CHAPTER ONE

Termite raiding behaviour of *Pachycondyla analis* at Mpala, a Kenyan savannah

Abstract

Predation on termites of the subfamily Macrotermitinae by the ant *Pachycondyla analis* was studied over a period of six months (April-September 2007) at Mpala, a semiarid savannah in central Kenya. A total of 37 nests of *P. analis* were studied and 330 raids were observed and recorded. There were 17.0 nests/ha, with most nests located under rocks. There were two peaks of raiding activity; one in the morning and the other in the evening. Foraging parties travelled a distance ranging from 0.7 m to 39.8 m, with speeds of outward journeys being slower than those of return journeys (6.70 cms^{-1} and 13.03 cms^{-1} respectively). Larger foraging parties spent more time and carried more termites than smaller ones. *Microtermes* spp. was the most frequently preyed upon termite species (66.0%), followed by *Odontotermes* spp. with a prey frequency of 34.0%. Ants spent more time during raids on *Microtermes* than during raids on *Odontotermes*. The results here indicate that prey choice by *P. analis* is not only based on the abundance of prey but also on the costs of foraging, which was influenced by prey defences, size and foraging behaviour.

Introduction

Ants are among the greatest enemies of termites in all regions of the world (Deligne *et al.*, 1981; Hölldobler and Wilson, 1990). They share the same habitats and are extremely abundant in terms of biomass and density (Fujiwara-Tsujii *et al.*, 2006). Predation by ants is thought to have favoured the development of a soldier caste specialised both in chemical and physical defence systems within termite colonies (Waller and LaFage, 1987). According to Hölldobler and Wilson (1990), during their 100 million years of coexistence, ants and termites have engaged in a co-evolutionary arms race, with ants evolving several predatory tactics while termites have responded with defensive strategies. In ants, the most specialised predatory species are concentrated in the morphologically primitive sub-families Ponerinae and Myrmicinae (Lévieux, 1966; Longhurst *et al.*, 1978, Longhurst *et al.*, 1979; Maschwitz and Schönegge, 1983; Lepage 1981; Corbara and Dejean, 2000).

Group raiding strategies are considered to be more advanced than solitary foraging because they involve cooperative behaviours among workers and enable the capture of large prey and hence energy saving (Corbara and Dejean, 2000).

The African poneromorp ant, *Pachycondyla analis* (Latreille) (formerly *Megaponera foetens* Fabr.), is widespread and relatively common throughout most of sub-Saharan Africa. The recorded average number of workers in a colony ranges from 400 in one locality (Lévieux, 1966) to 1475 in another (Lepage, 1981). Group predatory behaviour of the species was first described by Livingstone (1857) and became the focus of several subsequent studies (Wheeler 1936, Hölldobler and Wilson, 1990). The ant feeds exclusively on termites, mainly Macrotermitinae. Scout ants that detect a termite source lay scent trails directly back to their nests (Longhurst *et al.*, 1978; Longhurst *et al.*, 1979; Hölldobler *et al.*, 1994; Janssen *et al.*, 1995). Once in the nest, a scout recruits between 22 and 840 nestmates and guides the column back to the prey by following the trail. Both major and minor workers of *P. analis* take part in the raids (Crewe *et al.*, 1984; Villet, 1990). On arrival at a termite source, major worker ants break open termite galleries and the minor workers invade the galleries (Figure 1.1). Those that capture termites, sting them, carry them out of the galleries and place them near the gallery entrance, and then return to continue hunting. Piles of paralysed termites grow at the entrance. After about 13-20 minutes, the workers stop hunting and return to the pile of paralysed termites. Major workers grasp 1-7 termites between their mandibles, while minors grasp 1-3 termites. Some do not carry any termites, but lead columns of ants loaded with prey back to their nest (Longhurst *et al.*, 1978).

Figure 1.1 *Pachycondyla analis* during a raid on a termite source at Mpala, Kenya.

The raiding patterns and dynamics of *P. analis* as well as the effects of termite defences, prey size (reward) and abundance of termites on the raiding behaviour of *P. analis* at Mpala, Kenya is reported here. This was aimed at obtaining background information that will be used in understanding the chemical ecological interactions between *P. analis* and its termite preys.

Materials and methods

Study site

This study was conducted at Mpala (0°17’N, 37°52’E), on the research facility of Mpala Wild Life Foundation. Mpala is located in Laikipia district, Central Kenya 250 km north of Nairobi and about 50 km from the equator and 50 km north-west of Nanyuki (Figure 1.2). The northern two-thirds of Mpala is underlain by dissected Archean terrain with

