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Behavioral ecology of the neotropical termite-hunting ant *Pachycondyla* (= *Termitopone*) *marginata*: colony founding, group-raiding and migratory patterns

Abstract This study provides the first detailed field account of colony founding, group-raiding and migratory habits in the neotropical termite-hunting ant *Pachycondyla marginata*, in a semi-deciduous forest in south-east Brazil. New colonies can originate by haplometrosis, pleometrosis, or colony fission. Incipient colonies with multiple foundresses persisted longer in the field, and most excavated nests contained more than one dealated female. A total of 202 group raids by *P. marginata* were registered, and in all cases the raided termite species was *Neocapritermes opacus*. Nearly 20% of the workers within a colony engage with raiding activity. Colonies of *P. marginata* hunt for termites approximately every 2–3 weeks, and group-raids may last for more than 24 h. Target termite nests are up to 38 m from the ant colony, and occasionally two nests are simultaneously raided by one ant colony. Raiding ants carry 1 or 2 paralysed prey, and nearly 1600 termites can be captured during a 9-h raid. Migration by *P. marginata* colonies lasted over 2 days and covered distances of 2–97 m ($n = 48$). Average residence time at a given location was 150 days. Three basic migratory patterns were noted: colony fission (only part of the colony moves), long-distance migrations, and short-distance migrations. Both raiding and migratory activities appeared to be strongly affected by seasonal factors. The group raiding and migratory patterns of *P. marginata* are compared with other ant taxa with similar habits. It is concluded that *P. marginata* presents a rudimentary form of the so-called "army ant behavior", which is highly developed in the subfamilies Dorylinae and Ecitoninae. The extremely specialized diet of *P. marginata* and the associated high costs of migration are features likely to prevent it from evolving a full army ant life pattern.

Introduction

Ants (Formicidae) exhibit almost all degrees of prey specialization; some species may include in their diets many different types of arthropods while others may prey on a relatively restricted taxonomic group (Wheeler 1910). Members of the subfamily Ponerinae normally feed on soil arthropods such as collembolans, centipedes, millipedes, other ants, and termites (Hölldobler and Wilson 1990). Many of these prey organisms possess very sophisticated defense mechanisms, and specialized ponerine ants have a number of mechanisms for subduing them efficiently (e.g., Lepage 1981; Maschwitz and Schönegge 1983; Mill 1984; Attygalle et al. 1988). Ants frequently prey on termites, and the two groups have evolved many morphological and behavioral strategies to cope with one another in nature (Hölldobler and Wilson 1990).

Traniello (1981) defined three main predatory strategies utilized by termite-hunting ants: (1) facultative predation by solitary foragers, found in some species of *Pachycondyla*, *Ectatomma* and *Odontomachus*; (2) attacks organized in a short period of time through mass recruitment, as in *Solenopsis* and *Pheidole*; and (3) predation by obligate termitophagous ants, as in species of *Pachycondyla* (= *Termitopone*), *Megaponera*, *Leptogenys*, among others.

Obligate termitophagy has been reported for the following ant taxa: *Pachycondyla* (= *Termitopone*), *Acanthostichus* and *Cylindromyrmex* in Central and South America; *Megaponera*, *Pachycondyla* (= *Ophthalmopone*, see Bolton 1994) and *Decamorium* in tropical Africa; and *Leptogenys* and *Centromyrmex* in tropical Asia (Wheeler 1936; Brown 1975; Longhurst et al. 1979a; Overal and Bandeira 1985; Hölldobler and Wilson 1990). Obligate termitophagy through group

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raiding may be linked with migratory habits in a few species in the ant subfamily Ponerinae (Wheeler 1936; Wilson 1958).

The simultaneous occurrence of group predation and migratory behavior is regarded as a diagnostic characteristic of the so-called "army ant" life pattern (Wilson 1958), which is maximally developed in the subfamilies Ecitoninae and Dorylinae but also occurs to varying degrees in other ant subfamilies (reviewed by Hölldobler and Wilson 1990). An evolutionary pathway leading to fully developed army ant behavior was originally proposed by Wilson (1958), summarized as follows. In a first step, group raids were initiated through recruitment by successful scouts, and this capacity presumably allowed specialized feeding on social insects (e.g., ants or termites) or large arthropods. Some ponerines exhibiting this form of raiding also have migratory habits, as in some species of *Leptogenys*, *Pachycondyla* (= *Termitopone*), and *Megaponera* (Maschwitz and Schönegge 1983; Hölldobler and Traniello 1980a; Mill 1982a; Longhurst and Howse 1979). In later steps group raids became progressively more autonomous (no recruitment being necessary), massive and efficient, colonies began to migrate regularly to exploit new food sources, their diet expanded markedly, and colony size became extremely large. This stage has been achieved by the African driver ants and the neotropical *Eciton burchelli* (for further details see Wilson 1958; Hölldobler and Wilson 1990).

Available data on species with rudimentary forms of army ant behavior are still fragmentary, and more field data are needed in order to assess more precisely how the various features of the army ant life pattern might have arisen. Three neotropical *Pachycondyla* (= *Termitopone*) species exhibit both group-predatory and migratory behavior, namely *P. laevigata*, *P. commutata*, and *P. marginata* (cf. Hölldobler and Traniello 1980a; Mill 1982a; Wheeler 1936). *P. marginata* (Roger) occurs in South America, and is widely distributed in several regions of Brazil (Kempf 1972). In southeast Brazil this species is frequently found in humid forests. Here we provide a detailed account of the field biology of *P. marginata*, with special attention to its modes of colony founding, group-predatory behavior, and migratory habits. The following features are likely to distinguish *P. marginata* from the "true army ants":

1. Brood development and behavior cycles are not synchronized, with raiding and migratory activities being markedly connected to seasonal factors.

2. Diet is extremely specialized and group-raids are organized through conventional group recruitment.

3. Nest relocations are not frequent and nest building activities are costly.

4. New colonies can originate from one to seven foundresses, or from budding.

5. Mature colonies usually contain more than one non-physogastric queen.

These results are compared with other ant taxa presenting similar habits.

