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The efficacy of pitfall traps for determining the structure of a desert ant community

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Pitfall trapping was found to be an unreliable way of determining the structure of a Namib Desert epigaeic ant community. There were considerable intraand interspecific differences in the probability of encountering randomly distributed pitfall traps and in the vulnerability to capture when pitfall traps were encountered.

INTRODUCTION

Various methods for quantifying the structure of epigaeic ant communities have been reported in the literature. These methods are based on colony density (Briese & Macauley 1977; Whitford 1978; Bernstein 1979), censusing ants at baits (Culver 1974; Chew 1977; Davidson 1977), soil-core sampling (Boomsa & De Vries 1980), searching (Room 1975) and pitfall trapping (Muhlenberg et al. 1977; Majer 1978a; Samways 1981, in press). Pitfall trapping is a superior method in that it can be employed with ease on a regular basis to monitor temporal changes in community structure, it can be operated throughout the day and night thereby avoiding problems associated with interspecific differences in activity rhythm and several sites can be sampled concurrently for intersite/habitat comparisons. Furthermore, Samways (in press) found that in the citrus orchards of Nelspruit, South Africa, 'pitfall trapping gave the most individuals, the most species and the most constancy of proportions of ant species in each trap from week to week' when compared with other methods employing sticky traps, nest counting, quadrat sampling and counting by eye per unit time.

The mathematical model of Jansen & Metz (1979) indicates that pitfall trapping should give reliable data on the community structure of epigaeic arthropods, provided the animals move independently according to Brownian motion. This model also makes the implicit assumption that all individuals that encounter pitfall traps are equally vulnerable to capture regardless of species. Alternatively, it should be possible to derive specific correction factors which take into account differences in vulnerability to capture. Certain characteristics of ants, however, suggest that they may not be ideal pitfall trap candidates. All ant species have elaborate social behaviour and many exhibit recruitment responses to food sources such that the movements of foragers are not independent of one another (see Wilson 1971). Furthermore, owing to interspecific differences in size, shape, foraging behaviour and speed of locomotion it seems unlikely that all species within a community will be equally vulnerable to capture.

The purpose of the present investigation was to test the efficacy of pitfall trap-

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ping as a method to obtain reliable data on the structure of a Namib Desert epigaeic ant community. The following two questions were posed: 1) Do foraging workers of the component ant species in the community have the same probability of encountering randomly distributed pitfall traps? 2) Do all individuals that encounter pitfall traps have the same probability of capture?

METHODS

Study site and species

The study was conducted on the gravel plains near Ganab (28° 08′ S; 15° 37′ E) on the eastern edge of the Namib-Naukluft Park. The habitat is a uniform flat plain and was almost devoid of vegetation and litter during the investigation thus facilitating observations. Previous intensive searching using a variety of baits to attract ants revealed that 13 ant species occurred in this habitat. Only eight species were sufficiently common to provide adequate data for this study. Three of the species belong to the genus *Monomorium* which is currently being revised by B. Bolton of the British Museum (Natural History), London, and consequently it is not possible to use specific names. Reference specimens of these species are lodged at the British Museum (Natural History) as follows: *Monomorium* sp. A = M. Namib sp. A; *Monomorium* sp. B = M. Namib sp. B; *Monomorium* sp. C = M. Namib sp. C.

Probability of trap encounter

Most of the surface activity of ants is concerned with foraging and it is during foraging excursions that ants are likely to encounter pitfall traps. Typically, ants leave their nests and travel in one general direction when searcing for food. For example Messor denticornis Forel workers frequently travel up to 60 m from their nest to their foraging sites without deviating more than 10 cm from their path (pers. obs.). Likewise Ocymyrex barbiger Emery foragers regularly travel for 30 m or more in a path which deviates no more than 2 m from a straight course. The foraging behaviour of all the common ant species at Ganab conforms to this general pattern and the direction of leaving a nest is thus indicative of movement in the environment. This behavioural characteristic was therefore used to detect interspecific differences in foraging direction patterns and consequently interspecific differences in the probability of encountering randomly distributed pitfall traps. To avoid localized depletion effects, pitfall trap sample periods should be of limited duration. Majer (1978a) used seven day sample periods whereas Samways (1981) used three day sample periods. Here the foraging direction patterns of individual colonies were plotted over three day periods. Every day, for three consecutive days, the azimuth foraging directions of 20 randomly selected ants from each of 20 marked nests were determined as the ants crossed the circumference of a 50 cm radius circle drawn around the nest entrance. Observations were made during peak activity periods for each species and individual nests were observed at the same time each day. The 20 nests included 4 M. denticornis, 3 Tetramorium rufescens Stitz, 3 T. sericeiventre Emery, 1 Monomorium sp. A, 3 Monomorium sp. B, 2 Monomorium sp. C, 1 O. barbiger and 3 Pheidole tenuinodis Mayr. The Rayleigh test (Batschelet 1981) was used to determine whether the 60 azimuth directions obtained for each nest conformed to a random pattern or exhibited directionality. In one instance, where the foraging directions appeared to be trimodal, Rao's spacing test (Batschelet 1981) was used to test whether the pattern departed from random.