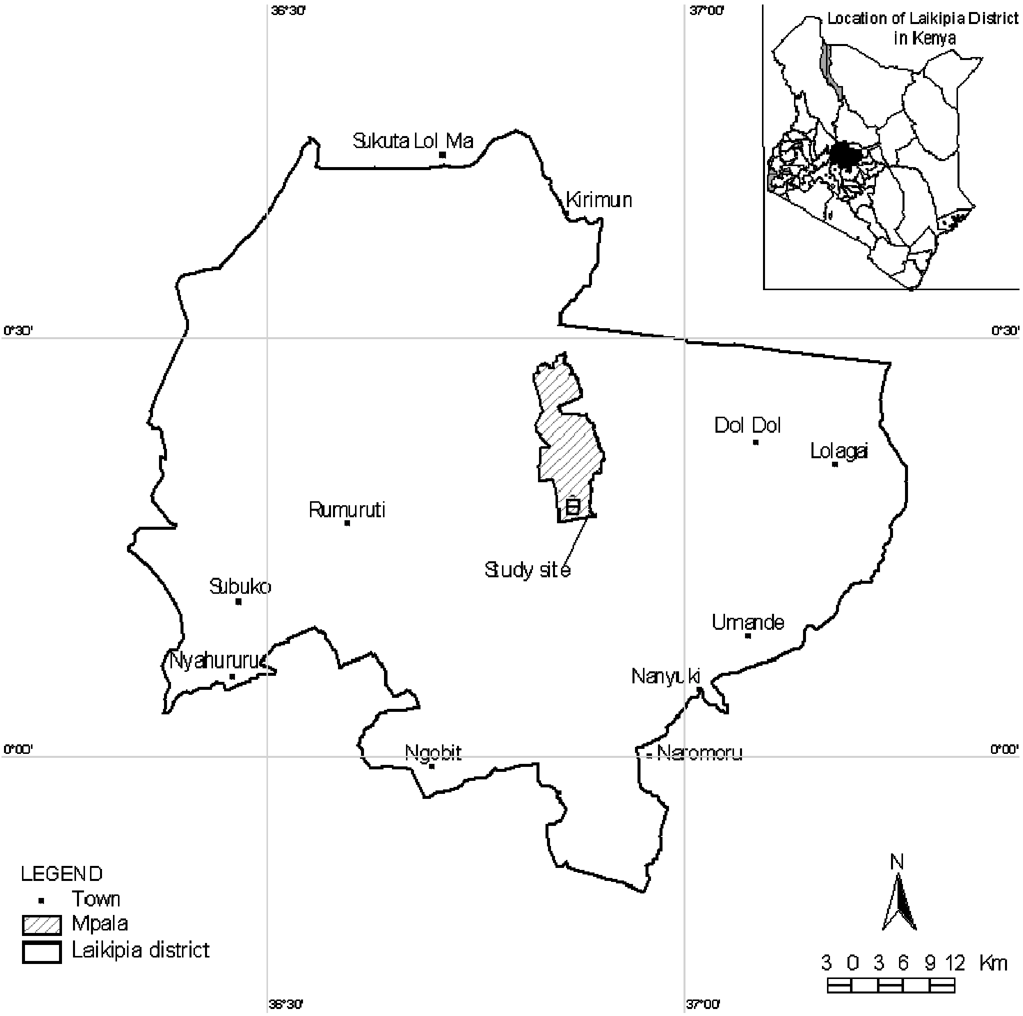


Figure 1.2 Map of Laikipia showing the study site (site) at Mpala research centre. Insert Map showing the location of Laikipia in Kenya).

thin dark red sandy loams (latosols). The southwestern one-third of Mpala is characterised by a 100m high phonolite lava flow. Soils developed on the flow consist of a catena of black clay vertisols with impeded drainage, with brown calcareous loams (chestnut soils) on the higher elevations and steeper slopes. Warm days and cool nights are predominant at Mpala, with very low humidity in the driest season (January-April), and moderate humidity at other times. Rainfall is weakly trimodal, with peaks in April-May, July-August, and October-November, and a distinct dry season in January-February.

Nest location, distribution and density

Nests of *P. analis* were located using three different approaches (Longhurst *et al.*, 1978; Bayliss and Fielding, 2002; Marcus Stüben; personal communication). These included following ants returning from raids, following scout ants, and looking for pupal cases, termite body fragments, or dead ants near likely nest sites. Nest density was calculated using standard methods (Lepage 1984; Bayliss and Fielding 2002; Diehl *et al.*, 2005). Eight quadrats (50 m x 50 m each) were set randomly within the study area, and the number of nests were counted and expressed as nests per hectare.

Foraging parties

To monitor morning (07.00-11.00hrs) and evening (16.00-19.30hrs) raids, nests were selected opportunistically from each of the eight quadrats. Ant colonies were also monitored for late evening raids between 2200-2400hrs. The monitoring periods were based on prior observations for 14 days of raiding behaviour. Raiding behaviour was monitored daily throughout the study period (April – September).

The number of ants in a raiding column, those carrying termites, and, number of termites carried per ant in a random sample of 10 ants from each raiding column were counted. Ants setting out on a raid were counted one after another if there were less than about 200 in the group. Where there were more than 200 ants, the number was estimated in groups of 10. The number of ants carrying termites was also recorded in the same way. The number of termites carried per ant was determined by carefully grabbing the ants by the thorax using entomological forceps. That triggered the ant to attack the forceps and release the termites. Termites were identified to the generic level by their caste information as outlined in Pearce *et al.* (1996). The number of injured ants during raids was also determined for each raid by counting the numbers of injured ants carried back to the nest by nestmates. Duration of the different phases in a raid (outward journey to termite source, time spent at termite source and time spent on return journeys to nest) was determined for each raid. Foraging distance (m) for each raid was measured. Ground temperatures at departure from ant nests for raids were recorded for each raiding column. Mean rainfall was also recorded for each month during the study period.

Foraging velocity

The foraging velocity was calculated using the time an ant took to travel a distance of 50 cm. This was repeated fourteen times on the outward and return journeys for randomly selected foraging parties with ants selected at random. Measurements were taken from ants travelling in the main body of the column as the activities of ants on the periphery showed a high level of variation. If an ant stopped during the timing period the record was discarded. These measurements were carried out on open ground to eliminate the effect of variable amounts of litter.

Predation

Predation rate was calculated for each month based on the number of termites taken per nest per day using the equation of Lepage (1981) as modified by Bayliss and Fielding (2002):

$$P = F \times T \times R \times N \times t$$

Where;

P= Termites predated per nest per day

F= Average number of ants carrying termites of that species per raid

T= Average number of termites per ant per calendar month

R= Average number of raids per day per nest per calendar month

N= Number of ant nests per hectare

t= Average duration of raid per calendar month

Predation was also analysed in relation to the abundance of termite genus in the field by comparing the frequency of raids on a given termite species in relation to their abundance within the study quadrats. Termite abundance was estimated in September using a modification of the Jones *et al.* (2003) method. Transects were set up within the same quadrats used to study *P. analis* raids on termites. Each termite transect was 50 m long × 2 m wide, and divided into 10 contiguous numbered sections (each 5 m × 2 m). Two collectors spent 30 minutes each per section. In each section the collectors searched the following microhabitats which are common sites for termites: surface soil to 5 cm depth; accumulations of litter and humus at the base of trees; the inside of dead logs, tree stumps, branches and twigs; the soil within and beneath very rotten logs; all subterranean nests, mounds, carton sheeting and runways on vegetation, arboreal nests up to a height of 2 m above-ground level and animal dung. The protocol was designed to offer a flexible approach to sampling, whereby the collectors used their experience and judgment to search for, locate, and sample as many species of termites in each section as time allowed. Specimens from each termite population encountered were collected, identified to generic level and sent to the National Museum of Kenya (NMK) Nairobi for confirmation. Voucher specimens were also deposited at the NMK. All castes were collected if present, but priority was given to soldiers and workers. Termites were placed in vials labelled with the section number and identified afterwards. This transect sampling method provided a semi-quantitative measure of the relative abundance of termites based on the number of encounters or 'hits' with each species within a transect (Jones *et al*., 2003).

