Prey choice and Raiding Behaviour of the Ponerine ant *Pachycondyla analis* (Hymenoptera: Formicidae)

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Abstract

Termite raiding behaviour of the African poneromorp ant *Pachycondyla analis* was studied at Mpala, Kenya. 330 raids were observed with the raiding activity showing peaks in the morning and evening. Time spent at the termites' source was positively correlated with the numbers of termites taken. The sizes of foraging parties, number of termites taken, distance travelled and time spent at termite sources also showed a positive correlation. *P. analis* preyed significantly more on *Microtermes* spp. than they did on *Odontotermes* spp.but no significant differences in terms of predator efficiency even though many ants were injured in raids on *Odontotermes* spp. than those on *Microtermes* spp. Our results indicate that, *P. analis* seems to forage optimally, balancing the costs of energy with prey reward and, prey choices were not only influenced by prey abundance, but also by the costs of foraging, as influenced by prey defences, size and foraging behaviour.

Keywords: Matabele ants, Macrotermitinae, foraging behaviour, poneromorph

Introduction

When an animal feeds, it makes a number of decisions, which includes the type of food to forage upon and the time to pursue the food when it is detected (Engen and Stenseth, 1984). This

foraging behaviour is shaped by behavioural, physical, physiological and ecological parameters which are related to detection, ingesting and processing of food items (Schoener 1971; Stephens and Krebs 1986; Houston and McNamara 1999). Studies on optimal foraging theory often use net-energy intake as a proxy for fitness, which the animal obviously wants to maximise. The three main assumptions of classical optimal foraging models often referred to as contingency model by Schoener (1974) are that: a) an increase in the abundance of a particular food leads to a specialised diet. b) In case of a fixed total food abundance, a food is either always attempted to be taken or not. c) A food type, which is not part of the diet, cannot be added to it even if that food item increases in abundance. These predictions were further discussed in Charnov's (1976) marginal value theorem which states that: for a particular environment an optimal predator would accept an item if it does not provide less energy per time than the energy per time available in the long run from a different diet not including that item (Engen and Stenseth 1984). However, the assumptions of Charnov's Marginal value theorem that a forager either accept or reject a particular food item is not always the case in nature with most foragers especially, with social animals like ants, because they encounter prey/food items simultaneously offered a number of options to choose from. Engen and Stenseth (1984) extended Charnov's optimal foraging theory taking into account the issue of simultaneous encounters of prey by foragers. Other factors such as prey distribution (Iwasa et al. 1981), biased time perception (Hills and Adler 2002), behaviour, size, defence (Pohl & Foitzik 2011), and micro-climatic factors could as well influence foraging patterns in ants.

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

The African poneromorph ant, *Pachycondyla analis* (Latr.) (formerly *Megaponera foetens* Fabr.), is widespread and relatively common throughout most of sub-Saharan Africa. Numbers of workers in a colony range from approximately 400 (Lévieux 1966) to 1475 (Lepage 1981). Group predatory behaviour or as termed raiding 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 of the subfamily 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 back to the nest, a scout recruits between 22 and 840 nestmates and guides the column back to the prey by following the trail (Longhurst et al. 1978). 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. 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 opening. 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 (Suplementary material). Some do not carry any termites, but lead columns of ants loaded with prey back to their nest (Longhurst et al. 1978; Yusuf 2010). The variable size and duration of the raiding party, the limitations of an individual worker to carry prey items, and the division of

labour between minor and major workers makes this species an ideal model organism to identify some underlying mechanism of optimal foraging theory.

We report here the raiding patterns and dynamics of *P. analis* and the effects of termite defences, prey size, and abundance on its raiding behaviour in a Kenyan Savannah. We hypothesise that *P. analis* forages effectively by showing adaptive foraging behaviour in keeping with Charnov's marginal value theorem by balancing the cost of foraging with those of reward, and that prey preference in *P. analis* is influenced by prey behaviour, abundance and prey defence.

Materials and methods

Study site. This study was conducted at Mpala Research Centre (0°17'N, 37°52'E) Laikipia District, Central Kenya, during the months of April to September 2007.

Nest location, distribution and density. Nests of *P. analis* were located using three different approaches (Longhurst et al. 1978; Bayliss and Fielding, 2002). 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. To obtain the nest density within the study site, eight quadrats (50 m × 50 m each) were set randomly. The numbers of nests were counted, and the average 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. These monitoring periods were based

on prior observations of raiding behaviour before the start of experiments. Raiding behaviour was monitored daily throughout the study period.

