

AGONISTIC INTERACTIONS AND REPRODUCTIVE
DOMINANCE IN *PACHYCONDYLA OBSCURICORNIS*
(HYMENOPTERA: FORMICIDAE)

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INTRODUCTION

In many animals, agonistic interactions among members of a social group have been demonstrated to be associated with the formation of dominance hierarchies, which result in a reproductive rank order within the group. This type of social structure has been shown to occur in both vertebrate and invertebrate taxa, and the general pattern observed consists of one or a few highly-ranked individuals being responsible for most of the reproductive activity within the group (Wilson 1975a).

Dominance orders leading to differential reproduction by colony members have already been documented for bees, wasps and ants (e.g., Pardi 1948, West-Eberhard 1969, Brothers and Michener 1974, Cole 1981, Franks and Scovell 1983, Bourke 1988, Heinze and Smith 1990, Röseler 1991). In more advanced ant societies, the morphologically differentiated queen usually holds her top position in the reproductive rank order of the colony by means of inhibiting pheromones which suppress the reproductive activity of workers (Fletcher and Ross 1985, Wheeler 1986). However, in phylogenetically more primitive ant species in which the queen and worker castes are often poorly differentiated, or in which the morphological queen caste has even disappeared entirely and reproduction is performed by mated workers (gamergates), the behavioral mechanisms regulating reproduction within the colony are complex and variable (Peeters 1987, Fukumoto et al 1989,

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Peeters and Higashi 1989, Oliveira and Hölldobler 1990, Ito and Higashi 1991).

In the present paper we report observations concerning the reproductive division of labor in the primitive ponerine ant *Pachycondyla obscuricornis* (Emery). We provide evidence that the agonistic interactions among colony members including aggression toward egg-layers and the destruction of their eggs, as well as the 'shuffling' of newly laid eggs within the egg pile may all be part of a "behavioral syndrome" associated with reproductive competition within the colony, leading ultimately to a differential production of eggs by individual colony members.

MATERIALS AND METHODS

The colony of *Pachycondyla obscuricornis* used in this study was collected in lowland rainforest at the Estacion Biologica La Selva, Costa Rica, in March 1985. The ants were cultured at 20–25° C in the laboratories in the Museum of Comparative Zoology, Harvard University. The artificial nest consisted of 4 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, dilute honey and synthetic ant diet (Bhatkar and Whitcomb 1970). At the beginning of our observations (17 October 1988) the colony of *P. obscuricornis* consisted of 11 dealated virgin queens, 4 winged females, 9 males, 19 workers, 10 pupae, 3 mature larvae, and 50–60 eggs. The single mated queen had died before our quantitative observations started. It appeared, however, that the reproductive competition among the remaining colony members became considerably more intense after the death of the mated queen.

By 22 November 1988 individual dealated queens (N = 9) were marked with colored dots of gloss enamel paint (Testors Corp., Rockford, IL, USA) on the thorax and/or gaster. The workers (N = 19) remained unmarked. Egg-laying by queens and workers, and agonistic encounters between ants were recorded intermittently in sessions lasting 15 to 60 minutes (during the daily period from 9.00 to 18.00). Special attention was given to aggressive displays towards egg-layers, and the fate of newly-laid eggs. An egg was considered as 'laid' only after it could be seen totally out of the egg-layer's gaster. A newly-laid egg was considered successfully

deposited provided that no ant ate it during a 20 minute period following its deposition on the egg pile.

In order to determine whether the fidelity at the egg pile by individual queens was related to their reproductive state, snapshot records were taken at 1-hour intervals (9.00 to 18.00 hours). Marked queens were assigned as being either at the egg pile (< 1 cm from the eggs), or elsewhere in the nest tubes or foraging arena.

After terminating the behavioral observations, the ovarian development of queens and workers of *P. obscuricornis* 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

Aggressive interactions between nestmates were very frequent in the colony of *Pachycondyla obscuricornis*, and involved both workers and dealated virgin queens. Agonistic encounters consisted of brief (5 to 15 seconds) mandibular strikes directed toward the head, antennae, mandibles, legs or thorax. Most contests were frontal but an attacking ant may also approach either from the side or rear of the opponent. The ant being attacked usually did not retaliate, and once released by its aggressor the subordinate ant normally walked away. No ant was ever observed to suffer any kind of physical injury or mutilation as a result of agonistic interactions with a nestmate.

