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Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo

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The diversity and abundance of epigaeic ant species were determined across three habitats (riverine areas, gently sloping grassland areas and steep slope areas) in summer (November–December) and winter (May–June) of 1998 at Tussen die Riviere Nature Reserve in the Karoo, to determine temporal and spatial variations in the availability of potential prey species of the aardvark *(Orycteropus afer)*. Pitfall trapping, dig sampling and quadrat sampling were used to ensure as complete a sampling effort as possible. Forty-five ant species of five sub-families and 17 genera were recorded. The grassland habitat yielded the highest abundance and diversity, followed by the steep slope and riverine areas. Ant abundance and diversity were higher during summer than winter in all three habitats. *Anoplolepis custodiens* was the most abundant species in summer, whilst *Monomorium albopilosum* was the most abundant species in winter. Pitfall trapping was responsible for recording more species than dig sampling or quadrat sampling. No method recorded all of the species present.

Keywords: Karoo; epigaeic ants; abundance; diversity; season; habitat; pitfall trap; dig samples; quadrats

Introduction

This research was conducted as part of a broader study based on the feeding ecology of the aardvark, incorporating aspects of prey selection, habitat utilization and seasonal patterns in feeding behaviour (Taylor *et al.,* unpublished data). Ants represent the dominant dietary component of the aardvark across all seasons and habitats in the southern Karoo (Taylor, 1998; Lindsey, 1999). The present study aim was to determine temporal and spatial patterns in the availability of potential aardvark food. Ant faunas tend to vary considerably between habitat types and seasons (Samways, 1990; Anderson, 1993) and consequently, sampling was done in three different habitats in summer and winter. Taylor *et al.* (unpublished data) discuss the diet and prey selection of the aardvark in detail and, as a result, the present paper focuses solely upon the abundance and diversity of ants across habitats and seasons in a little-studied area of the Karoo.

Despite the abundance and diversity of ants in South African ecosystems and their importance as a food source for a variety of species, understanding of the ant

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communities of this country remains very limited (Marsh, 1990). The work that has been done has focused largely on the Cape Fynbos (Donnelly & Giliomee, 1985*a* 1985*b*; Koen & Breytenbach, 1988), Mpumalanga (Samways, 1983, 1990, Swart *et al.*, 1999) and the Namib Desert (Marsh, 1986*a*).

The biota of the Karoo are very poorly known and many common species from a variety of taxa remain unidentified (Milton *et al.*, 1992). Work done on the ant communities of the Karoo is limited largely to studies of single species (Dean & Yeaton, 1993; Vorster *et al.,* 1992). Dean & Turner (1990) considered the use of stones as nesting sites for avoidance of predation by the aardvark, whilst Dean (1992) looked at the effect of temperatures on ant activity patterns in the southern Karoo. Willis *et al.* (1992) considered the diet of the aardvark relative to the availability of ants and termites in the Karoo. The present paper follows on from the work of Willis *et al.* (1992), with a significant intensification of sampling and the adoption of two additional methods in an attempt to achieve a more complete sampling effort.

Much consideration has been given to the merits of the various sampling techniques available (Andersen, 1991; Majer, 1997). Pitfall trapping is the most widely used method in surveys of ant faunae (Majer, 1997) and several researchers consider the technique to give reliable results (Andersen, 1991; Vorster *et al.*, 1992). It is a low cost way to obtain a large number of specimens (Marsh, 1984) and it enables continuous sampling over a prolonged period, avoiding the potential sampling bias arising from inter-specific differences in activity periods (Marsh, 1984; Andersen, 1991).

However, a number of problems are associated with the method and pitfall trapping alone is likely to under-sample the ant community (Majer, 1997). As a result, dig-sampling (the sampling of set volumes of soil) was employed to ensure a more complete survey. In addition, limited quadrat data from the broader study are incorporated where possible. The use of additional methods increases the likelihood of recording rare or localized species. Furthermore, these methods are more likely to sample species with all types of foraging patterns and speeds, and hypogaeic species ought to be adequately sampled.

Study Area

This study was conducted on Tussen die Riviere Nature Reserve (TdR), an area of 22,000 ha of Eastern Mixed Nama Karoo (Hoffmann, 1996) in the southern Free State, at a position of 30°30′S and 26°15′E at the confluence of the Orange and Caledon rivers. This area is of considerable importance in the conservation of one of the least well preserved vegetation types (Hoffmann, 1996). The reserve excludes livestock and is inhabited by a high diversity of indigenous mammal species. Of particular interest with regards to this study is the presence of the myrmecophagous aardvark (*Orycteropus afer*) and the insectivorous aardwolf (*Proteles cristatus*). The climate of the area is intermediate temperate-tropical. The winter months are cold and dry, with mean temperatures between 0–10°C, whereas summer mean temperatures exceed 18°C. Annual rainfall averages approximately 400 mm and falls between November and March (Werger, 1973). The vegetation of the area has been categorized by Werger (1973) into three major types:

(1) The riverine communities. The riverine habitat is dominated by the *Acacia karoo–Celtis africana* community in any areas. This generally consists of three layers: A tree layer of 6–10 m in height, a shrub layer characterized by *Rhus pyroides, Diospyros lycoides, Lycium hirsutum* and *Clematis brachiata.* Thirdly, there is a grass layer, characterized by a number of species, including *Altriplex*

semibaccata, *Asparagus setaceus*, *Bromus willdenowii* and *Chenopodium murale*. The percentage cover is variable, with large areas of open ground of sparse grass coverage. The soils are alluvial with a pH of between 6·5–7·5 and a depth of approximately 0·5 m.

