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Regulation of Reproduction in the Neotropical Ponerine Ant, *Pachycondyla villosa*

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Workers in queenless groups of the ant Pachycondyla villosa *engage in antennal boxing and biting and by these interactions establish social dominance hierarchies, in which several high-ranking individuals may lay eggs. We observed egg cannibalism by dominant workers. The presence of larvae negatively effects the number of worker-produced eggs in queenless colony fragments in two ways. First, larvae feed on the eggs, and second, workers lay fewer eggs when larvae are present. In queenright colonies, workers lay eggs at a low rate, which are eaten by the queen or fed to the brood, but apparently they do not compete aggressively for egg-laying.*

KEY WORDS: dominance; reproduction; queen inhibition; Ponerinae.

INTRODUCTION

The organization of reproductive division of labor in ants of the ponerine genus *Pachycondyla* is remarkably flexible and ranges from species without a morphological queen caste to species with a typical queen–worker dimorphism. In most species examined so far, reproduction is regulated by aggressive interactions among potential reproductives: in queenless *P. sublaevis*, mated and unmated workers compete aggressively (Ito and Higashi, 1991; Higashi *et al.*, 1994). In *P. tridentata*, mated and unmated queens and mated and unmated workers engage in dominance interactions (Sommer and Hölldobler, 1992; Sommer *et al.*, 1994). In *P. apicalis*, *P. obscuricornis*, and *P. unidentata*, workers

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or queens and workers were observed attacking each other, and workers apparently attempted to "hide" their eggs from nestmates by shuffling them within the egg pile (Oliveira and Hölldobler, 1990, 1991; Düßmann, 1994). The neotropical species *P. villosa* was thought to be remarkably different: in queenright colonies, no intracolony aggression of any kind and no egg-shuffling was observed (Oliveira and Hölldobler, 1990). We here examine the social organization of *P. villosa* in more detail and provide evidence for reproductive competition among workers at least in queenless colonies and for an "inhibitory" influence of the larvae on egg-laying by workers.

MATERIALS AND METHODS

Four colonies of *P. villosa* were collected by P.S.O. in July 1992 at the cerrado reserve of the Instituto Brasileiro de Geografia e Estatística (IBGE) near Brasília, Brazil (15°47′S, 47°55′W). The colonies nested in the trunk and roots of bushes (*Ouratea hexasperma*, *Acosmium dasycarpum*) or in the trunk of a dead tree. Six months after collection the ants were transferred to Würzburg and, from that time on, kept in 40 × 60 × 11- and 19 × 19 × 9-cm^3 nest boxes with a plaster floor at 25°C and 55% humidity. The ants were fed three times per week with diluted honey and cockroaches. The actual size of the colonies by the time the observations were started is given in Table I.

For behavioral studies, workers were marked individually with dots of enamel paint on the thorax and gaster. Behavior was recorded either directly or with time-lapse video recording. Data were collected by scan sampling (Altmann, 1977); in addition, all aggressive interactions were noted. These consisted of antennation bouts, biting, and pulling on the antennae and legs of another ant.

To study the effect of the queen's presence on worker fertility, the queen was separated from workers in a cage of copper gauze. To study the influence of larvae on worker fertility, 10 groups of 16 workers each (8 workers from the foraging arena and 8 workers from the nest) were isolated from the rest of the

Table I. Composition of the Colonies of the Ant *Pachycondyla villosa* Used for Experiments on Reproductive Competition

Colony	Queens	Alate female sexuals	Dealate female sexuals	Workers	Males	Pupae	Larvae	Eggs
7-07	1	0	0	18	0	2	13	31
13-07	1	2	26	143	0	63	35	81
17-07	1	1	14	167	14	31	27	75
18-07	1	10	11	237	0	35	55	85

colony. Two of these groups were isolated with brood and eight without brood. In six of these eight groups set up without brood, we removed the brood produced after 105 days and replaced it in four groups by 20 foreign larvae of various stages and in two groups by 5 foreign larvae. In the remaining two groups set up without brood, the brood produced was removed after 80 days and 20 foreign larvae were added. All groups were checked three times per week for the presence of eggs. Additionally, the number of larvae was kept constant by adding new larvae if necessary. The foreign larvae were also removed after 40 days and the groups were again checked for eggs.

