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# The feeding ecology of the aardvark *Orycteropus afer*

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Thirteen aardvarks (*Orycteropus afer*) were radio tagged at Tussen die Riviere Nature Reserve in the Nama Karoo between 1996 and 1998. Faecal contents were analysed and four habituated aardvarks closely followed to investigate feeding ecology. The diet of the aardvark consisted entirely of ants and termites, with ants predominating in all seasons and years. *Anoplolepis custodiens* was the most important prey species in all months, followed by *Trinervitermes trinervoides*. Termites were fed on more often in winter than summer at a time when ant numbers were generally reduced and the aardvarks may have been experiencing difficulty in meeting their nutritional requirements relative to summer. Predation from epigeal mounds took place at this time, coinciding with the presence of alates.



**Keywords:** aardvark; *Orycteropus afer*; Nama Karoo; feeding; ants; termites; *Anoplolepis*; *Trinervitermes*

## Introduction

There are at least 216 ant/termite-eating mammalian species, the second most important class of animals to feed on them (Redford, 1983). Most mammals that eat large quantities of ants also eat termites, being specialized not on prey of a particular taxonomy, but of a certain type: small, fairly homogeneous, social arthropods (Redford, 1983).

The aardvark *Orycteropus afer* is a large myrmecophagous mammal (40–60 kg) that is distributed locally throughout sub-Saharan Africa (Skinner & Smithers, 1990). It is the only member of the order Tubulidentata and, as a solitary and nocturnal animal, has been little studied. In southern Africa aardvarks feed primarily on ants, but termites also constitute an important part of their diet (Smithers, 1971; Smithers & Wilson, 1979; Melton, 1976; Melton & Daniels, 1986; Willis *et al.*, 1992). Most accounts of aardvarks' diet are based on limited stomach or faecal contents, while other information is anecdotal. The most extensive study to date was that of Willis *et al.* (1992), which included 10 summer and 10 winter faecal samples. No studies have had access to habituated wild aardvarks, and previously 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 knowledge of aardvark feeding ecology.

 

## Materials and methods

### *Study site*

The study was carried out at Tussen die Riviere Nature Reserve (TdR) (30°30′S, 26°07′E) in the Eastern Mixed Nama Karoo (Hoffman, 1996), part of the Nama Karoo Biome, between June 1996 and December 1998. With a total area of 22,000 ha, TdR has an average annual rainfall of 400 mm falling mostly in summer (Nov.–Mar.). Summer temperatures exceed 30°C, while in winter (May–Jul.) temperatures often decline below 0°C at night.

The vegetation of TdR comprises three major communities (Werger, 1973):

(1) Riverine communities. Mostly made up of the *Acacia karoo*–*Celtis africana* community on the levees of fine alluvial sand. Usually three-layered consisting of a tree layer, an open 2–4-m tall shrub layer, and a field layer up to 0·6 m consisting of grasses, herbs and small shrubs.
(2) Communities of the flats and gently sloping grassland. These are usually two-layered, with the most important being the grass and dwarf shrub layer between 0·15 and 0·6m high.
(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 0·05 m; a grass and small shrub layer up to 0·8 m; a tall shrub layer between 1 and 4m; and sometimes an open tree layer up to 6 m high.

### *Study animals*

One of the aims of the study was to habituate aardvarks in order to make feeding observations. To achieve this, aardvarks were radio tagged to enable location and following at night. Thirteen aardvarks were captured in cage traps set outside burrow entrances and immobilised using a combination of ketamine hydrochloride (Anaket-V, Centaur, Bayer A.H., Isando), medetomidine hydrochloride (Domitor, Novartis A.H., Isando) and halothane (Fluothane, Zeneca) (Nel *et al.*, 2000). Telonics® radio transmitters were implanted intra-abdominally (Telonics, Telemetry-Electronic Consultants, 932 E. Impala Avenue, Mesa Arizona 85204-6699). Four aardvarks were habituated (two in 1996 and two in 1998) by following them on foot for periods of 3 h every night. This process took up to 3 months for each animal. Once tame, these aardvarks could be approached at any time and observed from a distance of 1m. Nine aardvarks remained unhabituated despite months of attempted following. Telemetry also enabled the determination of home ranges, which made it possible to identify the source of faeces from unhabituated aardvarks.

### *Faecal analysis*

The heads of adult ants and termites remain intact while passing through the aardvark GIT and can be extracted and identified from faeces. Generally faecal analysis only gives an approximate indication of dietary composition. Differential digestibility of different food stuffs results in absolute proportions of residues in the faeces which may differ from the proportions in which the food stuffs were ingested (Putman, 1984). Few foods have constant digestibility, as is the case with the insect exoskeleton which varies between taxa and between developmental stages. Adult ants and termites, however, have a strong cuticle which is sclerotised on the head (Rockstein, 1978).

During faecal analysis there was never any evidence of partial digestion of the heads of adult prey species, so it was assumed that differential digestion did not occur within the heads of adults.

This assumption was not made for developmental stages. The outer coats of insect eggs do not generally contain chitin (Hinton, 1981), while larvae have a soft, easily ruptured chitinous integument. Pupae were the only developmental stages of ants to pass through in the faeces. Production of pupae coincides with that of eggs and larvae (Steyn, 1954), so the latter were possibly eaten but not detected in the analysis. Developmental stages were not included in the results.

The number and composition of aardvarks available for faecal collection varied throughout the study due to the capture of more animals or losses via transmitter failure and death. From June 1996 to December 1997, faecal samples were collected monthly. In 1998, faeces were collected in two distinct seasonal periods, May–Jul. (winter), and Oct.–Dec. (summer). All faeces collected were fresh.

In 1997, six faecal samples were collected every month from each of the two habituated aardvarks while they were being followed, and a total of 10 faecal samples per month were collected from unhabituated aardvarks. The latter comprised radio-implanted individuals as well as unknown animals in separate areas of the Reserve. Experience of aardvark behaviour gained from tracking was utilized to ensure that faeces were assigned to the correct animals. Although the number of aardvarks available varied, faeces were collected from an average of six animals per month.

In 1998 10 faecal samples were collected from each of the four habituated aardvarks in both winter and summer. Ten faecal samples from different aardvarks were also collected.

Aardvark faecal deposits normally comprised 20–50 small ovoid pellets with a dry mass of up to 300 g. To represent the contents of one faecal deposit, one sub-sample of 20 g dry mass was collected from different parts of the deposit. After soaking in water the pellets were carefully broken up with a pestle in a mortar, following Willis *et al.* (1992). This freed organic material from the soil, allowing it to float to the surface to be filtered off and dried. Fresh water was added to the sample several times to extract as much of the organic material as possible. A larger faecal mass was unnecessary because it had been found previously that 15 g were sufficient to accurately represent an entire faecal deposit (Daniels, 1984). This was confirmed during the present study (pers. obs.).