(2) The grassland communities of the gently sloping and flat terrain. These communities are generally poorer in plant species than the steep slope areas and generally have only two layers, with the most important being the grass and dwarf shrub layer between 0·1 and 0·6 m in height with a cover of up to 50%. The general absence of trees in the grassland habitat is notable. Werger (1973) recognized four vegetation communities within this habitat type: (1) *Eragrostis lehmanniana-Chrysocoma tenuifolia* community; (2) *Chrysocoma tenuifolia—Lessertia pauciflora* community; (3) *Chrysocoma tenuifolia* - *Nenax microphylla* community, and (4) *Chrysocoma tenuifolia—Polygala leptophylla* community. This habitat is characterized by relatively deep solonetzic soils.

(3) The steep slope communities. This habitat is the richest community in the reserve, both in terms of species numbers and structural complexity. There are three or four layers, including an open tree layer in some areas, a shrub layer with a ground cover of 10–30%; a grass and small shrub layer with a 35–50% ground cover and finally, a sparse ground layer of creeping rosette species covering less than 5%. *Rhus erosa* and *Olea africana* are the most important tree species in this habitat. The soils of this habitat are shallow and stony with a mean depth of 10 cm.

Sampling methods

Pitfall trapping was stratified by habitat type, with nine randomly selected sites within each habitat in summer (November–December) and winter (May–June). At each site, five traps, 10 m apart, were placed in a line of random direction. The traps were set between 1600 and 1800 hours and left open day and night for a total of 5 days, at which time the ants were collected. Trapping was staggered over a period of 6 weeks so as to reduce the potential effect of short-term extreme weather conditions over the sampling period. One set of three areas within each habitat was sampled initially, followed by a second set of three areas in each habitat 2 weeks later, and a third set 14 days later still. In total the number if trap nights was 1350 (five traps × nine sites × three habitats × five days × 2 seasons). The pitfall trap design was based upon those detailed in Majer (1978). Rimmed Pyrex tubes 16 mm in diameter and 160 mm in length were inserted into sunken plastic piping, with the lip of the tube level with the surface. Twenty millimetres of three parts glycerol, and seven parts 80% ethanol solution was added to each tube. Prior to the commencement of trapping, the pitfall traps were left for one week to reduce 'digging-in' effects (Greenslade, 1973).

Dig sampling was achieved by taking samples in the proportions of a typical aardvark dig [10 (d) × 10 (w) × 15 (l) cm] and collecting all ants within the soil removed. As with the pitfall trapping, dig sampling was done to the same intensity in nine randomly selected sites in each habitat in summer and winter, in a staggered fashion. At each site four digs were made in a line 10 m apart. The line of digs was made parallel to, and 50 m to the east of the pitfall trap line.

Quadrat sampling was restricted to summer and was conducted with an alternative sampling intensity and distribution from the above methods. However, the additional insight into the ant communities by using this method justifies the inclusion of the results. This sampling was conducted in three large sections of the reserve, with 10 randomly chosen locations per site. At each of the 10 sites, three 1 × 1 m quadrats were sampled in a line of random direction. The daytime quadrats were conducted between 1630 and 1800 hours in the afternoon so as to avoid the hottest hours of the day when surface activity is likely to be reduced. The night-time quadrats were conducted between 2330 and 0030 hours to ensure minimal overlap with the day time ant faunae. Each quadrat was sampled for a period of five min, during which the surface of the soil was overturned with a small trowel to aid in the search for ants. Again, the sampling was staggered over a 6-week period with three sites per field trip and four in the last. Both the quadrat and dig sampling methods were used solely to record the presence of ant species, with no record made of abundance.

All ant species were collected and stored for later identification.

Species richness estimator

An abundance-based coverage estimator (ACE) (Colwell, 1997) was used to estimate species richness in the three different habitats. ACE is a method based on those species with 10 or fewer individuals in a sample and overcomes the problem of overestimating species richness, a characteristic of data types in which some classes are very common and others very rare (Colwell, 1997).

Statistical methods of analysis

Multivariate analyses were carried out using the computer software package PRIMER. These were used to compare the similarity between ant communities from different habitats and seasons as indicated by the pitfall trapping data. Multivariate methods are characterized by the fact that they base their comparisons of two or more samples on the extent to which these samples share particular species at comparable levels of abundance (Clarke & Warwick, 1994). These are founded on similarity coefficients, calculated between every pair of samples which then facilitate a clustering of samples into groups which are mutually similar, or an ordination plot in which, for example, the samples are 'mapped' in such a way that the distances between pairs of samples reflect the relative dissimilarity of species compositions.

It is recommended, even when samples are strongly grouped, that cluster analysis be best used in conjunction with ordination. Superimposition of the clusters on an ordination plot will allow any relationship between the groups to be more informatively displayed. The two techniques are best thought of as complementary to each other: neither may present the full picture so the recommendation is to perform both and view them in combination (Clarke & Warwick, 1994).

Hierarchical agglomerative clustering was the clustering technique used, while non-metric multi-dimensional scaling (MDS) was the ordination method used.

A pre-requisite to interpreting community differences between habitats and seasons should be a demonstration that there are statistically significant differences to interpret. Subsequently, a test was used which is built on a simple non-parametric permutation procedure, applied to a (rank) similarity matrix underlying the ordination or clustering of samples. This is termed analysis of similarity (ANOSIM) and was carried out on the data representing the ant communities from different habitats and seasons.

Transformations in the PRIMER package are used to define the balance between contributions from common and rarer species in the measure of similarity of two samples. This is unrelated to the more common reason for transformation, that of validating statistical assumptions for parametric techniques (unnecessary in this case because the technique works on ranked data). The square root transformation was selected in this case because it allows the intermediate abundance species to play a part. When no transformation is carried out only the common species contribute to the similarity.

