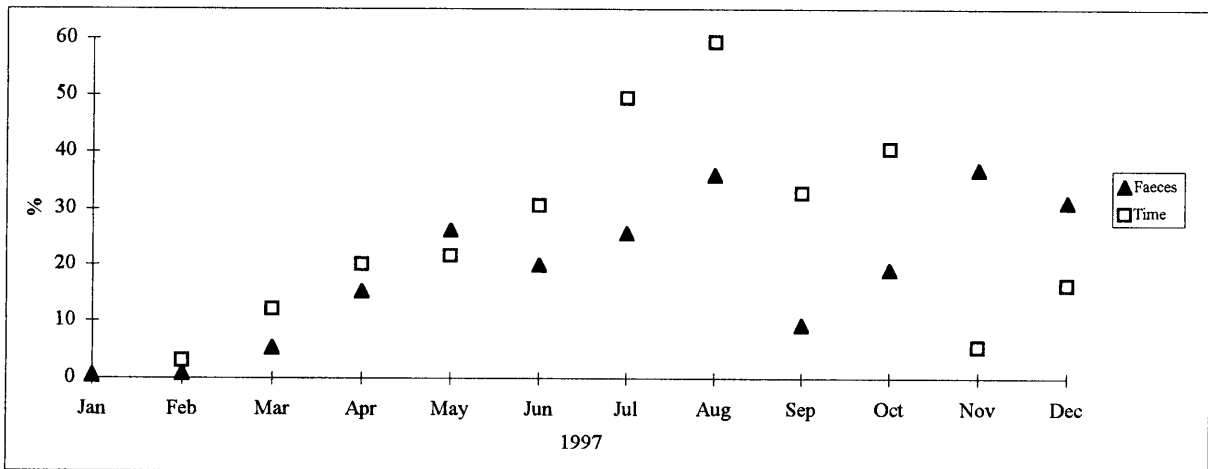


**Figure 49.** Comparison between the average monthly proportions of *T. trinervoides* in the faeces of aardvark F4 with the monthly proportion of time spent feeding on *T. trinervoides* (both from mound feeds and ground feeds) during observations.