Materials and methods

Field work was carried out in a semi-deciduous forest at the Santa Genebra Reserve, Campinas, Southeast Brazil (22°49′ S, 47°06′ W). A total of 83 colonies of *P. marginata* were marked and followed along two main trails in the study area. Demographic data of ant colonies are based on nine excavated nests. Field observations of nuptial flights, mating, and colony founding behavior of *P. marginata* were conducted in January 1993. Incipient nest chambers (*n* = 28) with different numbers of founding queens (assisted or not assisted by workers) were marked and monitored in the field during a period of 8 months (until September 1993). Within this period, the persistence of incipient colonies was checked at 2-day intervals.

Group-predatory behavior by *P. marginata* is described from over 200 raids observed in the field. For every raid we collected samples of workers and soldiers of the termite prey, and also registered the distance between the colony of *P. marginata* and the target termite nest. The proportion of worker and soldier termites being captured by *P. marginata* was evaluated during raids of three different colonies. Records of termite prey were taken at 1-h intervals, for 15 min.

The spatial distribution of foraging ants along a raiding column was evaluated from snapshot records (cf. Lehner 1979) of five different colonies. Although at any given time the ant traffic is in both directions along the raiding column, the snapshot records for outward-bound and returning ants were taken separately. We also recorded whether the ants were carrying or not termite prey.

The existence of division of labor during a raid, and the percentage of ants engaged with hunting activity in a given ant colony, were investigated during raids by three different colonies of *P. marginata*. All ants walking along the raiding column were marked on the thorax with colored dots (Enamel Paint, Testors, Rockford, Ill, USA). Ants were marked during a 15-min period, at 1-h intervals, until no unmarked ant could be seen on the trail. The nests were excavated in the following day for the census of marked and unmarked ants.

The percentage of colonies engaged in different activities (i.e., maintenance or foraging) was determined during the rainy/hot season (October to March) and the dry/cold season (April to September). All marked colonies were monitored for 3 days in each season. Climatic data and ant activity were recorded at every 2 h during a 24-h period.

In September 1992 all workers from seven colonies of *P. marginata* were marked on the thorax, using distinct colors for each colony. From October 1992 to September 1993, all observed migratory movements and raids to termite nests from each of the seven marked colonies were recorded and mapped. The description of the migratory behavior of colonies of *P. marginata* is based on 48 migration events observed in the field.

Results

General biology, demography, and colony founding in *P. marginata*

Nests of *P. marginata* are located on the ground, have up to 11 entrance holes (mean ± SD = 2.9 ± 2.6, *n* = 35 nests), and consist of several chambers connected by galleries. The nest chambers are distributed from 5 cm to 1.5 m below the ground surface (*n* = 9 excavated
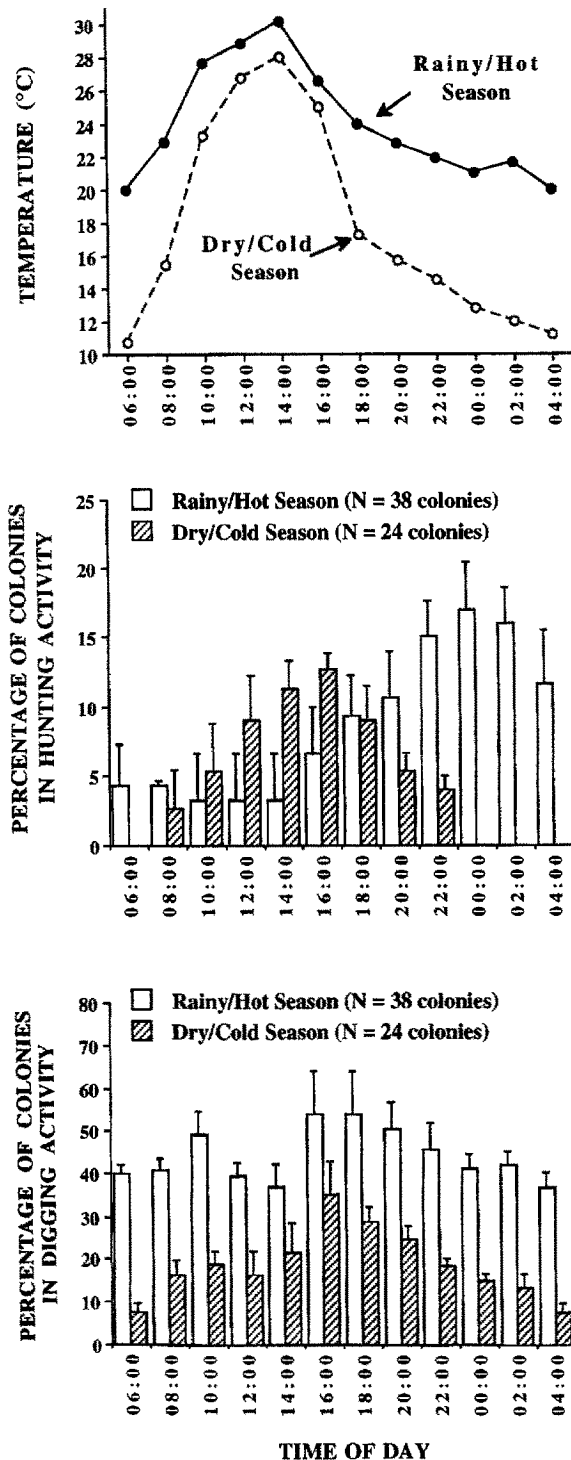
Fig. 1A–C Seasonal activity of *Pachycondyla marginata* colonies in a forest site in south-east Brazil. **A** Climatic data; temperature is expressed as the mean value between soil and air temperatures. **B** Hunting activity (+SE). **C** Digging activity (+SE). All data are means of 3 sampling days each season

Hunting activity by colonies of *P. marginata* presented a modal pattern throughout the day. During the rainy/hot season few colonies hunt during the day, and most of the raiding activity occurs at night, reaching a peak around 2400 hours (Fig. 1A, B). On the other hand, during the dry/cold season the peak of hunting activity occurred around 1600 hours, when temperatures are higher (Fig. 1A, B). No colony was seen hunting at temperatures near 10°C.