Results

Overall ant diversity

Forty-five ant species representing five sub-families and 17 genera were recorded (Table 1). Of the Formicidae, the Myrmicinae was the dominant subfamily in terms of species numbers (26 species) and abundance, followed by the Formicinae (15 species), the two subfamilies representing the vast majority of ant species present in the area. The most species-rich genera were *Tetramorium* (nine species), followed by *Monomorium* (seven species) and *Camponotus* (six species).

Temporal and spatial variation

The grassland habitat had the highest ant species richness count, at 41 species, or 91% of the total, followed by the steep slope habitat with 31 species (69%) and finally the riverine areas, which recorded only 15 species (33%). Twelve of the 45 species (27%) were recorded in all three habitats. Eighteen of the species (40%) occurred in two habitats, whilst 15 species (33%) occurred in one habitat type. The abundance figures obtained from the pitfall trapping provide a clearer picture of the inter-habitat and seasonal variations (Table 2). These results are presented as adjusted abundance (AA), calculated as follows;

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

Where A = abundance, and O = percentage occurrence.

This method reduces some of the problems associated with either abundance or percentage occurrence when used in isolation. Two species can have the same percentage occurrence even of they occurred at greatly different abundance. Conversely, abundance figures can be misleading when a species occurs in very high numbers in very few pitfall traps.

The most abundant species over all three habitats were *Monomorium albopilosum*, *Anoplolepis custodiens* and *Pheidole* sp 1. Twelve species were unique to the grassland habitat: *Aenictus rotundatus, Camponotus simulans, Camponotus*. sp. 2. *emarginatus* gp, *Camponotus*. sp. 3. *emarginatus* gp, *Camponotus vestitus*, *Lepisiota* sp. 4, *Monomorium* sp. 1, *Plagiolepis* sp. 1, *Meranoplus spininodis, Pheidole* sp. 3, *Tetramorium amaurum*, *Tetramorium* sp. 2 *simillum* gp. Only one species was unique to the riverine habitat, namely *Lepisiota* sp. 2, whilst one species was unique to the steep slope habitat, *Techonomyrmex albipes*. The habitats differed more in the abundance of individuals per species than in numbers of species. A far greater number of individuals were caught in the grassland habitat in both summer and winter than in the steep slopes, or riverine habitats. As with species numbers, fewest individuals were caught in the riverine areas.

The abundance and number of species of ants was greater in summer (3872 individuals of 44 species) than winter (2474 individuals of 25 species). Fifty-three per cent of the species were active in both seasons, whilst 97% were active in summer and 56% were active in winter. Twenty-nine per cent of ant species were active only during summer, whilst 2% were active only during the winter period.

The summer catches were less variable than the winter samples. In the grassland habitat in winter, the three most abundant species made up 91% of the total numbers caught, compared to a figure of 72% in summer. In the steep slope habitat, these figures were 90·9% and 71·5% in winter and summer respectively, and in the riverine habitat 91% and 50% in the riverine habitat.

Table 1. *A list of the species recorded by each of the three methods employed*

Ant species	Pitfall trapping	Dig	Quadrat
Aenictinae			
Aenictus rotundatus Mayr	0	0	1
Dolichoderinae			
Linepthema humile (Mayr)	1	0	0
Techonomyrmex albipes (Smith)	1	0	0
Formicidae			
Anoplolepis sp. 1	1	0	1
Anoplolepis custodiens (Smith)	1	1	1
Anoplolepis steingroeveri (Forel)	1	1	1
Camponotus fulvopilosus (De Geer)	1	0	1
Camponotus maculatus (Fabricius)	1	0	1
Camponotus nasutus Emery	1	0	0
Camponotus simulans Forel	1	0	0
Camponotus sp. 2 *emarginatus* gp	1	0	1
Camponotus sp. 3 *emarginatus* gp	0	0	1
Camponotus vestitus (Smith)	0	0	1
Lepsisiota capensis (Mayr)	1	1	1
Lepisiota sp. 1	1	1	1
Lepisiota sp. 2	1	0	0
Lepisiota sp. 4	0	1	0
Plagiolepis sp. 1	0	1	0
Myrmicinae			
Crematogaster melanogaster Emery	0	0	1
Crematogaster sp. 1	1	0	0
Meranoplus spininodis Arnold	0	0	1
Messor capensis (Mayr)	1	1	1
Monomorium albopilosum Emery	1	1	1
Monomorium havilandi Forel	1	1	1
Monomorium notulum Forel	1	0	1
Monomorium sp. 1	1	0	0
Monomorium sp. 2	1	1	0
Monomorium sp. 1 *salomonis* gp	1	1	0
Monomorium willomorense Bolton	1	1	1
Ocymyrmex weilzecher Emery	1	0	1
Pheidole sp. 1	1	0	1
Pheidole sp. 2	1	0	1
Pheidole sp. 3	1	0	0
Tetramorium clunem Forel	1	0	0
Tetramorium dichroum Santschi	1	1	1
Tetramorium erectum Emery	1	0	1
Tetramorium nr amaurum Bolton	1	0	0
Tetramorium sericeiventre Emery	1	0	0
Tetramorium setigerum Mayr	1	0	0
Tetramorium sp. 1	1	0	1
Tetramorium sp.nr frigidum Arnold	1	0	1
Tetramorium sp. 2 *simillum* gp	1	0	1
Ponerinae			
Anochetus levaillanti Emery	0	0	1
Pachycondyla ambigua Andre	0	0	1
Plectronectena mandibularis Smith	0	1	1

Table 2. *The adjusted abundance of the various ant species recorded in each habitat in summer and winter in the pitfall traps*