Aggressive behavior toward egg-laying workers and queens was extremely conspicuous, resulting in a high proportion of eggs being destroyed (Table 1). Ants took 11.3 ± 7.7 minutes (range 2–28; $n = 33$) to lay an egg, and during this period they were highly vulnerable to attacks from nestmates. While in the typical egg-laying posture (gaster curved forward) 33 ants were observed to each receive up to 19 mandibular strikes from other colony members. Typically, strikes were directed toward the tip of the gaster of the egg-layer, and clearly aimed at robbing the egg. If the attacker was successful, the egg was immediately eaten by the aggressor and/or other colony members. Fights for possession of robbed eggs were frequent and lasted up to 15 minutes during

Table 1. Oviposition and oophagy by dealated virgin queens and workers of *Pachycondyla obscuricornis*. Data are based on 28 hours of observation, from 21 October 1988 to 17 February 1989. At the beginning of the observations the colony contained nine queens and 19 workers (9 of which died during the study).

Egg-laying ant	No of eggs laid	No. of eggs destroyed by		No. of eggs successfully deposited
		workers	queens	
Queens	24	20	3	1 (4%)
Workers	39	15	4	20 (51%)
Total	63	35	7	21 (33%)

which the eggs were sometimes broken into pieces and eaten by 2–3 ants. Nineteen percent (8 out of 42) of the eggs destroyed were pulled out directly of the egg-layer's gaster. While laying eggs, ants conspicuously avoided encounters with nestmates, and on one occasion an egg-laying queen was seen fleeing to the arena (with the egg still attached to her gaster) as a result of 19 successive attacks from a worker in the nest tubes.

After seizing her newly-laid egg with the mandibles an egg-laying ant could either try to deposit it immediately on the egg pile ($n = 8$), or take from 1 to 77 minutes to do this ($n = 22$). Prior to the deposition of the egg on the pile, an ant carrying her newly-laid egg could receive up to 8 mandibular strikes ($n = 33$) from other colony members. During such fights the aggressor and the egg-layer antennate vigorously as the former attacks and tries to steal the egg. Fifty-five percent (23 out of 42) of the eggs destroyed were stolen from the egg-layer's mandibles. On two distinct occasions we observed a worker fleeing to the arena carrying her newly-laid egg after being attacked by nestmates in the nest tube; in both situations the egg-layer hid beneath the nest tube for nearly 15 minutes before returning to the nest.

Workers deposited successfully 51% of their eggs (Table 1), a far greater proportion than that achieved by the dealated virgin queens who succeeded only once (since this happened before the queens were marked, we do not know the identity of this queen) ($n = 24$; Table 1). Aggression near the egg pile was very

conspicuous and strikes toward egg-layers were obviously aimed at robbing newly-laid eggs before these were deposited on the pile. On one occasion we observed a worker being attacked 7 times as she attempted to approach the pile to deposit her recently-laid egg.

While depositing their eggs some ants may shuffle them within the pile for 5 to 10 minutes (observed on 9 occasions). Before walking to another place in the nest, egg-layers may still guard their eggs by sitting on the pile (or stand nearby) for up to 60 minutes after the deposition. Since the egg pile is constantly inspected by ants, we suspect that shuffling and guarding a newly-deposited egg may reduce the probability that it would be found and destroyed by other ants. In fact the stealing of newly-deposited eggs from the pile comprised 19% (8 out of 42) of all the eggs destroyed, and any behavior reducing this risk would be advantageous for an egg-layer. Although we have not gathered enough data for a more detailed and quantitative analysis concerning the fate of newly-deposited eggs, we believe that the following accounts provide circumstantial evidence for a protective role of both shuffling and guarding behavior by ants when depositing their eggs on the pile.