Statistical analysis

The Mann Whitney U (MWU) test and Student’s t-test were used to test for differences between morning and evening activities. Additionally Kruskal Wallis ANOVA (KWA) was used to test for differences in the raiding behaviour (duration of preying at the food source, those of outward and return journeys to and from food source) with respect to the prey species and time of the day. MWU tests were performed for pairwise comparisons. MWU statistics were also applied to test for differences in the efficiency of the ants preying on different termite species, with prey species being the independent variable. The ratio of ants carrying termites to the total raid size, number of termites carried per ant, number of termites per meter distance travelled, number of termites per minute travelled, or the number of injured ant workers carried back was the dependent variables. Only raids in which the prey was fully identified were used in the analyses. Spearman rank correlation was used to test the correlation between raiding party size, rainfall, number of termites taken, and months of study. Chi square (χ^2) tests were performed to compare the predation rates on the two genera of termites during the different months and to the data on prey abundance. All statistical analyses were performed using SAS (9.1) statistical package and at an α level of 0.05.

Results

During the study period in 2007, the month of June which was characterised by low rainfall in previous years, had the highest rainfall (mm): (Mpala Station Records: April, 86; May, 36.4; June, 152.2, July, 80.4; August, 34.9; September, 98.4).

Nest location, distribution and density

A total of 37 nests were located within the sampled quadrats. With regard to the location of the 37 nests, 43% were under rocks, 30% were in old termite mounds, 16% were under trees and 11% were in an open field (Figure 1.3, and 1.4). The distance between the nests ranged from 1.7 m to 29.7 m (Figure 1.5). Mean number of nests per quadrat was 4.25 ± 2.71 which is equivalent to ~17 nests per hectare.

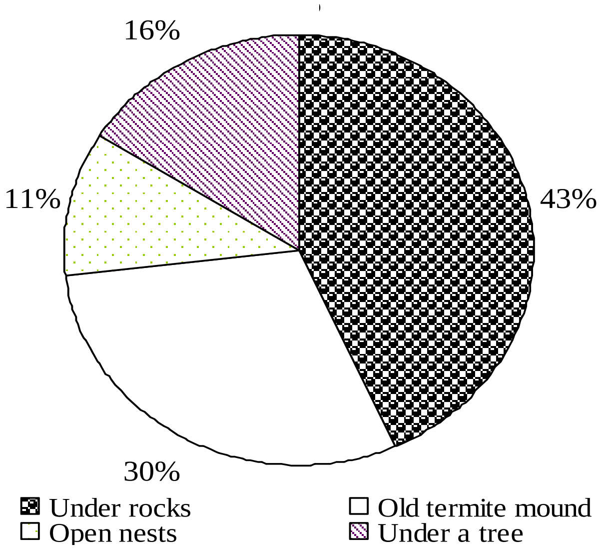


Figure 1.3 Distribution of *Pachycondyla analis* nests in the study area.

Foraging parties

There were 330 raids recorded from the 37 nests. Of these 56% occurred in the morning (0700-1100hrs), 42% in the evening (1600-1930hrs), and 2% were nocturnal (2000-2400hrs). The temperature at which raiding parties of ants departed from the nest to a

Figure 1.4.Nesting habitats of *Pachycondyla analis* at Mpala, Kenya. (A) nest under a rock, (B) nest under a tree, (C) nest in a deserted termite mound and, (D) an open field nest.

termite source was 23.1°C ± 0.21 (range: 17.8°C – 36.4°C). Ants took the same foraging path and direction regularly as long as the supply of termites was abundant. However, with diminishing supply of prey; the ants either changed the foraging direction or divided themselves into smaller foraging parties going in different directions.

The mean number of ants in a raiding party, the number carrying termites, and the total number of termites taken per raiding party varied between months (Figure 1.6). The size of the raiding parties increased significantly during the observation period (Spearman Rank correlation: r = 0.315, $P < 0.01$). The total number of termites taken per raiding party was not significantly different among the different months. However the percentage of ants carrying termites within a raiding party was significantly different and was highest from June to August (Kruskal Wallis ANOVA, $\chi^2 = 23.03$, $df = 5$, $P < 0.001$, Figure 1.7). The number of termites carried per ant was also significantly different (overall mean 2.69 ± 1.21; KWA $\chi^2 = 47.77$ $df = 5$, $P < 0.001$), peaking in July and falling to April levels by September. The raiding behaviour seems not to be affected by the amount of rainfall, because the number of termites taken (Spearman Rank correlation: r = 0.105, n.s.) and the size of the raiding party (Spearman Rank correlation: r = 0.107, n.s.) did not correlate significantly with rainfall.

