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# Multiple Queens in Founding Colonies of the Neotropical Ant *Pachycondyla striata* Smith (Formicidae: Ponerinae)

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**Abstract**

In social insects, the typical mode of colony foundation occurs when a single queen is inseminated by a male and establishes a new colony, although we can find interspecific and intraspecific variations in queen number and queen-mating frequencies in a single colony. This study aimed to verify the queen number in *Pachycondyla striata* (Smith) colonies and to evaluate the level of aggressiveness among workers. We collected 14 colonies of *P. striata*. The behaviors of individuals from five multiple-queen colonies maintained in laboratory were studied by the method of scan sampling. In order to evaluate aggressiveness, dyadic encounters among heterocolonial and homocolonial workers were performed. The results showed that colonies of *P. striata* can have two or more mated queens (polygynous colonies) besides to monogynous ones (colony containing one queen). Because in polygynous colonies the number of workers was relatively low, such colonies could represent colonies in the foundation phase that characterize a pleometrosis state. In fact, ovarian development analysis from queens showed that the number of queens in the colonies seemed to be unstable. Despite a few cases of oophagy (egg cannibalism), social hierarchy among queens is unclear in comparison to other *Pachycondyla* species. In addition, aggressiveness increased with distance among nests. Nearby colonies (less than 1 m apart) showed a low level of aggressiveness, suggesting the presence of polydomy, that is, a unique colony can occupy multiple nests. Polygyny associated to polydomy in founding colonies may confer benefits on growth and dispersion of colonies in the studied environments.

## Introduction

The cooperation among individuals of the same social group or of the same family exists in several species, which in some cases implicates in the abdication of their own reproduction to devote themselves to the care of the offspring of other individuals from the group. This system can involve a relationship of dominance and subordination (Walters *et al* 1992, Hatchwell & Komdeur 2000, Kokko *et al* 2000, Griffin & West 2002). This type of phenomenon occurs in various groups of the animal kingdom as in the red-cockaded woodpeckers (Walters *et al* 1988), naked mole-rat (Jarvis 1981), and is well-documented in invertebrates, most especially in social insects (Wilson 1971).

Ants, termites and some groups of bees and wasps have reached the highest degree of group living, that is, eusociality. This involves the cooperative care of the

offspring, the overlap of generations, and the evolution of a reproductive caste (queen) and a non-reproductive or partially reproductive caste formed by workers that give up their own reproduction to perform activities such as foraging, nest defense, cleaning, and brood care (Wilson 1971, Hölldobler & Wilson 1977, 1990, Bourke & Franks 1995). In such groups, monogyny is the typical mode of colony foundation and occurs when a solitary mated queen establishes a new colony (haplometrosis). However, especially among ants, there is much variation among species and even within the same species with respect to the number of queens in the colony (Hölldobler & Wilson 1977, 1990, D'Ettorre *et al* 2005, Wilson & Hölldobler 2005).

The presence of multiple mated queens in a colony characterizes the state of polygyny which may be primary, when the founding queens remain in the colony even when it is already established and well developed (e.g. *Atta texana* Buckley, Mintzer & Vinson 1985), or secondary when there is adoption of queens by established colonies (e.g. *Gnamptogenys striatula* Mayr) (Giraud *et al* 2000). Some species have polygynous and monogynous colonies in the same population, such as *Formica sanguine* Latreille (Seppä *et al* 1995) and *Ectatomma tuberculatum* Olivier (Hora *et al* 2005).

In the ant genus *Pachycondyla* (Ponerinae), the reproductive structure varies widely and aggressiveness seems to be an important factor in structuring the organization and reproductive division in the colony (Trunzer *et al* 1998, D'Ettorre *et al* 2005). Some types of social organization are peculiar, as the one reported for the species *Pachycondyla sublaevis* Emery, in which the disappearance of the queen caste occurs, and the dominant worker, called gamergate, is responsible for the reproduction (Higashi *et al* 1994). In *Pachycondyla tridentata* Smith the presence of the queen and gamergate in the same colony was reported. In this species the hierarchy is well defined: the gamergate is responsible for the reproduction, dominating even its own queen (Sommer & Hölldobler 1992).