27 December 1988 – A worker laid an egg at 13:35 hours and immediately deposited it on the pile, shuffling her egg among the others for approximately 5 minutes. At 13:42 hours the egg-laying worker abandoned the pile but stood nearby (less than 1 cm from the eggs) while two other workers began to inspect the pile. The recently-deposited egg was not destroyed by the inspecting workers during the 60 minutes that followed.

29 December 1988 – Queen GT laid an egg at 13:25 hours and deposited it on the pile at 13:26 hours, without shuffling her egg. The queen stood nearby the pile for 15 seconds before leaving the tube. A worker who had followed the queen on her way to the pile immediately seized and ate the recently-deposited egg. While eating the egg the worker was attacked by a nestmate who tried to take possession of the egg through several bites on the mandibles, head and antennae.

The above behavioral reports suggest that shuffling and guarding a newly-laid egg may reduce the chance that inspecting ants will find and destroy the egg. We noted, however, that sometimes several ants can simultaneously inspect/manipulate the egg pile. In

this case even recently-laid eggs that had been shuffled within the pile may be destroyed, as reported below.

27 December 1988 – Worker laid an egg at 10:50 hours and shuffled it within the pile at 11:10 hours, standing nearby. At 11:23 hours four workers were seen very excited on the pile as one of them picked up a recently-deposited egg (lighter in color than the other ones in the pile, and presumably the one deposited at 11:10 hours). The egg was entirely eaten by one of the workers after several fights with nestmates.

After terminating the behavioral observations, we dissected the dealated virgin queens and the workers of *P. obscuricornis* in order to determine the developmental stages of their ovaries. The results on egg production, constancy at the egg pile, and ovarian

Table 2. Data on ovarian development of dealated virgin queens of *Pachycondyla obscuricornis*. The number of eggs laid by each queen is based on 20 hours of observation, from 22 November 1988 to 17 February 1989. All queens had 6 ovarioles. Records of ants at the egg pile are based on 245 snapshots of the colony.

Queen	No. of Times eggs laid	at egg pile	No. of yolky oocytes	Yellow body	Fat body	Receptaculum
BL	4	149	6 mature	conspicuous	good	empty
GT	4	141	3 mature, 3 half-sized	just visible	good	empty
YT	4	90	2 mature, 2 half-sized	just visible	medium	empty
GA	3	53	0	conspicuous	weak	empty
RA	2	69	0	conspicuous	medium	empty
RT	0	52	some tiny ones	conspicuous	medium	empty
WT	0	39	0	conspicuous	weak	empty
GO	0	13	some tiny ones	conspicuous	weak	empty
BT	0	7	3 very small	conspicuous	weak	empty

development of individual queens are presented in Table 2. As expected, the queens most frequently seen at the egg pile were the ones with the greatest number of mature oocytes. Despite the fact that the three most common queens at the egg pile laid the same number of eggs during the observation sessions, queen GT was clearly the most aggressive one toward egg-layers approaching the pile to deposit their eggs. A total of seven eggs was destroyed by queens (see Table 1), four of which were eaten by queen GT after attacks toward egg-layers. Moreover, attacks toward egg-layers by queen GT were observed in 53% of the occasions (9 out of 17) on which queens were seen attacking egg-laying ants.

All dissected workers had 6 ovarioles and the presence of yellow bodies suggest that eggs had been laid previously, but in no case was sperm detected in the spermatheca (Table 3). The development of the ovaries clearly varied among the workers, with a few individuals carrying greater quantities of mature oocytes. Although this may suggest the existence of a dominance rank order, we were unable to follow and evaluate the reproductive performance of individual workers since these remained unmarked during the study.

DISCUSSION

Antagonistic behavior among nestmates has already been reported for many ant species (Wilson 1974, 1975b, Fowler and

Table 3. Data on ovarian development of workers of *Pachycondyla obscuricornis*. All workers had 6 ovarioles and in no case was sperm found in the spermatheca.