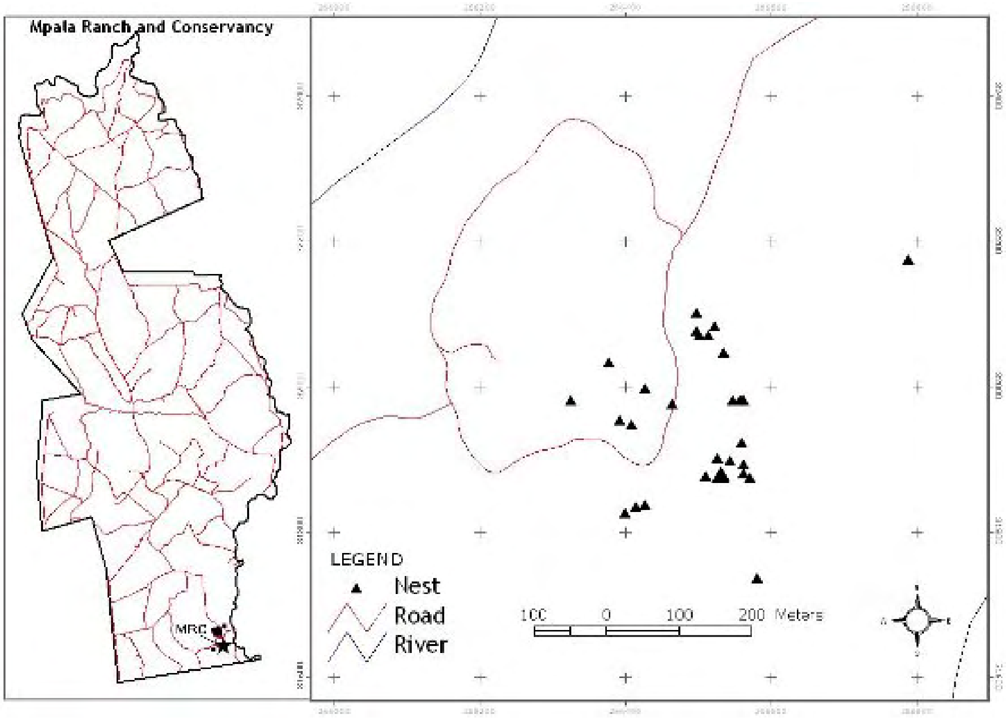


Figure 1.5 Map of Mpala Ranch and Conservancy showing the location of *P. analis* nests within the study area (Mpala Research Centre).

The mean number of ants per raid was significantly higher in the morning than in the evening (t = 2.48, *P* = 0.01, *df* = 323, Figure 1.8). The mean number of ants carrying termites during morning and evening raids was not significantly different (*t* = 1.88, *P* = 0.06, *df* = 309, Figure 1.8) nor was the number of termites carried per raiding party (t = 1.04, *P* = 0.29, *df* = 293) (Figure 1.8).

The foraging distances were longer in the morning than in evening raids, in May, August and September, but the reverse was the case for April, June and July (Table 1.1). The number of termites taken and the size of the raiding party were positively correlated with distance (Spearman rank correlation: party size, r = 0.38, *P* < 0.001, termites taken: r = 0.4, *P* < 0.001).

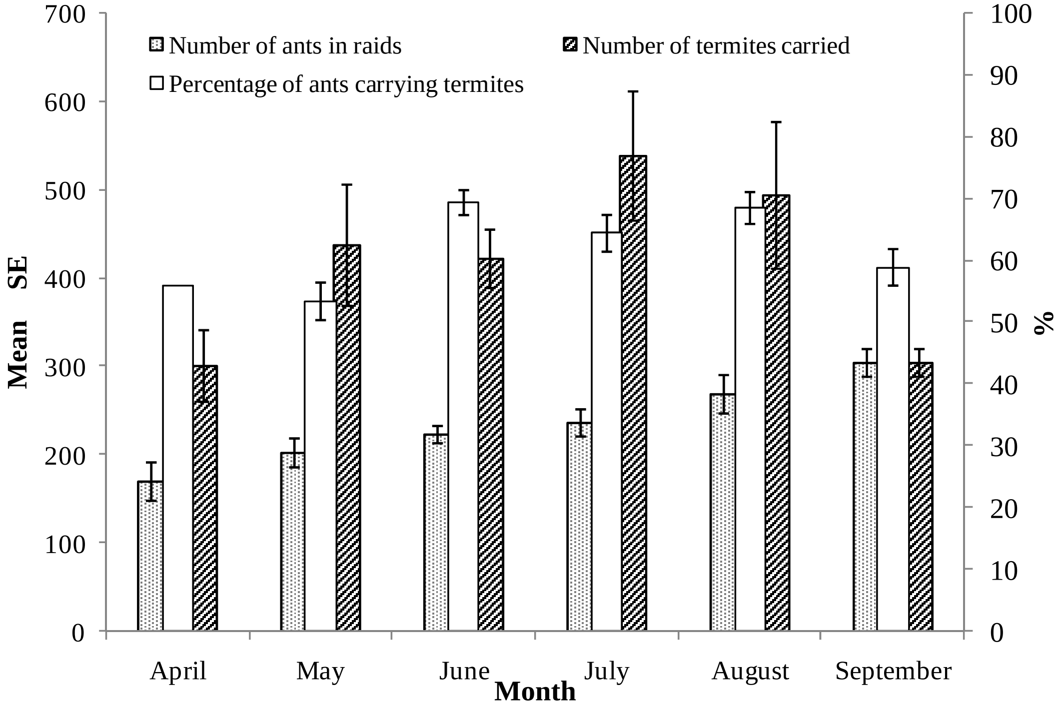


Figure 1.6 Mean numbers (± SE) of ants in a raiding group, percentage of ants carrying termites and number of termites carried.

Duration of raids

The total time spent by foraging parties on a raid ranged between 4 to 99 minutes and the duration of outward journeys (journey to termite sources) was as short as 1 minute and could last up to 35 minutes. Actual time spent in attacking termites at their nest (duration at termite colony) ranged from 2 to 69 minutes and the return journeys took between 1 to 29 minutes. The number of termites taken positively correlated with the time spent at the termite source; the longer the ants stayed at the termite source, the greater was the number of prey captured (spearman rank correlations: r = 0.252 *P* = 0.001).

There were no significant differences in duration of the outgoing or return journey between termite genera raided (KWA: outgoing: $\chi^2 = 3.8$, n.s.; return: $\chi^2 = 6.7$, n.s. Figure 1.8), but there was a significant difference in the length of time spent at the food source (KWA: staying: $\chi^2 = 3.8$, $P < 0.05$). The ants spent significantly more time at the *Microtermes* sites than at the *Odontotermes* ones (MWU: Z = -2.2, $P < 0.03$, Figure 1.8).