Mature colonies of *Pachydondyla goeldii* Forel are exclusively monogynous. Interestingly, in this species we can also find polydomous colonies, that is, the colony is distributed in several nests that are physically separated, maintaining their communication through the exchange of workers (Denis *et al* 2006); such phenomenon may justify the existence of colonies without queen. On the other hand, in *Pachycondyla obscuricornis* Emery the presence of two or more queens is considered common (Pezon *et al* 2005).

In Viçosa, Minas Gerais State, Brazil, some colonies of *Pachycondyla striata* Smith contain several queens in a single colony what would suggest polygyny (personal observation), even though monogynous colonies of this species have been reported for other Brazilian populations (Medeiros & Oliveira 2009, Silva-Melo & Giannotti 2010). Moreover, although this genus is considered highly aggressive against co-specifics (Oliveira & Hölldolbler 1991), preliminary observations show that workers of *P. striata* show no sign of aggressiveness against individuals from neighboring colonies. Thus, this work investigated the queen number in colonies of *P. striata* from Viçosa, the behavior of queens in colonies with more than one dealate queen, and if intercolonial aggression is influenced by the distance between the colonies.

## Material and Methods

### *Collection and maintenance of colonies in the laboratory*

Colonies of *P. striata* were collected from January to December 2008 in two fragments of semideciduous seasonal forest in Viçosa, state of Minas Gerais, southeastern Brazil: *Mata da Biologia* (20º 48'45 .8"S 42° 51'00 .8" W) and Estação de Pesquisa, Treinamento e Educação Ambiental Mata do Paraiso (20° 45'S and 42 55'W). Nest inspections were performed in the soil, and in wood trunks in decomposition. When the nest entrance was found, an area around the entrance was excavated. The soil in the area was excavated until the last room of the nest had being found (Antonialli Jr & Giannotti 1997, Silva-Melo & Giannotti 2010).

The colonies were taken to the laboratory for composition analysis (number of dealate queens, winged queens, males, workers, larvae, and pupae). Colonies were kept in artificial plaster nests (25 cm x 20 cm) connected to a foraging arena (10 cm x 5 cm). These nests were reared in the laboratory under controlled conditions (T = 25°C ± 5°C, RH = 75-80%, light/dark cycle 12h:12h). Larvae of *Tenebrio molitor* L. (Coleoptera: Tenebrionidae) and honey were offered daily in the foraging area.

To compare the composition of colonies with more than one queen to those with a unique queen or to an orphaned colony (that is without inseminated queen) we used the ANOVA followed by contrast analysis, in the free statistical software R (R Development Core Team 2006). All tests were performed at a significance level of 5%.

### *Behavioral observations*

In colonies with more than one dealate queen, all individuals were marked with numbered labels glued to their thorax following the protocol of Fresneau & Charpin (1977). The behavior of dealate queens, winged queens (when present) and workers was analyzed. Colonies were observed for a mean period of 12h through the method of scan sampling (e.g. Hora *et al* 2005), with intervals of 10 min between scans.

### *Dissections*

After the behavioral observations, all individuals were dissected in saline solution with the aid of a microscope Zeiss model 2000C. We estimated the reproductive condition of individuals by the presence of yolky oocytes, presence/absence of yellow bodies (that could indicate previous egg-laying), and mating status (i.e. filled or empty spermatheca).

### *Aggressiveness tests*

To check the level of intraspecific aggressiveness in *P. striata*, dyadic encounters between workers from different colonies were performed immediately after colony collection. The distances among the colonies ranged from 0.2 m to 70 m. The workers were confronted by a time of 5 min, in Petri dishes with 2.5 cm of diameter (Fénéron *et al* 1999). Ten colonies were used in this experiment and, in order to minimize the effect of manipulation, the tests were repeated five times for each pair of colonies using different workers (50 tests in total). For the control group we used five pairs of nestmate workers (four colonies, 20 tests in total).