Once dry, all individual ant and termite heads were extracted. Species identification was made from heads because they retained their shape and colour, allowing comparison with reference specimens. During sorting, morphologically distinct termite castes were categorised into soldiers and workers. Two ant genera were not separated into species due to the difficulty in distinguishing their heads; these were *Anoplolepis* spp. (comprising *A. custodiens* and *A. steingroeveri*) and *Camponotus* spp.

For each faecal sample the frequency of occurrence of every prey species was converted into a percentage occurrence, then monthly or seasonal averages estimated for each aardvark. Aardvark averages were then clumped with other aardvarks by month or season.

### *Feeding observations*

Habituated aardvarks were observed from a distance of 1m while they foraged. Observation periods lasted two hours and started at different times of the night. In 1997 two aardvarks (1 m, 1 f) were observed every month for total periods of 153 h and 173 h each, with the time spread fairly evenly between months. In 1998, each of the four habituated aardvarks (2 m, 2 f) were observed for an average of 32 h per season (winter: May–Jul.; summer: Oct.–Dec.), with a grand total of 256 h observation.

The following were recorded during each 2 h observation period:

(1) Prey species identification;
(2) Feed bout lengths (s). In 1997 the time was recorded from when aardvarks started digging into an ant nest, to when it stopped inserting its snout into the dig. In 1998 it was recorded as the length of time the aardvark collected food, indicated by movement of the hyomandibular apparatus. This difference was not important.
(3) Depth of food digs (cm).

Whenever an aardvark fed from an epigeal mound of *Trinervitermes trinervoides*, the following information was recorded:

(1) Mound height: small $< 20$ cm, medium 20–40 cm, and large $> 40$ cm. The height of a mound was used as an index of population size since the two measurements are highly correlated (Adam, 1993);
(2) Whether or not the mound had been previously excavated;
(3) The side of the mound opened up (north, south, etc.).

### *Calorific values of ants and termites*

Calorific values of six prey species eaten in large numbers were determined using a CP400 Mini Calorimeter (Cambridge Instruments). Soldiers, workers and alates of *T. trinervoides* were tested separately to compare calorific values between castes, while *A. custodiens* were collected in both summer and winter to compare seasons.

### *Estimation of densities of termite mounds*

One hectare sampling grids were temporarily marked out at 10 sites within known aardvark home ranges. Within each grid the number of epigeal *T. trinervoides* mounds were counted and categorized by height and whether or not they had been previously excavated.

### *Prey choice and prey value*

The major prey species in the diet of the aardvark were assessed according to five variables considered most likely to be important in affecting prey choice, using methods adapted from Swart *et al.* (1999). Variables were:

(1) The abundance of each species as indicated by pitfall trapping carried out at TdR (Lindsey & Skinner, 2001). Grassland results were used as this was the habitat in which aardvarks fed most often. Abundance figures were scaled from 1 to 50, with each increment of one indicating an increase in abundance of 50 ants. A figure of 1, therefore, indicates an abundance of 1–49, 2 = 50–99, etc. Abundance of *T. trinervoides* was estimated from the average density of epigeal mounds, from which termite density could be estimated using figures from Adam (1993);
(2) Prey size. A volumetric estimate was obtained using the equation:
Volume = Length (L) * Width (L/4) * Depth (L/5)
Each species length was measured and averaged from 10 specimens;
(3) Average dig depth. This was included to represent the depth of subterranean nests and, therefore, the effort expended by the aardvarks.

(4) Aggressiveness. A figure of 1–5 (1 low, 5 high) was given to each species to represent the defensive capabilities in the event of an attack on the nest by an aardvark. These figures were based upon observations made at feeding sites.
(5) Mobility. Values 1-5 as for aggression and based on observation.

These parameters were combined to generate a figure for prey value, using the following equation:

$$\text{Prey value} = (\text{Abundance} \star \text{Size})/(\text{Depth} \star \text{Defence} \star \text{Mobility})$$

### *Statistical analyses*

Parametric tests were preferred, but when data were not normally distributed, randomization testing (5000 permutations) was carried out. The software used for the randomization tests came from Manly (1991), converted from FORTRAN into Q-basic.

Analyses of seasonal variations in faecal prey species and their respective numerical contribution to the diet of the aardvarks were carried out using the software package PRIMER (Clarke & Warwick, 1994). This multivariate method bases its comparison of two or more samples on the extent to which these samples share particular species at comparable levels of abundance (Clarke & Warwick, 1994). Analysis of similarity (ANOSIM) is a test built on a simple non-parametric permutation procedure, applied to a (rank) similarity matrix underlying the clustering of samples (Clarke & Warwick, 1994). It was used on the frequency data of ants and termites in the faeces. For each season, 12 faecal sub-samples were randomly selected from six different aardvarks (two per aardvark) for the ANOSIM.

For analysis of mound predation by habituated aardvarks, $\chi^2$ tests were used. Circular statistics were used to test the orientation of digs into epigeal mounds. In the calculation of prey values it was assumed that each parameter was important to the aardvarks in terms of prey selection. This assumption was tested with the use of backwards stepwise regression.

## Results

### *Faecal analysis*

Table 1 shows the overall average contents of faecal samples collected at TdR for the entire study period. The mean % was calculated in the following way: for each faecal sample, species numbers were converted into percentages and an average obtained from all samples for each aardvark. All aardvark averages were then clumped for an overall average.

On average, ants (comprising 81·8% of faecal prey contents) were considerably more abundant than termites (18·2%) in the faeces. Six species, including four ants and two termites, made up 97·9% of the total intake. *Anoplolepis* spp. were the most numerous, followed by *T. trinervoides*. Faecal samples were occasionally dominated by a single species but no prey were found in every sample.

Table 2 shows the annual and seasonal variation in aardvark faecal contents for 1997 and 1998. *Anoplolepis* spp. were always the most abundant prey, while *T. trinervoides* occurred more in winter than summer, and *Monomorium albopilosum*, *Hodotermes mossambicus* and *Dorylus helvolus* occurred more in summer.

Table 3 shows the ANOSIM results for the faecal prey communities for winter and summer seasons from 1996 to 1998. There was strong evidence of differences between seasons and between years, with pairwise tests indicating that all three years were different from each other.

