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**Behavioral Ecology and Sociobiology**


# Dominance orders in the ponerine ant *Pachycondyla apicalis* (Hymenoptera, Formicidae)

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**Summary.** Intracolony aggression among workers of the neotropical ponerine ant species *Pachycondyla apicalis* leads to dominance orders. Antagonistic interactions can entail either overt physical attacks with the subordinate individual often exhibiting a submissive posture or the robbing and destruction of eggs laid by nestmates. The single queen, however, was never observed either attacking or being attacked by any colony member. The hierarchical structure among workers consists of one dominant individual and several subordinates; the relationships among subordinate workers are unclear, however. We report for the first time a natural (nonmanipulated) change in the social status of individuals within an ant dominance order. Dominant workers usually had better developed ovaries, laid more eggs and were more frequently observed attending the egg pile than subordinate individuals. This pattern became even more striking when the queen was excluded from the colony. These results indicate that workers of *P. apicalis* lay eggs even in the presence of the queen. It is possible that some of these haploid eggs may develop into males.

## Introduction

In a wide variety of social animals dominance orders are established as a result of agonistic encounters between group members. Such dominance patterns usually reflect the competitive abilities of individuals, with an individual's fitness being strongly influence by its rank within the group (Wilson 1975a). Although studied in greater detail and more widely in vertebrate societies (cf. Dewsbury 1982), dominance orders are also known from invertebrate species and are best documented in primitively organized social insects, such as bumblebees and paper wasps (Pardi 1946; Röseler 1985; Wilson 1971; West-Eberhard 1969), and more recently also in ants (Cole 1981; Franks and Scovell 1983).

Within most hymenopteran societies all females can potentially lay eggs, but the extent to which they do this is determined largely by dominance rank (Wilson 1971). In the primitively eusocial paper wasps (*Polistes*), for example, one or a few highly ranked individuals establish reproductive dominance by direct aggressive behavior toward the other wasps in the nest. This results in an order of ranking involving a principal egg-layer and the remainder of the associated females, who not only lay eggs less frequently but also take the role of workers (Pardi 1948; West-Eberhard 1969). However, in the more advanced insect societies, particularly those with strongly differentiated queen and worker castes, the queen usually controls reproduction in other colony members by means of inhibiting pheromones rather than by overt aggression (Fletcher and Ross 1985; Hölldobler and Bartz 1985; Wheeler 1986).

Very little information exists, however, concerning the mechanisms that regulate reproductive behavior in the phylogenetically more primitve ant species in which queen-worker dimorphism is only weakly developed (see Peeters 1987; Fukumoto et al. 1989; Peeters and Higashi 1989). In this paper we show that agonistic interactions among workers of the primitive ponerine ant *Pachycondyla apicalis* lead to the formation of dominance orders, which ultimately result in a differential production of eggs by individual workers. Data were collected both in the presence and in the absence of the queen. The unstable nature of the observed dominance orders enabled us to describe the behavioral means by which an individual worker may ascend in rank and dislodge the leading worker from her top position in the hierarchy.

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## Materials and methods

The colony of *P. apicalis* used in this study was collected in lowland rainforest at Estacion Biologica La Selva, Costa Rica, March 1989. The ants were cultured at 20°–25° C in the laboratories of the Museum of Comparative Zoology, Harvard University. The artificial nest consisted of 3 glass test tubes (2.2 cm diameter × 15 cm) containing water trapped behind a cotton plug. Nest tubes were placed in a box (32 × 23 cm) where the ants foraged for insect parts, diluted honey and synthetic ant diet (Bhatkar and Whitcomb 1970). At the beginning of our observations the colony of *P. apicalis* consisted of 1 mated queen, 23 workers, 9 pupae, 7 larvae, and 23 eggs.

By July 1989 individual workers ($n = 28$) were marked with colored dots of gloss enamel paint (Testors, Rockford, IL, USA) on the thorax and/or gaster. The queen remained unmarked. Egg-laying by the queen and workers and agonistic encounters between ants were monitored intermittently from 9.00 to 18.00 h in observation sessions lasting 15–60 min. An encounter was considered aggressive whenever one of the interacting ants seized the other by an appendage, head, thorax or gaster, often followed by tugging movements. Matrices of dominance relationships were constructed based on agonistic encounters between different ant workers, and the probability of linearity within hierarchies was calculated according to the method of Appleby (1983). Each ant in the matrices (Tables 1, 2, 4) was seen at least once being attacked or attacking another ant. Ants having very low scores (e.g 1 or 2 interactions) were not ordered on any particular basis with respect to one another. Ants which were not seen interacting aggressively with others (either attacking or being attacked) were not included in the tables. The spatial distribution of aggressive interactions within the nest box was also recorded and categorized as follows: (1) near the egg pile, (2) elsewhere in the nest tubes, or (3) in the arena.