Ant species	Gw	Gs	Sw	Ss	Rw	Rs	Total
Dolinchoderinae							
Linepithema humile	1·2	0	2	0	0·2	0	3·4
Techonomyrmex albipes	0	0	0	2·0	0	0	2·0
Formicinae							
Anoplolepis sp. 1	0	17	0	7	0	0·4	24·4
Anoplolepis custodiens	31	1111	0·4	255	0	7	1404·4
Anoplolepis steingroeveri	2	331	0	2	0	0	335
Camponotus fulvopilosus	0	0·2	0	0	0	0	0·2
Camponotus maculatus group	0·2	10	0	4	2	0	16·2
Camponotus nasutus	0	0·4	0	1	0	0	1·4
Camponotus simulans	0	0·2	0	0	0	0	0·2
Camponotus sp. 2 *emarginatus*	0	1	0	0	0	0	1
Lepsisiota capensis	0	0·2	2	1	1	0	4·2
Lepisiota sp1	0·2	0	0·4	0	0	0	0·6
Lepisiota sp2	0	0	0	0	0	0·2	0·2
Myrmicinae							
Crematogaster melanogaster	0	0	3	26	0	0	29
Crematogaster sp1	0	0	2	1	1	0	4
Messor capensis	48	13	5	6	0	14	86
Monomorium albopilosum	958	217	485	225	48	12	1945
Monomorium havilandi	6	225	1	219	0	7	458
Monomorium notulum	2	12	2	7	0	0	23
Monomorium sp. 1	0·2	0	0	0	0	0	0·2
Monomorium sp. 2	1	0	1	0	0	0	2
Monomorium sp.1 *salomonis* gp	0	7	0	0·2	0	7	14·2
Monomorium willomorense	0	3	0·4	2	0·2	2	7·6
Ocymyrmex weilzecher	0	36	0·2	10	0	4	50·2
Pheidole sp.1	350	110	59	70	0·8	4	593·8
Pheidole sp. 2	0	0·2	0	0	0	3	3·2
Pheidole sp. 3	0	0·2	0	0	0	0	0·2
Tetramorium clunem	7	0	0	0·6	0	0	7·6
Tetramorium dichroum	0	0	0	20	0	0	20
Tetramorium erectum	0·4	0·8	0·2	0·7	0	0	2·1
Tetramorium nr amaurum	0	0·2	0	0	0	0	0·2
Tetramorium sericeiventre	0·2	15	0·4	33	0	8	56·6
Tetramorium setigerum	1	2	2	3	0	0	8
Tetramorium sp. 1	0·2	0·2	0	0·3	0	0	0·7
Tetramorium sp· *Nr frigidum*	0	0·4	0	8	0	0	8·4
Tetramorium sp. 2 (*si’millum* gp)	0	8	0	0	0	0	8
Ponerinae							
Anochetus levaillanti	0	0·2	0	0·2	0	0	0·4
Pachycondyla ambigua	0	0	0	0·8	0	0	0·8
TOTAL AA	1414·6	2141·2	566	912·8	53·2	73·6	

Gw = grassland winter; Gs = grassland summer; Sw = steep slope winter; Ss = steep slope summer; Rw = riverine winter; Rs = riverine summer.

Table 3. *Two-way ANOSIM of the AA's of the various species in the pitfall traps in the three habitats and two seasons (10,000 permutations)*

Groups compared	Global (R)	*p* value
Summer *vs.* winter	0·501	0·0*
Habitats	0·398	0·0*
G *vs.* SS		0·2*
SS *vs.* R		0·0*
G *vs.* R		0·0*

G = grassland; SS = steep slopes; R = riverine. Significant statistics marked with asterisk.

Species richness estimator (ACE)

Values of species richness for the three habitats, as estimated by ACE, were 39·71, 27·06, and 11·96 from grasslands, steep slopes and riverine habitats respectively.

The AA's of the various ant species were compared between habitat and season, using a two-way ANOSIM (Table 3). There were significant differences between the seasons and habitats.

Figure 1 represents a dendrogram of the results. Here the similarity of the samples is reflected in their relative positions on the plot. Figure 2 shows a multi-dimensional scaling plot in which the distances between pairs of samples reflects the dissimilarity of species compositions. Figure 1 shows marked separation of samples from the various habitat and season categories, with the exception of the steep slope and grassland samples from summer which are interspersed. Figure 2 shows that the Riverine samples were very different from the samples of the other two habitats, which overlapped considerably. Clear seasonal groupings are also apparent from this plot.

Diel activity patterns

The quadrat sampling indicated that some species were predominantly diurnal whilst others were mainly nocturnal (Table 4).

Seven of the 26 species recorded in the quadrat samples were predominantly nocturnal, whilst 12 were mainly diurnal. Some species showed large differences in the percentage occurrence between day and night. *Camponotus fulvopilosus*, *C sp. 2 emarginatus* and *Pheidole sp. 1* were markedly nocturnal, whereas *A. custodiens* and *M. notulum* were largely diurnal in their activity patterns.

Sampling methods

Pitfall trapping caught more species (38 species) than either dig sampling or quadrat sampling. The quadrat sampling was also successful, yielding more species than the dig sampling (24) species, despite the limited spatial and temporal distribution of samples. The percentage of samples in which each species occurred in the three sampling methods in the grassland habitat during summer is compared in Table 5. The quadrat data were obtained only from the grassland habitat and therefore comparison between the three methods is only possible for this habitat.

