

Behavioral Strategies Used by *Macrotermes michaelseni* foragers to Avoid Ant Predation (Isoptera: Macrotermitinae)

by

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ABSTRACT

Macrotermes michaelseni, a dominant invertebrate herbivore in the semi-arid savanna of Kajiado, Kenya, was studied to establish what measures its foragers adopt to counteract ant predation while insuring adequate collection of food. Termites foraged under cover where possible. They kept foraging groups small. Distances travelled outside permanent structures were short. Finally soldiers functioned to guard foragers and entrances to foraging holes.

INTRODUCTION

A basic constraint in a central place foraging strategy (Bailey & Polis 1987) is that a successful forager is hampered by the food it carries in defending itself from a predator. The foragers' urgent need is to travel as quickly as possible to safety. The relatively soft cuticle of termites limits foraging activity to times when humidity is high such as at night or during dull and damp weather (Lepage 1981a). A further constraint, making an almost random search necessary, is the distribution of food items. There is, therefore, a constant threat of death during foraging, particularly from predatory ants, some of which have become specialized for a termite diet. Kaib (1985) emphasized that termite defense strategies have evolved mainly to counteract ant predation.

The present study was undertaken in the semi-arid savanna of Kajiado, Kenya, where *Macrotermes michaelseni* (Sjöstedt) is a common mound building termite. *M. michaelseni* forages mainly on dead grass during the night (Lepage 1981b). It constructs subterranean nests with conspicuous epigeal mounds and radial subterranean galleries extending up to 50m from the nest

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(Darlington 1982a). Termites travel along these galleries and emerge via foraging holes, of which there are 22,000–50,000 per colony (Lepage 1981b). Only a few of these holes are used in any 1 night. The area covered by foragers during 1 night varies from 133 to 552m² (Lepage 1981b). The subterranean galleries which terminate at these holes total up to 6km in length (Darlington 1982a). From the holes, foragers travel short distances above ground to gather food either in the open or under temporary surface galleries. Stuart (1967) suggested that most termite building activities are defensive in nature. The concern here is to understand how their various behavioral adaptations protect them from excessive predation.

MATERIALS AND METHODS

M. michaelseni forages either in the open where food (e.g. grass litter) is gathered outside protective earthen structures, or under cover where the food (e.g. dung pats) is completely or partially buried and its removal goes on with the forager unexposed. To investigate the size and composition of under cover foraging parties, 61 dung pats with termites were collected, 30 during the day and 31 during the night. The pats were quickly lifted and placed in plastic containers. The foraging termites were then sorted and counted in the laboratory. Open air foraging occurs only at night. A 1m² quadrat was placed on a foraging area at night (about 20:00 hr) where surface galleries were plentiful. The area enclosed by the quadrat was quickly swept with a soft broom and all the contents (termites, litter, soil) were collected in plastic containers and taken to the laboratory for sorting. Six samples were obtained in this way.

Twenty-eight foraging holes were examined at night by electric torch light. The numbers of each caste of soldiers guarding the entrances were recorded. The lengths of 72 surface galleries were measured using a tape measure.

RESULTS

The sizes of the under cover foraging parties are distributed as in Table 1. None had less than 50 nor more than 500 individuals. About 70% had less than 200 individuals. They included both major and minor soldiers and workers. The caste distribution (Table 2) was similar in all cases, with major workers most abundant followed by minor soldiers. There was no significant difference

Table 1. *M. michaelseni* foraging party sizes (dung pat samples).

Number of foragers in group	Number of groups of that size	Percent of total groups
0- 50	0	0.0
51-100	33	54.1
101-200	12	19.7
201-300	9	14.8
301-400	4	6.6
401-500	3	4.9
>500	0	0.0
Total	61	100.1

Table 2. Caste composition of foraging parties of *M. michaelseni* sampled either from dung pats of 1m² quadrats.