Whenever we noticed an individual in a typical egg-laying posture (gaster curved forward), we registered all aggressive interactions between the egg-layer and other ants, as well as the fate of the egg. An egg was considered successfully deposited provided that no ant ate it during a 20-min period following its deposition on the egg pile. After 20 min on the egg pile an egg was never seen to be eaten.

In order to determine whether the activities of individual ants differed according to their social status within the colony, snapshot records were taken at 1-h intervals (from 9.00 to 18.00 h). We registered whether the ant was at the egg pile (< 1 cm from the eggs) or at any place outside the nest tubes foraging or patrolling.

After the completion of our observations, the ovarian development of ants was determined from dissections performed on individuals killed by placing them for a few minutes in a freezer. The observer performing the dissections and scoring the ovarian development did not know the previous history of individual ants.

## Results

### *Dominance displays in Pachycondyla apicalis*

We noticed intracolony aggression in all four *P. apicalis* colonies cultured in the laboratory, but quantitive observations are based on one colony. Agonistic encounters between workers of *P. apicalis* were evident from the very beginning of our behavioral studies. The single queen, however, was never observed either attacking or being attacked by any colony member. In a typical aggressive episode, one worker approaches another quickly and seizes her usually by the antennae or legs, making vigorous tugging movements that may last from 5 to 15 s (Fig. 1). Encounters were normally frontal, but in some instances the aggressor also approached from the side or rear of the opponent. While being attacked an ant usually remained submissive and did not retaliate, although she often struggled to free herself (usually when the opponent attempted to hold her more firmly). Once having managed to break free, the subordinate ant usually walked away, rarely being pursued by her aggressor.

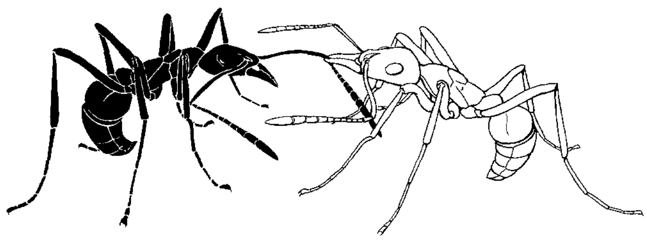


**Fig. 1.** A typical agonistic encounter between workers of *Pachycondyla apicalis*. The dominant ant (*white*) is pulling a nestmate by her antennae

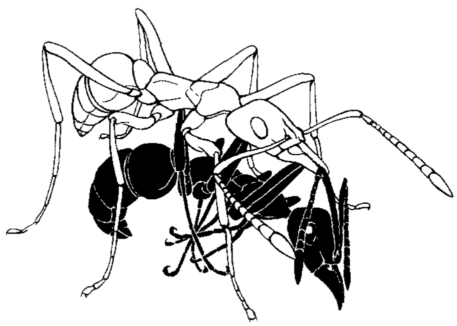


**Fig. 2.** Prolonged contest between workers of *Pachycondyla apicalis*. The dominant ant (*white*) attacks continuously the subordinate one (*black*), which assumes a pupal posture with the appendages tightly folded to the body

Prolonged contests occurred during the displacement of a worker from the top of the hierarchy (see below). In this case the once-dominant ant could be exposed to continuous attacks for up to 60 min, and she often responded by assuming a pupal posture, which appears to be an extreme submissive behavior (Fig. 2). Typically, the aggressor seized the opponent by the antennae or legs but sometimes also aimed her attacks at the head, thorax or gaster when the latter remained in a pupal posture. The strikes were vigorous, and the attacked worker could even be dragged around in the nest box. Occasionally a third ant joined such prolonged contests, in which case the submissive worker was simultaneously attacked by 2 nestmates. When released by its aggressor, the subordinate ant often remained in the pupal posture for 15–30 s before taking refuge in a safer place in the nest box (usually in a corner of the arena). These prolonged contests occurred many times within a period of 2–3 days, with the same ant worker being repeatedly attacked by several of her nestmates. The attacks were never found to cause any kind of physical injury or mutilation to any ant, irrespective of the duration or intensity of the contest.