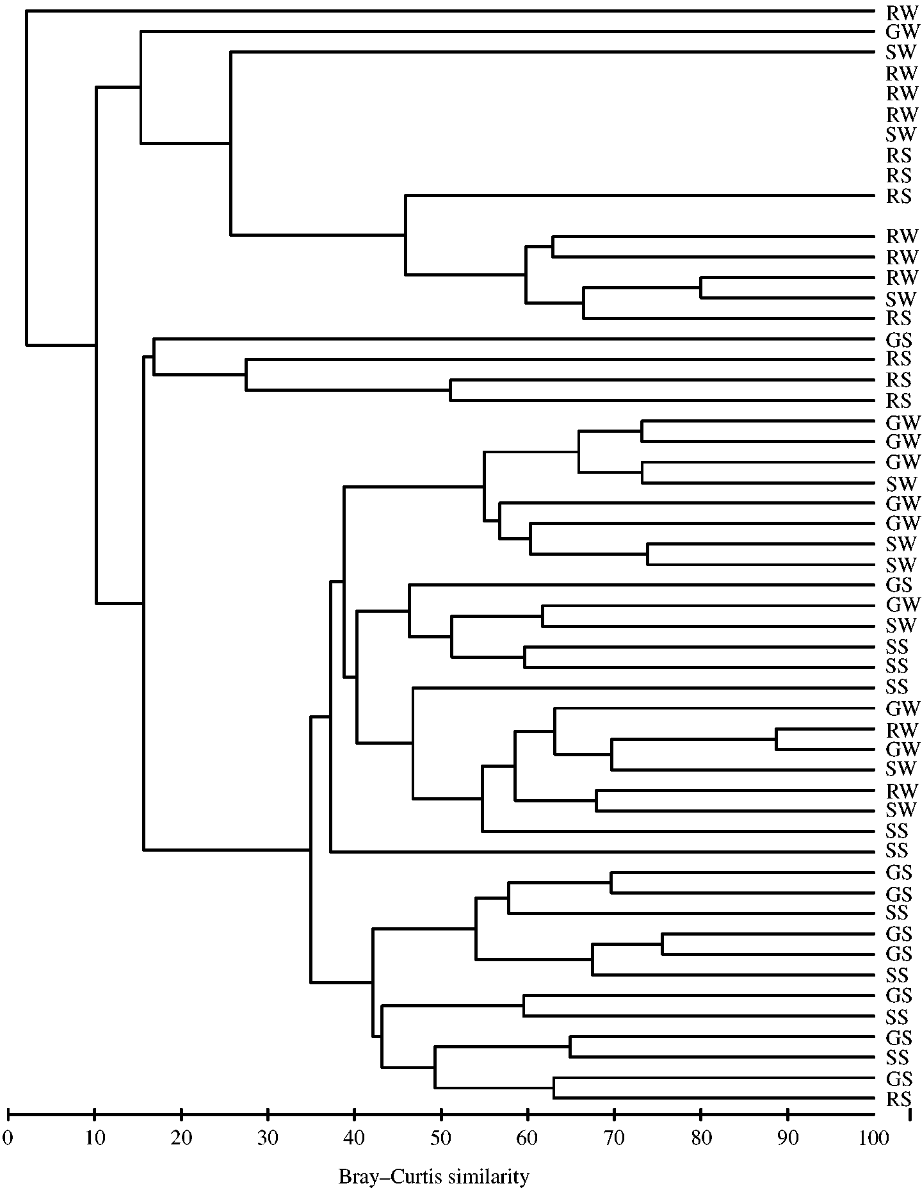

Figure 1. The dendogram derived from the species within each of the nine pitfall samples taken in each season and habitat. NB. GW = Grassland winter, GS = Grassland summer, SW = Steep slope winter, SS = Steep slope summer, RW = Riverine winter, RS = Riverine summer.

The vast majority of species occurred most frequently in the pitfall trap samples. The dig samples recorded the fewest species in the grassland in summer, whilst the pitfall traps yielded the most. The species that did occur in the dig samples occurred much less frequently than in the pitfall trapping. Several of the species not recorded or infrequently recorded by the quadrat or dig sampling occurred regularly in the pitfall samples (e.g. *Tetramorium setigerum*, *Camponotus maculatus* gp and *Anoplolepis* sp. 1), indicating that they were common but not recorded by the other techniques.

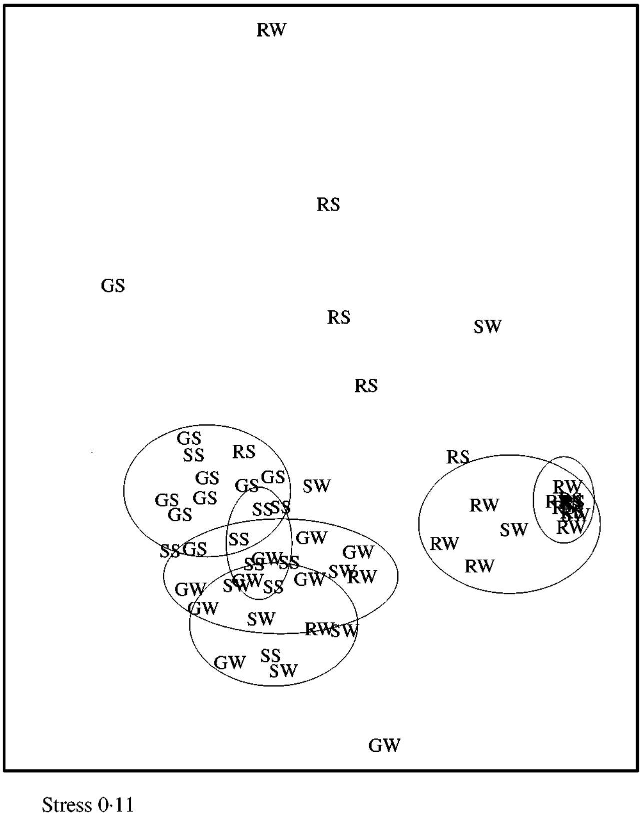

Figure 2. Non-metric MDS configuration of ant communities in three habitats in summer and winter, as suggested by pitfall trapping. Ellipses included to highlight groupings of habitat and season. NB. GW = Grassland winter, GS = Grassland summer, SW = Steep slope winter, SS = Steep slope summer, RW = Riverine winter, RS = Riverine summer.