Vulnerability to capture

A pitfall trap was inserted 0.5-1.0 m from the entrance of each of 36 selected nests. The nest included 6 M. denticornis, 5 O. barbiger, 5 T. rufescens, 5 T. sericeiventre, 5 P. tenuinodis, 5 Monomorium sp. A and 5 Monomorium sp. B. The structure and insertion of the pitfall traps was based on the design of Majer (1978b). A pitfall trap comprised a glass test-tube (18×150 mm), inserted into a PVC lined hole in the ground so that the rim was flush with the surface. Each test-tube contained 5 m ℓ ethylene glycol, a preservative commonly used in pitfall traps. Finely grated cheese was placed 0.5 m beyond the traps. The cheese was used as bait to lure ants in the direction of the traps so as to ensure a minimum of 50 encounters per nest per observation period. The response of each individual that encountered a trap was recorded. Individuals carrying bait were not considered in the analysis of the data.

To determine whether capture success was influenced by the type and presence of preservative used or by handling pitfall traps prior to insertion, the following procedure was adopted: One pitfall trap was inserted near each of 16 M. denticornis nests, 12 of these traps were inserted in the normal manner by hand whereas care was taken to ensure that four traps remained untouched. Ethylene glycol was added to four of the handled traps (the control group) and to the four untouched traps. Four traps remained empty and an alcohol-glycerine mixture (used by Majer (1978a) and Samways (1981, in press)) was added to the remaining four. All traps were monitored in the above mentioned manner and a Chi-square test was used to determine whether the capture success of any of the treatment groups differed from that of the control group.

RESULTS

Probability of trap encounter

Of the 20 colonies observed 8 exhibited statistically significant directional foraging patterns (Table 1). Typically M. denticornis travelled for up to 60 m along trunk trails less than 4 cm wide. Between one and three trunk trails were used per nest during any one foraging period. In this species individual trunk trails may be used for up to four weeks before other directions are favoured (pers. obs.). The foraging patterns of P. tenuinodis were variable and appeared to be related to the type and spatial distribution of food being exploited. The two colonies which exhibited directional foraging utilized one trunk trail each and these led to specific grass clumps which harboured honeydew secreting homopterans that were being tended by the ants. These trunk trails were approximately 1 cm wide and 5 m long. Ants from the P. tenuinodis colony which exhibited a random foraging pattern were collecting seed. Foraging patterns were also variable in the two Tetramorium species. Although these two species do not forage along trunk trails they occasionally show strong recruitment responses in which ten or more individuals emerge from the nest in quick succession behind an ant laying a pheromone trail and travel to the same foraging site.

Thus foraging patterns vary quite considerably in this community. Variation exists both within and between species. Whereas foragers from certain nests moved independently the movements of foragers from other nests were not independent of one another. Thus the probability of ants encountering pitfall traps while foraging would vary considerably and would be non-predictive for practical purposes.

Vulnerability to capture

Considerable intraspecific variation in vulnerability to capture was observed and this partially masked any interspecific differences (Table 2). Very few individuals

Table 1. Summary of foraging patterns for 20 nests. Mean vector length (r) ranges from one for a unidirectional pattern to zero for a perfectly random pattern. Angular deviation (s) is measured in radians and is a measure of dispersion equivalent to the standard deviation of linear statistics. The Rayleigh test was used in all cases with one exception (*) where the foraging pattern was trimodal and a Rao's spacing test was more appropriate (Batschelet 1981).