**Table 1.** Dominance order (phase 1) constructed from observation of 55 interactions in a queenright colony of *Pachycondyla apicalis* over 5 h. The probability of a linear hierarchy occurring by chance is $P>0.9$ (K=0.05). Note that worker WRT was not attacked by any ant. The numbers refer to agressive interactions between workers

| Dominant ants | Subordinate ants | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | WRT | GBG | LGG | RBT | YTG | RRG | GRG | SIG | GTG | WTG | GOB | GRR | RTY | WBG | Total |
| WRT | X | 20 | 12 | | | | | | | | | 1 | 1 | 1 | 35 |
| GBG | | X | | 6 | 5 | 2 | 1 | | 1 | 1 | 1 | | | | 17 |
| LGG | | 2 | X | | | | | | | | | | | | 2 |
| RBT | | | | X | | | | 1 | | | | | | | 1 |
| YTG | | | | | X | | | | | | | | | | 0 |
| RRG | | | | | | X | | | | | | | | | 0 |
| GRG | | | | | | | X | | | | | | | | 0 |
| SIG | | | | | | | | X | | | | | | | 0 |
| GTG | | | | | | | | | X | | | | | | 0 |
| WTG | | | | | | | | | | X | | | | | 0 |
| GOB | | | | | | | | | | | X | | | | 0 |
| GRR | | | | | | | | | | | | X | | | 0 |
| RTY | | | | | | | | | | | | | X | | 0 |
| WBG | | | | | | | | | | | | | | X | 0 |
| Total | 0 | 22 | 12 | 6 | 5 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | |

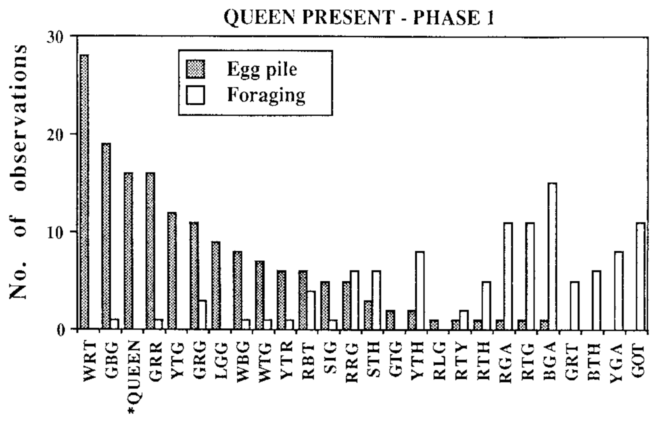
In the following series of observations we will demonstrate that the dominance order established as a consequence of such antagonistic interactions ultimately leads to differential production of eggs by individual workers. During these observations we witnessed a recordering of the dominance pattern among the workers. In order to document this temporal instability of the dominance structure better we present the data obtained prior to the experimental exclusion of the queen in 2 parts, which we label phase 1 and phase 2.

*Dominance orders in Pachycondyl apicalis*

*Queen present – phase 1*

Table 1 shows a dominance order based on 55 agonistic interactions between 14 workers of *P. apicalis* over 5.0 h of observation (phase 1, from 2 to 4 August 1989). Since the queen was never observed either attacking or being attacked by any ant, she is not included in the dominance matrix. Some 50% (14/28) of the workers in the colony were involved in the agonistic interactions. Attacks by worker WRT against workers GBG and LGG comprised 58% (32/55) of all the agonistic interactions observed in phase 1. Interestingly, worker WRT was never attacked by any ant within this period (Table 1). Snapshot records of the colony revealed that workers WRT and GBG and the queen were among the most frequently seen at the egg pile during phase 1, with virtually no foraging or patrolling activity (Fig. 3).

All agonistic interactions registered in phase 1 consisted of brief encounters between workers, as previously described and illustrated in Fig. 1. From 5 to 8 August, however, the general pattern of the contests between the ants changed markedly: Worker WRT began to be successively harassed by several nestmates, particularly