As the frequencies of egg-laying or aggressive interactions within colonies are likely to violate the assumption of independence, we did not use chi-square statistic to test differences between colonies. Rather, we subsetted data by calculating frequencies per observation hour (Kramer and Schmidhammer, 1992) and tested the differences with a nonparametric Mann–Whitney *U* test (Sachs, 1992).

RESULTS

Worker Reproduction and Antagonism

As already observed by Oliveira and Hölldobler (1990), in queenright colonies of *Pachycondyla villosa* workers occasionally laid eggs which were immediately fed to the queen (one observation in 20 h) or to larvae (three observations). Dissection showed that the ovaries of 9 of a total of 26 workers from a queenright colony were developed and that all of these fertile workers were young, according to the white coloration of their fat bodies. In the four queenright colonies, workers rarely interacted aggressively and dominance hierarchies could not be deduced. The frequency of aggressive acts did not increase when in one colony the queen was physically separated from her workers in a cage of copper mesh [with queen, 8 ± 2.4 (SD) aggressive acts/h, 10 h; queen caged, 9 ± 2.0 acts/h, 10 h; two-tailed *U* test, $z = 1.3$, $P = 0.19$]. Aggression was similar to that observed in other *Pachycondyla* species, i.e., workers attacked their nestmates with antennation bouts or bites and pulled their antennae and legs. Attacked workers usually crouched with retracted antennae in a submissive posture.

Similarly, when we isolated six groups of 16 workers each without queen and brood, the rate of aggression initially did not change (10 ± 3.4 acts/h, 10 h) and no eggs were laid. However, with the beginning of egg-laying by workers, on average 7 weeks after queen removal (51 ± 4.6 days), the frequency of antagonistic behavior increased significantly (26 ± 5.5 acts/h; $z = 4.5$, $P < 0.001$). Aggression led to the formation of social dominance hierarchies but not to the monopolization of reproduction by the α-worker (Table II). In three colony fragments, between 5 and 8 of a total of 16 workers each laid eggs, and

Table II. Dominance Interactions and Reproductive Status of a Group of Workers of *Pachycondyla villosa* Isolated from Their Queen[a]

	Subordinate																	
Dominant	A	B	C	D	E	F	G	H	I	K	L	M	N	O	Total	Eggs laid	Eggs fed to larvae	Ovarian development
A	X	13	17	9	21	4	1	3	1	4	2	6	3	2	86	6		+
B	1	X	6	16	21	9	1	5	1	3	2	5	7	6	83	1		+
C	1		X	9	6	7	3	3		1	4	4	2	2	42			+
D				X	8	6	7	6	1	4	6	9	7	2	56	4	1	+
E				1	X	10	2	6	2	2	4	5	3	3	38	4	2	−
F						X	5	3	2	5	3	6	6	5	35			+
G							X	1	1	3	2	1	5	1	14			−
H								X	1	1	8	7	6	2	25			−
I				1				1	X			1	3	1	7			−
K										X	1	1	3	3	8			−
L								1			X	5	2	1	9			−
M										1		X	7	4	12			−
N										1	1	3	X	4	9			−
O										1	1			X	2			−
Total	2	13	23	36	56	36	19	29	9	26	34	53	54	36				

[a]Total observation time was 20 h within 4 weeks.

dissection 8 weeks after hierarchy establishment proved that all their ovaries were still well developed (Table II). In two groups, the α-worker laid more eggs than any other worker. The fat bodies of workers collected in the foraging arena were yellowish, but those of egg-layers were white, suggesting that egg-laying workers were younger than foragers.