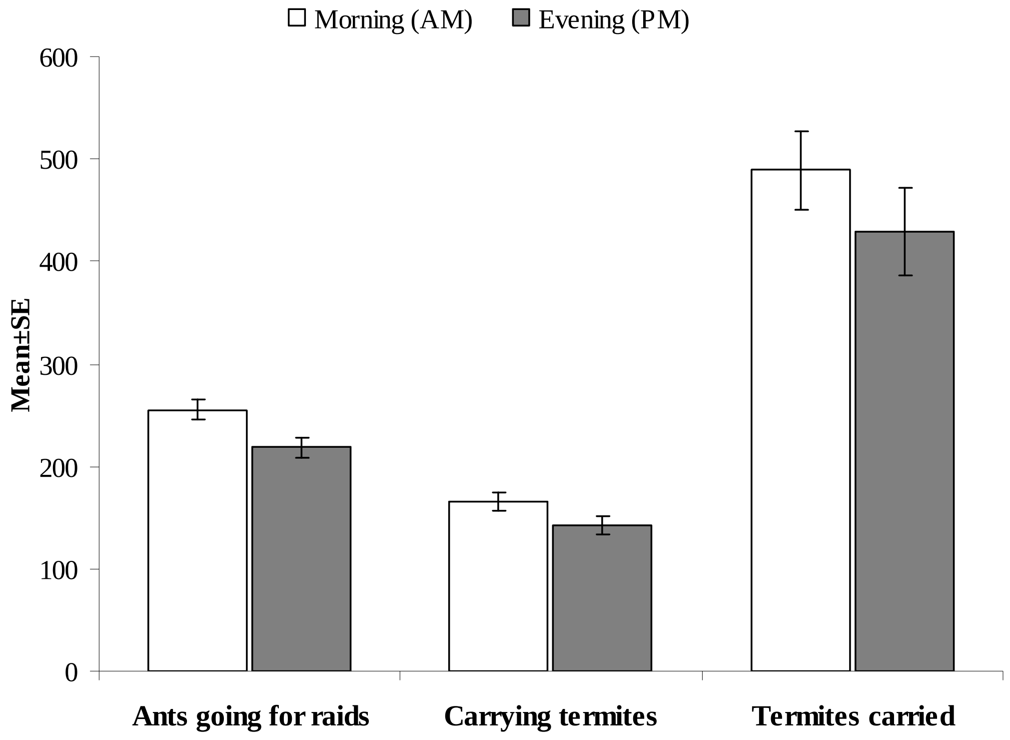


Figure 1.7 Mean numbers (± SE) of ants going on raids, carrying termites and termites carried in morning and evening raids at Mpala. White bars = morning, grey bars = evening

Foraging velocity

Speeds for outward journeys from ants nests were between 3.21 cms^{-1} and 11.06 cms^{-1} (mean = 6.70 ± 2.3 cms^{-1}). Return journeys (mean = 13.03 ± 6.4 cms^{-1}) were significantly faster than outward journeys (MWU: Z = -2.9, $P < 0.003$, n = 28), with a minimum of 3.72 cms^{-1} and a maximum of 22.83 cms^{-1}.

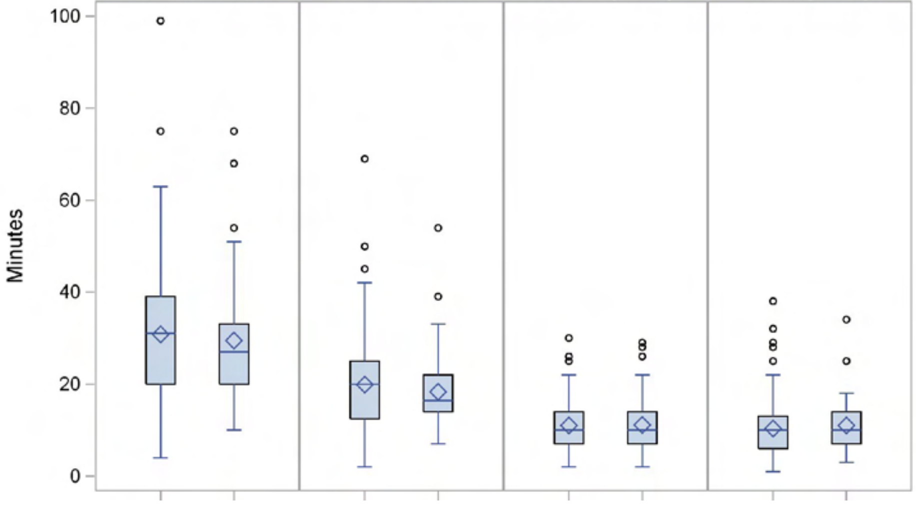
Table 1.1 Number of raids (N), minimum, maximum and mean (± SD) of foraging distances of *P. analis* raiding parties at Mpala between months and time of raids (mornings and evenings). Means were separated using Student-Newman-Keuls (SNK). Means in the same column followed by same letters are not significantly different (α = 95%).

		Foraging distance (m)			
Month	**Period of the day**	***N***	**Min**	**Max**	**Mean ± SD**
April	Morning	3	3.7	10.7	6.6 ± 2.2a
	Evening	15	2.4	29.9	11.1 ± 1.8b
May	Morning	27	2.5	25.6	10.9 ± 1.2a
	Evening	35	1.9	29.6	10.1 ± 0.9b
June	Morning	40	1.5	26.5	9.3 ± 0.6a
	Evening	20	3.4	26.3	11.1 ± 1.1b
July	Morning	49	1.6	39.8	11.4 ± 2.7a
	Evening	18	4.2	31.0	13.6 ± 0.8b
August	Morning	43	0.7	38.2	13.4 ± 1.4a
	Evening	19	1.1	17.3	9.5 ± 1.0b
September	Morning	38	4.5	39.7	12.1 ± 1.0a
	Evening	18	5.2	32.9	11.5 ± 1.6b

Note: Five late night (nocturnal) raids observed in April were not included in the table because it was difficult collecting data from those raids when they occurred.

Predation

P. analis was only observed to prey on two genera of termites at Mpala during the study period. Of the 330 raids, it was only possible to identify prey for 237 raids. *Microtermes* was targeted on average in 66% of these raids and *Odontotermes* in 34%. The latter was more preyed on in April and August (75% and 59%), while *Microtermes* was the main prey in subsequent months (69%, 74%, 75% and 70% respectively).