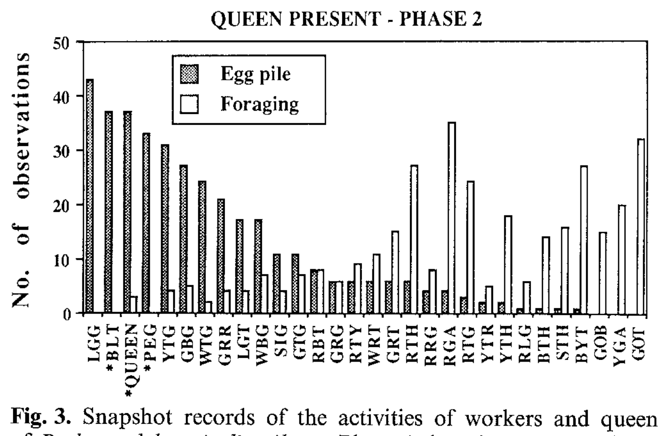




**Fig. 3.** Snapshot records of the activities of workers and queen of *Pachycondyla apicalis*. *Above*: Phase 1, based on 29 snapshots. *Below*: Phase 2, based on 66 snapshots. The queen and callow workers are indicated by *asterisks*. Compare the scores of workers WRT and LGG in both graphs

workers GBG and LGG. Contests between WRT and each of these two workers were usually of the prolonged type, with the former laying in pupal posture while being continuously attacked by her opponents (cf. Fig. 2). We

**Table 2.** Dominance order (phase 2) constructed from observation of 69 interactions in a queenright colony of *Pachycondyla apicalis* over 13 h. The probability of a linear hierarchy occurring by chance is $P > 0.9$ (K = 0.10). Note that 43 interactions (62%) were attacks by other ants on worker WRT. See also Table 1

| Dominant ants | Subordinate ants | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | LGG | GBG | WTG | GRR | SIG | GTG | STH | WRT | RTG | BGA | GRG | YTR | RGA | Total |
| LGG | X | 9 | | | | | | 10 | | 1 | 1 | | | 21 |
| GBG | 1 | X | 8 | 1 | | | | 17 | 2 | | | | | 29 |
| WTG | | | X | 1 | | | | 7 | | | | 1 | | 9 |
| GRR | | | | X | | | | 5 | | | | | | 5 |
| SIG | | | | | X | | | 3 | | | | | | 3 |
| GTG | | | | | | X | | 1 | | | | | | 1 |
| STH | | | | | | | X | | | | | | 1 | 1 |
| WRT | | | | | | | | X | | | | | | 0 |
| RTG | | | | | | | | | X | | | | | 0 |
| BGA | | | | | | | | | | X | | | | 0 |
| GRG | | | | | | | | | | | X | | | 0 |
| YTR | | | | | | | | | | | | X | | 0 |
| RGA | | | | | | | | | | | | | X | 0 |
| Total | 1 | 9 | 8 | 2 | 0 | 0 | 0 | 43 | 2 | 1 | 1 | 1 | 1 | |

**Table 3.** Egg production by a queenright colony of *Pachycondyla apicalis* containing 28 marked workers. Data are based on 20 h of observation, from 27 July to 18 August 1989

| Egg-laying ant | No. of eggs laid | No of eggs eaten by | | No. of eggs successfully deposited |
|---|---|---|---|---|
| | | Workers | Queen | |
| Queen | 5 | 0 | 0 | 5 |
| Workers | | | | |
| WRT | 2 | 1[a] | 0 | 1 |
| LGG | 3 | 3[a] | 0 | 0 |
| GBG | 1 | 0 | 1 | 0 |
| RRG | 1 | 0 | 1 | 0 |

[a] These eggs were eaten by the workers who laid them

consider this phenomenon as characteristic of a transitory period in the dominance structure of the colony, resulting in the establishment of a new hierarchical order among workers which will be described in phase 2.

*Queen present – phase 2*

A dominance order based on 69 agonistic encounters between 13 workers of *P. apicalis* over 13.0 h of observation is shown in Table 2 (phase 2, from 7 to 18 August). As in the previous phase, the queen did not take part in any of the contests registered in this period. Some 43% (13/30) of the workers in the colony were involved in the agonistic interactions. Worker WRT was constantly harassed by several nestmates, and attacks on her comprised 62% (43/69) of the interactions recorded, although she herself was never seen initiating an attack (Table 2). It is worth noting, however, that workers LGG and GBG were together responsible for 63% (27/43) of the attacks on WRT, and occasionally these attacks were carried out simultaneously by both nestmates. Incidentally, attacks involving these three ants in phase 1 were in the opposite direction (i.e., from WRT towards LGG and GBG; cf. Table 1). These changes are also reflected in the snapshot records of the activities of the workers in phase 2: Worker LGG, the queen, and two callow workers were now among the ants most frequently seen at the egg pile (Fig. 3). On the other hand, worker WRT was not as frequently at the egg pile and spent most of her time outside the nest (see Fig. 3).