The number of colonies engaged in digging activity (removal of soil particles from the nest) remained relatively constant throughout the day in the rainy/hot season (Fig. 1A, C). A smaller proportion of colonies engages in digging activity during the dry/cold season, and this behavior was most commonly observed around 1600 hours (Fig. 1A, C).

Table 1 provides the demographic data from nine excavated nests of *P. marginata*. Colonies contained approximately 550–1600 workers, and most of them had more than one dealated female. Dealated queens were not physogastric but could be distinguished from the workers by having a thicker gaster and larger thorax. Colony size was not correlated with the number of dealated females (Spearman's $r = 0.25$, $P > 0.60$, $n = 8$; data from queenless colony not used). Except for two colonies excavated at the beginning of the dry/cold season (April), all other colonies contained sexual alates (Table 1).

P. marginata colonies may be founded either by a single female (haplometrosis) or by multiple foundress associations of up to seven queens (pleometrosis) (Fig. 2). On 26 January 1993, reproductive activity by alate males and females was recorded for nearly 42% of the monitored colonies ($n = 40$). Alates were observed flying up to 2 m high; matings took place either during flight or on the ground. Founding nest chambers were always close to (2–5 m) an established mature colony. On several occasions groups of dealated females were seen in intense excavation activity in the vicinity (2–5 m) of their natal nests, being assisted by many resident workers. Colony founding by single females was also observed, and the founding queen may excavate the new nest alone or in the company of worker nestmates. Pleometrotic associations accounted for 82% ($n = 28$) of the founding events recorded; one to seven founding queens (mean ± SD = 3.2 ± 1.8 per nest) were observed digging nest chambers (see Fig. 2). Persistence of incipient colonies was positively correlated with the number of foundresses (Spearman's $r = 0.91$, $P < 0.05$, $n = 7$; see Fig. 2). Founding chambers with higher numbers of queens were more likely to be assisted by workers during foundation than those with single queens (Spearman's $r = 0.91$, $P < 0.05$, $n = 7$). The continuous monitoring of founding nest chambers revealed that workers assisting founding queens remain with the incipient colonies.

Fission may occur when colonies reach maturity, as observed once in the field for colony 15 (Fig. 3).

nests). Brood chambers may contain all developmental stages (eggs, larvae and pupae), or each of these separately. Live termites were also observed in two excavated nests.

Table 1 Demography of *Pachycondyla marginata* colonies in a forest site in south-east Brazil

| Colony code	Date of collection	Workers	Dealate females	Alate females	Males	Pupae	Larvae
3	10 Dec 91	1073	01	04	24	253	53
4	14 Dec 91	930	02	02	05	130	41
7	16 Jan 92	756	03	01	05	60[a]	20[a]
26	19 Jan 92	642	03	0	03	20[a]	10[a]
32	19 Feb 92	673	02	01	08	50[a]	20[a]
1	14 Oct 92	561	01	08	13	30[a]	40[a]
8	30 Dec 92	1115	03	21	36	100[a]	80[a]
12	29 Apr 93	602	02	0	0	0	70[a]
13	30 Apr 93	1581	0	0	0	30[a]	280[a]
Mean ± SD		881.4 ± 331.7	1.9 ± 1.1	4.1 ± 6.8	10.4 ± 12.2		

[a]Approximate counts
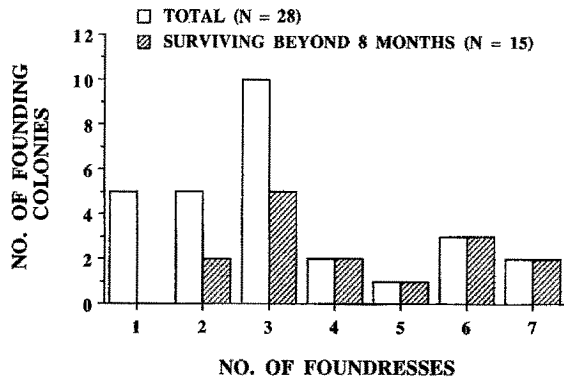
Fig. 2 Number of founding colonies with different number of queens, and persistence of incipient colonies of *P. marginata* in a forest site in south-east Brazil. The proportion of incipient colonies surviving beyond 8 months is positively correlated with the number of foundresses

Fig. 3 Map showing the raiding and migration routes of colony 15 of *P. marginata*, from October 1992 to September 1993, in a forest site in south-east Brazil. (Key to symbols: *N1* ant nest before migration, *N2* ant nest after migration, *N1'* part of colony N15 after its fission, *T1,2...* raided termite nests). *Dashed arrows* indicate migration routes, and *solid arrows* show raiding routes. *Thick arrows* show routes to termite nests which were raided twice. Termite nests are different from those shown in Fig. 4

Colony 15 was first recorded in June 1991, and by January 1992 a total of 171 workers were counted in a snapshot record of its raiding column to a termite nest. Therefore by the time of its fission the colony was at least 1.5 years old, and presumably had a few hundred workers. After the fission of colony 15 (7 November 1992) no traffic of ants was observed between the mother and daughter colony, and raids on termite nests were conducted independently by the two colonies (see Fig. 3). Reproductive activity by alate males and females was observed near the entrance of both colonies on 26 January 1993 (see above).