Dominant workers attacked mainly lower-ranking egg-layers and also ate their eggs. In an experimental group consisting of 27 workers and 7 virgin queens, we observed egg-laying by 14 individuals (2 virgin queens and 12 workers) during 264 h. Three of the workers laid a total of 18 eggs, one of which was immediately eaten by a virgin queen. The remaining 11 egg-layers produced 12 eggs, 7 of which were eaten directly after laying by the three major egg-layers, and 2 by a lower-ranking worker and a virgin queen, respectively. Whereas egg shuffling was not observed in three extensively observed queenright colonies, workers apparently attempted to ''hide'' their eggs in the egg pile in the six queenless colony fragments.

Larval Inhibition

In eight worker groups, each consisting of 16 workers without brood, the first eggs appeared on average 51 days after queen removal. In contrast, in two groups of 16 workers and 20 larvae, no eggs were found in the colony for more than 105 days. Eggs which were laid in these groups were immediately fed to the larvae or eaten by other workers. After removal of the brood, the number of eggs in the colony increased immediately. On the other hand, when larvae were added to four worker groups without brood after 105 days, the number of eggs decreased dramatically, regardless of the added larvae being offspring of the own mother queen, an alien queen, or alien workers. After removal of the larvae some 40 days later, the number of eggs increased again (Fig. 1a). To exclude the possibility that egg-laying follows internal rhythms independent of the presence of brood, we added larvae to two colony fragments already 80 days after queen removal and observed the same decline in egg-laying (Fig. 1b).

A negative correlation between the presence of larvae and the number of eggs in the nest was also evident from the number of brood produced in the eight queenless colony fragments. Whereas over the first 40 days, the number of eggs increased steadily, with the eclosion of larvae the number of eggs dropped and the total number of brood and eggs remained at a rather constant level (Fig. 1a).

The negative influence of larvae on the number of eggs in the colonies can be explained in part by larval egg cannibalism: in the absence of larvae, in three worker groups 10% of the eggs were eaten by workers and 90% developed into larvae, whereas in the presence of larvae, 60 to 80% were fed to the larvae. Eggs fed to the larvae were both produced by the high- and low-ranking egg-