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 or about 200 in the group. Where there were more than 200 ants, the number was estimated in groups of tens. The number of ants carrying termites was also recorded in a similar manner. The number of termites carried per ant was determined by carefully grabbing the ant by the thorax using an entomological forceps. That triggered the ant to attack the forceps and release the termites. Termites were identified to the generic level using their caste information as outlined in Pearce et al. (1996).

Foraging velocity. The foraging velocity was calculated using the time it took an ant to travel a distance of 50 cm from the nest to a termite source. This was repeated for fourteen different foraging parties on the outward and return journeys for randomly selected foraging parties. 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. These measurements were carried out on open ground to eliminate the effect of variable amounts of litter.

Factors affecting prey preferences

Duration of raids. The 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) were determined for each raid. The foraging distance covered for each of the raid was also measured. Ground temperatures at departure from ant nests for raids were recorded for each raiding column.

Injured ants during raids. 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 their nestmates.

Predation rates on preyed termite genus. 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 rate in relation to termite abundance. Predation in relation to the abundance of termite genera in the field were determined by comparing frequencies of raids on a given termite genus in relation to its abundance within the study quadrats. Termite abundance was estimated 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 × 2 m wide, and divided into 10 contiguous numbered sections of 5 m × 2 m each. Two collectors who were previously trained for two weeks, spent 40 min each per section. In each section the collectors searched microhabitats which are common sites for termites. Specimens of all castes from each

termite population encountered were collected. 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 analyses

A Mann Whitney U (MWU) test was used to test for differences between morning and evening activities. Spearman's Rank correlation was used to compare the size of raiding parties between months. 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 genera 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 genera, with prey genera 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 distance travelled, number of termites per minute travelled, and the number of injured ant workers carried back were the dependent variables. Only raids in which the prey was 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 termite genera during the different months and to the abundance of the prey data. Student's t- test was used to test differences in variables between morning and evening raids. All statistical analyses were performed using the SAS (9.2) statistical package.

Results

Nest location, distribution and density. A total of 37 nests were located within 8 random placed quadrats within the study site. Of these, 43% were under rocks, 30% in old termite mounds, 16% were under trees and 11% were in cavities in the soil. The distance between the nests ranged from 1.7 m to 29.7 m, while the mean number of nests per quadrat was 4.25 ± 2.71, equivalent to ~17 nests per hectare.

Foraging parties. Of the 330 raids recorded from the 37 nests, 56% (184) occurred in the morning (0700 - 1100hrs), 42% (138) in the evening (1600 - 1930hrs), and 2% (7) were nocturnal (2000 - 2400hrs). The mean temperature at which raiding parties of ants departed from the nest to a termite source was 23.1 ± 0.21 °C (range: 17.8°C – 36.4°C).

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 (Fig. 1). The size of the raiding parties increased significantly during the study period (Spearman's Rank correlation: r = 0.315, $P < 0.01$). The total number of termites carried were not significantly different between months. However the percentage of ants carrying termites within a raiding party was significantly different (Kruskal Wallis ANOVA, $\chi^2 = 23.03$, $df = 5$, $P < 0.001$, Fig. 1), and was highest from June to August. 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. Raiding behaviour was not affected by the amount of rainfall, while 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.

The mean number of ants per raid was significantly higher in the morning than in the evening (t = 2.48, $P = 0.01$, $df = 323$, Fig. 2). The mean number of ants carrying termites during morning and evening raids was not significantly different ($t = 1.88$, $P = 0.06$, $df = 309$, Fig. 2) nor was the number of termites carried per raiding party (t = 1.04, $P = 0.29$, $df = 293$) (Fig. 2).

Foraging distances were not significantly different between the morning and evening raids, except for the months of April, June and August (Table 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, $P < 0.001$).

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}.

Factors affecting prey preferences

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 total number of termites taken correlated positively with the time spent at the termite source; the longer the ants stayed at the termite source, the larger were the number of prey captured (Spearman's 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. Fig. 3), 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 sites of *Microtermes* than at the sites of *Odontotermes* (MWU: Z = -2.2, $P < 0.03$, Fig. 3).

Predation. P. analis was only observed to prey on two genera of termites at Mpala during the study period. Out of the 330 raids recorded, it was only possible to identify prey from 237 raids. *Microtermes* was targeted on average in 66% of these raids and *Odontotermes* in 34%. The latter was significantly preyed upon in April and August (75% and 59%), while the former was the main prey in other months (69%, 74%, 75% and 70% 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%). However, when comparing the predation rate on the two termite genera for each month against their abundance, the ants preyed significantly more often on *Microtermes* in June ($\chi^2 = 4.9$, $P < 0.05$) and more on *Odontotermes* in August ($\chi^2 = 8.14$, $P < 0.01$; Fig. 4).

