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Ecological factors affecting the feeding behaviour of pangolins (*Manis temminckii*)

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Abstract

The diet and foraging behaviour of 15 radio-tagged pangolins were studied in the Sabi Sand Wildtuin for 14 months, together with the community composition and occurrence of epigaeic ants and termites. Fifty-five ant and termite species of 25 genera were trapped in pitfalls of which *Pheidole* sp. 2 was the most common (27% occurrence). Five termite and 15 ant species were preyed on by pangolins. Six of these species constituted 97% of the diet while ants formed 96% of the diet. *Anoplolepis custodiens* constituted the major component of the pangolins' diet (77% occurrence) while forming only 5% of the trapped ants. Above-ground ant and termite activity was higher during summer than during winter (an 11-fold difference for *A. custodiens*), and the above-ground activity was also higher during the day than at night. Pangolins fed for 16% of their foraging time. However, 99% of the observed feeding bouts (mean duration 40 s) were on subterranean prey. The mean dig depth was 3.8 cm. Prey from deeper digs were fed upon for longer periods. A model taking into account various ant characteristics suggests that ant abundance and ant size are the two most important factors determining the number of feeding bouts that pangolins undertake on a particular ant species. Temperature effects on ant activity and their nest characteristics may exclude pangolins from parts of southern Africa.

Key words: pangolin, *Manis temminckii*, diet, feeding behaviour, termites

INTRODUCTION

Ants or termites are known to be included in the diet of about 216 mammal species, of which only 12% are obligate myrmecophages ($> 90\%$ ants or termites; Redford, 1987). Cape pangolins *Manis temminckii* feed exclusively on ants and termites and they have several morphological adaptations that enable them to gain access to the concealed galleries and nests of ants and termites (Sweeney, 1956; Kingdon, 1971; Smithers, 1983). The larger myrmecophages such as the aardvark *Orycteropus afer*, the giant pangolin *Manis gigantea*, and the giant armadillo *Priodontes maximus* are able to dig deep and peneterate the impervious structures of the mound building termites. In contrast, *M. temminckii* feed close to the soil surface since they are smaller and are less powerful diggers. The availability of ant and termite prey close to the soil surface would thus be an important factor in determining the distribution of *M. temminckii.*

Of the many behavioural ecological studies published on myrmecophagous mammals (e.g. Melton, 1976; Richer, Coulson & Heath, 1977; Lubin & Montgomery, 1981; Redford, 1983; Richardson, 1987), there are few on the ecology of pangolins of which none is a detailed study. This may be due to the elusive and nocturnal behaviour of pangolins or because they occur in relatively low densities compared with other myrmecophagous mammals.

Several studies have been conducted on the feeding behaviour of the Cape pangolin. Jacobsen *et al.* (1991) recorded 13 ant species and three termite species in the diet of a Cape pangolin in the Northern Province of South Africa, and Richer *et al.* (1997) recorded seven ant species in the diet of *M. temminckii*. Coulson (1989) analysed some stomach samples from pangolins from Zimbabwe and found that diurnal ants and termites were frequently taken by Cape pangolins. Although these studies, as well as those of Sweeney (1956, 1973), Kingdon (1971) and Smithers (1983), documented some of the prey species of pangolins, no emphasis was placed on the frequency with which the prey species were taken or the amount of time that pangolins spent feeding on each species. This information is crucial for determining the basic dietary requirements of pangolins, a basic factor which co-determines their distribution and status. In addition, nothing is known about the insects' characteristics that are instrumental in prey selection by pangolins.

The objectives of this study were to determine:

(a) the seasonal composition of the diet of Cape pangolins;

(b) the seasonal availability of ants and termites with the purpose to predict their availability as prey;
(c) whether the behaviour of these insects determine their availability as prey and consequently the activity of pangolins;
(d) whether the duration of pangolin feeding bouts is reduced by anti-predator defences of ants and termites;
(e) factors which make ant species suitable as prey of pangolins.

MATERIALS AND METHODS

Study area

The research was conducted in an area of approx. 15 000 ha within the Sabi Sand Wildtuin (SSW) Mpumalanga, South Africa (24°44′S, 31°19′E). The mean rainfall in this area is 570 mm/annum (Gertenbach, 1980), falling mainly during the southern hemisphere summer (October–March).

Pangolin foraging behaviour and diet

Pangolins were located either on foot or by vehicles and were captured, radio-tagged and released where caught. Pangolins weighing < 8 kg were regarded as sub-adults. Transmitters were attached to a large scale on the mid-region of the tail. Radio-tracking was carried out using a hand-held yagi antenna. Pangolins were followed on foot from the time that they became active until they returned to their den, and were observed with a flashlight from a distance of approx. 10 m. One pangolin was focused on at a time for 3–4 days (focal sampling; Martin & Bateson, 1986), and while the animal could be seen data were recorded continuously so that true frequencies, durations and times at which behavioural patterns started and stopped were measured. The duration of feeding bouts on each prey species was timed with a stop-watch and the depth of all holes excavated while foraging was measured. Digging time was excluded from feeding duration. Prey species exposed by the pangolins during feeding were collected, sorted and preserved in alcohol. All ant species were identified by Dr H. G. Robertson, and housed in the South African Museum collection, Cape Town, while termite species were identified by Ms V. M. Uys (National Collection of Insects, Pretoria). Since the actual numbers of insects consumed by pangolins could not be observed or determined in another way, the relative importance of prey taxa in the pangolins' diet was calculated as the proportion of time pangolins spent feeding on each species (see definitions below).

Sampling of ant and termite populations

The seasonal abundance and occurrence of ant species were determined with pitfall traps, a method useful for determining relative abundance (Luff, 1975) and species distribution (Greenslade, 1964). Most ground-nesting ants shelter and raise their brood within a nest below the soil surface, while up to 75% of the colony may leave the nest to forage above ground (Sudd, 1982). Thus, although Cape pangolins feed below the soil surface, a useful estimate of the relative abundance of different ant species (i.e. community structure) could be determined on a seasonal basis by measuring their above-ground occurrence with pitfall traps (Samways, 1983; Donnelly & Giliomee, 1985). An inverse relationship between above-ground abundance and below-ground abundance should hold in the short term for a particular ant nest. However, the interpretation of long-term changes of above-ground ant activity is less clear. Pitfalls were modified from Majer (1978). Traps consisted of an outer case of 160 mm long hard plastic tubing with a 20 mm internal diameter sunk into the ground, and containing a rimmed Pyrex test tube (145 mm deep, 16 mm internal diameter). A soap–water solution (40 mm deep) was placed in each tube to act as a surfactant to prevent the ants or termites from escaping.