The behaviors observed were ranked according to the level of aggressiveness: level 0 indicating no aggressiveness, 1 opening mandibles, 2 antennal boxing, 3 bite, and 4 stinging (one worker bites and stings the other), following standard protocol (e.g. Giraud *et al* 2002, Tsutsui *et al* 2003, Zinck *et al* 2008).

Data were analyzed through free statistical software R (R Development Core Team 2006), using the model LMER (Linear mixed model) to remove the effect of pseudo-repetition. In the case of count data, we used the Poisson distribution. All tests were performed at a significance level of 5%.

## Results

### *Colony composition*

A total of 14 colonies of *P. striata* were collected in the soil (n = 8) or in dead wood (n = 6) and they contained on average 36.7 ± 27.51 workers. Four colonies contained a single dealate queen, five contained two or more dealate queens, and in five colonies no queen was found. In colonies containing several dealate queens, the number of queens varied from two (colony code P8) to 10 (colony code P2). A unique male was found in one colony and the presence of immature (larvae and pupae) was observed in 50% of the collected colonies (Table 1). No connection was found among nests.

The average number of workers in monogynous colonies (50.8 ± 12.00) and queenless colonies (47.75 ± 13.71) was significantly higher than in colonies with several dealate queens (17.4 ± 4.29; ANOVA, $F_{1,13} = 9.43$, P = 0.009; Fig 1). When considering the number of immature found (larvae and pupae) in the three colonies types, no statistical difference was found (ANOVA, $F_{2,10}$ P = 0.02).

Table 1 Composition of 14 colonies of *Pachycondyla striata* collected in the region of Viçosa, MG, Brazil.

| Colony | Dealate queens[1] | Winged queens[2] | Males | Workers | Pupae | Larvae |
|---|---|---|---|---|---|---|
| P1 | 7 | 0 | 0 | 21 | 0 | 0 |
| P2 | 10 | 0 | 0 | 31 | 0 | 18 |
| P3 | 3 | 0 | 0 | 7 | 0 | 23 |
| P4 | 0 | 4 | 0 | 42 | 0 | 0 |
| P5 | 1 | 2 | 0 | 37 | 5 | 0 |
| P6 | 0 | 32 | 1 | 74 | 0 | 0 |
| P7 | 0 | 0 | 0 | 44 | 0 | 0 |
| P8 | 2 | 2 | 0 | 10 | 0 | 0 |
| P9 | 0 | 0 | 0 | 11 | 0 | 2 |
| P10 | 1 | 0 | 0 | 77 | 4 | 21 |
| P11 | 7 | 0 | 0 | 18 | 3 | 7 |
| P12 | 1 | 5 | 0 | 80 | 17 | 10 |
| P13 | 1 | 0 | 0 | 18 | 0 | 0 |
| P14 | 0 | 0 | 0 | 62 | 0 | 0 |

[1]29 dealate queens were inseminated; [2] all uninseminated.

### *Behavioral profile*

A total of 11 behaviors were observed in the five studied colonies: immobility, walking, self-grooming, brood care, food manipulating, allogrooming, feeding, agonistic behavior, oviposition, oophagy, and activities in the foraging area (Table 2).

In colonies P8 and P11 the most common behavior exhibited by the dealate queens was brood care, while in

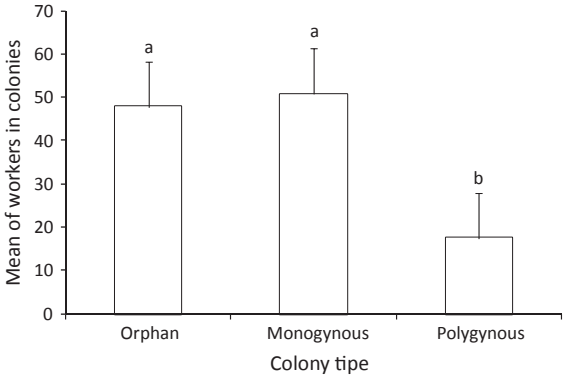


Fig 1 Worker number (mean) in 14 colonies of *Pachycondyla striata* collected in Viçosa, MG, Brazil. Bars with different letters are significantly different (ANOVA, $F_{1,13} = 9.43$, P = 0.009).