**Table 1.** *The overall contents of aardvark faecal samples at TdR from 1996 to1998 (standard deviation in parentheses). Mean % were calculated from 12 individual aardvarks and a total of 350 faecal samples. They were calculated in the following way: for each faecal sample, species numbers were converted into percentages and an average obtained from all samples for each aardvark. These were then clumped with other aardvark averages to give the overall average. % occurrence is the percentage of faecal samples in which a prey species was found*

| | Mean % | Range % | Occurrence | IV |
|---|---|---|---|---|
| *Anoplolepis* spp. | 68·4 (27·1) | 0–100·0 | 95·8 | 65·50 |
| *Monomorium albopilosum* | 7·4 (11·8) | 0–92·2 | 78·6 | 5·81 |
| *Dorylus helvolus* | 2·8 (11·1) | 0–90·3 | 23·9 | 0·67 |
| *Messor capensis* | 1·1 (3·3) | 0–35·3 | 55·1 | 0·61 |
| Formicidae sp. 1 | 0·4 (1·3) | 0–11·6 | 17·7 | 0·07 |
| *Crematogaster* spp. | 0·4 (3·3) | 0–50·4 | 8·5 | 0·03 |
| *Camponotus* spp. | 0·3 (1·2) | 0–16·4 | 27·4 | 0·08 |
| Other species | 0·3 (1·7) | 0–27·7 | 15·5 | 0·05 |
| *Solenopsis punctaticeps* | 0·3 (2·7) | 0–34·2 | 4·5 | 0·01 |
| *Monomorium havilandi* | 0·1 (0·4) | 0–3·4 | 46·6 | 0·05 |
| *Pheidole* spp. | 0·1 (0·1) | 0–1·1 | 7·5 | 0·01 |
| Formicidae sp. 2 | 0·1 (0·5) | 0–4·3 | 7·0 | 0·01 |
| Formicidae sp. 3 | 0·1 (0·4) | 0–6·9 | 6·7 | 0·01 |
| *Trinervitermes trinervoides* | 15·3 (22·3) | 0–98·9 | 82·5 | 12·63 |
| *Hodotermes mossambicus* | 2·9 (10·6) | 0–100·0 | 44·4 | 1·29 |

Importance value (IV) = (Mean % * % Occurrence)/100.

Table 4 shows average monthly variation in aardvark faecal contents for one year. In every month *Anoplolepis* spp. were the most abundant prey, followed by *T. trinervoides* and *M. albopilosum*. Within all species there was considerable variation between months but there were no apparent seasonal patterns.

Seasonal differences in the predation of *A. custodians* and *T. trinervoides* were tested statistically. May, June and July data were clumped as winter, while November, December and January data made up summer. Average percentages from nine aardvarks were used. For *Anoplolepis* spp. there was no seasonal difference ($t = 0{\cdot}84$, df. = 16, $p = 0{\cdot}41$), while for *T. trinervoides* there was evidence for a seasonal difference (albeit not at the 0·05% level) ($t = 2{\cdot}02$, df. = 16, $p = 0{\cdot}06$). In winter aardvarks ate more *T. trinervoides* than summer.

In 1997 *T. trinervoides* comprised an average of 64% soldiers and 36% workers in the faeces. Worker numbers increased in winter then decreased again in the following summer. January and December had the lowest proportions of workers (25% and 24% respectively) while the winter months May to July had an average of 39%. October was the only month when workers outnumbered soldiers (54% workers).

Soldiers occurred in the faeces in larger numbers than expected ($\chi^2 = 3184$, df. = 1, $p < 0{\cdot}001$). Expected values were calculated by multiplying the percentage of a caste available (25% soldiers, 75% workers) (Adam, 1993) by the total number of soldiers and workers in the faeces.

### *Feeding observations*

At TdR aardvarks fed at night and exclusively from ant and termite nests. Ground feeds for ants were mostly 5–30 cm deep, while digs as deep as 2 m were observed for the

**Table 2.** *The annual and seasonal variation in aardvark faecal contents between 1997 and 1998. Mean % calculated in the same way as for Table 1*

| | Winter 97 | | Summer 97 | | Winter 98 | | Summer 98 | |
|---|---|---|---|---|---|---|---|---|
| | Mean % | % occ. | Mean % | % occ. | Mean % | % occ. | Mean % | % occ. |
| *Anoplolepis* spp. | **68·9** | 100·0 | **63·5** | 100·0 | **63·6** | 97·9 | **65·3** | 100·0 |
| *Monomorium albopilosum* | **4·1** | 85·4 | **11·4** | 95·5 | **4·4** | 77·1 | **9·8** | 85·3 |
| *Dorylus helvolus* | **1·6** | 16·7 | **3·8** | 28·8 | **1·9** | 33·3 | **8·1** | 52·9 |
| *Messor capensis* | **0·8** | 54·2 | **0·8** | 40·9 | **2·0** | 60·4 | **0·5** | 32·4 |
| *Camponotus* spp. | **0·2** | 39·6 | **0·1** | 24·2 | **0·5** | 39·6 | **1·7** | 70·6 |
| *Crematogaster* spp. | **0·2** | 2·1 | **1·9** | 19·7 | **0·1** | 2·1 | **0·1** | 5·9 |
| *Monomorium havilandi* | **0·1** | 14·6 | **0·2** | 21·2 | **0·0** | 0·0 | **0·2** | 17·6 |
| *Pheidole* spp. | **0·1** | 2·1 | **0·1** | 4·5 | **0·0** | 0·0 | **0·1** | 5·9 |
| Other spp. | **0·0** | 0·0 | **0·6** | 16·7 | **0·8** | 35·4 | **0·8** | 52·9 |
| Formicidae sp. 1 | **0·0** | 0·0 | **1·6** | 57·6 | **0·1** | 2·1 | **0·6** | 52·9 |
| Formicidae sp. 2 | **0·0** | 0·0 | **0·2** | 28·8 | **0·0** | 0·0 | **0·0** | 0·0 |
| *Solenopsis punctaticeps* | **0·0** | 0·0 | **0·1** | 7·6 | **0·0** | 0·0 | **0·0** | 0·0 |
| Formicidae sp. 3 | **0·0** | 0·0 | **0·5** | 33·3 | **0·0** | 0·0 | **0·0** | 0·0 |
| *Trinervitermes trinervoides* | **21·5** | 91·7 | **12·2** | 81·8 | **22·7** | 85·4 | **0·7** | 29·4 |
| *Hodotermes mossambicus* | **2·5** | 37·5 | **3·1** | 72·7 | **3·9** | 31·3 | **12·1** | 79·4 |

Winter 97 = 6 aardvarks, 80 samples; Summer 97 = 7 aardvarks, 75 samples; Winter 98 = 7 aardvarks, 45 samples; Summer 98 = 8 aardvarks, 40 samples.

subterranean termite *H. mossambicus*. Feeds were discreet and of short duration, lasting from 5 s to 2 min, and aardvarks made up to 200 feeds per night. The termite *T. trinervoides* was often eaten out of epigeal mounds and these feeds sometimes lasted more than 30 min. The aardvarks dug into the centre of the mounds where the adult and larval termites were most highly concentrated (Adam, 1993).