The production of eggs by the queen and workers of *P. apicalis* is shown in Table 3. No aggessive interactions were recorded during egg-laying by either the queen or workers. All eggs laid by the queen were successfully deposited on the egg pile. On three occasions workers were observed picking up queen-laid eggs from the ground and depositing them on the egg pile. In contrast, only one worker egg (laid by WRT during phase 1) was successfully deposited on the pile. The others were either given to the queen or eaten by the egg-layers themselves (Table 3). The fact that two workers ate their own eggs was probably caused by a lack of protein in the ants' diet, for it never happened again once the quantity of insect food (beetle larvae, grasshoppers and cockroaches) given to the colony had been increased.

*Queen excluded*

The queen was removed from the colony on 19 August 1989. A 3-day interval was allowed before new observations on agonistic interactions between workers and snapshot records of the worker' activity were made. Table 4 shows a dominance order based on 194 interactions between 24 workers of *P. apicalis* over 32.0 h of observation (from 22 August to 20 September). Some 77% (24/31) of the workers in the colony were involved in the

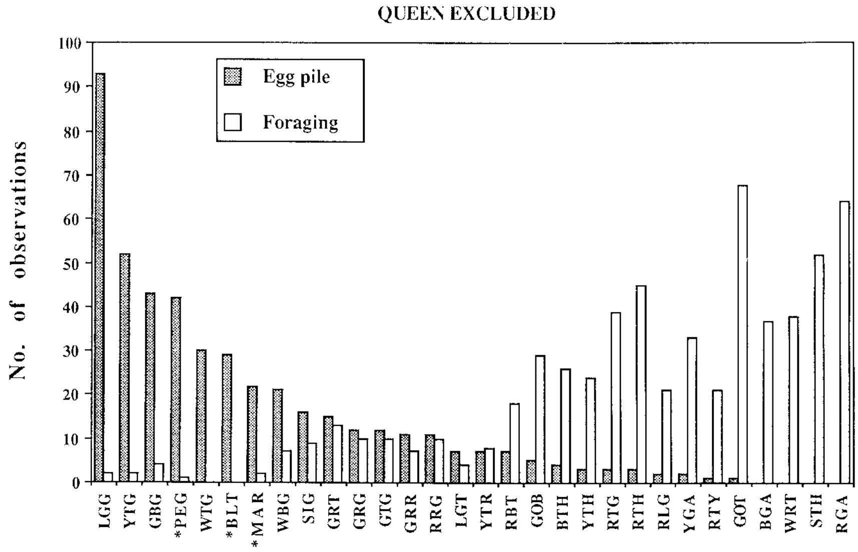



**Fig. 4.** Snapshot records ($n=132$) of the workers' activities of the *Pachycondyla apicalis* colony after the queen had been excluded. Callow workers are indicated by *asterisks*. Note the score of worker WRT and compare it with Fig. 3

agonistic interactions, a proportion significantly greater than those observed in the presence of the queen ($P<0.05$; $G=4.69$; df=1; when compared with phase 1; $P<0.01$; $G=7.37$; df=1; when compared with phase 2; G-tests). Worker LGG was not attacked by any ant and directed 69% (24/35) of her attacks towards worker GBG. Interestingly, in the previous observations (queen present, phase 2) these were the two ants who most frequently attacked worker WRT when the latter was being dislodged from the top of the hierarchy (see Table 2). In the new situation worker WRT continued being attacked by several ants and was never observed harassing any of her nestmates (Table 4). Snapshot records of the workers' activities after the queen had been excluded revealed that worker LGG stayed most frequently at the egg pile, while WRT was recorded only outside the nest tubes (Fig. 4).

The spatial distribution of agonistic interactions between workers of *P. apicalis* is shown in Table 5 for the period in which the queen was present (phases 1 and 2 grouped) and after her exclusion. Only 6% of the interactions occurred in the arena in either situation, but contests taking place inside the nest tubes were more scattered in the absence of the queen ($P<0.001$; $G=36.14$, df=2; G-test). Agonistic interactions occurred at equal rates in the presence (6.9 contests per hour) and absence of the queen (6.1 contests per hour), and such differences in the spatial distribution of the contests are probably due to the fact that workers were themselves more scattered within the nest tubes after the queen had been excluded ($P<0.01$; $Z=-2.833$; $n=21$; Wilcoxon's signed ranks test).