Species	Nest	r	s	Foraging pattern	Significance level
M. denticornis	I	1,000	0	Directional	p < 0,001
M. denticornis	2	1,000	О	Directional	p < 0,001
M. denticornis	3	0,333	66,1	Directional	p < 0,001
M. denticornis *	4	0,341	65,8	Directional	p < 0.050
P. tenuinodis	ī	1,000	o	Directional	p < 0,001
P. tenuinodis	2	1,000	0	Directional	p < 0,001
P. tenuinodis	3	0,140	75, I	Random	NS
T. rufescens	ī	0,327	66,5	Directional	p < 0,001
T. rufescens	2	0,105	76,6	Random	NS
T. rufescens	3	0,094	77,1	Random	NS
T. sericeiventre	I	0,361	64,7	Directional	p < 0,001
T. sericeiventre	2	0,168	73,9	Random	NS
T. sericeiventre	3	0,050	78,9	Random	NS
Monomorium sp. A	ī	0,237	70,8	Random	NS
Monomorium sp. B	I	0,080	77,7	Random	NS
Monomorium sp. B	2	0,070	78,1	Random	NS
Monomorium sp. B	3	0,048	79,0	Random	NS
Monomorium sp. C	I	0,298	67,9	Random	NS
Monomorium sp. C	2	0,120	76,0	Random	NS
O. barbiger	I	0,168	73,9	Random	NS

Table 2. Variation in the number of ants captured by pitfall traps. The data are expressed as percentages of the number of individuals that encountered a trap. N1 represents the total number of individuals that encountered the traps and N2 represents the number of nests from which observations were made.

Species	Ants trapped (%)	Nı	N ₂	
Messor denticornis	I-I2	550	6	
Ocymyrmex barbiger	o-8	270	5	
Tetramorium rufescens	16-79	507	5	
T. sericeiventre	6-47	522	5	
Pheidole tenuinodis	15-72	4 61	5	
Monomorium sp. A	23-81	457	5	
Monomorium sp. B	3-71	341	5	

seemed to be captured by surprise upon first encountering a pitfall trap. Most paused at the trap lip and sensed the air with their antennae before further movement. This behaviour suggested that the preservative or human odour on the test-tubes may have been influencing the ants. The tests on *M. denticornis*, however, indicated that there

were no detectable differences in behaviour at traps whether they were empty, contained ethylene glycol, an alcohol-glycerine mixture or whether they had been touched or not (p > 0,2) for all treatment groups).

Having paused at the trap lip many individuals moved around it and continued on their journey. In one instance most individuals from a *M. denticornis* nest consistently avoided the pitfall trap by deviating from their path when about 2 cm from the trap, by-passing the trap and then returning to their original path. This behaviour suggests that a pheromone trail had been laid around the trap.

Many ants, particularly the relatively large species such as *M. denticornis* and *O. barbiger*, partially entered the traps, by maintaining contact with the trap lip via their meta-thoracic tarsal claws and dangling the remainder of their body in the trap, before resuming their journey. Other ants, particularly the smaller species, entered the traps and walked about on the vertical glass walls. Many of these individuals reemerged to continue their journey while others fell or were blown into the preservative as they reappeared at the trap lip.

DISCUSSION

The two simple experiments documented in this paper indicated that the major assumptions underlying the use of pitfall trap data to describe community structure were invalid for this Namib Desert ant community. Furthermore, in view of the large intraspecific variation in vulnerability to capture and probability of trap encounter it was not possible to derive correction factors which adequately took into account interspecific differences in trapability. In contrast, at Nelspruit relatively constant proportions of ant species were obtained in each trap through time implying that intraspecific variation in capture success is slight (Samways, in press), however, no data on intertrap comparisons in each habitat was presented. Although it is possible that pitfall trapping may be a more reliable way of obtaining data to describe ant community structure in areas other than the Namib Desert, it is prudent to test the efficacy of the technique before initiating large scale trapping programmes. In view of the possibility of selective trapping it seems unwise to place much reliance on pitfall trapping for obtaining measurements of single communities unless the response of all species to pitfall traps is known and predictable. Similar observations about the reliance of pitfall traps for invertebrates in general have been made by Southwood (1978) and Koch & Majer (1980). Pitfall trapping remains a useful method for interhabitat comparisons (e.g. Muhlenberg et al. 1977; Majer 1978a; Samways 1981, in press) provided intraspecific variation in vulnerability to capture is minimal.

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