Table 2 Behaviors of dealate queens (Q), winged queens (WQ), and workers (W) in five colonies of *Pachycondyla striata* collected in the region of Viçosa, MG, Brazil.

| Colony | P1 | | P2 | | P3 | | P8 | | | P11 | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Caste | Q | W | Q | W | Q | W | Q | WQ | W | Q | W |
| Individuals | 7 | 21 | 10 | 31 | 3 | 7 | 2 | 2 | 10 | 5 | 18 |
| Scan total | 1468 | | 1529 | | 500 | | 1314 | | | 2747 | |
| Immobility | 19.81 | 23.02 | 14.85 | 23.54 | 24.80 | 12.80 | 7.61 | 8.52 | 16.89 | 8.05 | 30.54 |
| Walking | 6.13 | 14.03 | 3.99 | 21.19 | 5.00 | 16.00 | 1.75 | 3.27 | 14.84 | 2.00 | 16.31 |
| Self-grooming | 1.09 | 6.13 | 0.85 | 6.28 | 0.40 | 7.40 | 0.38 | 1.53 | 6.85 | 0.95 | 10.52 |
| Activity in foraging area | 0.34 | 15.12 | 1.44 | 13.47 | 2.20 | 20.20 | - | - | 4.11 | - | 4.70 |
| Brood care | 5.66 | 2.05 | 4.12 | 2.75 | 2.20 | 4.00 | 8.75 | 4.41 | 8.90 | 10.2 | 7.28 |
| Food manipulation | 0.41 | 5.25 | 0.39 | 4.38 | 0.40 | 2.60 | 0.08 | 1.22 | 2.13 | 0.15 | 3.39 |
| Allogrooming | 0.14 | 0.34 | 0.20 | 2.09 | 0.60 | 0.80 | 0.08 | 0.53 | 5.02 | 0.36 | 1.27 |
| Feeding | 0.14 | 0.34 | - | 0.39 | - | 0.20 | - | 0.23 | 0.46 | 0.80 | 2.83 |
| Agonistic behavior | - | - | - | 0.07 | - | 0.40 | 0.53 | 0.08 | 0.76 | 0.25 | 0.11 |
| Oviposition | - | - | - | - | - | - | 0.08 | - | 0.23 | 0.11 | 0.07 |
| Oophagy | - | - | - | - | - | - | 0.30 | - | 0.46 | 0.07 | 0.04 |

*inseminated; **uninseminated

the other three colonies the queens remained immobile most part of the time. Winged queens (n = 2, P8) presented a distinct behavioral profile compared to nestmate dealate queens, performing less frequently brood care and more often behavioral acts such as walking, self-grooming, and food manipulation (Table 2).

Most of the activities in the foraging area were conducted by workers. In three colonies some dealate queens visited the foraging area (queen code 40 colony P1, queens 45 and 49 colony P2, and queens 16, 37 and 60 colony P3), although with relatively low frequencies (see Table 2).

Agonistic behaviors (antennal boxing and biting) were observed in colony P8. Such behaviors were performed for both winged (four observations in 20h) and dealate queens (one observation in 20h) and only against workers. Aggression toward queens were observed in colony P11, and occurred when dealate queens (codes 32, 34, and 37) exhibited the egg-laying behavior; they were attacked by other dealate queens (n = 3) and workers (n = 2).

Oophagy, i.e. the destruction of eggs, by queens was observed in one colony (P11, n = 7), but the origin of the eggs could not be determined; they were very similar to those laid by queens and probably were not trophic eggs. However, three eggs produced by queens 33 and 39 were not destroyed. Egg-laying by workers (n = 3) could be observed in two colonies and were always consumed by the queens.

A total of 118 individuals were dissected (29 dealate queens, two winged queens, and 87 workers). The 29 dealate queens were inseminated and presented yellow bodies in the ovarioles indicating previous oviposition. However, only the queens from colonies P8 and P11 had developed oocytes. Winged queens were uninseminated and had undeveloped ovaries. Dissected workers had no spermatheca and only two of them had developed oocytes.