Panchromatic black-and-white aerial photographs of the study area were used to interpret vegetation stratification. Five vegetation types were identified from the photographs and each area was inspected to ensure that it was homogeneous. For each habitat, 12 sites were selected from the photographs and 1 pitfall trap was placed in each site (total of 60 traps over 5 habitats). Sites were chosen to be representative of the chosen habitat in terms of smaller scale habitat characteristics. Traps were inserted for 1 day (24 h) every week and checked at dawn and dusk once a week from July 1993 to July 1994. To avoid a bias towards emphasis on high abundance at single pitfall samples, calculations were based on the number of times each species was caught in a pitfall trap rather than the number of individuals caught. The following measures of ant abundance were used:

Relative importance (RI) = proportion of feeding time pangolins fed on a particular species;
Occurrence (N_1) = the number of pitfall samples which included a particular species;
Abundance (N_2) = the number of individuals of each species sampled in all pitfalls.

$$\%\ \text{Contribution} = 100 \cdot N_{1_i} \Big/ \sum_{i=1}^{\#\,of\ species} N_{1_i}$$

Prey mobility and prey aggression were scored into 4 classes of increasing value, based on observations in the field.

For modelling the factors contributing to prey importance, we defined an index termed prey value (PV) which included various characteristics of the prey taxa considered to be important for determining the food preference of pangolins. Large prey size and high prey abundance (N_2) increase PV whereas high levels of aggression and mobility, as well as deep nests, decrease

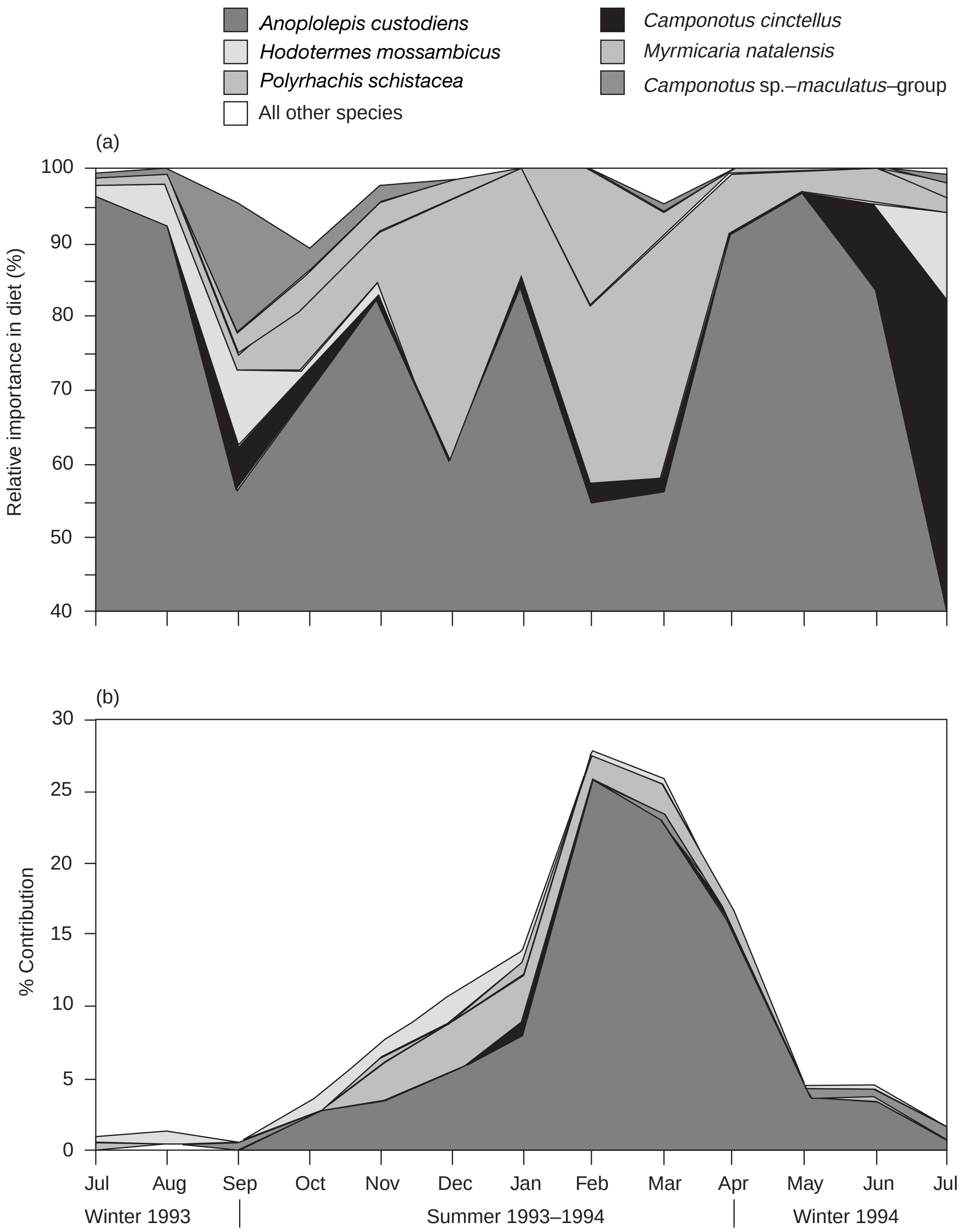

Fig. 1. The seasonal variation in the composition of the six most important prey species that occurred in the diet of pangolins (a) and in pitfall traps over 14 months (b).

PV. Prey value therefore represents the expected relative importance (RI) of a particular prey species within the pangolin's diet, measured as the number of insects consumed. Within this model, prey length was cubed to relate to a volumetric measurement, and the numerators were scaled by 1000 to reduce the numerical value of any of these variables to a value of < 20. All the variables therefore had values within the same order of magnitude and it was not possible for a particular variable to overshadow the effects of the others.