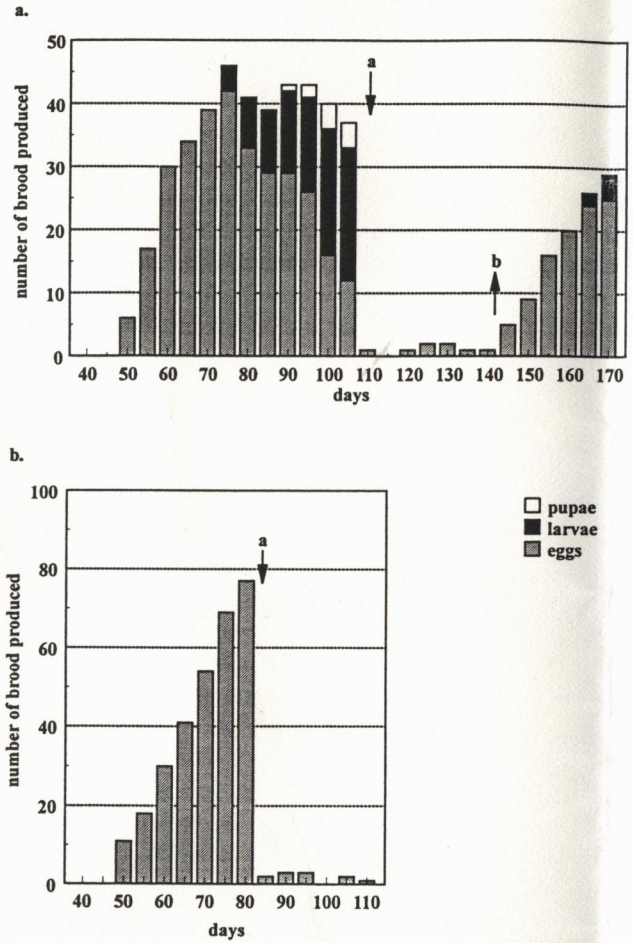

Fig. 1. Mean number of total brood produced in six groups, each consisting of 16 workers of *Pachycondyla villosa*, with and without larvae. (a) In four groups, the brood produced during 105 days was removed and 20 foreign larvae were added (arrow a). This led to a decrease in the number of eggs produced. Forty days later, the 20 foreign larvae were removed (arrow b) and the number of eggs laid increased again. (b) In two worker groups the eggs produced were removed already after 80 days. During this period, no larvae had eclosed. The addition of 20 foreign larvae also led to a decline in the number of eggs laid.

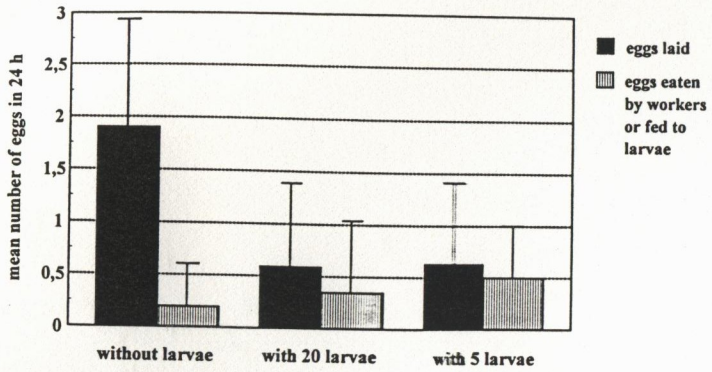

Fig. 2. Mean number of eggs (±SD) laid per hour during 24 h in three groups of 16 *P. villosa* workers, and mean number of eggs eaten by workers or fed to the larvae during the same period. Three situations were compared: groups of workers without larvae, with 20 larvae, and with 5 larvae. In the worker groups without larvae many more eggs were laid than in the groups with the larvae ($P < 0.001$); the egg-laying rate was similarly low in the groups with 20 or 5 larvae ($P = 0.69$).

layers but data do not suffice to conclude whether the proportion of eggs fed and eggs developing into males was correlated with the egg-layer's rank. In addition, however, egg-laying rates dropped from 1.9 ± 1.1 eggs per day in the absence of larvae to 0.6 ± 0.8 eggs per day when 20 larvae were added (three colonies; $z = 3.5$, $P < 0.001$; Fig. 2). Egg-laying rates were similarly low in two groups of 16 workers with 20 and 5 larvae, respectively ($z = 0.40$, $P = 0.69$; Fig. 2).

DISCUSSION

Workers of the neotropical ponerine ant, *Pachycondyla villosa*, do not engage in aggression for reproductive rights in queenright colonies and worker-laid eggs are immediately fed to larvae or the queen. In orphaned colony fragments, on the other hand, the workers begin to interact aggressively and form hierarchies, and they lay viable eggs which can develop into males. Several young workers can have developed ovaries, but it appears that due to egg-eating only a small number of high-ranking individuals actually produce males. The presence of larvae decreases the number of eggs in the colony, first, because larvae feed on the eggs and, second, because the presence of larvae somehow decreases egg production by workers.

Reproductive conflict among workers in queenless colonies of *Pachycondyla villosa* is thus resolved in a similar manner as in numerous other species

of ponerine ants (Oliveira and Hölldobler, 1990; Ito and Higashi, 1991; Sommer and Hölldobler, 1992; Peeters and Tsuji, 1993; Heinze *et al.*, 1994), i.e., aggressive interactions, such as antennal boxing and biting lead to the formation of dominance hierarchies. As in *P. sublaevis* (Higashi *et al.*, 1994), younger workers are typically dominant over older workers. It is surprising, however, that after queen removal aggression started and the first eggs were laid only after a latency of 37 to 56 days. In other *Pachycondyla* species, queen removal almost immediately leads to a significant increase in aggressive interactions among workers (Oliveira and Hölldobler, 1990; Düßmann, 1994).