Discussion

Ant diversity of the semi-arid Karoo

The 45 ant species and 17 genera recorded in the present study (and 58 species recorded to date in the area) compare well with the figures obtained by other authors who used pitfall traps in South Africa. For example, in Mpumalanga, Samways (1983, 1990) recorded 49 species and 56 species respectively in grassland associated with citrus, whilst Swart *et al.* (1999) recorded 50 species in the Arid Lowveld. In the Fynbos of the south Western Cape Province, Donnelly & Giliomee (1985*a*) recorded 45 species in two habitats. Considerably more species were recorded in the present study than in the survey of Marsh (1986*a*) in the Namib desert (27 species). The higher productivity of the Karoo relative to the extremely arid conditions that prevail in the Namib probably explains this discrepancy. The limited work done on ants in the Karoo has indicated a positive correlation between species richness and rainfall (Vernon, 1999). The site of the present study experiences relatively high annual rainfall and has a correspondingly high ant species richness. Comparisons with the ant species richness of other biogeographical regions is hampered by differences in sampling intensity and design. However, the ant faunas of semi-arid Australia are some of the most species rich known

Table 4. *The percentage of samples in which each species occurred during the day and at night, in quadrat samples*

Ant species	Average percentage occurrence in the day	Average percentage occurrence at night
Aenictinae		
Aenictus rotundatus	3·3	1·1
Formicidae		
Anoplolepis custodiens	26·6	7·7
Anoplolepis steingroeveri	15·5	6·6
Camponotus fulvopilosus	1·1	54·4
Camponotus sp.2 *emarginatus* gp	3·3	24·4
Camponotus sp. 3 *emarginatus* gp	0	1·1
Camponotus vestitus	1·1	0
Lepisiota capensis	0	2·2
Myrmicinae		
Crematogaster melanogaster	3·3	5·5
Meranoplus spininodis	1·1	3·3
Messor capensis	11·1	1·1
Monomorium albopilosum	5·5	26·6
Monomorium havilandi	10	6·6
Monomorium notulum	61·1	0
Monomorium willowmorense	13·3	0
Ocymyrmex weilzecher	5·5	0
Pheidole sp. 1	1·1	30
Pheidole sp. 2	13·3	1·1
Tetramorium erectum	0	1·1
Tetramorium dichroum	1·1	0
Tetramorium nr frigidum	3·3	7·7
Tetramorium sericeiventre	1·1	0
Tetramorium sp. 2 *simillum* gp	8·9	7·8
Ponerinae		
Plectronectena mandibularis	1·1	0

(Andersen & Burbridge, 1992). In a comparative study of harvester ant communities in arid areas of Australia and North America, Morton & Davidson (1988) noted that greater between-habitat diversity existed in Australia. Likewise, the diversities recorded in semi-arid areas of Australia tend to be considerably higher than that recorded in the present study and at other sites in South Africa. The species richness of ant communities generally increases with decreasing latitude (Kusnezov, 1957) and this effect may, in some cases, partially explain the comparatively lower diversities recorded in semi-arid parts of South Africa. For example, the 111 species recorded by Andersen (1993) in the Gulf Region of Australia were captured at a latitude of 18°43′S, in comparison to the latitude of 30°30′S of the present study.

The ant faunae in the present study were dominated by the Myrmicinae, which made up 58% of the total species, followed by the Formicinae, which made up 33%. The Myrmicinae and Formicinae are the largest ant subfamilies and the dominant ant groups in most terrestrial habitats (Marsh 1986*a*). Several other researchers in South Africa have recorded similar patterns to those found in the present study: Donnelly & Giliomee

Table 5. *The percentage of samples in which each species occurred as recorded in the three sampling methods in the grassland habitat during summer*

Ant species	Pitfall trapping	Dig	Quadrat
Aenictinae			
Aenictus rotundatus	0	0	2·2
Formicidae			
Anoplolepis sp. 1	28·9	0	1·1
Anoplolepis custodiens	53·3	16·6	11·1
Anoplolepis steingroeveri	26·7	2·7	17·2
Camponotus fulvopilosus	2·2	0	27·7
Camponotus maculatus-group	22·2	0	3·8
Camponotus nasutus	2·2	0	0
Camponotus simulans Forel	2·2	0	0
Camponotus sp. 2 *emarginatus* gp	4·4	0	13·8
Lepisiota sp. 4	0	8·3	0
Lepsisiota capensis	2·2	5·5	1·1
Plagiolepis sp. 1	0	2·7	0
Myrmicinae			
Crematogaster melanogaster	0	0	4·4
Messor capensis	31·1	16·6	6·1
Meranoplus spininodis	0	0	2·2
Monomorium albopilosum	77·8	25	15·6
Monomorium havilandi	48·9	8·3	8·3
Monomorium notulum	26·7	0	30·6
Monomorium sp. 1 *salomonis* gp	17·8	8·3	0
Monomorium willomorense	11·1	5·6	6·7
Ocymyrmex weilzecher	28·9	0	2·7
Pheidole sp. 1	66·7	0	15·6
Pheidole sp· *2*	2·2	0	7·2
Pheidole sp. 3	2·2	0	0
Tetramorium sp. 1	2·2	0	1·6
Tetramorium nr amaurum	2·2	0	0
Tetramorium erectum	4·4	0	0·6
Tetramorium sp·nr frigidum	4·4	0	5·6
Tetramorium sericeiventre	*26*·7	0	0
Tetramorium setigerum	8·9	0	0
Tetramorium sp. 2 *simillum* gp	17·8	0	8·3
Ponerinae			
Plectronectena mandibularis	0	0	0·6
Anochetus levaillanti	0	0	2·2