Worker number	No. of yolky oocytes	Yellow body	Fat body
1	4 mature, 3 small	just visible	medium
2	3 mature, 3 small	just visible	medium
3	3 mature, 2 small	just visible	good
4	3 mature, 1 small	just visible	good
5	1 mature, 3 half-sized	none	good
6	4 small	conspicuous	weak
7	a few small	conspicuous	medium
8	0	conspicuous	weak
9	0	conspicuous	medium
10	0	not clear	brownish

Roberts 1983, Hölldobler and Taylor 1983, Wilson and Brown 1984, Evesham 1984, Hölldobler and Carlin 1985, Peeters and Higashi 1989, Heinze and Smith 1990, Heinze and Lipski 1990, Oliveira and Hölldobler 1990). Reproductive competition is thought to underlie such dominance interactions which ultimately result in a differential production of eggs by individual colony members (Cole 1981, Franks and Scovell 1983). More recently an array of complex behavioral mechanisms were shown to mediate the reproductive activity within ant colonies, particularly in the primitive subfamily Ponerinae (e.g., Fukumoto et al. 1989, Peeters and Higashi 1989, Oliveira and Hölldobler 1990, Ito and Higashi 1991).

In the neotropical ponerine ant *Pachycondyla apicalis* Oliveira and Hölldobler (1990) have demonstrated that a reproductive rank order among workers is established through dominance displays identical to the ones described here for the closely related species *P. obscuricornis*. In these species aggressive interactions among colony members consist of brief encounters in which one individual tugs the opponent usually by the antennae or legs. The robbing and consumption of newly-laid eggs were shown to be extremely conspicuous in both *Pachycondyla* species and resulted in a disproportionate net production of male eggs by individual colony members. The destruction of one another's eggs has also been shown to be associated with reproductive competition in colonies of the ant *Leptothorax curvispinosus* (Wilson 1974), paper wasps (West-Eberhard 1969) and honeybees (Ratnieks and Visscher 1989). In this context the suggestion that the shuffling and guarding of newly-laid eggs on the pile by *P. obscuricornis* has a protective function needs further experimental investigation. Incidentally, intra-colony aggression and shuffling behavior by egg-layers were also commonly seen in a colony of *Pachycondyla unidentata* (Oliveira and Hölldobler, unpublished). In *P. apicalis*, however, which also exhibits strong intra-colony aggression, egg shuffling occurred only rarely (Oliveira and Hölldobler 1990).

The dominance structure in *P. apicalis* consisted of one dominant individual and several subordinates, and the social status of individual workers correlated well with their egg production, ovarian development and constancy at the egg pile (Oliveira and Hölldobler 1990). Since dominance interactions were not quantified in

the *P. obscuricornis* colony, we are unable to determine the rank position of individual ants based on their behavioral performances during domination contests. Nevertheless our data on egg production, ovarian development and frequency at the egg pile clearly demonstrated a differential reproductive activity by individuals of *P. obscuricornis*; (concerning other parameters of division of labor and ovarian development see also Fresneau 1984). The dealated queens (individually marked) having better developed ovaries were also the ones that laid more eggs and that more frequently attended the egg pile. The greater aggressiveness toward egg-layers exhibited by the high-ranked queen GT in the *P. obscuricornis* colony confirms the pattern observed for *P. apicalis* (Oliveira and Hölldobler 1990) and paper wasps (West-Eberhard 1969).

Our results therefore support the existence of a dominance order in *Pachycondyla obscuricornis*, and strengthen the suggestion that such reproductive division of labor may be more widespread among ants than previously thought, being particularly relevant for more primitively organized ant taxa such as the Ponerinae.

SUMMARY

In the present paper we investigate the reproductive division of labor within a queenless colony of the primitive ponerine ant *Pachycondyla obscuricornis*. Aggressive interactions between workers and dealated virgin queens were very frequent, and attacks toward egg-laying ants resulted in a high proportion of eggs being destroyed. The robbing and consumption of one another's eggs leads ultimately to a differential net production of male eggs by individual colony members. It is suggested that the shuffling and guarding of newly-laid eggs on the pile by *P. obscuricornis* may have a protective function, reducing the risk that newly-deposited eggs would be found and destroyed by inspecting ants. Results on egg production, ovarian development and the frequency of being at the egg pile clearly demonstrated a differential reproductive activity among individually-marked dealated virgin queens.

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