(B) Evening Raids

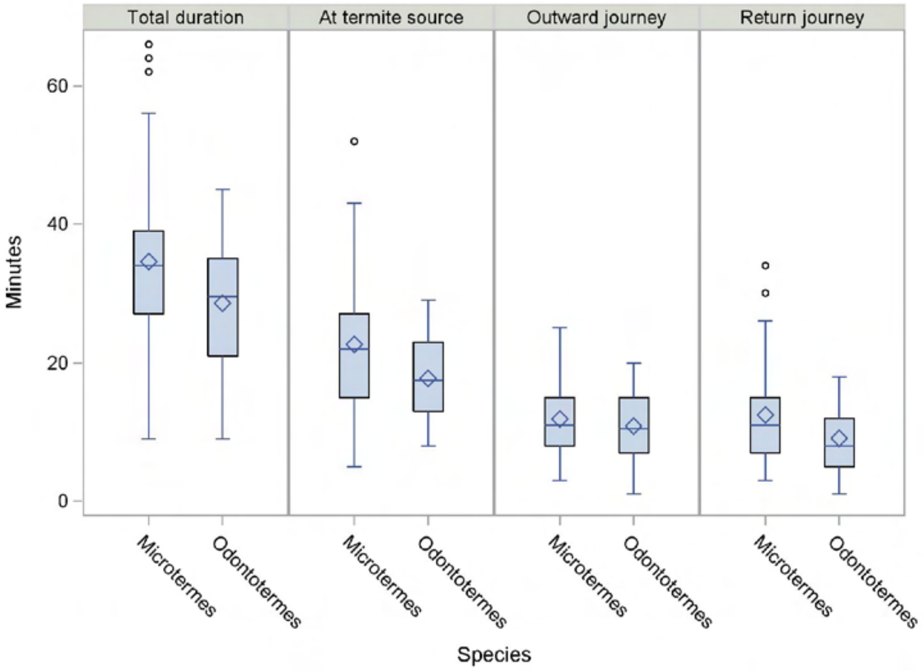


Figure 1.8 Total duration of raids, outward journey, time spent at termite colonies, return journey from raids for (A) morning and (B) evening raids for the two termite genera preyed upon by *P. analis* at Mpala. Circles represent outliers, squares represents the median, middle lines represent the mean, while lower and upper lines represents the 1st and 3rd quartiles respectively.

The average abundance (81%) of *Microtermes* was higher, based on transects surveys in the field compared to the observed prey frequency by *P. analis* (70%) in September (n = 21). However, when comparing the predation rate on the two species for each month relative to their abundance, the ants were preying significantly more often on *Microtermes* in June ($\chi^2 = 4.9$, $P < 0.05$) and more on *Odontotermes* in August ($\chi^2 = 8.14$, $P < 0.01$; Figure 1.9).

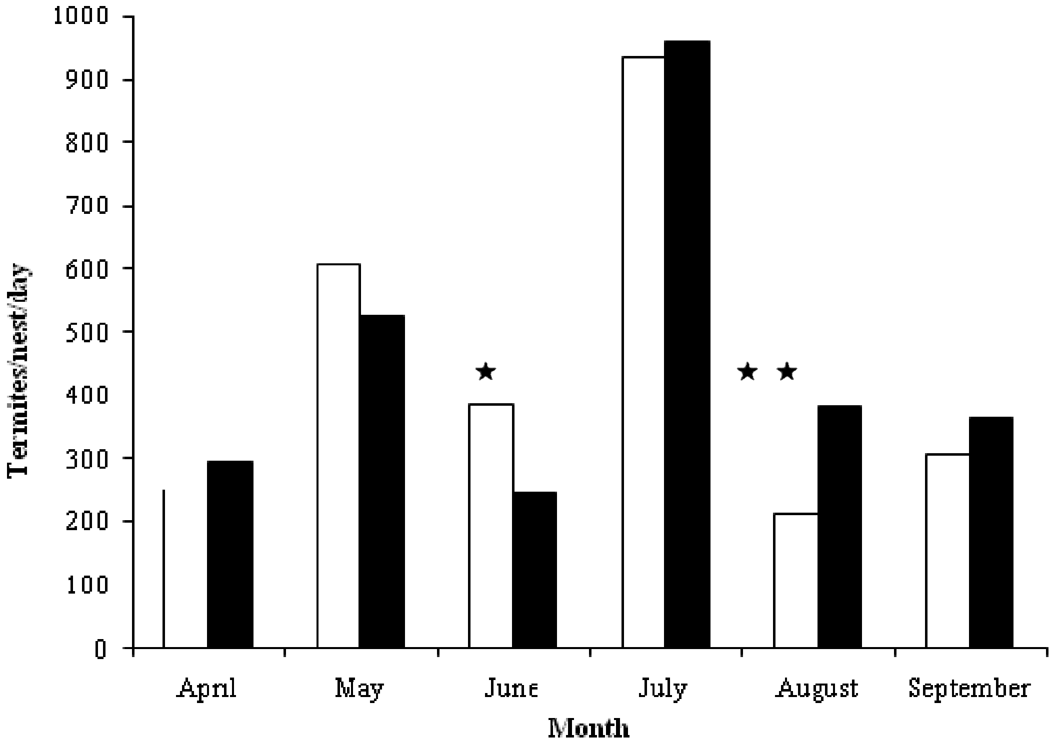


Figure 1.9 Monthly predation rates by *P. analis* based on termite genera prey captures. White bars represents predation rates on *Microtermes* and black bars represent predation rates on *Odontotermes*. χ^2- test, * significant at $P < 0.05$ and ** significant at $P < 0.01$.

Overall, the percentage of ants carrying termites (64.62 ± 22.03 for *Microtermes*; 64.25 ± 20.08 for *Odontotermes*) and the total number of ants in the raiding party (259 ± 138.25 for *Microtermes*; 260.60 ± 142.29 for *Odontotermes*) was not significantly different between prey species (MWU: Z = -0.16, n.s.). Similarly, no significant differences were recorded when comparing the termites carried per ant (2.59 ± 1.29 for

Microtermes; 2.89 ± 1.16 for *Odontotermes*) (MWU: Z = -0.89, n.s.) and the termites carried per meter (43.30 ± 35.02 *Microtermes;* 52.16 ± 54.26 for *Odontotermes*) or per minute (25.39 ± 24.74 for *Microtermes*; 34.02 ± 44.09 for *Odontotermes*) (MWU: per meter: Z = -0.55, n.s., per min: Z = -1.79, n.s.) as measures of predator efficiency. However, significantly more injured workers (see Appendix I-ii) were carried back when preying on *Odontotermes* spp. (2.25 ± 2.71) compared to (1.63 ± 2.18) *Microtermes* spp. (MWU: Z = -2.2, $P < 0.03$).