The production of eggs by workers with in a period of 3 weeks in the absence of the queen is summarized in Table 6. Data on egg production are based on 93.0 h of diurnal and 10.5 h of nocturnal intermittent sessions. In contrast to the lack of aggression associated with egg-laying in the presence of the queen, aggressive interactions between the egg-laying workers and their nestmates were extremely common in her absence, enhancing the disproportionate contribution of eggs among workers of different social status. Ants took $21.4 \pm 8.3$ min ($X \pm SD$; $n=18$) to lay an egg, during which they were highly vulnerable to attacks from other workers. Typically, attacks toward egg-layers consisted of mandibular strikes which were obviously aimed at robbing the egg. If the aggressor succeeded, the egg was eaten immediately. A total of 28 eggs were laid during observation sessions, 12 of which were eaten by the workers and 16 successfully deposited on the egg pile (Table 6). On 4 occasions a robber was seen pulling an egg directly out of the nestmate's gaster (Fig. 5), while in 4 other instances the egg was stolen from the egg-layer's mandibles. In either situation the strikes were vigorous and were usually followed by antennation bouts between the egg-layer and her opponent. While laying eggs workers conspicuously avoided encounters with nestmates, and on several occasions egg-laying workers were seen fleeing to the arena as a result of attacks in the nest tubes.

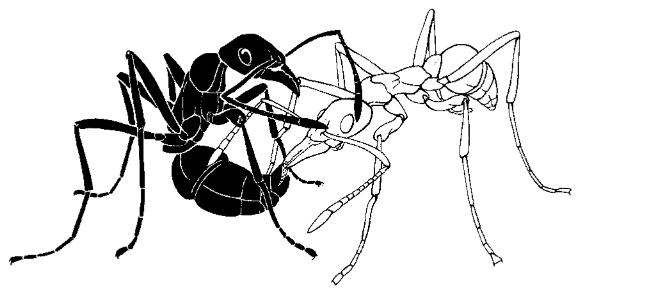


**Fig. 5.** Worker (*white*) of *Pachycondyla apicalis* pulling an egg out of the gaster of a nestmate (*black*). The egg eventually will be eaten by the aggressor

In the nest tubes workers constantly manipulate the egg pile, and on three occasions recently laid eggs were destroyed by inspecting ants soon after they had been deposited on the pile. 7 workers were observed laying eggs, 39% (11/28) of which were laid by worker LGG. The latter was also the most aggressive ant toward egg-

**Table 4.** Dominance order constructed from observation of 194 interactions over 32 h, in a colony of *Pachycondyla apicalis* from which the queen had been excluded. The probability of a linear hierarchy occurring by chance is $P > 0.5$ (K = 0.09). Note that workers LGG was not attacked by any ant. See also Tables 1 and 2

| Dominant ants | Subordinate ants | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | LGG | GBG | YTG | GRT | WBG | WTG | RLG | YTR | GRG | GTG | RRG | WRT |
| LGG | X | 24 | 1 | | 2 | 4 | | | | | | 2 |
| GBG | | X | 4 | | 5 | 24 | 1 | 2 | 1 | 1 | | 9 |
| YTG | | | X | 3 | 11 | | | 1 | 6 | 1 | 1 | 1 |
| GRT | | 1 | 7 | X | 6 | 11 | 1 | | | 2 | | |
| WBG | | 10 | | | X | | | 1 | | 1 | | 3 |
| WTG | | | 8 | | | X | | | 1 | | | 2 |
| RLG | | | | | | | X | | | | | |
| YTR | | | | | | | | X | | | | 2 |
| GRG | | | | | | | | | X | | | |
| GTG | | | | | | | | | | X | | 1 |
| RRG | | | | | | | | | | | X | |
| WRT | | | | | | | | | | | | X |
| GRR | | | | | | | | | | | | |
| SIG | | | | | | | | | | | | |
| RBT | | | | | | | | | | | | |
| LGT | | | | | | | | | | | | |
| RGA | | | | | | | | | | | | |
| RTG | | | | | | | | | | | | |
| YTH | | | | | | | | | | | | |
| RTH | | | | | | | | | | | | |
| BTH | | | | | | | | | | | | |
| PEG | | | | | | | | | | | | |
| BLT | | | | | | | | | | | | |
| MAR | | | | | | | | | | | | |
| Total | 0 | 35 | 20 | 3 | 24 | 39 | 2 | 4 | 8 | 5 | 1 | 20 |