Table 5 shows the annual and seasonal variations in numbers of observed feeds as well as the percentage time spent feeding on prey species. *A. custodiens* was the most commonly consumed species, but percentages of time feeding showed some variation. *T. trinervoides* was fed on for the longest periods during both winters while *A. custodiens* was fed on for the longest only in the summer of 1998.

### *Depth of food digs*

The relationship between the dig depth and duration of feeds in summer and winter was tested using linear regression (Winter: $r = 0{\cdot}50$, df. = 4, $p = 0{\cdot}75$; Summer: $r = 0{\cdot}35$, df. = 6, $p = 0{\cdot}43$). There was no correlation, therefore, no association between deeper digs and longer feeds.

### *Feeding on* T. trinervoides *mounds*

Figure 1 shows the average monthly predation frequencies from *T. trinervoides* mounds by aardvarks M5 and F4 in 1997. The results were obtained by dividing the number of

**Table 3.** *Analysis of similarity (ANOSIM) of the faecal prey communities for winter and summer seasons from 1996 to 1998*

Tests for differences between seasons (averaged across all year groups)
Sample statistic (Global $R$): 0·318
Number of permutations: 5000
Number of permuted statistics greater than or equal to global $R$: 0
Significance level of sample statistic: 0

Tests for differences between years (averaged across all season groups)
Sample statistic (Global $R$): 0·124
Number of permutations: 5000
Number of permuted statistics greater than or equal to global $R$: 2
Significance level of sample statistic: 0·001

Pairwise tests

| Groups used | Number permutations | Number greater than stat value | Significance level |
|---|---|---|---|
| 1996, 1997 | 5000 | 55 | 0·011 |
| 1996, 1998 | 5000 | 8 | 0·002 |
| 1997, 1998 | 5000 | 31 | 0·006 |

observed mound feeds in a month by the total observation time (hours) for the same period.

Predation frequencies were higher in winter than summer. Randomization showed strong evidence of variation between months, but not between aardvarks (two-way-ANOVA randomized: between months $p = 0{\cdot}001$; between aardvarks $p = 0{\cdot}65$). The relationship between monthly predation frequencies and monthly feeding bout lengths from epigeal mounds was tested using a Spearman rank correlation coefficient (Aardvark M5: $r = 0{\cdot}50$, $n = 8$, $p = 0{\cdot}21$; Aardvark F4: $r = -0{\cdot}357$, $n = 7$, $p = 0{\cdot}43$). There was no correlation, therefore, no association between feeding frequency and feed length.

Table 6 shows counts and percentages of the different categories of *T. trinervoides* mounds determined from the sample grids, as well as the observed counts of predation on these mounds by the habituated aardvarks. Small mounds were most numerous followed by medium then large mounds. Moreover, more undug mounds were available than predug mounds. Large mounds were fed on more often than expected ($\chi^2 = 46$, df. = 2, $p < 0{\cdot}001$), as were predug mounds ($\chi^2 = 683{\cdot}3$, df. = 1, $p < 0{\cdot}001$). Expected frequencies were calculated by comparing the number of termite mounds present (grids) with the number of mounds eaten.

Aardvark M5 fed for an average of 177 (199), 370 (385) and 353 (362) s from small, medium and large mounds respectively, while aardvark F4 fed for an average of 111 (135), 233 (303) and 242 (268) s (standard deviations in parentheses). Small mounds were fed on for significantly shorter periods than the other mounds (ANOVA: $F = 12{\cdot}5$, df. = 2, $p < 0{\cdot}001$) ($Log_{10}$ transformation: variance > mean).

Aardvark M5 fed for an average of 324 (316) and 359 (416) s from undug and predug mounds respectively, while aardvark F4 fed for an average of 322 (349) and 205 (232) s. There were no significant differences between the length of average feeding bouts on undug and predug mounds (ANOVA: $F = 0{\cdot}2$, df. = 1, $p = 0{\cdot}64$) ($Log_{10}$ transformation).

**Table 4.** *Monthly variation in aardvark faecal contents for 1997 (values are percentages). Each month represents approximately 22 faecal samples from six aardvarks. Average percentages were calculated for each faecal sample first, then each aardvark, before being clumped*

| | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Anoplolepis* spp. | 87·9 | 80·3 | 64·8 | 82·4 | 71·7 | 76·1 | 73·7 | 61·2 | 63·6 | 67·6 | 57·4 | 65·1 |
| *Monomorium albopilosum* | 2·2 | 13·6 | 12·1 | 2·7 | 4·2 | 2·9 | 5·1 | 2·0 | 17·5 | 11·6 | 11·1 | 11·6 |
| *M. havilandi* | 0·1 | 0·1 | 0·1 | 0·2 | 0·2 | 0·3 | 0·2 | 0·0 | 0·1 | 0·4 | 0·1 | 0·1 |
| *Messor capensis* | 0·9 | 0·5 | 3·8 | 2·0 | 1·1 | 0·6 | 1·4 | 0·4 | 0·1 | 0·6 | 1·2 | 0·7 |
| *Dorylus helvolus* | 0·1 | 0·1 | 0·1 | 0·1 | 0·4 | 4·3 | 1·5 | 1·4 | 9·4 | 6·5 | 4·0 | 0·7 |
| *Camponotus* spp. | 0·0 | 0·1 | 0·3 | 0·0 | 1·2 | 1·0 | 0·5 | 0·3 | 0·1 | 0·3 | 0·1 | 0·1 |
| *Pheidole* spp. | 0·1 | 0·1 | 0·1 | 0·1 | 0·1 | 0·1 | 0·1 | 0·0 | 0·1 | 0·1 | 0·1 | 0·1 |
| Formicidae sp. 1 | 0·1 | 0·1 | 0·1 | 0·0 | 0·0 | 0·0 | 0·0 | 0·0 | 0·0 | 0·5 | 1·4 | 2·9 |
| Formicidae sp. 2 | 0·1 | 0·1 | 0·4 | 0·1 | 0·1 | 0·0 | 0·0 | 0·0 | 0·0 | 0·1 | 0·2 | 0·2 |
| Formicidae sp. 3 | 0·0 | 0·1 | 0·1 | 0·0 | 0·0 | 0·0 | 0·0 | 0·0 | 0·1 | 0·3 | 0·4 | 0·8 |
| *Solenopsis punctaticeps* | 0·1 | 0·0 | 5·3 | 1·3 | 0·0 | 0·1 | 0·0 | 0·0 | 0·0 | 0·1 | 0·1 | 0·1 |
| *Crematogaster* spp. | 0·0 | 0·1 | 1·4 | 0·1 | 0·0 | 0·0 | 0·4 | 0·0 | 0·4 | 0·9 | 4·0 | 0·6 |
| Other species | 0·1 | 0·1 | 0·1 | 0·1 | 0·3 | 0·0 | 0·0 | 0·0 | 0·1 | 0·0 | 1·6 | 0·2 |
| *Trinervitermes trinervoides* | 8·0 | 4·4 | 10·8 | 10·4 | 17·3 | 13·2 | 15·3 | 31·3 | 8·0 | 7·7 | 13·8 | 15·3 |
| *Hodotermes mossambicus* | 0·3 | 0·3 | 0·5 | 0·5 | 3·4 | 1·4 | 1·8 | 3·4 | 0·5 | 3·3 | 4·5 | 1·5 |