### *Aggressiveness tests*

The level of aggressiveness observed between neighboring colonies (< 1 m apart) was relatively low (0.6 ± 0.87, four colonies). In these colonies the only agonistic behavior observed was the opening of mandibles (level 1), which was observed in six of the 10 tests performed. Workers from distant colonies showed a high level of aggressiveness, and behaviors such as biting and stinging were observed in all tests. The results showed that the level of aggressiveness increases significantly with the distance between colonies (ANOVA, $X^2 = 10.96$, $P < 0.01$, Fig 2). After the trials, two colonies (P4 and P5) previously collected at a distance of 0.8 m were joined and this did not cause any aggressive behavior.

## Discussion

Previous studies conducted with *P. striata* populations from Campinas and Rio Claro, São Paulo State, Brazil, showed that the colonies of this species are always monogynous or queenless (Medeiros & Oliveira 2009, Silva-Melo & Giannotti 2010). Nevertheless the present study showed that colonies of *P. striata* from another

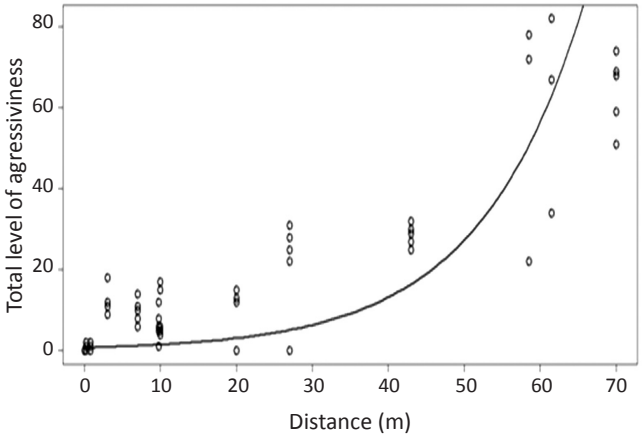


Fig 2 Level of aggressiveness between workers of *Pachycondyla striata* from Viçosa, MG, Brazil (ANOVA $X^2 = 10.96$, $P < 0.01$).

Brazilian population may contain more than one mated queen per colony. In fact several ant species show intraspecific variation in queen number, that is, both monogynous and polygynous colonies can be found in the same population (e.g. Seppä *et al* 1995, Hora *et al* 2005).

In our study, even if only seven of the 29 inseminated queens had developed oocytes, all of them showed yellow bodies in the ovarioles which indicate previous oviposition. According to D'Ettorre *et al* (2005), the absence of developed oocytes associated to the presence of yellow bodies in ovarioles may indicate interruption in egg production. However, the factors linked to such egg-laying interruption in our study are unknown. All colonies with several mated queens had relatively few workers (< 35) and in some cases a high number of immature, suggesting young colonies or colonies in the foundation phase (for example colony P3). Thus the species of *P. striata* can be considered, at least in the foundation phase, as being polygynous (pleometrosis foundation). In this way, the difference in queen number found in this study could be related to the development phase of the colony. In this case the colonies collected in Campinas and Rio Claro could represent mature colonies whereas those collected in Viçosa could represent young ones.

The cooperation among queens in the phase of colony foundation has been described in other species of the genus *Pachycondyla* as *P. marginata* Roger (Leal & Oliveira 1995), *P. inversa* Smith (Kolmer & Heinze 2000), and *P. villosa* Fabricius (Heinze *et al* 2001). Founding queens of *P. inversa* form a social hierarchy system, mediated by aggressive interactions, and the queen which is worst placed in the hierarchy is responsible for foraging, while the other queens are egg layers (Kolmer & Heinze 2000). Moreover, the queen that is best placed in hierarchy can eat the eggs produced by the other queens (Kolmer & Heinze 2000, D'Ettorre *et al* 2005). This mode of colony foundation reduces the risks to which the queens are exposed, since that before the emergency of the first workers, the queen feeds the larvae with its own body tissue and/or leaves periodically to forage (D'Ettorre *et al* 2005), reducing the life expectancy due to physical use or to external pressures (Keller 1995). Moreover, polygynous colonies developed faster (i.e. produce more brood) than colonies formed by a single queen (Hora *et al* 2005).