Overall, the ratio between ants carrying the two different genera of termites, and the total number of ants in raiding parties was not significantly different between prey species (MWU: Z = -0.16, n.s.). The same was the case when comparing the termites carried per ant, termites carried per meter or per minute (MWU: per meter: Z = -0.55, n.s., per min: Z = -1.79, n.s.) as measures of predator efficiency. However, significantly more injured ant workers were carried back when preying on *Odontotermes* (2.25 ± 2.71) compared to (1.63 ± 2.18) *Microtermes* (MWU: Z =- 2.2, $P < 0.03$) (Fig. 5).

Discussion

The thirty seven nests of *P. analis* encountered in this study were mainly under rocks and in abandoned termite mounds. Studies in other localities (Longhurst and Howse 1979; Bayliss and Fielding 2002) have indicated a preference for sites that are provided by the particular habitat, thus *P. analis* at Mpala exhibit a different nesting pattern. These nesting patterns at Mpala could have advantages in the regulation of the nest temperature and provide protection against rains. The results shows a relatively higher 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 in Tanzanian coastal dry forest (16.0 nests/ha, Bayliss and Fielding 2002). Savannah woodlands and secondary costal dry forests are normally richer in biodiversity than semiarid savannah; other habitat factors like conservation status and the consequent lack of agricultural and other disturbances at Mpala may favour the abundance of *P. analis* nests.

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 (e.g. Longhurst et al. 1978; Bayliss and Fielding 2002). However, our observations revealed another 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. Nocturnal raids at Mpala were absent in wet months (June, July, August and September). This behaviour may reflect the need to avoid high daytime temperatures and low humidity with the attendant risk of losing trail pheromones laid by scouts and workers during foraging and raids. It may also accounts for the increased raiding activity in

the evenings in April. Alternatively but not mutually exclusive, termite forage mostly in the cooler hours of the day (mornings and evenings) and this may influence an increase in the raiding behaviour by *P. analis* during this period. This had been demonstrated in the Asian *Odontotermes* spp. which showed increased foraging activity in the pre-monsoon season (Rajagopal 1990). At Mpala where the present study was conducted, April constituted the end of the dry season while the long wet season commence in June and end in November. Soil texture e.g. loose soil, environmental conditions, especially low ground temperatures, and relative humidity favours the foraging activity of termites especially *Microtermes* spp. and *Odontotermes* spp. (Badawi 1984; Sattur et al. 2007). This suggests that foraging activity of *P. analis* is synchronised by its prey behaviour.

Ground temperatures for departing *P. analis* foraging parties at Mpala were within the range of 19 - 34°C (average 23° C). The average temperature was lower than those reported by Inara and Paulo (1995) for raids of the Neotropical termite-hunting ant, *Pachycondyla marginata* from a semi-deciduous forest in Brazil during wet (30°C) and dry (28°C) seasons. At Mpala, no foraging party was observed leaving the nest at midday, presumably because of heat stress and/or the volatility of their trail pheromone.

In this study, ants in raiding columns were fewer than those reported elsewhere (Longhurst et al. 1978; Lepage 1981; Bayliss and Fielding 2002). This suggests that *P. analis* colonies at Mpala may be smaller, as the number of ants per foraging party may reflect the size of the colony and its food requirements (Bayliss and Fielding 2002). The nests of these ants excavated for chemical ecological studies had between 270 to 425 individuals per colony (n = 6).

Results from this study indicate that *P. analis* forages economically, balancing energy used in foraging with rewards in raids, since the number of ants in a raiding party, distance travelled to termite source and time spent in raid is proportional to the number of termites taken during a raid. This phenomenon follows the theory of optimal foraging in ants (Orians and Pearson 1979), which states that resources are balanced with efficiency of group foraging and food reward to favour the success of the whole colony. These results confirmed earlier reports by Duncan (1995), that *P. analis* workers use energy efficiently especially in carrying prey during their raiding expeditions.