**Table 5.** *The annual and seasonal variation in numbers of feeds and time spent feeding during observations on aardvarks. Each % time feeding was calculated by dividing the total time feeding on one species by the total time feeding on all species. 1997 observations represent two aardvarks and 1998 represents four aardvarks. Observation periods lasted 2 h, and the overall observation time, spread fairly evenly between aardvarks was 552 h (326 h in 1997, 256 h in 1998)*

| | % number of feeds Winter 97 | % of time feeding Winter 97 | % number of feeds Summer 97 | % of time feeding Summer 97 | % number of feeds Winter 98 | % of time feeding Winter 98 | % number of feeds Summer 98 | % of time feeding Summer 98 |
|---|---|---|---|---|---|---|---|---|
| *Anoplolepis custodiens* | **66·8** | 31·3 | **48·9** | 21·5 | **19·3** | 18·8 | **51·6** | 54·3 |
| *Messor capensis* | **8·7** | 21·3 | **8·2** | 34·3 | **25·8** | 24·3 | **3·5** | 4·5 |
| *Anoplolepis steingroeveri* | **0** | 0 | **9·5** | 6·4 | **5·6** | 7·1 | **17·2** | 14·6 |
| *Monomorium albopilosum* | **1·6** | 0·4 | **4·2** | 3·9 | **0·4** | 0·4 | **2·2** | 2·3 |
| *Camponotus* spp. | **0·2** | 0 | **0** | 0 | **0·5** | 0·3 | **1·5** | 0·5 |
| *Crematogaster melanogaster* | **0** | 0 | **0·2** | 0·1 | **0** | 0 | **0·4** | 0·1 |
| *Dorylus helvolus* | **0·3** | 0·2 | **0·1** | 0·1 | **0·1** | 0·1 | **1·8** | 1·1 |
| *Pheidole* sp. 1 | **0·1** | 0·1 | **0** | 0 | **0** | 0 | **0·1** | 0·1 |
| *Trinervitermes trinervoides (ground)* | **7·7** | 4·5 | **19·9** | 5·8 | **39·3** | 18·4 | **1·2** | 1·4 |
| *Trinervitermes trinervoides (mound)* | **14·6** | 42·2 | **6·6** | 22·5 | **2·1** | 29·4 | **0·4** | 1·4 |
| *Hodotermes mossambicus* | **0·1** | 0·1 | **2·3** | 5·4 | **6·9** | 1·2 | **20·1** | 19·7 |

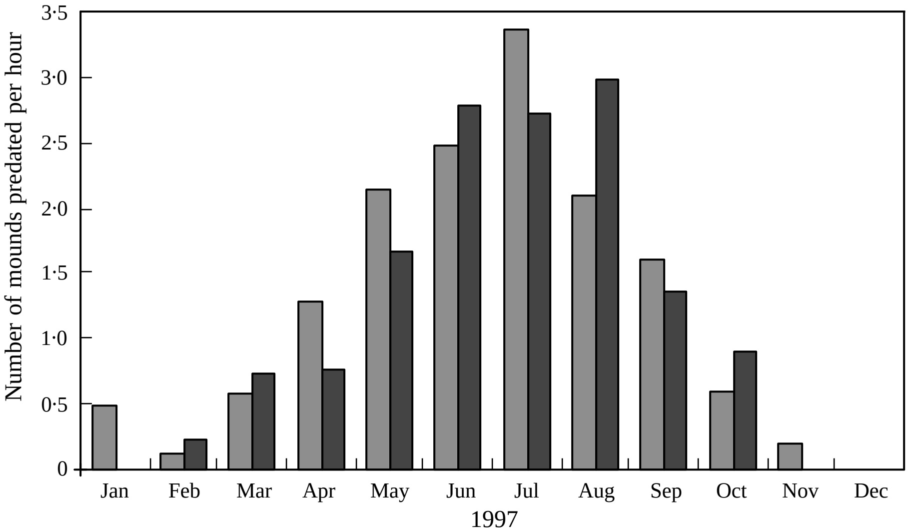


**Figure 1.** Average monthly feeding frequencies from *T. trinervoides* mounds by aardvarks M5 (■), and F4 (■) in 1997. The number of observed mound feeds in a month were divided by the total observation time for the same period.

### *Orientation of digs into* T. trinervoides *mounds*

The orientation of the aardvark digs into *T. trinervoides* mounds were categorised into eight compass sections starting at 0° (e.g. 0–45°, 45–90°). The Rayleigh test was used to investigate whether digs occurred randomly on all sides of mounds or whether there was any one-sidedness (Batschelet, 1981). The mean bearing at which aardvarks dug into mounds was 190·5°. The orientation of digs into termite mounds was not random, indicating that the sampled mounds were excavated significantly more on their south sides ($n = 302$, $\kappa = 1{\cdot}67$, $p < 0{\cdot}001$).

**Table 6.** *Counts and percentages of termite mounds from sampling grids (grids) and counts and percentages of termite mounds fed on by aardvarks M5 and F4 during 1997 (predation)*

| | Small frequency | % | Medium frequency | % | Large frequency | % | Total frequency | % |
|---|---|---|---|---|---|---|---|---|
| Grids | | | | | | | | |
| 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 |
| Predation | | | | | | | | |
| Undug | 32 | 6·6 | 34 | 7·0 | 56 | 11·5 | 122 | 25·1 |
| Predug | 8 | 1·6 | 64 | 13·1 | 293 | 60·2 | 365 | 74·9 |
| Total | 40 | 8·2 | 98 | 20·1 | 349 | 71·7 | 487 | 100·0 |

**Table 7.** *Calorific values of six common prey species of aardvark at TdR*

| | Calorific value | (MJ $kg^{-1}$) |
|---|---|---|
| *Anoplolepis custodiens* | 20·300 | (0·305) |
| *Anoplolepis steingroeveri* | 20·597 | (0·663) |
| *Messor capensis* | 20·081 | (0·436) |
| *Dorylus helvolus* | 21·793 | (0·230) |
| *Hodotermes mossambicus* | 19·195 | (0·244) |
| *Trinervitermes trinervoides* | | |
| Soldiers | 23·870 | (0·579) |
| Workers | 18·743 | (0·568) |
| Alates | 27·002 | (1·462) |

Standard deviations in parentheses.