**Table 5.** Spatial distribution of aggressive interactions between workers of *Pachycondyla apicalis*. Data are based on 124 interactions over 18 h of observation in the presence of the queen and 194 interactions over 32 h of observation in her absence. For further explanation see text

| Condition | Number of aggresssive interactions | | | *P* (G-test) |
|---|---|---|---|---|
| | Egg pile | Other parts of the nest | Arena | |
| Queen present | 92 | 25 | 7 | <0.001 |
| Queen excluded | 81 | 102 | 11 | |

**Table 6.** Egg production by workers of *Pachycondyla apicalis*. The observations started 14 days after the queen had been excluded from the colony and comprised 103.5 h from 2 to 22 September 1989

| Egg-laying worker | No. of eggs laid | No. of eggs eaten by others | No. of eggs of others eaten | No. of eggs successfully deposited |
|---|---|---|---|---|
| LGG | 11 | 0 | 10 | 11 |
| WTG | 6 | 5 | 0 | 1 |
| GBG | 4 | 2 | 0 | 2 |
| WBG | 3 | 2 | 0 | 1 |
| GRT | 2 | 1 | 1 | 1 |
| YTG | 1 | 1 | 1 | 0 |
| RLG | 1 | 1 | 0 | 0 |

layers, stealing and eating a total of 10 eggs laid by other workers. On the other hand, worker LGG was never observed being harassed by any ant, and all her eggs were successfully deposited on the egg pile, comprising 69% (11/16) of the net egg production by workers in the absence of the queen (Table 6).

*Ovarian development*

After terminating the observations, we dissected 26 workers in order to assess the developmental stages of the ovaries. The results are given in Table 7. All workers possessed 6 ovarioles, all of which contained yellow bodies indicating that eggs had been produced, but in no case did we detect sperm in the spermatheca. Worker LGG clearly had the best developed ovaries. This fact correlates well with LGG's dominant status when the observations were terminated. However, it is not obvious why LGG directed most of its attacks toward GBG whose ovaries were only weakly developed. On the other hand 5 workers among the top 11 individuals of the dominant group (see Table 4) carried at least one mature oocyte, whereas in none of the bottom 13 workers could

| Subordinate ants | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GRR | SIG | RBT | LGT | RGA | RTG | YTG | RTG | BTH | PEG | BLT | MAR | Total |
| | | | | 1 | | | | | | 1 | | 35 |
| | | | | | | | | | | | | 47 |
| 2 | 3 | 3 | 2 | 1 | 1 | | 1 | 2 | 4 | | 4 | 47 |
| | 1 | 1 | | | | 1 | | | | | 1 | 32 |
| | | | | | | | | | | | | 15 |
| | | | | | | | | | | | | 11 |
| | | | | 2 | | | | | | | | 2 |
| | | | | | | | | | | | | 2 |
| | | | | | | 1 | | | | | | 1 |
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| | | | | | | | | | | | X | 0 |
| 2 | 4 | 4 | 2 | 4 | 2 | 2 | 1 | 2 | 4 | 1 | 5 | |

**Table 7.** Data on ovarian development of workers ($n=26$) of *Pachycondyla apicalis*. All workers had 6 ovarioles, and in no case was sperm found in the spermatheca

| Worker | No. of oocytes |
|---|---|
| LGG | 2 mature, 4 half-sized, many tiny ones |
| WTG | 1 mature, 1 half-sized, many tiny ones |
| GBG | 2 tiny ones |
| WBG | many tiny ones |
| GRT | 2 mature, 2 tiny ones |
| YTG | 1 mature, 5 tiny ones |
| RLG | a few tiny ones |
| RRG | 2 mature |
| GRG | 1 tiny one |
| All others[a] | 0 |

[a] WRT, GRR, GTG, LGT, RGA, RTY, GOB, YTH, RTH, BTH, SIG, YTR, RTG, RBT, BLT, PEG, MAR

we detect any developing oocyte. It is possible that the three exceptions in the top group (GBG, RLG, GRG) were younger workers whose ovaries were still developing, although the presence of yellow bodies indicates that they had laid eggs previously. Nevertheless, these data indicate that generally the most dominant worker have the best developed ovaries. Like the workers, the queen of *P. apicalis* possessed only 6 ovarioles, but the spermatheca was inseminated.