Maximum foraging distance (39.8 m) obtained in this study was longer 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 also 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. Foraging patterns are influenced by the behaviour of termites during wet 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 high abundance of termites in close proximity to ant nests could explain these shorter foraging distances at Mpala. Previous studies by Davidson (1978) on *Pogonomyrmex barbatus* and Crist and MacMohan (1992) on *P. occidentalis* showed that ants increasingly select their foraging distance with food availability (although these were shown outside their foraging range). Similar experiments on harvester ant (Rissing and Pollock 1984; Ferster and Traniello 1995) and on leaf cutting ants (Wetterer 1991) did not show any significant difference between size of food and

foraging distances. However, it is worth noting that the above studies were conducted either in the laboratory or under semi-field conditions using food baits.

The duration of raids at Mpala were shorter than earlier reports from a Tanzanian coastal dry forest (Bayliss and Fielding 2002) with the longest raid lasting just over 90 minutes. Time spent at a termite source strongly correlated with the number of termites taken, with ants spending significantly more time in raids on *Microtermes* than *Odontotermes*. This is an indication that ants encounter more resistance from *Odontotermes* than *Microtermes* during raids, as suggested by the higher number of *P. analis* ants injured during the encounters.

Therefore, *Microtermes* was the most frequently raided among the two genera during the study period at Mpala. Although *Trinervitermes* was encountered in lower proportion (~5%) during termite abundance sampling, *P. analis* were not seen preying on these termites. This may be due to the advanced defence strategy involving the secretions of terpenoids employed by soldiers of Nasutitermitinae, thereby making them unlikely candidates for assault by these ants. Longhurst et al. (1978) suggested that several factors might influence prey selection. These include relative abundance of termite species (as observed here in the case of *Microtermes*), seasonal foraging patterns and foraging behaviour of termites, size, and the interactions between the ants and termites. This may also be attributed to the relative body mass between the two termite genera. *Odontotermes* being bigger than *Microtermes* are a more rewarding food source per individual prey for the ants (Longhurst et al. 1978). The foraging behaviour of a termite species can also influence its predation by *P. analis*. *Odontotermes* forages principally on wood, grass or litter on the surface and covering their food with a thin layer of soil. They therefore feed beneath this

protective cover. *Microtermes* forage on the surface only occasionally and are within their food sources which include roots, grasses and wood litter., They move into these materials at points of contact with the soil that are perhaps more difficult for *P. analis* workers to access. *Microtermes* forage less at the surface during the dry season, whereas *Odontotermes* forage mainly during the dry season (Bayliss and Fielding 2002). These results therefore showed the likelihood that abundance of *Microtermes* contributed to its predation by *P. analis* as the ants had about a six-fold greater chance of encountering them compared with *Odontotermes* (which is bigger in size). 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 than on *Microtermes*. Similar behaviour of favouring reward against defences was reported for the slave-making ant *Protomognathus americanus* (Pohl and Foitzik 2011).

To conclude, our data suggests that *P. analis* forages optimally by balancing the cost of foraging with reward in order to satisfy their colony food requirements. Prey preferences in *P. analis* also appears to be synchronised with prey behaviour, reward as well as prey's physical and or chemical defence mechanisms.