Prey value (PV) =

$$\mathrm{Log}\left(\frac{(\text{prey length (mm)})^3/1000)\cdot(N_2/1000)}{\text{aggression}\cdot\text{mobility}\cdot\text{mean dig depth (cm)}}\right)$$

Multiple regression was used to measure the effects of each of the above variables on the fit between PV and RI, the latter 2 indices representing expected and observed values. Parameters which did not contribute to the fit of the model were dropped from the equation.

RESULTS

Composition and activity of the ant and termite fauna

During July 1993 to July 1994, 6480 pitfall sample checks were carried out over 54 days. A total of 27 067 insects from 5449 trap records representing 25 genera and 55 species were recorded (Appendix). The Formicidae were represented by 20 genera and 50 species while only five genera and five species of termites were recorded. The occurrence (N_1) of all the ant and termite species samples in pitfall traps along with the abundance (N_2) are given in the Appendix. The closer the value of (N_1) is to (N_2) the more evenly the abundance of a species is distributed. Four species of ants accounted for 65% of the total pitfall catches. Of these the most common species was *Pheidole* sp. 2 which constituted 27% of occurrences (Appendix). The above-ground abundance of all species combined was significantly higher during summer compared to winter ($\chi^2 = 281.5$; d.f. = 1; $P < 0.001$). In addition, the overall nocturnal above-ground abundance was significantly lower than the corresponding diurnal abundance (Mann–Whitney *U*-test, $U = 52$; $n = 13$; $P < 0.001$). Six of the 10 most abundant species were predominantly diurnal while the remaining taxa were predominantly nocturnal. The termite species *Hodotermes mossambicus* switched from being mainly diurnal during summer to mainly nocturnal during winter. The seasonal availability of the six most important species of ants and termites preyed on by pangolins are represented in Fig. 1b. The above-ground abundance of *Anoplolepis custodiens*, the most important food source of *Manis temminckii*, was low during winter (only 8.1%), gradually increasing in early summer with a sudden peak during February and then a steep decrease at the end of summer (Fig. 2). There is a significant correlation between the above-ground abundance of *A. custodiens* and the corresponding daily minimum temperatures ($r = 0.56$; d.f. = 11; $P < 0.05$). In addition, the nocturnal above-ground abundance of this species was significantly lower than the corresponding diurnal value ($U = 26$; $P < 0.001$; Fig. 2).

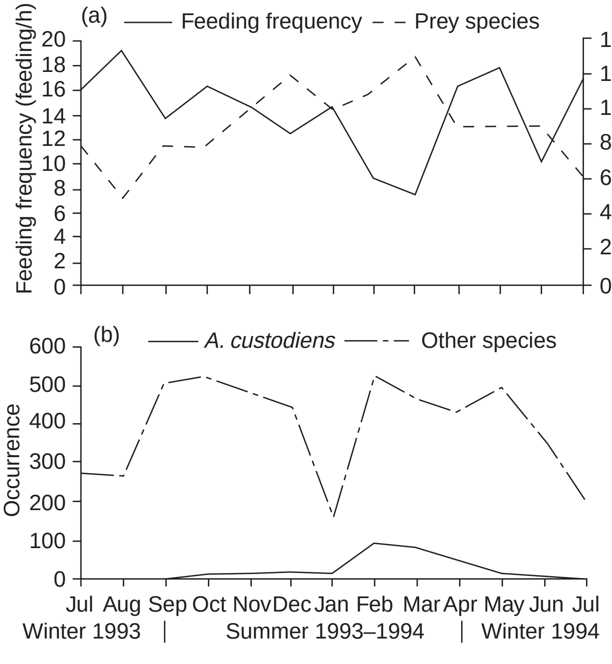

Fig. 2. (a) Seasonal variation of the mean feeding frequency of pangolins recorded for each month, in relation to the mean number of prey species caught in pitfall traps ($r_s = -0.81$; $n = 13$; $P < 0.001$). (b) The occurrence of prey species in pitfall traps over the same period.

Diet and foraging behaviour of pangolins

Fifteen Cape pangolins were radio-tagged and the foraging behaviour of 11 of these (10 adults and one sub-adult) was recorded. Of the 50 ant species and five termite species identified in the study area during this period, only 15 ant species and five termite species were preyed on by pangolins (Table 1). Data on feeding behaviour were recorded for a total of 331.6 h during 375 observation periods. During this period a total of 4672 feeding bouts were observed. Although most of the pangolin's activity period was devoted to foraging for ants and termites, only 15.7% of this time was spent actually feeding. The mean duration of feeding bouts was only 40 s (SE = 0.63; range = 2–1198; $n = 4672$) with a mode of 15 s (Table 1).

The RI of ants (Hymenoptera: Formicidae) was 96.7% whereas termites (Isoptera) constituted only 3.3% of the prey. The most important prey species in the pangolins' diet was the ant *A. custodiens* with a RI value of 77.3%. Six of the 20 taxa (five ant and one termite species) constituted 97.7% of the pangolins' diet. All of these are larger than 0.5 cm in length. While the RI of *A. custodiens* as a prey species decreased from 83% during winter to 72% during summer (Fig. 1a), the RI of *M. natalensis* increased eight-fold from 2% to 16% during the same period. The ant species *Polyrhachis schistacea* was also preyed on considerably more during summer, particularly during February 1994 when the RI of this species was 19% (Fig. 1). In contrast, *Camponotus cinctellus* and *H. mossambicus* were preyed on more during winter when 71% of the feeding bouts on *H. mossambicus* took place. *Hodotermes mossambicus* was the only termite species that made a significant contribution to the pangolins' diet. The feeding frequency (number of feedings per hour) of pangolins appears to be inversely related to the number of prey species recorded above ground (Spearman's $r_s = -0.81$; $n = 13$; $P < 0.001$). Thus an increase in their availability above ground and consequently a decrease below the soil surface appears to decrease the pangolins' feeding frequency. This is particularly pronounced by the above-ground occurrence of *A. custodiens*. During February and March 1994, when the occurrence of *A. custodiens* was the highest, the overall frequency of feedings by pangolins was the lowest (Fig. 2).