Raiding behavior in *P. marginata*

P. marginata preyed exclusively on the abundant termite species *Neocapritermes opacus* (Hagen) (Termitidae). The termite prey nests within roots or rotting wood, and occurs at an approximate density of one nest at every 3 m (survey along a 50-m transect). *P. marginata* is found at a density of one nest at every 30-40 m (survey along a 700-m trail). A single ant colony can simultaneously exploit two termite nests. On the other hand we never observed, either at the
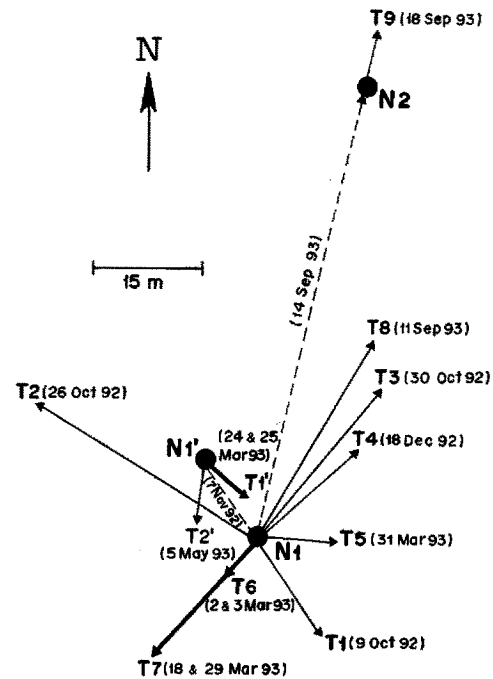
same or different times, a given termite nest being raided by two ant colonies. Figures 3 and 4 illustrate the raiding routes taken by colonies of *P. marginata* at different nest locations in the study area (symbols in each figure refer to different termite nests).

The raiding of a termite colony usually starts with a few ant workers leaving the nest in the same direction, and exhibiting trail-laying behavior. The signals employed by the ants to locate the termite nest are unknown. Once having found a termite nest, the ants immediately begin to excavate and penetrate into the nest. Shortly after the first scout ants return to their
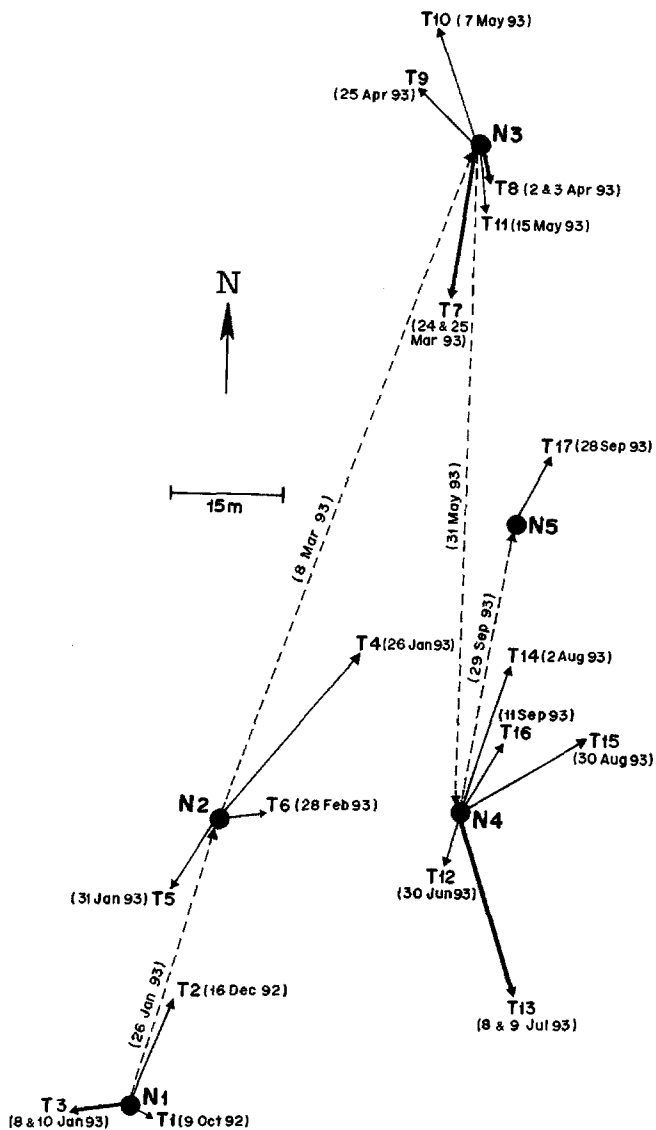
Fig. 4 Map showing the raiding and migration routes of colony 2 of *P. marginata*, from October 1992 to September 1993, in a forest site in south-east Brazil. (Key to symbols: *N1* ant nest before migration, *N2,3...* ant nests after migrations, *T1,2...* raided termite nests). *Dashed arrows* indicate migration routes, and *solid arrows* show raiding routes. *Thick arrows* show routes to termite nests which were raided twice. Termite nests are different from those shown in Fig. 3
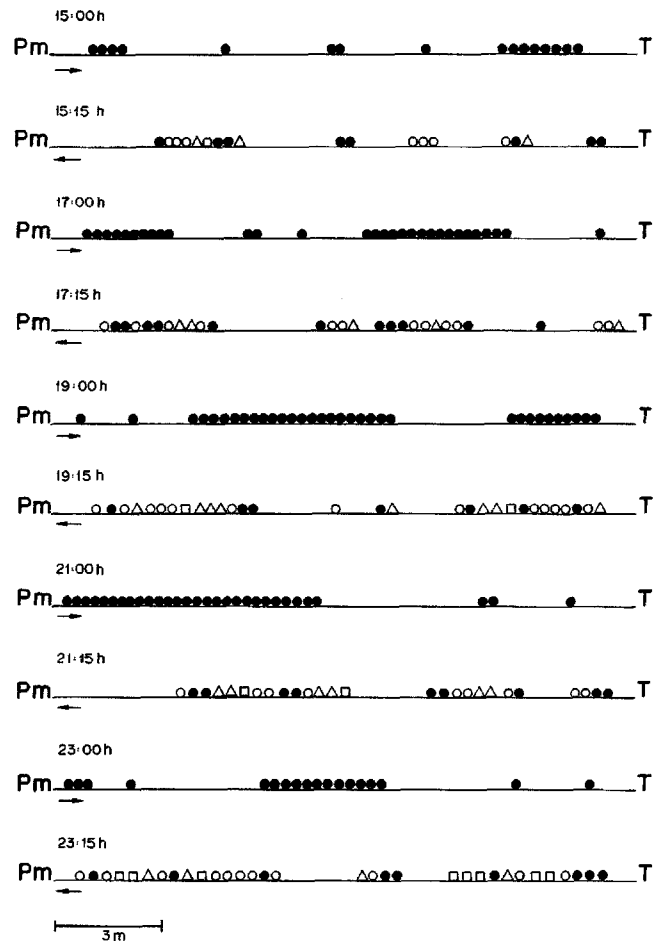