(1985*a*) recorded figures of 59% and 19% of the species belonging to the Myrmicinae and Formicinae respectively in the Fynbos. Likewise, Swart *et al.* (1999) recorded figures of 64% and 22% for these two groups. The prevalence of these two subfamilies has been reported to increase with increasing aridity and Marsh (1986*a*) reported a much higher dominance of these two genera (81% Myrmicinae, 18% Formicinae) in the Namib Desert. In contrast, Australian and North American semi-arid areas are characterized by a more even spread of species across sub-families such as the

Dolichoderinae, Dorylinae and Ponerinae (Andersen, 1986; Briese & Macauley, 1977; Whitford, 1978). This reflects the different evolutionary histories of the ant faunae of the arid areas in these countries (Marsh, 1986*b*).

In keeping with the findings of a number of South African studies (Donnelly & Giliomee 1985*a*, Koen & Breytenbach, 1988; Samways, 1983) *Tetramorium* was the largest genus in the area with nine species. Indeed, the Ethiopian zoogeographical region contains more *Tetramorium* species than the rest of the world combined (Bolton, 1980). The most abundant *Tetramorium* species in the present study, *T. sericeiventre* has been described as being the commonest member of this genus in Africa (Marsh, 1986*b*) and is capable of existing anywhere the soil is sandy or well drained (Bolton, 1980). The other *Tetramorium* species all occurred at low densities. The present study did not record a species found to be the sixth most abundant species in a previous study (Willis *et al.*, 1992). It has been suggested that ants occur in mosaic distributions whereby in areas of apparently homogeneous vegetation, different species dominate (Majer, 1972; Samways, 1983; Miller & New, 1997). The absence of this species from the present study, despite intensive sampling in an area of the same habitat as that of the previous study may indicate the presence of such a mosaic distribution.

Monomorium was the most abundant genus, due largely to the high numbers of two species: *M. albopilosum* and *M. havilandi. M. albopilosum* was very abundant in all of the habitats. Samways (1983), in contrast, found this species to be very habitat selective, being typical of sparse grassland. This discrepancy may be due to greater inter-habitat differences in terms of floral and structural diversity between the habitats compared by Samways (1983) relative to those compared in the present study.

The genus *Anoplolepis* consists of only four species (Marsh, 1986*b*), of which three were recorded in the present study. *Anoplolepis custodiens* showed a higher abundance than any other species during summer in the grassland habitat and was the second most abundant species overall. *Anoplolepis custodiens* occurs very widely across southern Africa and is thought to be the most abundant Camponotine species in South Africa (Steyn, 1954). *Anoplolepis custodiens* and *A. steingroeveri* both occurred with greater abundance in the grassland habitats than in the other two habitats. *Anoplolepis steingroeveri* does not nest under stones (Dean & Turner, 1990) and probably occurs at low density on the steep slopes as a result of the high density of stones and rocks in this habitat.

Spatial variation: habitat differences

Little is known of the habitat requirements of many ants, but the limited research done indicates that ant assemblages are influenced by a number of habitat variables including; landform, geology, soil type, soil moisture, physiognomy, vegetation cover, plant structural diversity and leaf litter cover (Koen & Breytenbach, 1988; Andersen, 1993). Positive correlation between plant structural diversity and the abundance and diversity of ants is frequently reported (Culver, 1974; Room, 1975).

Marked habitat differences in the present study were reflected in differences in the ant assemblages between the three habitats. Of the three habitats, the ant communities of the riverine areas were the most distinct both in terms of habitat structure and ant assemblage. A lower ant diversity and abundance was recorded in this habitat than the other habitats in summer and winter. These areas are exposed to seasonal flooding followed by the desiccation and deep cracking of the soil. Consequently, the fauna is likely to be limited to species adapted to the rapid colonisation of available habitat. The percentage cover of vegetation of large areas of the riverine habitat was lower than the other two habitats. The winter sampling in this habitat recorded only 116 individuals of seven species. The low-lying nature of this habitat makes it likely that the temperatures in these areas are lower than in the other habitats. This factor may partly explain the relative lack of ant activity in this habitat during winter. Finally, the presence of various tree species in restricted parts of this habitat suggests that a number of arboreal ant species not sampled by the methods of the present study may occur.

The steep slope and grassland areas were more similar, both in terms of their vegetation, and in the ant fauna. In floristic and structural terms, the steep slope habitat is the most diverse in the reserve (Werger, 1973), providing wide scope for exploitation by ants. In addition, the shrub layer provides a source of decaying wood for utilisation and inhabitation by ants. The slightly lower ant species numbers of this habitat relative to the grassland areas may be due to the constraints that shallow, stony soils impose upon the construction of nests (Dean & Turner, 1990). Furthermore, it has been suggested that the levels of insolation reaching the ground can affect ant diversity (Donnelly & Giliomee, 1985*a*). The steep slopes receive less insolation per day than the flatter grassland areas and this factor may account for the slightly lower ant diversity recorded in this habitat. In contrast, the bare soil of the grassland is ideal for ant foraging and nest construction, whilst the diversity of vegetation provides food and shelter (Greenslade & Greenslade, 1977).