Discussion

The thirty seven nests of *P. analis* encountered in this study were found in various nesting places. Most nests were under rocks and in old abandoned termite mounds. Studies in other localities have indicated a preference for sites that are provided by the particular habitat. Thus *P. analis* at Mpala exhibits a different nesting pattern than observed in the Tanzanian coastal dry forest (Bayliss and Fielding, 2002) and the Nigerian savannah region (Longhurst and Howse 1979). These nesting patterns at Mpala could have advantages in the regulation of the nest temperature and provide protection against rains. A relatively high nest density per hectare of *P. analis* in a savannah habitat with 17.0 nest/ha was observed in this study, compared to 3.8 nests/ha at Kajiado in Kenya (Lepage, 1981), 9.0 nest/ha in a Nigerian guinea savannah (Longhurst *et al.*, 1978) and Tanzanian coastal dry forest (16.0 nests/ha, Bayliss and Fielding, 2002). However, the observed density was lower than reported in a gallery forest in the Ivory Coast (Lévieux 1966, 20.0 nests/ha). Although savannah woodlands and secondary costal dry forests are normally richer in biodiversity than semiarid savannah, other habitat factors may favour the abundance of *P. analis* in Mpala.

The main raiding activities of *P. analis* were in the mornings (0700 - 1100hrs) and evenings (1600 - 1930hrs), similar to the behaviour reported in other habitats. Longhurst *et al*., (1978) recorded two raids daily per nest in a Nigerian savannah between 0700 - 0930h and 1630 - 1830hrs. Bayliss and Fielding (2002) also reported two similar peaks of activity per day in a Tanzanian coastal dry forest. However, observations revealed a minor raiding activity in the early part of the night (nocturnal) between 2000 - 2400hrs during the month of April, which represented about 2% of the total raids observed. Lepage (1981) recorded three peaks of activities during the rainy season and two peaks of activities in the dry season at Kajiado, a Kenyan savannah. Nocturnal raids at Mpala were only observed in the drier month of April rather than in wet months (June, July and September) similar to earlier results (Lepage 1981). This may reflect the need to avoid high daytime temperatures and low humidity and reduce the risk of losing the trail pheromone laid by scouts and workers during foraging and raids in the morning. Alternatively, but not mutually exclusive the foraging activity of the prey (termites) might be increased at that time resulting in an increase in the raiding behaviour by *P. analis* at night or the evening. Indeed, Asian *Odontotermes* spp. show increased foraging activity in the pre-monsoon season (Rajagopal, 1990) and April 2007 constituted the end of the dry season with the long rainy season commencing in June. This is because soil texture, environmental conditions, especially ground temperatures, and relative humidity favours the foraging activity of termites especially *Microtermes* spp. and *Odontotermes* spp. (Sattur *et al*. 2007; Badawi *et al.*, 1984). This suggests that the change in foraging activity of the ants might be as a result of the changes in termites foraging activity.

Ground temperatures for departing *P. analis* foraging parties at Mpala fell in the range of 19 - 34 °C (average 23°C) similar to that reported by Bayliss and Fielding (2002). The average temperature is lower than that reported by Inara and Paulo (1995) for raids of the Neotropical termite-hunting ant *Pachycondyla marginata* in a semi-deciduous forest in Brazil during rainy (30°C) and dry (28°C) seasons. No foraging party was observed leaving the nest at midday, presumably because of heat stress and perhaps the volatility of their trail pheromone. On one occasion, ants coming back from a raid were disoriented when it rained making it difficult for them to detect the trail laid on their way out.

At Mpala, the average number of ants in raiding columns was smaller than those previously reported by other workers from a Nigerian savannah (Longhurst *et al.* 1978), in Kajiado Kenya (Lepage, 1981), and a Tanzanian coastal dry forest (Bayliss and Fielding, 2002). This suggests that *P. analis* colonies at Mpala may be smaller than those previously reported elsewhere if the number of ants per foraging party as suggested by Bayliss and Fielding (2002) reflects the size of the colony. Indeed, nests excavated for chemical ecological analysis had 270 - 425 individuals per colony (n =

11), which is fewer than the average of 400 individuals (Lévieux, 1966) and 1475 (Lepage, 1981) from Ivory Coast and Kajiado in Kenya respectively.

The maximum foraging distance (39.8 m) was higher than 35.4 m reported by Lepage (1981), but shorter than 44.0 m from a Tanzanian coastal forest (Bayliss and Fielding, 2002). It was considerably shorter than the 95.0 m reported by Longhurst *et al.* (1979) in a Nigerian savannah and 97.0 m for *P. marginata* (Inara and Paulo, 1995) in a Brazilian semi-deciduous forest. In general, mean foraging distances at Mpala were shorter than those reported previously by Longhurst and Howse (1979), Lepage (1981) and Bayliss and Fielding (2002). Longhurst and Howse (1979) observed shorter foraging distances at the beginning of the rainy season in June, which then increased in July, August and September. This foraging pattern is influenced by the behaviour of termites during rainy seasons when the colony increases in numbers with reproductive alates flying away to form new nests (Pearce *et al.*, 1996), thus increasing the abundance of prey items for *P. analis*. Therefore the observed shorter foraging distances might be a result of a higher abundance of food in closer proximity to the ant nests.

The duration of raids at Mpala for both morning and evening was shorter than those in a Tanzanian coastal dry forest (Bayliss and Fielding, 2002), and at Kajiado Kenya (Lepage, 1981). The longest raids lasted for just over 1.5hrs. This is much shorter than raids of *P. marginata* which usually last up to 24hrs covering distances of about 38 m (Inara and Paulo, 1995). Raids in *P. marginata* occur approximately after every 2-3 weeks, whereas in *P. analis* they occur more frequently with at least one raid per week. The length of the stay at the termite source was longer than in previous studies (e.g. Longhurst and Howse, 1979; Lepage, 1981; Bayliss and Fielding, 2002) which might be related to differences in the prey species. In the previous studies (Longhurst and Howse, 1979; Lepage, 1981; Bayliss and Fielding, 2002) *Macrotermes* was the main prey which has a formidable soldier caste which when recruited to a site of attack may reduce the duration of foraging by the ants. The time spent at a termite source is strongly correlated with the number of termites taken thus supporting some of the earlier findings (Bayliss and Fielding, 2002). Furthermore, the ants spent significantly more time in raids on *Microtermes* than *Odontotermes*. This might be due to defence by the soldier caste of *Odontotermes* that resulted in significantly more ants workers being injured when raiding *Odontotermes.*

Foraging velocities for return journeys were faster than those of outward journeys. This is in agreement with reports by Longhurst and Howse (1979), but contrary to findings in a coastal dry forest (Bayliss and Fielding, 2002). The foraging velocity of outward journeys is likely to be lower because all the ants in the foraging party rely on the scout ant who leads in following the original trail laid by the scout. In a situation where the scout was unable to locate the trail, the foraging columns went back to the nest. This may partly explain why group-raiding ants prepare to raid at lower temperatures when trail pheromones are likely to persist for longer (B. Torto, personal communication). Return journeys from raids may be faster because of a better defined and more concentrated trail laid collectively during the outward journey.