### *Calorific values*

Table 7 shows the calorific values of six of the common prey species. There was no difference between *A. custodiens* and *A. steingroeveri* ($t = 0{\cdot}698$, df. = 10, $p = 0{\cdot}49$), and no difference in the calorific value of *A. custodiens* between summer and winter ($t = -0{\cdot}071$, df. = 17, $p = 0{\cdot}944$). There was, however, a difference between the three *T. trinervoides* castes (ANOVA: $F = 132{\cdot}1$, df. = 2, $p < 0{\cdot}0001$).

### *Prey values*

Table 8 shows the prey values of the major prey species and the values of associated variables for both winter and summer. *T. trinervoides* had the highest prey values in both seasons. *A. custodiens* had the second lowest prey value in winter, while in summer it ranked in the middle.

The assumption that the parameters used in the calculation of prey values were important was tested by a backwards stepwise regression (BSR) on the summer and winter data. A threshold $F$ value of 4·00 was used to determine which parameters were removed from the model.

Utilisation of prey species in winter could be predicted from a linear combination of the following independent variables: abundance (BSR: $F = 7{\cdot}1$, df. = 3, $p = 0.032$), size (BSR: $F = 4{\cdot}8$, df. = 3, $p = 0{\cdot}066$) and mobility (BSR: $F = 19{\cdot}6$, df. = 3, $p = 0{\cdot}003$). In summer, utilization could be predicted only by mobility (BSR: $F = 13{\cdot}8$, df. = 1, $p = 0{\cdot}05$).

## Discussion

The diet of the aardvark varies considerably between different localities within southern Africa (Smithers, 1971; Smithers & Wilson, 1979; Melton & Daniels, 1986; Willis *et al.*, 1992), yet all studies concur that the Formicidae predominate over the Isoptera.

### *Species contributions*

*Anoplolepis* spp. were by far the most common and important prey species in aardvark faeces at TdR. This is in agreement with the results of Willis *et al.* (1992) who found 14

**Table 8.** *The value of each factor determining the prey value in winter and summer*

| | Size B | Agg B | Mob B | Depth W | Depth S | RI W | RI S | Ab W | Ab S | PV W | PV S |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Anoplolepis custodiens* | 10·8 | 4 | 5 | 8·9 | 12·9 | 46·3 | 53·8 | 1 | 20 | 0·06 | 0·84 |
| *Anoplolepis steingroeveri* | 6·3 | 4 | 4 | 8·5 | 12·3 | 17·5 | 13·8 | 1 | 7 | 0·05 | 0·22 |
| *Camponotus* sp. | 36·5 | 3 | 3 | 3·0 | 2·7 | 0·5 | 1·7 | 1 | 1 | 1·35 | 1·50 |
| *Dorylus helvolus* | 10·8 | 5 | 3 | 9·0 | 9·0 | 1·9 | 8·4 | 1 | 2 | 0·08 | 0·16 |
| *Monomorium albopilosum* | 2·1 | 2 | 2 | 9·8 | 9·3 | 4·4 | 9·6 | 19 | 5 | 1·04 | 0·29 |
| *Monomorium havilandi* | 1·2 | 1 | 1 | 8·7 | 8·7 | 0·1 | 0·1 | 5 | 1 | 0·68 | 0·14 |
| *Messor capensis* | 17·2 | 1 | 2 | 6·0 | 8·9 | 2·0 | 0·5 | 1 | 1 | 1·43 | 0·96 |
| *Pheidole* sp. | 1·5 | 1 | 1 | 4·0 | 4·0 | 0·1 | 0·1 | 3 | 7 | 1·12 | 2·61 |
| *Crematogaster* sp. | 3·2 | 1 | 2 | 6·0 | 6·0 | 0·5 | 0·1 | 1 | 1 | 0·27 | 0·27 |
| *Trinervitermes trinervoides* | 3·2 | 3 | 1 | 3·8 | 14·4 | 22·7 | 0·7 | 41 | 41 | 11·51 | 3·04 |
| *Hodotermes mossambicus* | 66·6 | 1 | 4 | 2·7 | 9·4 | 3·9 | 11·9 | 1 | 1 | 6·16 | 1·77 |

Agg = aggression, Mob = mobility, RI = relative importance, Ab = abundance, PV = prey value, B = both summer and winter, W = winter, S = summer.

prey species compared to 15 in the present study. Willis *et al.* (1992) found that *A. custodiens* was present in all faecal samples, making up an average of 44% of the diet. *Anoplolepis* spp. occurred in 96% of faecal samples during the present study and made up an average of 68% in the diet. The abundance of *Anoplolepis* spp. is the probable cause of them being so common in the aardvarks diet.

*Trinervitermes trinervoides* was the second most important prey species in the present study, compared to third in that of Willis *et al.* (1992). The average proportions of total numbers were similar between the two studies (13·8% 1992 cf. 15·3% present) but the percentage occurrence was different (30% 1992 cf. 83% present). Willis *et al.* (1992) found *H. mossambicus* in every faecal deposit, compared to 44% occurrence in the present study.

The differential contributions made by the latter two prey species during the two studies may be explained by temporal and spatial mosaics in their distributions. There was a time lapse of 10 years between studies, while data were collected from different sites within TdR. Ant and termite populations are known to have mosaic distributions (Samways, 1983) and this was shown to be the case at TdR (Lindsey & Skinner, 2001).

### *Seasonal variation in diet*

Numbers of *A. custodiens* are lowest between May and July (Steyn, 1954; Lindsey & Skinner, 2001) when developmental stages are virtually non-existent. This suggests summer is a relatively good time to eat them. However, no pattern of increased feeding on *A. custodiens* occurred in summer. This might be explained by two factors. First, even though *A. custodiens* numbers were low in winter, they were actually high relative to numbers of other ant species (Lindsey & Skinner, 2001). Secondly, there was no difference in the energy value of *A. custodiens* between seasons, making individual ants just as valuable in winter.

*Trinervitermes trinervoides* differ from *Anoplolepis* spp. in several ways. First, they nest in hard mounds which require more effort to break into (pers. obs.). Secondly, large *T. trinervoides* mounds hold over 80,0000 termites (Adam, 1993), compared with *A. custodiens* nests which contain little over 1000 adult ants (Steyn, 1954). Thirdly, populations of adult *T. trinervoides* do not decrease significantly in winter months (Adam, 1993) so the number of termites per colony is not a limiting factor on predation.