Fig. 5 Snapshot records at 2-h intervals of a column (15 m) of *P. marginata*, showing the spatial distribution of ants during the raiding of a termite nest of *Neocapritermes opacus*. Ant movement is always in both directions, but records of outward-bound (*right arrow*) and returning (*left arrow*) ants were taken separately. (Key to symbols: *Pm* ant nest, *T* termite nest, ● ants with no prey, o ants carrying one termite worker, Δ ants carrying two termite workers, □ ants carrying one termite soldier). Note that termite soldiers are captured in greater numbers during the final phase of the raid

nest, a column of ants emerges from it and follows the same trail. On their way to the termite nest the ants frequently antennate with the returning nestmates, and the whole recruiting process may last 2–4 h (mean ± SD = 3.44 ± 1.02 h, *n* = 8 raids) before the first termites are captured by the ants. Ants arrive at the target termite nest in groups of 10–30 individuals (23.33 ± 20.26, *n* = 8 raids), seize one or two paralysed prey within their mandibles, and return to the nest in groups (Fig. 5). Nearly 1600 termites are captured during a 9-h raid (1617 ± 275, *n* = 3 raids). Termite castes are captured by the ants at a mean proportion of 1 soldier to 12.70 ± 3.15 workers (*n* = 3 raids). The

proportion of soldier to worker termites being captured changes from nearly 1:28 at the beginning of the raid to 1:2 during its final phase (see also Fig. 5).

The marking of raiding ants indicated that nearly 20% of the workers from a single colony are engaged in foraging activities. The speed with which the ants walk along the raiding column increases significantly with time (beginning of raid: mean ± SD = 1.64 ± 0.39 m/min, *n* = 8; end of raid: 4.49 ± 0.62 m/min, *n* = 8; *t*-test: *t* = −11.09, *df* = 14, *P* < 0.0001; Fig. 6A), probably due to the progressive accumulation of recruiting pheromone deposited on the trail. At the beginning of the raiding process the number of ants returning to the nest is significantly smaller than the number of ants leaving it (leaving: mean ± SD = 35.58 ± 6.57 ants, *n* = 8; returning: 14.95 ± 4.88 ants, *n* = 8; *t*-test: *t* = 7.13, *df* = 14, *P* < 0.0001), while during the final phase the opposite occurs (leaving: mean ± SD =
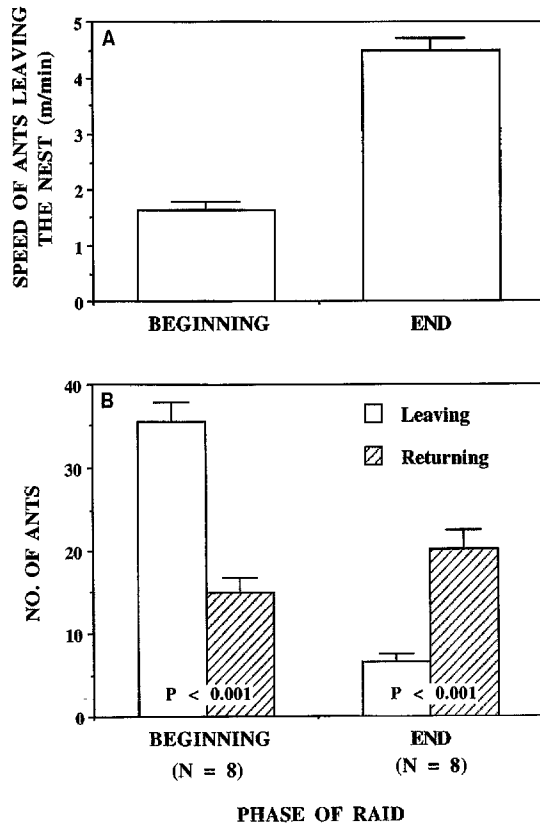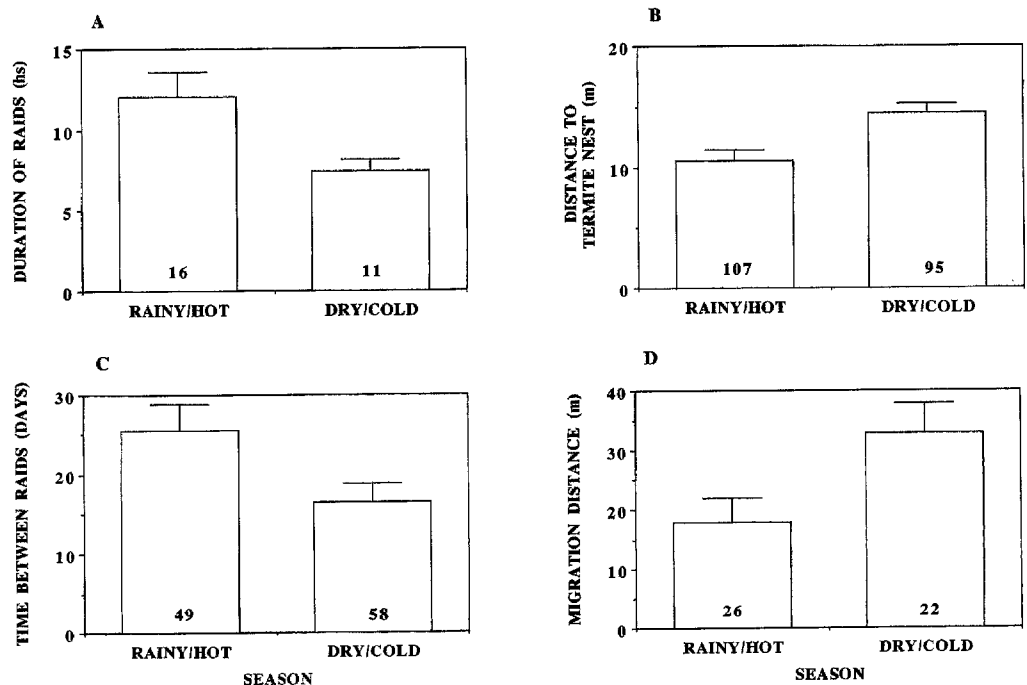
Fig. 6A, B Performance and quantity of *P. marginata* workers at different phases of raiding activity. **A** Speed of ants along the raiding column. **B** Number of ants walking in either direction along the raiding column. Data are means + SE