In addition, our data suggest an inhibitory effect of larvae on worker egg-laying activity. A similar correlation is known in honey bees (Pain, 1954; Jay, 1970, 1972; Jay and Jay, 1976; Kropácová and Haslbachová, 1971) and ants (Bier, 1954; Mamsch, 1967) and has been explained by either inhibitive pheromones produced by the larvae (Jay, 1972) or nutritional contraints. Various authors suggested that workers produce glandular secretions ("profertile" or "fertility substances") which are typically fed to the larvae or the queen but which are utilized to produce own eggs in the absence of queens or brood (Pain, 1954; Bier, 1954; Mamsch, 1967). In *P. villosa*, workers do not feed the larvae with secretions or by trophallaxis, hence the latter explanation does most likely not apply in this case.

Whereas worker antagonism is an obvious consequence of selection favoring those workers which invest most in males to which they are closest related (e.g., Bourke, 1988; Heinze *et al.*, 1994), the significance of larval inhibition is less clear. Workers might decrease their own reproductive efforts when the number of larvae becomes so high that additional brood could no longer be taken care of, or when energetical constraints by brood care, such as grooming, divert resources from egg production. It appears that in a colony fed ad libitum, 16 workers could easily nurse far more than 5 or 20 larvae without impairing their own egg production. Before orphaning, the ratio of workers to larvae ranged from approximately 1.4:1 to 6:1, i.e., did not differ strongly from the experimental conditions (0.8:1 and 3.2:1). Nevertheless, numerous eggs were present in these unmanipulated colonies. Alternatively, the presence of larvae might typically signal the presence of a highly fertile queen and workers might respond to this signal by refraining from reproduction (Seeley, 1985; Keller and Nonacs, 1993). Seeley (1985) explained the inhibitory effects of brood on egg-laying by honey bee workers with the possibility of rearing a replacement queen from the present larvae. Only in colonies which are "hopelessly queenless," i.e., without queen and female brood, workers should begin egg-laying. One might thus expect that workers respond differently to female and male larvae, but preliminary experiments in *P. villosa* do not substantiate this difference.

Finally, egg cannibalism by larvae might lead dominant *Pachycondyla* workers to save their resources for periods after the pupation of the present brood, when their freshly laid eggs no longer risk to be eaten.

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The Effects of Season, Pretraining, and Scent on the Efficiency of Traps for Capturing Recruited Honey Bees (Hymenoptera: Apidae)

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A portable trap was designed to capture honey bees recruited to the field by dancers. An infrared phototransistor placed in the entrance tunnel of the trap sensed an incoming bee and turned on a talking clock, which in turn activated a voice-actuated audio tape recorder that recorded the time. We tested the effectiveness of traps for capturing bees recruited by four dancer bees (1) during two seasons when local flower densities differed, (2) with or without a group of bees pretrained to enter traps for food, and (3) when the scent used in traps and at the dancers' feeding station was changed just prior to recruitment trials or was not changed. One trap was put out at each of four distances (50, 100, 150, and 200 m) from the hive, while dancers fed on concentrated sucrose at the feeding station located at 150 m in the same direction. Recruited bees that approached the traps but did not enter were counted by observers. More bees were recruited and captured in traps when the local flora was sparse (fall) than when flowers were abundant (summer), when bees were pretrained versus not pretrained, and when the scent was not changed just prior to recruitment trials versus changed. The distributions of number of bees counted at the four distances at scented recruit stations and trapped were similar only when bees were pretrained and the scent was not changed during recruitment trials. However, the highest proportion of bees trapped in a trial at 150 m (distance to dancers' feeding station) was when bees were pretrained and the scent was changed.

KEY WORDS: *Apis mellifera*; honey bee; recruitment; trap.

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