Table 1. The total time pangolins spent feeding on the various species of ants and termites, their relative importance (RI) in the pangolin's diet, and the prey value which is based on the aggression, mobility and size of the prey species

Ant and termite species	Prey aggression	Prey mobility	Prey size (mm)	Prey value	Total feeding time (s)	Total feeding bouts	RI in diet (%)	Mean feed time per bout (s) ± SE)	Mean dig depth (cm) ± SE)
Aenictus eugenii Emery	2	1	3.9	−1.27	6	1	<0.1	6.0 ± 0	1.0 ± 0
Pheidole sp. 3	2	2	3.5	−1.38	25	2	<0.1	12.5 ± 3.2	4.0 ± 0.71
Tetramorium longicorne Forel	2	1	3.7	−2.47	40	2	<0.1	20.0 ± 7.1	3.0 ± 1.41
Crematogaster sp. – *castanea*-group	2	1	3.9	−1.27	6	1	<0.1	6.0 ± 0	1.0 ± 0
Ocymyrmex fortior Santschi	2	4	7.2	0.14	58	2	<0.1	29.0 ± 6.4	7.5 ± 0.35
Tetramorium weitzeckeri Emery	2	1	3.5	−2.67	59	1	<0.1	59.0 ± 0	4.0 ± 0
Rhadinotermes coarctatus Sjöstedt[a]	2	1	3.8	−1.20	99	2	0.1	49.5 ± 27.2	10.0 ± 0
Dorylus badius Gerstäcker	2	2	5.7	−2.08	215	2	0.1	107.5 ± 27.2	3.4 ± 0.35
Termitidae[a]	–	–	–	–	281	12	0.1	23.4 ± 4.9	2.5 ± 0.32
Trinervitermes rapulum[a]	2	1	4.3	–	319	3	0.2	106.3 ± 67.1	
Camponotus congolensis Emery	2	2	8.5	−1.09	685	13	0.4	52.7 ± 10.4	4.5 ± 0.55
Pheidole sp. 2	2	2	3.7	0.97	741	13	0.4	57.0 ± 15.8	4.6 ± 0.75
Monomorium junodi Forel	1	1	3.2	0.28	749	11	0.4	68.1 ± 14.1	5.6 ± 0.81
Odontotermes sp.[a]	2	1	6.2	−0.58	1034	45	0.6	23.0 ± 4.4	1.9 ± 0.19
Camponotus sp. – *maculatus*-group	2	2	10.8	−0.91	2739	60	1.5	45.7 ± 5.0	4.1 ± 0.32
Hodotermes mossambicus Hagen[a]	4	1	11.3	1.41	4517	529	2.4	8.5 ± 0.3	1.3 ± 0.02
Polyrhachis schistacea Gerstäcker)	1	1	11.6	−0.89	5251	77	2.8	68.2 ± 7.2	6.1 ± 0.42
Camponotus cinctellus (Gerstäcker)	2	2	8.9	−1.22	8893	178	4.7	50.0 ± 3.0	3.5 ± 0.14
Myrmicaria natalensis (Mayr)	2	1	7.5	−0.22	16 878	187	9.0	90.3 ± 8.9	6.6 ± 0.31
Anoplolepis custodiens (Smith)	3	3	5.6	1.60	144 373	3530	77.2	40.9 ± 0.6	3.6 ± 0.04
Values for all species combined	–	–	–	–	187 015	4672	100.0	40.0 ± 0.6	3.8 ± 0.04

[a] Termite species.

Ninety-nine percent (4633) of the 4672 feeding bouts were on ants and termites situated below the soil surface. The overall mean dig depth was 3.8 cm (SE = 0.04 cm; Table 1). Of the ant and termite species recorded in at least 10 ground digs, the mean depth of the holes excavated to expose the ant species *M. natalensis* was the deepest whereas the shallowest digs were recorded for the termite species *H. mossambicus* (Table 1). The duration of feeding bouts on each species of prey correlated with their depth below the soil surface; those species preyed on from deeper digs were also fed on for longer periods. Consequently a highly significant inter-species correlation existed between the mean duration of feeding bouts and the mean depth of the diggings required to expose the various species of ants and termites ($r = 0.95$; $P < 0.001$; Fig. 3). This correlation was significant for each individual pangolin except for one sub-adult (Table 2). In addition, there was a highly significant correlation between the mean duration of feedings and the mean dig depth when pangolins preyed on *A. custodiens* ($r^2 = 0.17$; $F_{1,2785} = 562.6$; $P < 0.001$; Fig. 4).

Pangolins occasionally preyed on the egg, larval and pupal (ELP) stages of ants, however, they were never

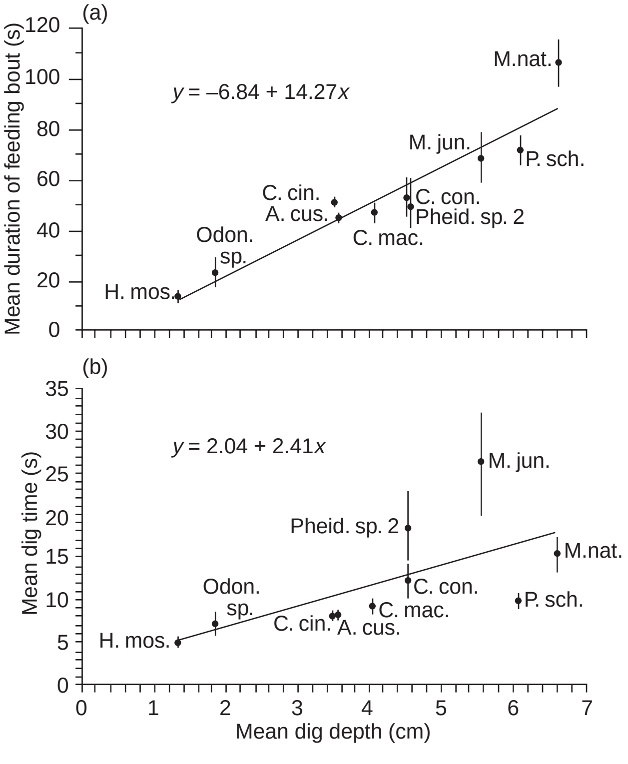

Fig. 3. The linear regression of: (a) the mean feeding duration *vs* mean dig depth ($r_s = 0.90$; $n = 10$; $P < 0.005$) and (b) the mean dig time *vs* mean dig depth ($r_s = 0.85$; $n = 10$; $P < 0.01$) while feeding on eight species of ants and two species of termites. Only species that were recorded in more than 10 feeding bouts were used for the regression. Vertical bars indicate 1 SE. M nat., *Myrmicatia natalensis*; P. sch., *Polyrhachis schistacea*; M. jun., *Monomorium junodi*; C. con. *Camponotus congolensis*; Pheid. sp. 2, *Pheidole* sp. 2; C. mac., *Camponotus* sp. – *maculatus* group; A. cus. *Anoplolepis custodiens*; Odon. sp., *Odontotermes* sp.; H. mos., *Hodotermes mossambicus*; C. cin., *Camponotus cinctellus.*