The grassland ant assemblage consisted of approximately the steep slope ant fauna, upon which were superimposed a set of rare species. Furthermore, the abundance of ants was greater in the grassland habitat than in the steep slope areas. The abundance-based species richness estimators corroborated the observation that ant species richness is higher in the grassland habitat. This indicates that the differences in the ant communities between the habitats are not an artefact caused by the effects of substrate on ant movement.

The most abundant species tended to be widely distributed across habitats. For example, *A. custodiens* and *M. albopilosum* both occurred in all three habitats. In contrast, the rare species were highly restricted in their spatial distribution, generally occurring in one of the three habitats.

Some differences were noted within habitats between sites, indicating the presence of a mosaic distribution of ant communities. For example, *A. steingroeveri*, was the dominant ant in localised areas where *A. custodiens* (the dominant species over larger areas) was absent. In this instance, the patchy distribution appears to be related to soil type, with *A. steingroeveri* dominating on sandier soils. However, competitive interactions are known to occur between these species (Dean, 1992) and the spatial separation noted in the present study may be the result of competitive displacement.

Temporal variation: seasonal differences

It is thought that temperature controls overall temporal patterns in activity through its definition of physiological limits to activity (Andersen, 1983). The activity patterns of *Messor* spp., for example, are thought to be determined to a large degree by temperature (Steinberger *et al.* 1992). However, contrary to these findings and those of Vorster *et al.* (1992), *M. capensis* showed little seasonal preference in the present study, presumably because of the warmer than average conditions over the winter period.

Semi-arid and arid regions are noted for the great ranges in seasonal and daily temperatures. In congruence with this, the site of the present study experienced considerable seasonal and daily fluctuations. The summers are very hot, whilst winter temperatures are frequently very low.

Other abiotic factors such as humidity and light undoubtedly play a role in determining activity patterns (Briese & Macauley, 1980). Low relative humidity and relatively short daylight hours typify winter in the southern Karoo and these factors may partly explain the relative lack of ant activity in winter.

Within the limits to activity set by the climate, a variety of other factors are likely to be responsible in isolation or in combination for the seasonal patterns in the foraging schedules of individual species. For example Whitford & Ettershank (1975) noted that foraging in Chihuahua Desert by harvester ants was primarily controlled by forage availability. Plant productivity is at its lowest during winter and as a result, this period is likely to represent a period of food shortage for many species. Competition and predation are likely to have had some influence in causing the activity patterns observed. However, in the absence of manipulative studies the implication of these factors is speculative.

Marked seasonal differences were noted in the ant communities. Greater abundance and diversity of ants were recorded in summer than winter in keeping with the majority of surveys done at similar latitudes (Andersen, 1983, 1986; Samways, 1990; Swart *et al.*, 1999). Thirty species were more active in summer, whilst only three species were more active in winter. A survey of ants in the arid Lowveld indicated that winter ant activity was considerably greater than that recorded in the present study (Swart *et al.,* 1999). This is likely to be the result of the relatively mild winter conditions typical of the Lowveld.

Few species were responsible for the majority of the individuals trapped in winter, whilst in summer, the abundance of individuals was more evenly spread across the various species. These patterns indicate that relatively few species are able to cope with the extreme conditions of the winter period. Of the species that were recorded in the winter period, many exhibited marked reductions in activity relative to the summer period. In contrast, two species (*M. albopilosum and Pheidole* sp. 1) showed considerably greater activity during winter than during summer. It is possible that the ability of these species to cope with the harsh winter conditions has resulted in a degree of competitive release.

In summer, several species were very abundant, with *A. custodiens* representing by far the most abundant species. Irrespective of the cause, the observed variation in ant species composition between the seasons indicates the presence of a temporal dimension to the ant species mosaic of the area (Samways, 1983).

Diel activity patterns

The present study also revealed pronounced diel patterns in activity. Forty percent of the species recorded in the quadrats were predominantly diurnal, whilst 27% were most active during the night. In Mpumalanga, Swart *et al.* (1999) also found that more species (58%) were mainly diurnal, whilst 42% were mainly nocturnal. Several species are known to change their behaviour from being predominantly nocturnal in summer to being largely diurnal in winter (Briese & Macauley, 1977). This probably explains the greater proportion of diurnal species (69%) noted by Willis *et al.* (1992) at TdR, whose summer data were taken from March, when temperatures are cooler than the months considered here. Bernstein (1979) suggested that the avoidance of simultaneous foraging periods by competing species may have resulted in selection for restricted, non-overlapping foraging times. For example, Dean (1992) suggested that the separate foraging times displayed between *A. custodiens* and *A. steingroeveri* in the southern Karoo was the result of competitive displacement. However, the present study indicated that both species were predominantly diurnal and that if competition does occur between these two species, it is manifested in spatial, not temporal separation.

Sampling methods

Pitfall trapping yielded more species in each habitat and each season than the dig sampling and quadrat sampling. However, pitfall trapping did not record all of the species known to occur in the area and the absence of the common hypogaeic ant

Dorylus helvolus compounds the belief that this method is inadequate for recording hypogaeic ant species. In addition, several species were recorded in the dig sampling and quadrat sampling that were not caught in the pitfall traps. This indicates the importance of using a variety of methods to obtain an adequate impression of the local ant faunae. However, even the intensive use of three different methods failed to record all species known to occur in the area. The pitfall survey and extended searching of Willis *et al.* (1992) yielded 13 species not recorded in the present study, bringing the total number of recorded ant species in the area to 58. Willis *et al.* (1992) conducted his sampling during different times of the year than the present study. The limited temporal extent of sampling in the present study is the likely cause of the failure to sample all of the species known to occur in the area. However, species not recorded were likely to be rare or very localised and in the context of the broader study, which considered the availability of food for the aardvark, the effect of this was not significant.

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