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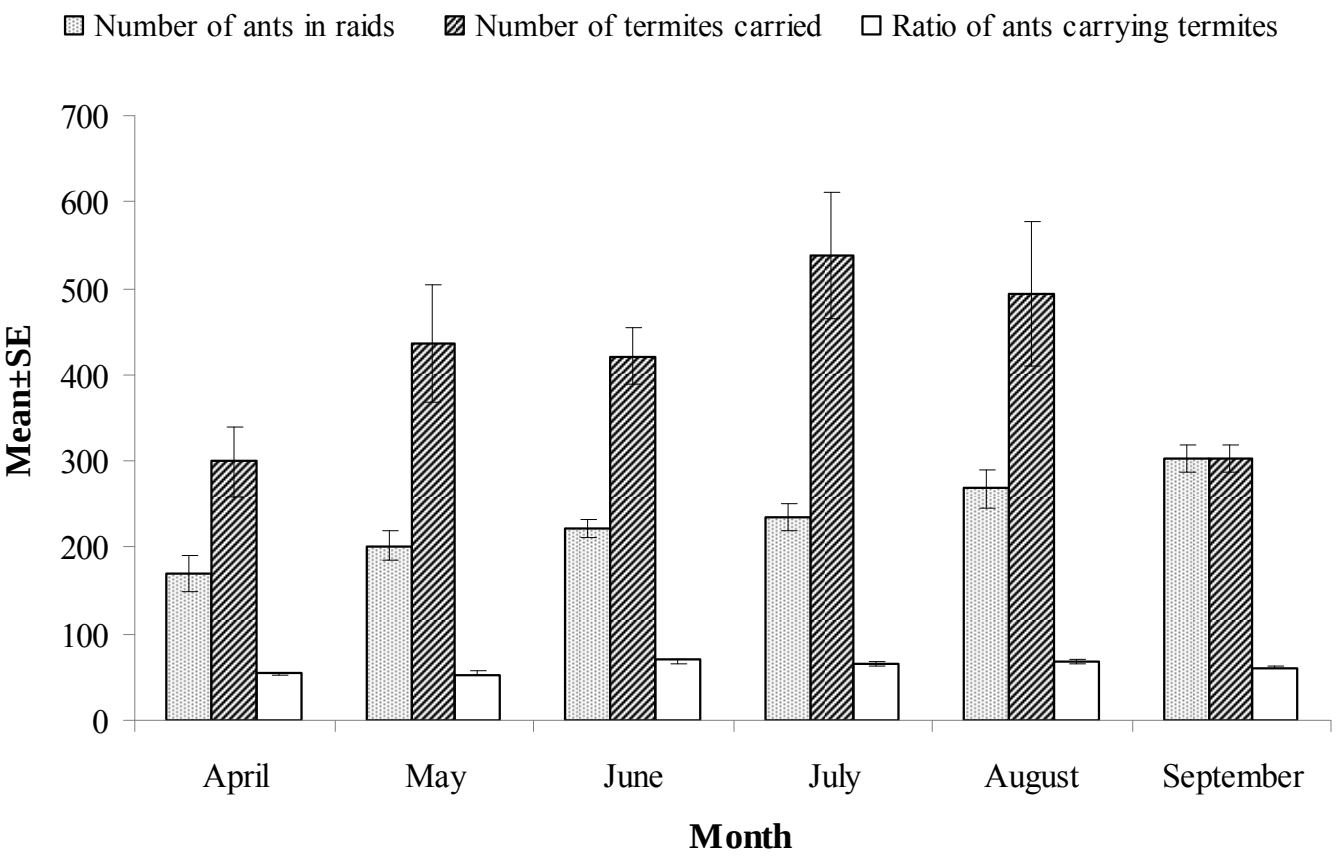
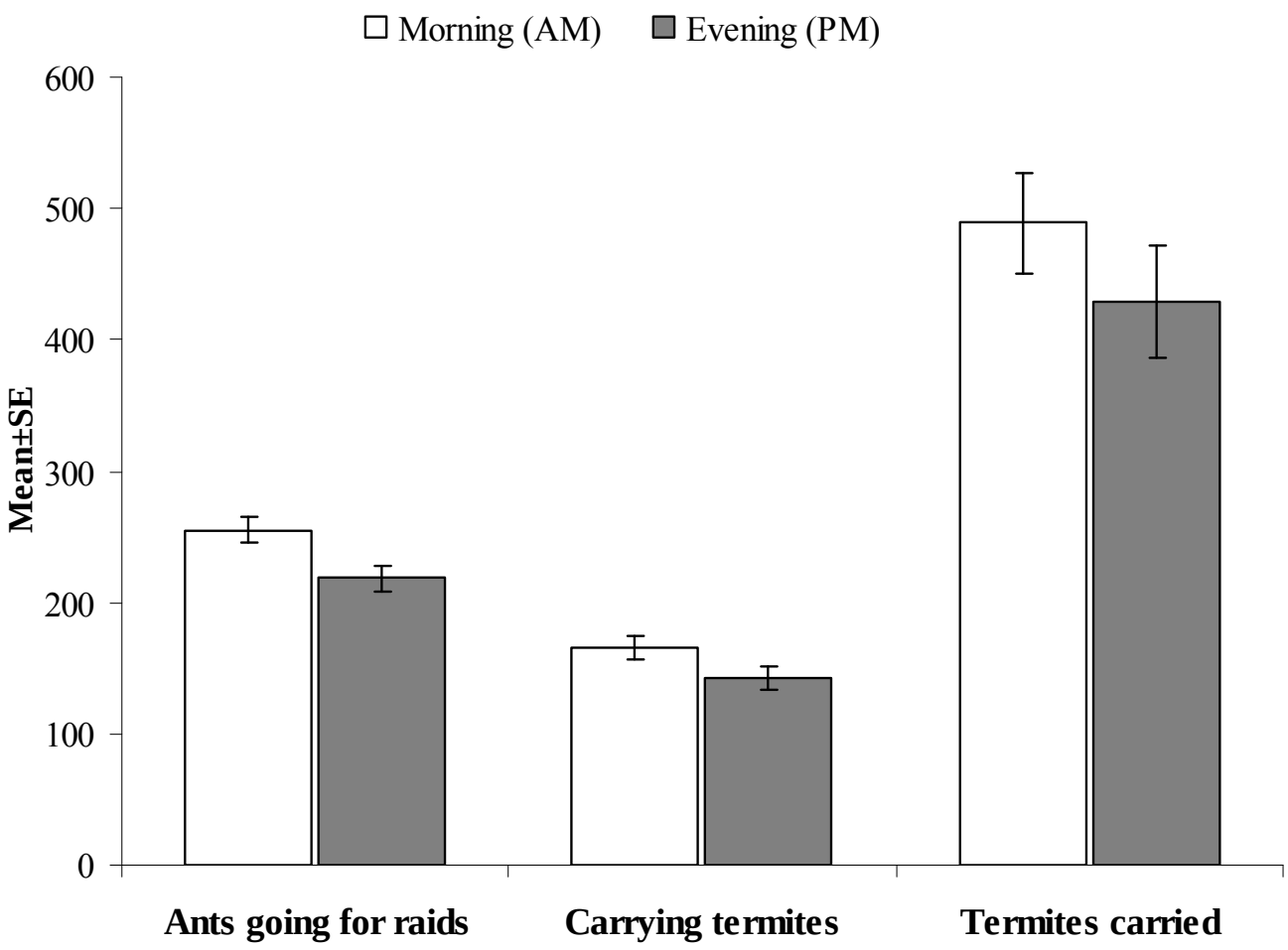