remain inside the termite nest, probably paralysing and storing prey. This suggestion is further supported by our observations on marked ants along the raiding column. After having marked all ants seen along the hunting column, unmarked ants emerged from the raided termite nest only at the final phase of the raid.

Raids on termite nests occurred both day and night, and could last for more than 24 h ($n = 27$ raids). Raids lasted significantly longer during the rainy/hot season than in the dry/cold season (rainy/hot: mean ± SD = 12.03 ± 6.21 h, $n = 16$; dry/cold: 7.45 ± 2.21 h, $n = 11$; t-test: $t = 2.61$, $df = 20, 6$, $P < 0.02$; Fig. 7A). The distance between a colony of *P. marginata* and a target termite nest varied from 0.12 to 38 m ($n = 202$ raids). The raids covered significantly shorter distances in the rainy/hot season than in the dry/cold season (rainy/hot: mean ± SD = 10.60 ± 7.86 m, $n = 107$; dry/cold: 14.42 ± 8.90 m, $n = 95$; t-test: $t = -3.21$, $df = 200$, $P < 0.002$; Fig. 7B). Colonies hunted more frequently in the dry/cold season (rainy/hot: mean ± SD = 25.43 ± 24.03 days, $n = 49$; dry/cold: 16.41 ± 18.29 days, $n = 58$; t-test: $t = 2.15$, $df = 88, 6$, $P < 0.04$; Fig. 7C).

6.51 ± 2.83 ants, $n = 8$; returning: 20.19 ± 6.55 ants, $n = 8$; t-test: $t = -5.42$, $df = 9, 5$, $P < 0.001$; Fig. 6B). This difference may indicate that some raiding ants

Migratory behavior in *P. marginata*

Migration by colonies of *P. marginata* was recorded on 48 occasions in the study area. Nest relocations lasted over 2 days and covered distances of 2–97 m ($n = 48$). Migration distances were significantly shorter in the rainy/hot season (rainy/hot: mean ± SD = 17.96 ± 20.16 m, $n = 26$; dry/cold: 32.86 ± 23.76 m, $n = 22$; t-test: $t = -2.35$, $df = 46$, $P < 0.03$; Fig. 7D). The mean

Fig. 7A–D Seasonal parameters concerning raiding and migratory activity of *P. marginata* colonies in a forest site in south-east Brazil. **A** Duration of raid. **B** Distance to raided termite nest. **C** Time between raids. **D** Migration distance. Data are means + SE. *Numbers inside bars* refer to sample sizes
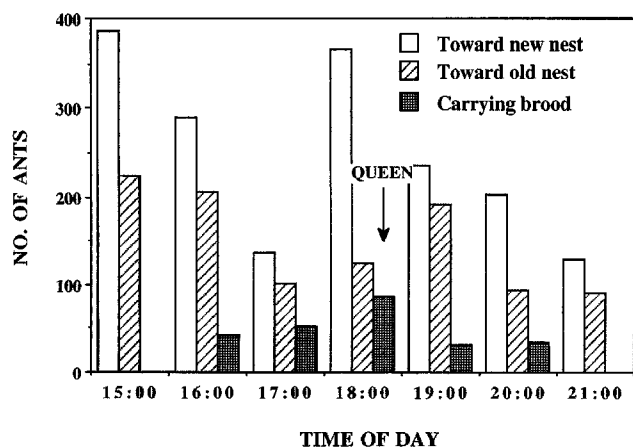
Fig. 8 Snapshot records of part (7 h) of the migratory process of a *P. marginata* colony. Data represent the migration of colony 2 on 29 September 1993. The *arrow* indicates the time the queen moved to the new nest

residence time of ant colonies at a given location was 150.97 ± 91.48 days (based on 17 migratory events from six marked colonies).

The behavioral description provided below is based on partial observations of 17 migratory events (the whole migration process was observed in greater detail for colonies 33 and 2). Migrations usually started in the afternoon and continued throughout the night until the next morning. Sometimes the migratory process was interrupted in the middle of the day and resumed in the following evening. Pupae, larvae and eggs are transported to the new nest by the workers; alates and the queen migrate by themselves but are closely followed by many worker nestmates all the way to the new nest.

Figure 8 illustrates part (7 h) of the migratory process of colony 2 on 29 September 1993; the new nest site was located 42 m away from the old one. At the beginning of our observations (1500 hours) many workers were already actively excavating the new nest. Only workers were observed along the trail; the ants walked very slowly in a single column and exhibited trail-laying behavior. At 1600 hours the eggs began to be transported by the workers, being deposited next to the entrance of the new nest (mean ± SD = 3.7 ± 2.5 eggs per ant, *n* = 41 ants). Additional brood (pupae, larvae and eggs) were successively transported and deposited in the same place (Fig. 8). At 1800 hours alates (males and females) and the dealated queen were closely followed to the new nest by an aggregation many workers. At 2100 hours some workers were still transporting larvae (Fig. 8). The migration to the new nest site continued throughout the night and in the next morning no traffic of ants could be seen anymore. At 0900 hours all ants were already in the new nest and the migration process was complete. The old nest was excavated and no ants were found inside it.