Table 2. The correlation coefficient (*r*) for the mean duration of feeding bouts *vs* mean dig depth, calculated for all ant or termite species preyed on by each pangolin

Name	Weight (kg)	Total no. of digs	Mean duration of feeding bouts (s) ± SE	No. of species preyed	Mean duration of feeding bouts (s) *vs* mean dig depth (cm)		
					r	d.f.	*P*
Males							
Jobu	12.6	728	43 ± 1.1	7	0.83	5	< 0.05
Shumi	13.2	615	50 ± 1.5	8	0.8	6	< 0.05
Zinga	13.0	38	53 ± 6.0	1	–	–	–
Zimu	16.1	4	184 ± 66.0	1	–	–	–
Females							
Nina	14.1	608	43 ± 1.6	10	0.93	8	< 0.001
Ozela	14.0	504	52 ± 3.4	9	0.84	7	< 0.01
Yela	12.7	229	35 ± 1.9	7	0.93	5	< 0.01
Vunga	10.8	152	57 ± 4.9	4	0.99	2	< 0.001
Penula	10.2	12	57 ± 5.5	1	–	–	–
Lola	12.6	9	52 ± 10.3	2	–	–	–
Azana	11.4	5	15 ± 4.0	1	–	–	–
Thamo	11.8	2	107 ± 52.3	1	–	–	–
Sub-adult							
Imini	6.2	393	56 ± 2.1	9	0.32	7	> 0.1[a]
All pangolins	–	3299	48 ± 0.8	20	0.59	17	< 0.01

[a] Not significant.

Table 3. A comparison between the feeding bouts on egg, larvae and pupal (ELP) stages, and adult stages of three ant species. Ground digs indicate feedings from excavations in the soil to access ant galleries. Port feeds indicate feedings from active ant nest entrances

	Feeding bouts on ELP stages			Feeding bouts on adult stages		
	Mean feed time (s) ± SE	Mean dig depth (cm) ± SE	*n*	Mean feed time (s) ± SE	Mean dig depth (cm) ± SE	*n*
Ground dig						
A. custodiens	72 ± 10.1	4.5 ± 0.7	25	45 ± 0.7	3.6 ± 0.04	2741
M. natalensis	142 ± 45.8	5.7 ± 0.9	30	93 ± 8.2	6.7 ± 0.40	98
P. schistacea	99 ± 18.4	6.4 ± 1.0	23	57 ± 6.1	5.9 ± 0.46	46
Port feed						
A. custodiens	0	–	0	27 ± 0.8	–	755
M. natalensis	86 ± 30.3	–	3	56 ± 5.0	–	52
P. schistacea	56 ± 25.4	–	4	29 ± 2.5	–	4
Totals						
A. custodiens	72 ± 10.1	–	25	41 ± 0.6	–	3496
M. natalensis	137 ± 41.8	–	33	80 ± 5.7	–	50
P. schistacea	93 ± 16.4	–	27	55 ± 5.7	–	50

observed preying on the alates of ants or the alates and ELP stages of termites. Although pangolins preyed on the adult stages of 19 species of ants and termites, they were observed preying on ELP stages of only five species. In addition, the ELP stages of ants were preyed upon almost exclusively during summer with only 1% of winter feedings. A total of 87 feeding bouts were recorded on ELP stages, a mere 1.9% of the total feeding bouts, and 85 (97.7%) of observations were on the three species: *A. custodiens*, *M. natalensis* and *P. schistacea* (Table 3). The proportion of feeding bouts on ELP stages was almost negligible (0.7%) for *A. custodiens*, but was 18% for *M. natalensis* and 35% for *P. schistacea*. The mean duration of feedings from ELP stages was significantly longer than from adult stages (*t*-test assuming unequal variances; $t = 3.6$; d.f. = 85.2; $P < 0.001$). The mean duration of feeding bouts from ELP stages was 101 s (SE = 10.8 s) whereas from adult stages it was only 39 s (SE = 0.55 s).

Forward stepwise multiple regression analysis indicated that the prey values of different ant species was successful in predicting the RI on each of the prey taxa (Fig. 5; multiple $R = 0.75$; $F = 3.0$; d.f. = 5, 12; $P < 0.05$). We performed a sensitivity analysis of this model by dropping parameters from the full model (defined in Methods) one each time. This indicated that not all ofthe variables in the model contributed equally to the importance of prey. Prey abundance and prey size were

Table 4. Results of a multiple regression model of factors affecting prey value. SS change, Increase in sums-of-squares brought about by dropping variables, one each time, from the full model. Positive values indicate variables which contribute to the accuracy of the model; ρ, partial correlation of variable with RI of prey taxa; *P*, statistical significance of the correlation of this variable with RI values of prey taxa, resulting from a forward stepwise regression analysis

Variable	SS change	ρ	*P*
Body size	−0.48	0.66	0.007
N_2 (abundance)	0.18	0.58	0.019
Depth of nest	0.09	0.07	0.745
Prey mobility	−0.03	−0.04	0.863
Prey defence	−0.02	0.04	0.856

the two parameters which contributed most to the predictive precision of the model with partial correlation values > 0.5 (Table 4). The inclusion of prey mobility and prey aggression values actually decreased the precision of the model and these two variables were therefore omitted from the final model. The depth of diggings had a small but positive effect on the accuracy of the model.