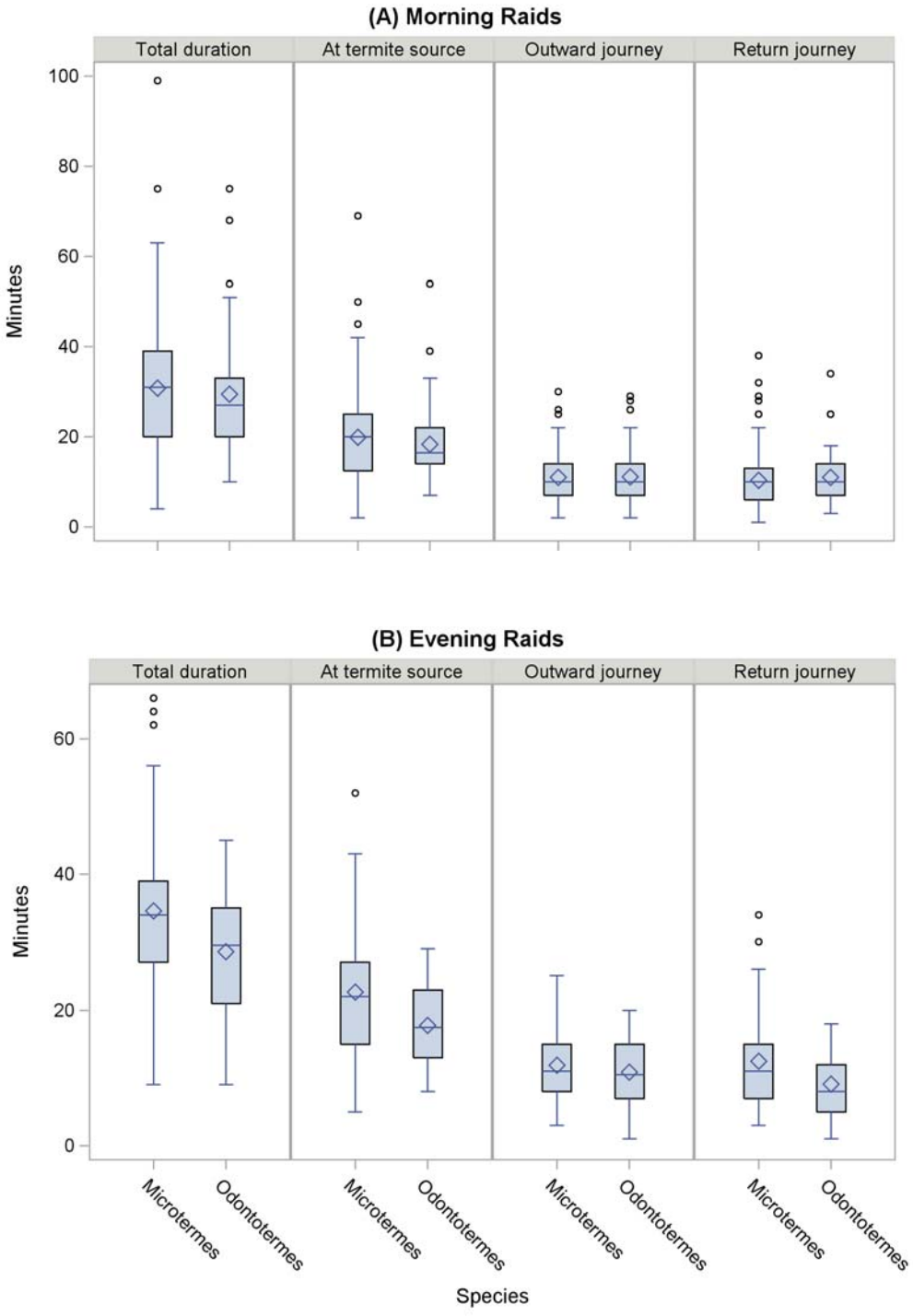
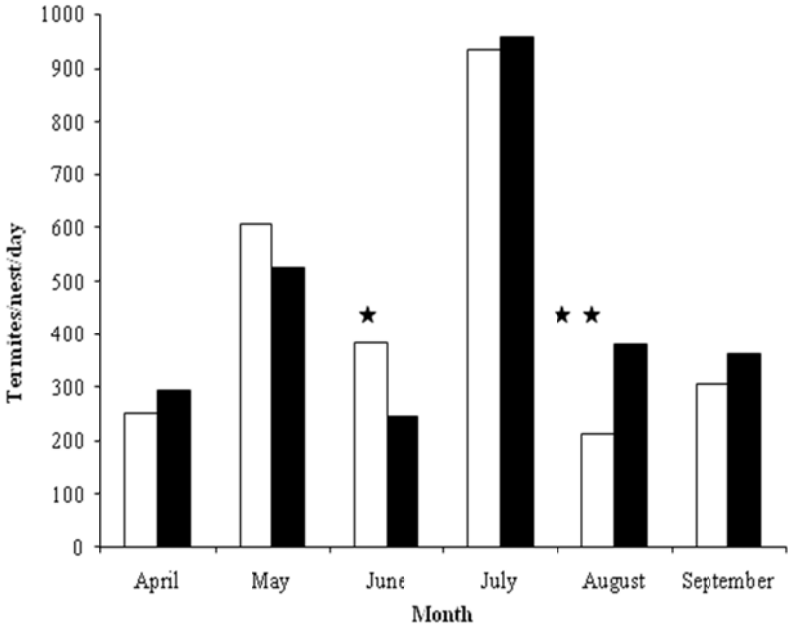