Discussion

The field data revealed that colony founding in *P. marginata* can be remarkably diverse. New colonies can potentially originate from a single foundress (haplometrosis), groups of two to seven foundresses (pleometrosis), or even by colony fission. Pleometrotic associations comprised 82% of the founding events recorded in the field, and data on persistence of incipient colonies revealed that such a strategy is much more successful than solitary founding. Similar results have been reported for several other ant species (Bartz and Hölldobler 1982; Hölldobler and Carlin 1985; Rissing and Pollock 1988; and citations therein). Although we have not tested the factors that could be promoting pleometrotic advantage in *P. marginata*, our field observations indicate that associated queens are more likely to be assisted by resident workers during colony founding than isolated foundresses (see also Hölldobler and Carlin 1985). The presence of workers at initial stages of colony development presumably may result in better protection of the incipient colony against predators (Greaves and Hughes 1974), greater ability to overcome unfavorable physical conditions, and increased foraging efficiency. Although we have no data on hunting success by incipient colonies of *P. marginata*, it is possible that pleometrotic colonies produce a larger initial worker force more rapidly than haplometrotic ones, and therefore enjoy an advantage in raiding termite nests. Available data from pleometrotic species with inter-colonial raiding behavior indicate that the rapid production of a larger worker force by incipient colonies makes them more successful at brood raids and territorial fights against other colonies (Bartz and Hölldobler 1982; Tschinkel and Howard 1983; Rissing and Pollock 1987).

The colony founding data, the fact that most of the excavated nests of *P. marginata* contained more than one dealated female in the mature colony, and the occurrence of colony budding, strongly suggests that this species is facultatively polygynous in nature. The occurrence of more than one queen in colonies of *P. marginata* would be particularly important if there is an associated risk of queen loss during the migratory process (see below). A shift in the frequency distributions of the number of queens from initial to later stages of colony development (see Fig. 2, Table 1) may suggest some type of elimination of supernumerary queens as the colony grows (see Hölldobler and Wilson 1977). Unfortunately, we have no data on this for *P. marginata*. However, the execution of initial co-foundresses has recently been recorded in pleometrotic colonies of the ponerine ants *Pachycondyla villosa* and *Gnamptogenys* sp. (P. S. Oliveira, unpublished work). When collected in the field, the incipient colony of *P. villosa* contained 2 queens, 5 workers and 3 eggs, while that of *Gnamptogenys* had 2 queens, 3 workers, 2 pupae and 5 eggs. The queens coexisted peacefully

in the laboratory for 5 months in the *P. villosa* colony (15 workers, 8 larvae, 5 pupae, 15 eggs), and for 2 months in the *Gnamptogenys* colony (9 workers, 5 pupae, 3 larvae, many eggs). In both colonies one of the queens was dragged off the nest by 2–3 workers, being fiercely attacked and mutilated to death in the foraging arena. The remaining queen of *Gnamptogenys* also joined the workers in the elimination of the rival queen (see also Ward 1981; Bartz and Hölldobler 1982; Rissing and Pollock 1988; Keller et al. 1989).

The hunting behavior of *Pachycondyla marginata* is similar to that of other obligate termitophagous ants. A group of leader ants locates a termite nest and organizes the raid through conventional recruitment, as also reported for *P. laevigata* (Hölldobler and Traniello 1980a). For other termite-hunting species, the raiding process can be initiated by a single leader ant who locates the termite nest and initiates the raiding process after the recruitment of nestmates, as reported for *Megaponera foetens* (Fletcher 1973; Longhurst and Howse 1979; Lepage 1981), *Leptogenys chinensis* (Maschwitz and Schönegge 1983), and *Decamorium uelense* (Longhurst et al. 1979b). Group-raids to termite nests by the neotropical species *Pachycondyla commutata* can be initiated either by a group of foragers or by a solitary leader ant (Wheeler 1936; Mill 1982b, 1984). However, some obligate termitophagous ponerines are strict solitary hunters, and no cooperation among foragers is ever observed (Peeters and Crewe 1987).

As opposed to most obligate termitophagous ants, which may include several species and genera of termites in their diets (even from different families), *P. marginata* presented a high degree of prey specialization and only raided colonies of the termite *Neocapritermes opacus* (*n* = 202 raids). Prey specificity by *P. marginata* does not seem to be a function of the study area (we recorded six termite species nesting within roots and rotting wood along a 50-m transect). In fact, the geographical distributions of *P. marginata* and *N. opacus* largely overlap (cf. Kempf 1972; Krishna and Araujo 1968). In his faunal studies in the Amazon Basin, where more 40 termite species were recorded in each of three localities (1 ha surveyed at each site), Mill (1982b) reports that *P. marginata* preys on two species of *Neocapritermes*, *N. opacus* being the principal prey. Krishna and Araujo (1968) also mention that *N. opacus* is frequently preyed upon by *P. marginata*, and further report that the asymmetrical snapping mandibles of the termite soldier can toss the ant up to 20 cm.

As also reported for many other predatory ponerines, including non-termitophagous ones (see Hölldobler 1982; Steghaus-Kovac and Maschwitz 1993), *P. marginata* workers paralyze their prey before storing them in the nest. Several termitophagous species (obligate or not) show this behavior and it is possible that the storage of prey by paralysis allows the ant colony to overcome less favorable climatic conditions affecting hunting success (Hölldobler 1984; Maschwitz and Schönegge 1983; Hölldobler and Wilson 1990).

There seems to be a division of labor among *P. marginata* workers during raids on termite nests. Nearly 20% of the workers in a colony are involved with the hunting activity, and foraging ants are apparently engaged with different tasks (paralyzing or transporting prey) while raiding a termite nest. Similar behavioral patterns have been described for other termitophagous species such as *P. laevigata*, *P. commutata*, *Megaponera foetens* and *Decamorium uelense* (Hölldobler and Traniello 1980a; Mill 1982b; Longhurst et al. 1978, 1979a, b; Longhurst and Howse 1979).