DISCUSSION

Composition and activity of the ant and termite fauna

In arid and semi-arid regions where temperatures are often extreme, above-ground ant activity is controlled by changes in temperature and food supply, and regulated by daily weather fluctuations (Andersen, 1983, 1986; Greenslade & Greenslade, 1984; Koen & Breytenbach, 1988). In particular, the effects of temperature, as a major factor influencing above-ground ant activity, has frequently been noted (Briese & Macauley, 1980; Andersen, 1983). It also seems to be a major factor controlling numbers of above-ground ant prey during this study since a low activity of ants above the soil surface would leave higher densities of ants in their underground galleries where they are more available as prey to pangolins and *vice versa*. The above-ground activity of *A. custodiens* (the main prey species of pangolins) seemed to decrease considerably with cold temperatures thus making them more available as prey below the soil surface. During winter their presence was 11 times lower than during summer. This was probably because most of the major and median workers hibernated during winter while the rest of the workers, mainly minor workers, continued to forage above ground (Steyn, 1954). The sudden rise in the above-ground presence of *A. custodiens* during February 1994 can probably be ascribed to the high rainfall recorded during December 1993, similar to sudden increases in the above-ground occurrence of this species reported elsewhere (Louw, 1968). The 2-month delay between rainfall and the increased above-ground activity of *A. custodiens* is possibly related to ant breeding as well as the life cycle of the homopterans that supply the ants with honeydew; the diet of *A. custodiens* consists mainly of honeydew (Steyn, 1954) and the number of homopterans would thus limit the population size of these ants.

Since the study area is rich in ant species and several species are abundant, there appears to be a readily available supply of prey for pangolins. The daily availability, size of the various species and the pangolins' ability to locate and expose the underground nests and galleries, however, may be as important in determining their viability as prey. *Anoplolepis custodiens*, for example, had a high surface activity during summer that probably caused them to be less available underground than during winter. That is probably the reason why this ant species was preyed upon less during summer, even though it still constituted a major dietary component of pangolins. In contrast, the termite species *H. mossambicus* (the pangolins' most common termite prey) was only preyed on when they were abundant at the nest entrances. This species switched from being predominantly diurnal during summer to predominantly nocturnal during winter, thus making them more available to pangolins during winter.

Diet and foraging behaviour of pangolins

Diet composition

Our study largely extends the list of species previously recorded in the diet of Cape pangolins. Coulson (1989) recorded nine insect species, Jacobsen *et al.* (1991) 16 species and Richer *et al.* (1997) seven species. Sixteen of the 20 prey species recorded during our study were not recorded in previous studies, indicating some geographical variation in their diet. *Anoplolepis custodiens*, however, is the only prey species recorded in all these studies. Since the proportion that the various prey species contributed to the diet of pangolins was not indicated in these publications, ours is the first study to quantify the prey composition of *M. temminckii*. Our study also suggests that *A. custodiens* is probably the key species in their diet within the Southern African region. Thus, the distribution of *A. custodiens* in Southern Africa is probably important in determining the distribution of *M. temminckii*.

Richer *et al.* (1997) suggested that *A. custodiens* was important only to juveniles and diurnal foraging pangolins and not to nocturnal foragers. Feeding data from 11 of our pangolins (10 adults and one sub-adult) during the present study revealed that *A. custodiens* is an important prey species for all the pangolins that we observed, including individuals and adults feeding at night.

Selectivity

Kingdon (1971) rated pangolins as selective feeders of ants and termites, and the present study verified their selectivity for certain prey species. Firstly, the number of species available during the study period did not appear to determine the number of species that was preyed upon by pangolins (Table 1, Appendix). Secondly, pangolins preyed predominantly on larger species (> 0.5 cm) such as *A. custodiens* which constituted only 5% of the overall species composition of the area, yet made up 77% of the pangolins' diet. However, when compared with the other 10 species of the same size or larger, its contribution to the diet composition was 43%. Thirdly, pangolins were not preying on the most abundant above-ground species, since the six most frequently taken species accounted for 97.7% of the overall diet. Moreover, these six species were not the most abundant species in the study area (Fig. 1, Appendix). This selectivity for such a high proportion of *A. custodiens* is mainly because its nest galleries are close to the soil surface making it easily accessible as prey for Cape pangolins.

Ants and termite alates and their larval and pupal stages are nutritionally more valuable and have a substantially higher fat content (and a higher prey value) than other castes (Redford, 1984). Therefore, when these castes are available they should be selected by pangolins. Our Cape pangolins, however, never preyed upon ant or termite alates. Alates within a nest can change the food value of an ant or termite colony (Redford, 1987) since the presence of alates or prealates in a nest has been highly correlated with longer feeding bouts by echidnas (Griffiths & Simpson, 1966) and *Tamandua* anteaters (Lubin & Montgomery, 1981). When our Cape pangolins preyed on the ELP of ants, the average duration of feeding bouts was also significantly longer. Kingdon (1971) recorded *M. temminckii* in East Africa preying predominantly on the juvenile stages of *Crematogaster* ant species and *Odontotermes* and *Microcerotermes* termite species. In the present study, however, these juvenile states (ELP) did not make a significant contribution to their diet since they were recorded in only 1.9% of the total feeding bouts. Two main factors probably contributed to this low incidence of ELP stages in the pangolin diet in our study. Firstly, very few ELP stages occur in the nests of *A. custodiens* during winter (Steyn, 1954). Secondly, the availability of the ELP stages to pangolins also depends on their depth below the soil surface and their accessibility to the tongues of pangolins via the underground galleries. In the nests of *A. custodiens*, ELP stages are usually widely distributed in several queen cells between 10 and 50 cm below the soil surface that are linked to one of numerous horizontal galleries via a single vertical tunnel (Steyn, 1954). This structure would make the queen cells far less accessible to the pangolin's tongue than the numerous horizontal galleries where many of the nest inhabitants can be found. The complexity of factors that may affect food availability to pangolins, including prey availability, mobility and defence, is evident.