Number of ants in raids
Number of termites carried
Ratio of ants carrying termites
700
600
500
400
300
200
100
0
Mean±SE
April
May
June
July
August
September
Month


Morning (AM)
Evening (PM)
600
500
400
300
200
100
0
Mean±SE
Ants going for raids
Carrying termites
Termites carried


(A) Morning Raids
Total duration
At termite source
Outward journey
Return journey
Minutes
100
80
60
40
20
0
(B) Evening Raids
Total duration
At termite source
Outward journey
Return journey
Minutes
60
40
20
0
Microtermes
Odontotermes
Species


1000
900
800
700
600
500
400
300
200
100
0
Termites/nest/day
April
May
June
July
August
September
Month

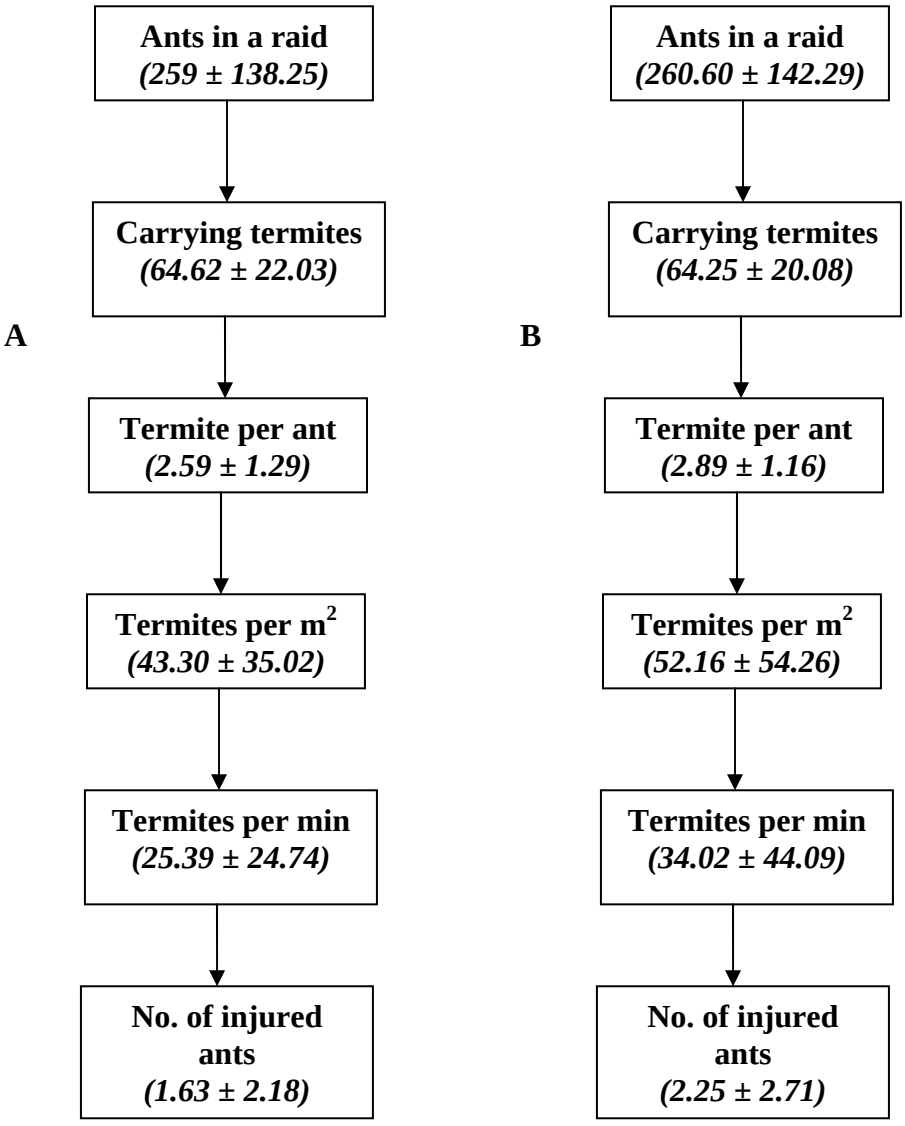

A
Ants in a raid
(259 ± 138.25)
Carrying termites
(64.62 ± 22.03)
Termite per ant
(2.59 ± 1.29)
Termites per m2
(43.30 ± 35.02)
Termites per min
(25.39 ± 24.74)
No. of injured ants
(1.63 ± 2.18)
B
Ants in a raid
(260.60 ± 142.29)
Carrying termites
(64.25 ± 20.08)
Termite per ant
(2.89 ± 1.16)
Termites per m2
(52.16 ± 54.26)
Termites per min
(34.02 ± 44.09)
No. of injured ants
(2.25 ± 2.71)

Figure Captions

Fig. 1 Mean numbers (±SE) of ants in a raiding group, number of termites carried and ratio of ants carrying termites.

Fig. 2 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

Fig. 3 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.

Fig. 4 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.* * $P < 0.05$ and ** $P < 0.01$.

Fig.5 Raiding dynamics of *Pachycondyla analis* on the two genera of termites at Mpala (A) *Microtermes* and (B) *Odontotermes*

Table

Table 1 Number of raids (N), minimum, maximum and mean (±SE) foraging distances of *P. analis* raiding parties at Mpala between months and time of raids (mornings and evenings).

			Foraging distance (m)		
Month	**Period of the day**	***N***	**Min**	**Max**	**Mean ± SE**
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 ± 1.2b
	Evening	35	1.9	29.6	10.1 ± 0.9b
June	Morning	40	1.5	26.5	9.3 ± 0.6c
	Evening	20	3.4	26.3	11.1 ± 1.1b
July	Morning	49	1.6	39.8	11.4 ± 2.7b
	Evening	18	4.2	31.0	13.6 ± 0.8d
August	Morning	43	0.7	38.2	13.4 ± 1.4d
	Evening	19	1.1	17.3	9.5 ± 1.0c
September	Morning	38	4.5	39.7	12.1 ± 1.0d
	Evening	18	5.2	32.9	11.5 ± 1.6b

Note: Means in the same column followed by same letters are not significantly different (α = 95%).