The predation rates per nest per day by *P. analis* on *Odontotermes* spp. and *Microtermes* spp. at Mpala were higher (Figure. 1.9) than those reported by Longhurst and Howse (1979) and Lepage (1981). This reflects a higher prey capture in this study that may be due to the higher relative abundance of prey.

The two genera of termite prey of *P. analis* at Mpala were also reported in Nigerian savannah (Longhurst *et al.*, 1978). Lepage (1981) found *Macrotermes* spp. and *Odontotermes* spp. to be the main prey of *P. analis* at Kajiado Kenya with a few predating on *Synacantothermes* spp. The most frequently raided genus of termites at Mpala during the study period was *Microtermes* which was taken more in the months of June through to September. Although *Trinervitermes* was encountered in lower proportions (~5%) during termite sampling, *P. analis* were not seen preying on these termites. Longhurst *et al.* (1978) suggested that several factors might influence prey selection. These include relative abundance of termite species, seasonal foraging patterns, foraging behaviour, size, and the interactions between the ants and termites. At Mpala, *Microtermes* were most frequently preyed upon (66%); however, this was significantly lower than their relative abundance (81%) within the study site. This may be attributed to the relative body mass between the two termite genera. *Odontotermes* being bigger than *Microtermes* are a more rewarding food source for the ants (Longhurst *et al.*, 1978) and fewer individuals may be taken as a result. Moreover, foraging behaviour of a termite species can also influence its predation by *P. analis*. *Odontotermes* spp. forages principally on wood, grass or litter on the surface, covering their food with a thin layer of soil and feed beneath this protective cover. Foraging ants usually break open these soil sheathings and remove the termites. Other species such as *Microtermes* forage on the surface only occasionally. They principally forage within their food sources that include roots, grasses and wood litter, entering it at points of contact with the soil that are perhaps more difficult for *P. analis* workers to enter. *Microtermes* forage less at the surface during the dry season, whereas *Odontotermes* forage mainly during the dry season (Bayliss and Fielding, 2002). This results show likelihood that abundance of *Microtermes* contributed to its preference by *P. analis* as the ants had about a six-fold greater chance of encountering *Microtermes* compared with *Odontotermes* (see termite abundance results in Appendix I). In addition, physical interactions between *P. analis* and its termite prey may also play a role in the choice of prey, since preying on *Odontotermes* resulted in more injured ant workers (Appendix I-ii). Although *Odontotermes* spp. is more defensive the greater weight per termite provides a greater reward. Our results indicate that prey choice by *P. analis* may not only be based on prey abundance, but also on the costs involved in foraging.

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APPENDIX I-i

Termite abundance within sampling quadrats at Mpala

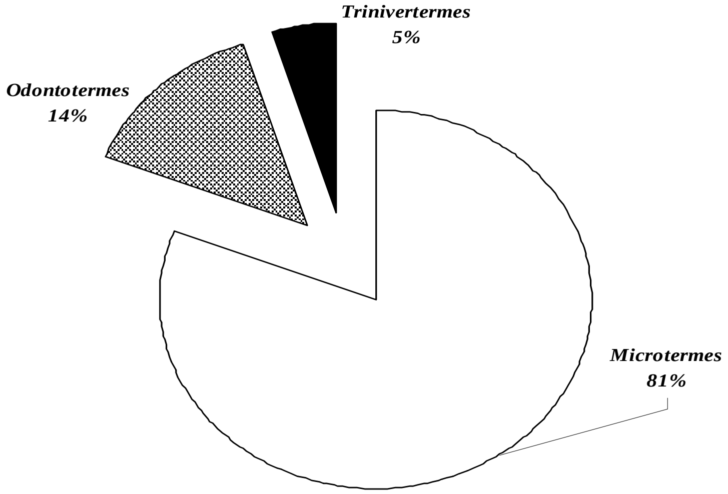

Figure 1. Relative abundance of termite genera within sampling quadrants at Mpala.

Appendix I-ii

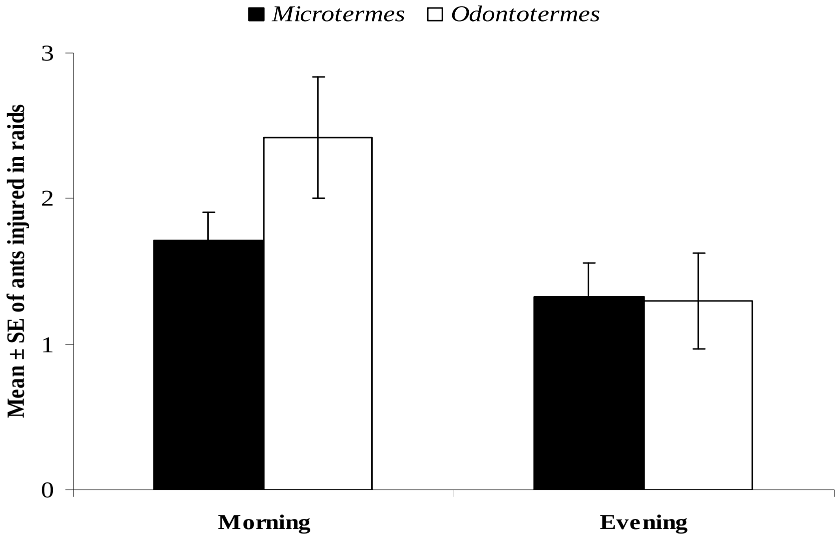

Figure 2. Number of ants injured calculated from the number of ants carried by con-specifics when returning from a raid. Black and white bars represents injured ants from *Microtermes and Odontotermes* raids respectively.