Prey availability

Redford (1984, 1987) suggested that myrmecophagous mammals probably prey on the most available species rather than attempting to select species with higher nutritional value. A distinction must be drawn between prey abundance and prey availability since the most abundant species is not necessarily the most available. Ant and termite availability to pangolins is determined by two prominent factors. The first factor is the depth below the soil surface of the ant and termite nests. The morphological adaptation that pangolins share with some of the other typical myrmecophagous mammals is strong forelimbs with hard claws modified for digging. They are not, however, as well adapted for digging deep into hard soil as the aardvark *Orycteropus afer* (Melton, 1976), the giant armadillo *Priodontes maximus* (Redford, 1985*b*) and the giant pangolin *Manis gigantea* (Kingdon, 1971). Several common termite species, especially of the genus *Macrotermes*, were not available because their nests are either too deep or they are constructed with a hard outer crust of compacted soil (Skaife, 1979) making the nest galleries impenetrable to pangolins. On the other hand *A. custodiens* store grass seeds and honeydew in a mass of horizontal channels and galleries 4–7 cm below the soil surface (Bond & Slingsby, 1983). The foraging efficiency of pangolins on *A. custodiens* was probably high because their digging effort was just sufficient to expose the relatively dense aggregations of these ants within the active galleries. Secondly, the activity periods of ants and termites and their foraging activity within the underground galleries also largely determines whether they are available as prey. The harvester termite *H. mossambicus* nests were approx. 1.5 m below the soil surface (Hartwig, 1965), which is inaccessible to pangolins and they were preyed on only when they were active in secondary aggregations in the nest ports at the soil surface. This was the only termite species that made a perceptible contribution to the pangolin's diet and it was preyed on almost exclusively during the dry season when they were at or near the soil surface collecting dry grass (Botha & Hewitt, 1978).

Prey defence

?twb=.33w>From the time that a myrmecohagous predator begins feeding on an ant or termite colony it experiences a decrease in the prey value as a result of the rapid response of the ants and termites following predator attack (Redford, 1985*a*). This decrease in prey value is caused by colony defence mechanisms exhibited by different prey species. This limits predation and results in feeding bouts of short duration typical of mammalian myrmecophages (Redford, 1985*a*, 1987). This is supported by the present study as the average duration of pangolin feedings were only 40 s and most were shorter than 1 min (Table 1). The prominent prey species of pangolins, *A. custodiens*, swarms and bites fiercely following predator attack, and like other members of the Formicinae they also spray formic acid from a poison gland or inject it into the bite

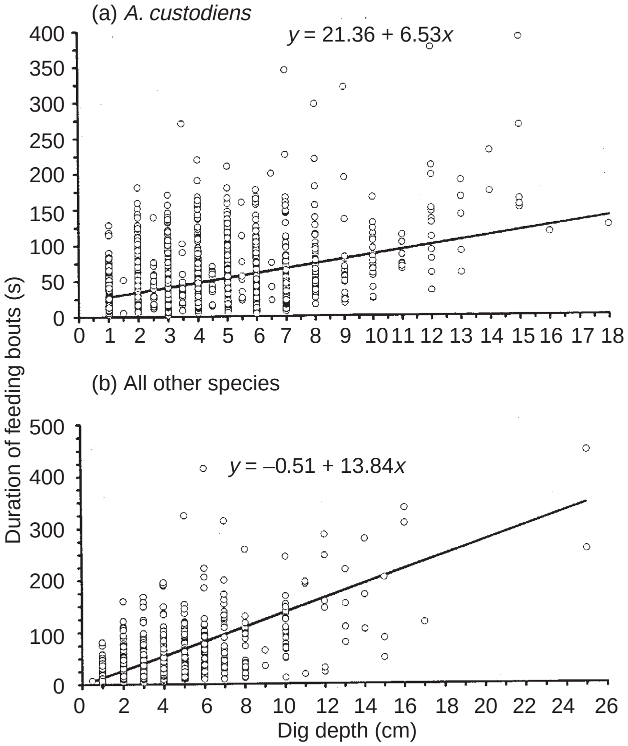

Fig. 4. A linear regression of the duration of feeding bouts as a function of the depth of the holes excavated by pangolins while feeding on: (a) *A. custodiens* ($r^2 = 0.17$, $P < 0.001$) and (b) all other species ($r^2 = 0.3$, $P < 0.001$).

wounds (Skaife, 1979). The soldiers of the termite *H. mossambicus* also have powerful mandibles that function solely to defend the colony against predator attack (Wilson & Clarke, 1977). These soldiers are effective in deterring pangolins as the duration of feeding bouts were very short (usually <10 s) and pangolins displayed considerable discomfort when preying on this species (Swart, 1992; pers. obs.). In contrast, the ants *M. natalensis* and *P. schistacea* are less aggressive and have poor defence against predation (pers. obs.) and thus are fed on for longer durations (90 s and 68 s, respectively; Table 1).

Prey mobility

An equally important factor responsible for reducing the prey value to pangolins appears to be the mobility of the different prey species. *A. custodiens* are fast moving ants that disperse quickly while swarming (pers. obs.) thus reducing their density in the underground galleries soon after being attacked. On the other hand *M. natalensis* and *P. schistacea* are relatively slow moving (pers. obs.) with the result that higher densities are maintained for longer durations and feeding bouts are longer when pangolins prey on the latter two species (Table 1).

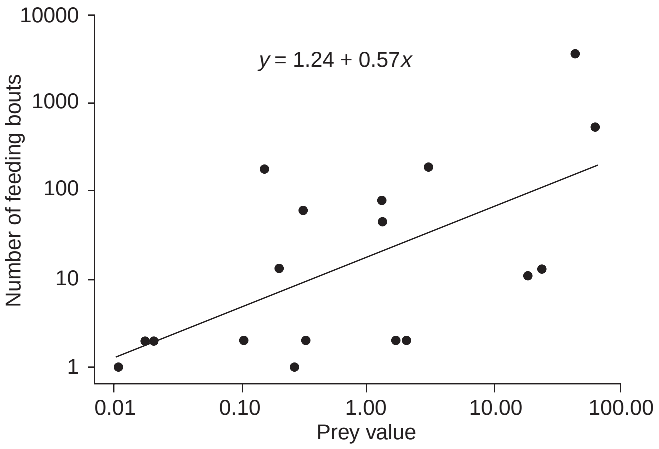

Fig. 5. The linear regression of the number of feeding bouts as a function of the prey value of the various species of ants and termites ($r_S = 0.58$; $n = 18$; $P < 0.01$). All species preyed on are shown, except *Trinervitermes rapulum* and unidentified Termitidae.