The aggression and formation of hierarchy among queens in polygynous colonies is also common in other species of ants, as for example, *Odontomachus chelifer* Latreille. In this species the dominant queen reproduces more when compared to nestmate ones (Medeiros *et al* 1992). Moreover, in *Leptothorax gredler* Mayr only the queen best placed in the social hierarchy system is responsible for the egg production (Heinze & Lipski 1990, Heinze & Smith 1990). The colonies of *P. striata* studied here presented a low frequency of agonistic behaviors, which were more common in colony P11 and only at the time of queen oviposition. Moreover, in the colonies P1, P2 and P3 the queens observed in the foraging area were inseminated, and this might reflect a hierarchy system among queens that would be more subtle in comparison to other phylogenetically close species (Heinze & Keller 2000, D'Ettorre *et al* 2005).

Oviposition by workers was observed a few times in the studied colonies, but all eggs were destroyed by nestmate workers or by the queens, and they may represent trophic eggs (e.g. Dietemann *et al* 2003). In social insects, egg cannibalism may be associated with competition for reproduction. In the eusocial bee *Apis mellifera* L. the oviposition by workers is common, but only 0.01% of the males produced by a colony are originated from eggs of workers. These eggs are often destroyed by other workers, a common behavior in social insects, known as worker policing (Visscher 1996, Monnin & Ratnieks 2001, D'Ettorre *et al* 2004). In *P. obscuricornis* the destruction of unfertilized eggs by the queen and/or workers is relatively common, and is probably due to intense intracolonial conflicts. In this species, about 70% of eggs produced in the colony end up being destroyed (Oliveira & Hölldolbler 1991).

Our results showed a relatively low level of aggressiveness between workers from nearby colonies, and aggressiveness increased significantly with the distance between colonies. The low hostility showed by neighboring workers from queenless and queenright colonies may indicate the presence of polydomy in *P. striata*. Medeiros & Oliveira (2009) suggested a polydomous structure of this species because the colonies presented from two to eight nest entrances and when the nests were excavated, five and six interconnected chambers could be found. The polydomy is common the polygynous species *Pachycondyla luteola* (Verhaagh

1994), *Hypoponera opaciceps* Mayr and *Hypoponera opacior* Foroel (Foitzik *et al* 2002), and *E. tuberculatum* (Zinck *et al* 2008). In these species, the queen nuptial flight is absent or reduced and the growth of the colony may occur by budding (Vander Meer *et al* 1992, Gadau *et al* 1998).

The polydomous structure has already been reported for the monogynous species *P. apicalis* (Fresneau 1994) and *P. goeldii* (Denis *et al* 2006). Though no connection among nests neither worker exchange was observed in *P. striata* from Viçosa, polydomy may occur both in monogynous and polygynous colonies from this populatoin, as showed by our results. Colonies that have polydomous nests have a greater foraging area, which leads to an increase in the number of sources of resources that can be exploited (Hölldobler & Lumsden 1980, Denis *et al* 2006, Zinck *et al* 2008). Another advantage of this type of structure is the greater efficiency in escaping from possible predators and/or competitors, since the individuals from the colony are able to escape to another satellite nest when the colony is attacked (Cerdá & Retana 1998).

In conclusion, this study shows that *P. striata* may present both monogynous and polygynous colonies in the same population, at least in the foundation phase. In fact, the interruption of queen oviposition may suggest that polygyny can be unstable. The presence of polygyny associated with polydomy may confer benefits to growth and dispersal of colonies in the studied environments. This association could also provide a greater use of the resources and it is a key factor in ensuring the success of species in places where there is high inter- and intraspecific competition. Future studies related to the genetics of this group can be a useful tool to measure the degree of relatedness among heterocolonial workers that could confirm the presence of polygynous and polydomous colonies in *P. striata*.

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