Caste	Mean number of foragers per sample		
	Under cover		Open air
	Day	Night	Night
	No. (%)	No. (%)	No. (%)
Major workers	116.5 (82.6)	97.5 (87.1)	84.0 (68.4)
Minor workers	10.0 (7.1)	0.8 (0.7)	1.3 (1.1)
Major soldiers	1.1 (0.8)	1.9 (1.7)	0.5 (0.4)
Minor soldiers	13.4 (9.5)	11.8 (10.5)	37.0 (30.1)
N	30	31	6
Ratio of workers to soldiers	8.7	7.2	2.3

between day time and night time under cover foraging parties in ratios of workers (major and minor) to soldiers (major and minor). However, the ratio of minor to major workers was greater during the day ($\chi^2=5.99$, $P<0.05$). There were significantly more soldiers in the open air than in the under cover foraging parties ($\chi^2=21.4$, $P<0.001$). In dung pats at least, the number of soldiers is strongly correlated with the total number of termites in the foraging party ($r=0.94$, $P<0.005$).

The entrances to the foraging holes were guarded by soldiers. Three major and 40 minor soldiers were recorded from the 28 holes examined (average 1.5 soldiers/hole). None of the holes

Table 3. Length of surface foraging galleries of *M. michaelsoni*.

Length of gallery (cm)	Number	Percentage
1- 5	2	2.8
6-10	15	20.8
11-15	24	33.3
16-20	16	22.2
21-25	5	6.9
26-30	6	8.3
31-35	2	2.8
>35	2	2.8
Total	72	99.9

Mean length of gallery \pm S.E. = 17.5 \pm 7.8 cm

were unguarded.

The mean length of the surface galleries was 17.5cm with 79% less than 20cm (Table 3). These galleries were sometimes completely covered and sometimes partially open at the top. They were temporary structures whose role may be partly protective but also partly for enhancing homing speed by the concentration of pheromone trails.

DISCUSSION

M. michaelsoni is an important invertebrate herbivore in the savanna grasslands of Kenya (Darlington 1982b), feeding mainly on dead vegetal matter. In Kajiado, they are also important in the removal of the plentiful dung of both domestic and wild mammalian herbivores. Termites are central place foragers (Oster & Wilson 1978) and during foraging predation is a major risk. The major predators of *M. michaelsoni* are ants and in Kajiado, *Megaponera foetans* (F.) is especially important (Nyamasyo & Khamala in prep.). The termites seem to have a number of adaptations facilitating food gathering while minimizing loss due to ant predation.

Under cover foraging is used to obtain food existing in large discrete patches (e.g. dung pats) while open air foraging is necessary when small items of food (e.g. grass litter) are scattered and demand random foraging. Open air foraging is practiced only at night. Risk of desiccation is probably too great during the day.

Open air foragers are probably more at risk from predators.

Strategies countering ant predation were: (i) Foraging groups were small so that in case a whole foraging party was successfully preyed upon the loss to the colony, whose population may number over 1.3 million individuals (Darlington 1982b), would be negligible. (ii) The distances travelled beyond permanent galleries were small. Abe (1982) estimated that the distance travelled by foragers totally exposed was 15cm. Mean length of the surface galleries was 17.5cm; so that the total distance travelled beyond the foraging hole would be 32.5cm. (iii) Soldiers were always present among the foragers. Where the risk from predation was high (open air foraging), the proportion of soldiers was also high.

Minor soldiers predominated among soldiers protecting foraging parties and among those guarding the entrances to the foraging holes. The role of major soldiers is not clear. Lepage (1981b) speculated that they remained within protective structures and only emerged on the surface in case of an attack. The observations here showed that minor soldiers accompanied workers during foraging while major soldiers remained within permanent galleries. It is possible that after an attack, very few foragers actually succeed in escaping into the foraging holes. Since the ants do not pursue the termites past the entrances to the foraging holes, the defensive role of the major soldiers is not certain.

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