Prey value

Foraging efficiency appears to be governed largely by a combination of the above factors. Since prey value is largely determined by the body size, population density and nest structure of ant species (Table 4), pangolins are expected to have a preference for large species found in high densities and with nests close to the soil surface. This expectation is supported by our model of prey value (Fig. 5). The sensitivity analysis of this model indicated that species-specific differences in prey density and prey size are the two most important factors affecting the choice of prey by pangolins. On the other hand, prey aggression and prey mobility did not have a measurable effect. We suspect, however, that the nest depth of ants has an overriding effect on this and that its importance is grossly underrepresented in the model (Table 4). This is because only the depth of ant nests found by pangolins were measured. We suspect that many deeper nests not found by pangolins went unrecorded. The ants *M. natalensis* and *P. schistacea* appear to have nests that are deeper and concentrated in a smaller area than those of *A. custodiens* (pers. obs.) and this could explain their small RI in the overall pangolin diet.

The correlation between dig depth and feeding duration (which excludes digging time, Fig. 3) seems to be more fundamental than merely reflecting between species differences in ant nest structure: it was recorded within single species such as *A. custodiens*. Several explanations are available. Firstly, optimal foraging theory would predict that ant nests which required more digging would, on average, be fed upon for longer durations. Alternatively, given that all the nests used were shallow, digging deeper into a nest may result in more ants being exposed and longer feeding durations. These alternatives need to be tested in order to obtain a fundamental understanding of pangolin feeding behaviour.

What does this mean in terms of an understanding of the ecological requirements of pangolins? Although *A. custodiens* is a widespread and relatively abundant species occurring throughout South Africa, it is not necessarily available to pangolins throughout the year. Winter minimum temperatures in the Sabi Sand Game Reserve are usually mild and although they occasionally drop to below 5 °C, this usually lasts for only a few days. In contrast, many of the temperate regions of South Africa above the great escarpment experience cold winters where the temperature often falls below 5 °C and even below 0 °C. The ants escape the cold by hibernating deep below the soil surface where they are out of reach of the shallow-digging pangolin. In this situation pangolins would be left without their primary food source for extended periods during winter in these regions, and this is probably the reason that the pangolin's range does not extend into these temperate regions.

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Appendix. The frequency of occurrence (N_1) and the abundance (N_2) of each species of epigaeic ant and termite sampled with pitfall traps from July 1993 to July 1994. The percentage contribution of the 10 most abundant species recorded during winter and summer are also included

Ant and termite species	% Contribution		N_1	N_2
	Winter	Summer		
Formicidae				
Aenictinae				
Aenictus eugenii Emery	–	–	7	9
Dolichoderinae				
Tapinoma sp. 1	–	–	15	16
Tapinoma sp. 2	–	–	9	14
Technomyrmex albipes (Smith)	4.1	1.7	132	305
Formicinae				
Anoplolepis sp. 1	–	–	2	7
Anoplolepis custodiens (Smith)	1.4	6.6	274	8127
Camponotus sp. – *maculatus* – group	–	–	4	4
Camponotus cinctellus (Gerstäcker)	–	–	3	3
Camponotus congolensis Emery	–	–	6	6
Lepisiota capensis (Mayr)	–	–	55	91
Lepisiota spinosior (Forel)	–	–	14	15
Lepisiota submetallica Arnold	–	–	83	117
Plagiolepis sp. 1	–	–	40	82
Plagiolepis sp. 2	–	–	1	1
Polyrhachis schistacea (Gerstäcker)	–	–	5	5
Myrmicinae				
Crematogaster sp. 1	–	–	38	139
Crematogaster sp. 2	–	–	4	6
Crematogaster sp. – *castanea* – group	2.5	2.2	125	414
Melissotarsus beccarii Emery	–	–	1	1
Meranoplus inermis Emery	–	–	1	1
Meranoplus magrettii André	–	–	10	10
Meranoplus nanus André	–	–	1	1
Meranoplus sthenus Bolton	–	–	4	4
Monomorium damarense Forel	28.0	21.4	1273	3013
Monomorium emeryi Mayr	–	–	15	20
Monomorium havilandi Forel	–	–	2	2
Monomorium junodi Forel	28.0	11.8	569	3250
Monomorium mictilis Forel	–	–	40	322
Monomorium sp. – *mediocre* – complex	–	–	8	30
Myrmicaria natalensis (Mayr)	–	–	39	95
Ocymyrmex fortior Santschi	0.7	4.2	173	278
Pheidole sp. 1	–	–	5	5
Pheidole sp. 2	28.1	27.2	1498	8570
Pheidole sp. 3	–	–	22	39
Pheidole sp. 4	–	–	8	12
Solenopsis sp. 1	–	–	12	10
Tetramorium constanciae Arnold	–	–	2	10
Tetramorium do Forel	2.0	2.3	121	141
Tetramorium inezulae (Forel)	–	–	68	258
Tetramorium longicorne Forel	–	–	2	2
Tetramorium mossamedense Forel	–	–	3	3
Tetramorium notiale Bolton	–	–	6	7
Tetramorium oculatum Forel	–	–	1	1
Tetramorium sericeiventre Emery	3.1	5.6	266	435
Tetramorium setigerum Mayr	–	–	42	50
Tetramorium setuliferum Emery	–	–	36	185
Tetramorium sp. – *oculatum* – complex	5.8	3.9	242	386
Ponerinae				
Odontomachus troglodytes Santschi	–	–	63	72
Pachycondyla kruegeri Forel	–	–	34	35
Plectroctena mandibularis Smith	–	–	3	3
Termitidae				
Termitidae (unidentified sp.)	–	–	18	230
Hodotermitidea				
Hodotermes mossambicus Hagen	–	–	18	230
Macrotermitinae				
Macrotermes falciger Gerstäcker	–	–	1	27
Odontotermes sp.	–	–	16	21
Nasutitermitinae				
Rhadinotermes coarctatus Sjöstedt	–	–	6	116
Trinervitermes Sjöstedt	–	–	4	8
Totals	–	–	5449	27 067
Total number of species	–	–	55	