## Discussion

Antagonistic behavior within ant colonies has been documented for several species in different subfamilies (e.g., Wilson 1974, 1975b); Fowler and Roberts 1983; Hölldobler and Taylor 1983; Wilson and Brown 1984; Evesham 1984; Hölldobler and Carlin 1985; Peeters and Higashi 1989; Heinze and Smith 1990). The establishment of dominance hierarchies among worker ants has been shown in *Leptothorax* (Cole 1981), *Harpagoxenus* (=*Protomognathus*) *americanus* (Franks and Scovell 1983) and *H. sublaevis* (Bourke 1988a). Such hierarchies among workers are explained in terms of competition for the production of sons within the colony, and Cole (1981) showed that highranking *L. allardycei* workers produce more than 20% of all eggs in the queen's presence. In *H. americanus*, Franks and Scovell (1983) have shown that the queen solicits food preferentially from high-ranking workers, possibly to limit their production of eggs. The destruction of eggs associated with reproductive competition among nestmates has also been shown in colonies of paper wasps (West-Eberhard 1969) and honeybees (Ratnieks and Visscher 1989). The relevance of worker reproduction for colony organization and function in eusocial hymenopterans has recently been reviewed by Bourke (1988b) and Choe (1988).

In the present study we demontrated that in the neotropical ponerine species *P. apicalis* workers establish dominance orders through agonistic interactions which ultimately lead to a diferential production of eggs by individual workers. As opposed to the linear pattern observed in other ant hierarchies (Cole 1981; Franks and Scovell 1983; Bourke 1988a; Heinze and Smith 1990), the dominance structure among workers of *P. apicalis* consists of one dominant individual and several subordinate workers. The relationhips within the group of subordinates are unclear, however. In any case we were unable to delineate a dominance structure among the workers below the leader, although they lay eggs and exhibit aggressive behavior. An inseminated queen maintains the unchallenged top position in the reproductive dominance order, although she was never seen initiating an agonistic act or being attacked by any of her nestmates. However, the dominance pattern among the workers is not stable, and we documented for the first time a natural (nonmanipulated) change in the social status of individuals within an ant dominance order. After the queen had been excluded from the colony, an increased number of workers participated in the agonistic interactions, the attacks toward egg-laying workers became more frequent, and the differential egg production more striking. This suggests that the queen's presence has an inhibitory effect on the workers. The social status of individual workers was closely correlated with their ovaian develoment, that is, the top group in the dominance order had the best developed ovaries and was most frequently seen attending the egg pile. The fact that yellow bodies were detected in the ovaries of all workers may suggest an age-based dominance order in *P. apicalis*. Additional data concerning the division of labor confirm the basic pattern recently described for *P. apicalis* by Fresneau and Dupuy (1988).

We observed similar dominance behavior in a total of four *P. apicalis* colonies, and in one case we were able to follow the development of males out of worker-laid eggs. In this context it is worthwhile to report briefly some of the results of still unpublished studies with several other *Pachycondyla* species (Oliveira and Hölldobler, unpublished). In *P. obscuricornis*, which is closely related to *P. apicalis*, we found a similar dominance behavior among workers and dealated virgin queens. In this case, too, the most dominant individuals laid most of the eggs. While depositing their eggs, *P. obscuricornis* usually shuffled them within the pile, a behavior that may reduce the probability that newly laid eggs will be found and destroyed by the other ants that frequently inspect the pile. Other aspects of the social structure of *P. obscuricornis* were described by Fresneau (1984). Although "shuffling" by egg-layers was rarely seen in *P. apicalis*, it was quite common in a colony of *P. unidentata* in which agonistic interactions were also frequent. Interestingly, no intracolony aggression of any kind had been observed in a queenright colony of *P. villosa*. Eggs laid by *P. villosa* workers were always given to the queen. Eggs laid by the queen, however, were deposited safely in the egg pile. No egg-shuffling has been observed in *P. villosa*.

Finally, in the queenless ponerine ant *Diacamma australe* Peeters and Higashi (1989) recently demonstrated that reproductive dominance within a colony is established by a single mated worker ("gamergate") attacking her nestmates and forcefully removing from them the so-called vestigial wings, a "pair of bladder-like appendages on the thorax."

Our results and those of Peeters and Higashi (1989) demonstrate that the reproductive division of labor and its underlying behavioral mechanisms in ponerine ants are surprisingly complex and diverse (see also Peeters 1987). The establishment of reproductive dominance orders by overt aggressive behavior by one or a few individuals has now been demonstrated in several ponerine species. It is possible that this is an ancestral trait which might be common in the phylogenetically more primitive subfamily Ponerinae.

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