The orientation of *P. marginata* workers during both hunting and nest relocation seems to rely on odour trails. As demonstrated for the related species *P. laevigata* by Hölldobler and Traniello (1980a), the trail pheromone in *P. marginata* also originates from the pygidial gland (Hölldobler et al. in press). The pygidial gland is widely employed in the Ponerinae, and in *Pachycondyla* species its secretions may be used during nest relocations and recruitment to food sources (Hölldobler and Traniello 1980b; Traniello and Hölldobler 1984).

The migratory behavior of *P. marginata* is similar to that described for the closely related termite-hunters *P. laevigata* and *P. commutata* (Hölldobler and Traniello 1980a; Mill 1982a), as well as for other group-raiders such as *Megaponera foetens* and *Leptogenys* spp. (Fletcher 1973; Longhurst and Howse 1979; Maschwitz and Schönegge 1983). However, the migratory behavior of *P. marginata* differs from *Leptogenys* sp. 1 in that in the latter species the males are carried by the nestmates, and the queen is not protected by the workers during migration (Maschwitz et al. 1989)

As opposed to other species which may relocate their nests every few days, migration by *P. marginata* colonies is less frequent, with a residence time of approximately 150 days. Colonies of *P. marginata* are relatively large compared to other ponerines (see Peeters 1993), and their nests may have several chambers 1.5 m below the ground surface. According to Smallwood (1982), species with large colonies tend to relocate their nests less frequently since they are better able to keep stable temperature and humidity conditions inside the nest. Moreover, colonies of *P. marginata* spend a considerable time (several hours) excavating the new nest as the migration proceeds. These characteristics suggest that migration is costly for *P. marginata*. On the other hand, for some *Leptogenys* species whose nest sites are rarely modified by the ants (i.e., leaf litter, rotten logs, ground cavities), nest relocation may be as frequent as more than once a week (Maschwitz and Schönegge 1983; Maschwitz et al. 1989).

There are three basic patterns of nest relocations in *P. marginata*.

1. Colony fission: only part of the colony migrates and a new nest is established away from the parental colony (Fig. 3).

2. Short-distance relocations: migration distances are shorter than those covered during raids to termite nests.

3. Long-distance relocations: migration distances are greater than those covered during raids to termite nests (Fig. 4).

Most authors have proposed that the search for new food sources would be one of the main stimuli for nest relocation in ants (e.g., Schneirla 1971; Gotwald 1982; Franks and Fletcher 1983; Maschwitz and Hänel 1985; Maschwitz et al. 1989). For *P. marginata*, however, this may not always be the case, since we have observed nest relocations over very short distances. On several occasions, especially after rains, we have observed the ants removing dead termites from their nests (see also Peeters and Crewe 1987), and one might speculate whether the progressive decaying of termite prey inside the nest chambers could stimulate nest relocation by *P. marginata* colonies. In this case migratory behavior could prevent the dissemination in the colony of pathogens associated with rotten termites (e.g., fungi and/or bacteria). This hypothesis could be tested in the laboratory using groups of colonies being reared in nests with different sanitary conditions. In fact, short-distance relocations have been related to factors such as: (1) environmental fluctuations provoking flood, drought, and shading by vegetation (Cole 1940; Talbot 1946; Brian 1965); (2) fungal and bacterial growth resulting from the accumulation of debris in the nest (Brian 1965; Brian et al. 1966); (3) avoidance of parasites and predators (Brian 1952, 1956).

Group-raids and migrations by *P. marginata* colonies covered greater distances during the dry/cold season, and this may be related to a decrease in the availability of termites during this season (cf. Wilson 1971). For instance the African termite-hunter *Decamorium uelense* (Myrmicinae) preys on *Microtermes* during the wet season, but includes a range of soft-bodied insects during the dry season, when termites are less abundant (Bolton 1976; Longhurst et al. 1979b). Although this type of variation was not observed in the diet of *P. marginata* at the Santa Genebra Reserve, it is commonly reported for other termitophagous ants (Hölldobler and Wilson 1990).

Wilson (1958) characterized the behavior of the "army ants" as a combination of two diagnostic traits: nomadism or migratory behavior and group predation. These two traits have reached their highest development in the subfamilies Dorylinae and Ecitoninae. So-called army ant behavior also exists, at least to a limited extent, in the subfamilies Ponerinae, Leptanillinae and Myrmicinae (Hölldobler and Wilson 1990). This idea originated with the observations of Wheeler (1910) on the raiding behavior of certain ponerine species, and is

supported by recent field studies (e.g., Maschwitz and Schönegge 1983; Maschwitz et al. 1989; Moffett 1984).

One distinctive feature of the "true army ants" is the correlation between brood development and the change between migratory and stationary phases (Fletcher 1973; Franks and Fletcher 1983). Such a synchronization is not observed in the migratory pattern of *P. marginata*, which seems to depend largely on climatic factors. Moreover, as opposed to the massive group raiding exhibited by ecitonine and doryline ants, *P. marginata* employs conventional group recruitment by successful scouts to organize its raids to termite nests (see above).

A predetermined foraging pattern has been reported in *Eciton burchelli* (Franks and Fletcher 1983) and *Leptogenys* sp. 1 (Maschwitz et al. 1989), and is related with the avoidance of own (or other's) previous raiding paths. Due to the extremely specialized diet of *P. marginata*, the raiding routes taken by its colonies may depend largely on the location of the nests of its sole prey, *Neocapritermes opacus*. The re-utilization of the same raiding route apparently does not lead to an immediate depletion of prey by *P. marginata*, since a given ant colony can raid the same termite nest at different occasions within a short period of time (see Figs. 3, 4).

The current field study showed that in spite of exhibiting both group-predation and migratory behavior, *P. marginata* also possesses several characteristics that differentiate it from the true army ants of the subfamilies Ecitoninae and Dorylinae. The extremely specialized diet of *P. marginata* (one termite species) and the associated high costs of migration (excavation of a deep subterranean nest) are features likely to prevent it from evolving a full army ant life pattern. More detailed field studies with other species presenting rudimentary army ant behavior are needed in order to understand the evolutionary steps leading to the true army ant habit.

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