*Trinervitermes trinervoides* is a nocturnal forager (Adam, 1993), while *A. custodiens* is predominantly diurnal (Steyn, 1954; Willis *et al.*, 1992). Surface activity of *T. trinervoides* virtually ceases in winter (Adam, 1993) and they are confined to their mounds. In warmer months the termites travel along shallow tunnels to foraging areas and are often eaten out of these.

Calorific values of *T. trinervoides* workers and soldiers do not vary between seasons, neither do their overall numbers. However, calorific values and numbers of alates do vary. Alate production begins in March and by October they are fully developed, with maximum calorific value (Adam, 1993). The availability of alates might induce aardvarks to feed more from mounds in winter, but there was no evidence for this because any ingested alates would have been fully digested due to their soft bodies (Adam, 1993).

*Trinervitermes trinervoides* occurred in higher percentages in the faeces in winter when aardvarks fed from epigeal mounds. Aardvarks also eat *T. trinervoides* from foraging parties in summer, but as concentrations are higher in mounds, winter feeding predisposes a higher intake rate and possibly more termites eaten overall. This contradicts the findings of Melton (1976) and Willis *et al.* (1992), who found that termites were taken more in summer than winter.

ANOSIM showed that the prey communities within the faeces were different between seasons and years. This indicates that, although *T. trinervoides* were eaten more in winter than summer, there was no seasonal pattern in the overall prey community selection. Again, this can best be explained by temporal and spatial mosaics in prey distributions.

### *Predation of* T. trinervoides *castes*

The relatively high proportion of workers ingested in winter compared to summer can perhaps be explained by the differing caste compositions of mounds and foraging parties. Foraging parties comprise 17% fewer workers than mound populations (Adam, 1993), so the termites that aardvarks eat in summer comprise less workers. Moreover, the high proportion of soldiers ingested by aardvarks in 1997 contradicts the idea that aardvarks are deterred from eating soldiers by the distasteful terpenes contained within the soldiers heads (Richardson, 1987).

### *Predation of* T. trinervoides *mounds*

The energy expended digging into a mound should be retrieved due to the large numbers of prey inside. Observations of mound feeding indicated that aardvarks often dug into the centre below ground level, where both adult and larval termites were highly concentrated (Adam, 1993). Rather than inhibiting the predation of *T. trinervoides*, the inactivity of this termite in winter makes it more accessible by concentrating its numbers in one place. Aardvarks preferentially selected large mounds over small ones, probably because large mounds have larger termite populations. They form a bigger resource allowing aardvarks to spend more time feeding without depleting termite numbers too much. Moreover, alates are only produced in mounds over 30 cm, while 83% of mounds between 41 and 50 cm produce alates (Adam, 1993). In the present study mounds were considered large when over 40 cm high, so it can be assumed that 83% or more contained alates.

Predug mounds were also positively selected, probably as a result of the relative ease in which they could be re-excavated compared to the hard outer layers of untouched mounds.

### *The orientation of aardvark digs on* T. trinervoides *mounds*

As aardvarks fed from the central point of termite mounds, the digging effort should have been the same from all sides. However, mounds were excavated significantly more on their south sides. A possible explanation for this is that mound construction by *T. trinervoides* occurs most frequently on the southern side (Adam, 1993). This is in contrast to the study of Bernard & Peinke (1993) who found that most diggings occurred on the northern (32%) and eastern (28%) quadrants. They suggest that this was because in the southern hemisphere these quadrants of termitaria are the warmest and should contain most termites at night. Excavations into northern quadrants would then be explained by optimal foraging theory based on the temperature differential that exists within the termite mound.

### *Prey values and choice*

Of the 45 ant and termite species recorded at TdR (Willis *et al.*, 1992; Lindsey & Skinner, 2001), only 15 were recorded in the diet of aardvarks during the present study. The Formicines were highly preferred, while the Myrmicines were under-utilized, conforming to the findings of Redford (1987). The abundance of prey has been suggested as an important factor in determining prey choice in myrmecophagous mammals (Redford, 1987; Abensperg-Traun, 1990). In the present study, abundance was found to be predictive of utilization by aardvarks in winter, but not summer. Some species were not utilized in proportion to their abundance. *T. trinervoides* and *M. albopilosum* were both under-utilized relative to *A. custodiens*.

Aardvark forage in a haphazard manner, and this makes it likely that prey species abundance is important in determining their diet selection. For example, *A. custodiens* is more widespread and numerous at TdR than *A. steingroeveri* (Lindsey & Skinner, 2001) and, if no preferential selection occurs between the two species, *A. custodiens* should be utilized more. This is indeed the case. In fact all the species of major importance in the diet of the aardvarks at TdR are extremely abundant in the area.

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

Prey size was predictive of prey utilization in winter but not in summer, even though most aardvark prey in summer were large. As the prey species have similar calorific values per unit mass it might be expected that the size of the various prey species would be significant in prey choice. Greater calorific gains per ant would be achieved from larger ants.

Prey defence was not found to be predictive of prey utilization in the present study although it has been found to be important in a number of other myrmecophages, including the pangolin *Manis temminckii* (Swart, 1996), the giant anteater *Myrmecophaga tridactyla* (Redford, 1985), the vermilinguas *Cyclopes didactylus* and *Tamandua mexicana* (Montgomery, 1985), and the echidna *Tachyglossus aculeatus* (Abensperg-Traun, 1990). Prey defences may cause irritation and premature cessation of feeding bouts in a number of species (Redford, 1987). It has been suggested that the preference of myrmecophages for formicines over myrmicines can be explained in terms of prey defences.

The only prey species to visibly cause the aardvarks discomfort during feeding was *D. helvolus*. The rest, including *A. custodiens* and *H. mossambicus*, which are recorded as causing discomfort to pangolins (Swart, 1996), did not appear to affect the aardvarks. The defences of *T. trinervoides* did not deter aardvarks either. The hard mounds of this termite are an effective barrier to other myrmecophages, including the aardwolf (Richardson, 1987) and pangolin (Swart, 1996), but the aardvark is able to dig into them with consummate ease. The chemical defences of *T. trinervoides* soldiers do not prevent predation by aardvarks either, despite suggestions to the contrary (Richardson, 1987, 1994; Anderson, 1994). The proportions of soldier *T. trinervoides* in aardvark faeces were significantly higher than proportions in mounds, indicating that the aardvark is not too careful to avoid their ingestion. Therefore, the effect of prey defences upon the feeding patterns of the aardvark appears limited.

The effect of prey defences may be reduced by certain behavioural characteristics of aardvark. First, on reaching prey nests they dig rapidly and feed frantically, enabling prey consumption to occur before the concentration of soldiers can increase significantly. Secondly, frequent digging during feeding probably has the effect of removing any build up of soldiers. Thirdly, aardvarks do not chew their food (aside from

*M. capensis*) and this reduces the release of chemical defences of certain prey. Redford (1983) showed that the efficacy of prey defences depends upon the size of the predator and the aardvark is likely to be less affected than smaller species.

If energy is limiting, one would expect the cost of prey extraction to be of importance in prey selection. Digging is energetically costly and differences in the depths of the various species may affect their value as prey items. However, several points suggest that this factor is of little importance in prey choice by the aardvark. For example, the depth at which the various species were fed upon was not correlated with utilization or feed length in either season, suggesting that digs were made to the depth required to expose prey regardless of value. Moreover, aardvarks did not spend longer feeding in previously undug mounds that would have used up more energy to dig open than predug mounds. In contrast, the pangolin has been shown to make longer feeds upon species where the depth of the digs is greater, indicating that more effort was expended for species of higher value (Swart, 1996). In addition, the difference between the average depths of the feeds upon the various species of major importance in the diet was small and in energetic terms, probably insignificant.

## *Summary*

In keeping with previous studies, aardvarks fed predominantly on ants, with *A. custodiens* being the most important prey species in all seasons and years. Out of 15 prey species identified, almost 98% of the aardvarks diet comprised only six species. There were no clearly defined seasonal patterns in prey species selection, although the termite *T. trinervoides* was eaten more in winter than summer. This disagrees with previous findings. It is possible that increased termite predation in winter may have supplemented the aardvarks diet at a time when numbers of *A. custodiens* were at their lowest. *T. trinervoides* soldiers were consumed in larger numbers than expected indicating that they are not avoided as previously suggested.

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## References

Abensberg-Traun, M. (1990). Patch selection and patch use in the Echidna *Tachyglossus aculeatus* Shaw 1792 (Monotremata: Tachyglossidae), in western Australian wheatbelt reserves. Ph.D. thesis, University of Western Australia, Perth. 252 pp.

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, Bloemtontein. 226 pp.

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, Pretoria. 176 pp.

Batschelet, E. (1981). *Circular Statistics in Biology*. London: Academic Press. 371 pp.

Bernard, R.T.F. & Peinke, D. (1993). Is the orientation of aardvark diggings into termitaria optimal? *Naturwissenschaften*, **80**: 422–424.

Clarke, K.R. & Warwick, R.M. (1994). *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*. Plymouth Marine Laboratory. Bournemouth, UK: Bourne Press Limited. 144 pp.

Daniels, C. (1984). Some aspects of habitat utilization and feeding ecology of the aardvark *Orycteropus afer*. B.Sc. (Hons) thesis, University of Natal, Pietermaritzburg. 71 pp.
Hinton, H.E. (1981). *Biology of Insect Eggs*, Vol. 1. New York: Pergamon Press. 172 pp.
Hoffman, T. (1996). Eastern Mixed Nama Karoo. In: Low, A.B. & Rebelo, A.G. (Eds), *Vegetation of South Africa, Lesotho and Swaziland*, pp. 52–57. Pretoria: Dept Environmental Affairs and Tourism. 85 pp.
Lindsey, P.A. & Skinner, J.D. (2001). Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. *Journal of Arid Environments*, **48**: 551–568.
Manly, B.F.J. (1991). *Randomization and Monte Carlo Methods in Biology*. London: Chapman and Hall. 281 pp.
Melton, D.A. (1976). The biology of aardvark (Tubulidentata-Orycteropodidae). *Mammal Review*, **6**: 75–88.
Melton, D.A. & Daniels, C. (1986). A note on the ecology of the aardvark, *Orycteropus afer*. *South African Journal of Wildlife Research*, **16**: 112–114.
Montgomery, G.G. (1985). Impact of vermilinguas (*Cyclopes*, *Tamandua*: *Xenartha = Edentata*) on arboreal ant populations. In: Montgomery, G.G. (Ed.), *The Evolution and Ecology of Armadillos, Sloths and Vermilinguas*, pp. 351–363. Washington: Smithsonian Institution Press. 451 pp.
Nel, P.J., Taylor, W.A., Haupt, M.A. & Meltzer, D.G.A. (2000). Capture and immobilization of aardvark (*Orycteropus afer*) using different drug combinations. *Journal of the South African Veterinary Association*, **71**: 58–63.
Putman, R.J. (1984). Facts from faeces. *Mammal Review*, **14**: 79–97.
Redford, K.H. (1983). Mammalian myrmecophagy: feeding, foraging and food preference. Ph.D. thesis, Harvard University, Cambridge, MA. 299 pp.
Redford, K.H. (1985). Feeding and food preference in captive and wild giant anteaters. *Journal of Zoology*, **205**: 559–572.
Redford, K.H. (1987). Ants and termites as food: patterns of mammalian myrmecophagy. In: Genoways, H.H. (Ed.), *Current Mammalogy*. Vol. 1. pp. 349–399. New York: Plenum Press. 513 pp.
Richardson, P.R.K. (1987). Aardwolf: the most highly specialised myrmecophagous mammal? *South African Journal of Science*, **83**: 405–410.
Rockstein, M. (1978). *Biochemistry of Insects*. New York: Academic Press. 649 pp.
Samways, M.J. (1983). Community structure of ants (Hymenoptera: Formicidae) in a series of habitats associated with citrus. *Journal of Applied Ecology*, **20**: 833–847.
Skinner, J.D. & Smithers, R.H.N. (1990). *The Mammals of the Southern African Subregion* (2nd Edn), Pretoria: University of Pretoria. 771 pp.
Smithers, R.H.N. (1971). The Mammals of Botswana. *Museums Memoir. National Museums and Monuments of Rhodesia*, **4**: 188–199.
Smithers, R.H.N., & Wilson, V.J. (1979). Check list and atlas of the mammals of Zimbabwe Rhodesia. *Museum Memoir*, **9**: 147 pp.
Steyn, J.J. (1954). The pugnacious ant (*Anoplolepis custodiens* Smith) and its relation to the control of citrus scales at Letaba. *Memoirs of the Entomological Society of South Africa*, **3**: 1–96.
Swart, J.M. (1996). Foraging behaviour of the Cape pangolin *Manis temminckii* in the Sabi Sand Wildtuin. M.Sc. thesis, University of Pretoria, Pretoria. 149 pp.
Swart, J.M., Richardson, P.R.K. & Ferguson, J.W.H. (1999). Ecological factors affecting the feeding behaviour of pangolins (*Manis temminckii*). *Journal of Zoology*, **247**: 281–292.
Werger, M. J. A. (1973). An account of the plant communities of Tussen die Riviere Game Farm, Orange Free State. *Bothalia*, **11**: 165–176.
Willis, C.K., 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*. *African Journal of Ecology*, **30**: 322–334.