OBSERVATIONS ON THE SOCIAL ORGANIZATION OF *PACHYCONDYLA CRASSINODA* LATREILLE, 1802 (HYMENOPTERA: FORMICIDAE: PONERINAE)¹

Alda Henriques & Paulo R.S. Moutinho

Departamento de Psicologia Experimental, Centro de Filosofia et Ciências Humanas, Universidade Federal do Pará, 66075-100 Belém, PA, Brazil

Abstract²

In this work we present some behavioral observations about the social organization of the Neotropical ant *Pachycondyla crassinoda*. The individual behavioral catalog of workers is described by studying three colonies and compared with that of other Ponerinae ant species. A total of 33 categories are described from 42 hours of observations. *P. crassinoda* presents a social organization similar to other species of the genus. The queen participates in parental care, and the foragers are recruited by tandem running. Casual observations of agonistic encounters were registered between nestmates that laid eggs, suggesting the existence of reproductive dominance among workers.

Keywords²: dominance orders, Pachycondyla, Ponerinae, social organization

Introduction

Studies of the social behavior of insects have made an important contribution to understanding mechanisms in the organization and evolution of animal societies (Wilson 1975). Among the social insects, ants are a group of especial significance in this regard, on account of their great diversity of species and abundance of individuals. This allows for a great number of interspecific comparisons of adaptations and organizational patterns (Hölldobler & Wilson 1990). Many authors have carried out studies of the mode of social organization in ants (reviewed by Hölldobler & Wilson 1990), mainly in the subfamilies regarded as more highly evolved. These are characterized by a division of labor based on physical castes and a strong regulation of the colony's reproduction and other social activities, mediated by chemical signals (pheromones). In contrast, our knowledge of social organization in the more primitive ants (Ponerinae: Ponerini), in which worker castes are not physically distinct and workers interact through physical contact -- which may even be aggressive -- is still poorly developed. Studies of the social behavior of ponerine ants are needed if we are to gain a more complete view of the social evolutionary mechanisms and social organization of ants.

Pachycondyla is a pantropical genus of predatory ponerine ants with broad distribution in the New World (Kempf 1972). Behavioral studies of these ants have focused on aggression (e.g. in *P. apicalis* and *P. obscuricornis*, Oliveira & Hölldobler 1990, 1991) and division of labor within the colony (Lachaud & Fresneau 1985, Pérez-Bautista et al. 1985). However, information on other *Pachycondyla* spp. is all but nonexistent. *P. crassinoda* is very common in forested areas of the Brazilian Amazon, where it is easy to capture with baits placed on the soil surface (pers. obs.). The only study of this species to date refers to the morphology of the ovary (cited by Fresneau 1984).

Our purpose here is to describe some aspects of the social organization of *P*. *crassinoda* in comparison with other ponerine ants. We describe its social behavior by way

of a behavioral catalog, or ethogram, developed according to the method of Fagen & Goldman (1977). This approach was chosen in order to facilitate comparison with results from other authors (Wilson 1976, Brandão 1978, Paiva & Brandão 1989).

Materials and Methods

Colonies of *P. crassinoda* were collected in a small stand of secondary forest on the grounds of the Emílio Goeldi Museum of Pará in Belém, Pará from September to November, 1991. This forest has a canopy height of 10-18 meters and is dominated by such fast-growing trees as *Cecropia* spp., *Tapirira guianensis*, *Jacaranda copaia*, *Euterpe oleracea*, *Liconia* sp. and *Hevea brasiliensis*.

Collection of colonies

Nests of *P. crassinoda* were located by following foraging workers that carried food in their mandibles as they returned from baits of commercial meat paste that we had set out. Three nests were excavated and the ants, eggs, pupae and larvae counted and transferred to plastic boxes. Of 24 workers, four alate queens, eight pupae and two larvae were collected from colony A; one dealate queen, 18 workers, three alate queens, one pupa, four larvae and eight eggs from colony B; and one dealate queen, 38 workers, seven pupae, 10 larvae and 20 eggs from colony C.

The nests were found in the soil between tree roots or under fallen trunks. They have a simple structure, consisting of a main chamber at 5-10 cm depth, with a tunnel leading to a single opening to the outside. Voucher specimens of *P. crassinoda* are deposited in the Emílio Goeldi Museum of Pará.

Observation nests

In the laboratory each colony was kept in a white plastic tray (10 by 35 by 45 cm) with four or five test tubes (2.5 by 20 cm) placed side by side, each half-filled with water. The water was held in the tubes by a cotton plug. The opening of each tube was partly closed with polyethylene tape in order to maintain a high humidity inside. The tray-nest was connected to a feeding arena (6 by 30 by 35 cm) by means of transparent plastic tubing (1.2 by 12 cm). Workers could not scale the tray walls, so there was no need for an escape barrier.

Colonies were fed once daily with fragments of grasshoppers or cockroaches and occasionally with tenebrionid larvae. As a supplement, honey diluted 1:2 with water was available ad libitum. Dishes of water were also available throughout the study.

Observation procedure

The initial behavioral catalog was compiled by recording all behavior patterns shown by members of colonies A and B over a total of 20 hours between September and November, 1991.

The quantitative treatment was conducted by visual scanning of colony C for a total of 42 hours during 24 days in December 1991 and January 1992. It was recorded each time a member of the colony performed one or another behavior pattern. Workers were not marked for individual recognition. All three colonies were subject to additional observation outside this period of systematic tabulation of acts.

An estimate of the total number of behavior patterns and the statistical analysis of *P*. *crassinoda*'s behavioral catalog followed the method of Fagen & Goldman (1977).

Results

The behavioral catalog of *P. crassinoda* is based on 9257 acts of workers tabulated during 42 hours of observation. These represent 33 behavior patterns (Table 1). The expected number of behavior patterns, according to the method of Fagen & Goldman (1977), is 32.4 (range 26-40). The known behavioral catalog is, therefore, believed to be highly consistent with this species's total behavioral repertory (p<0.001). Queens manifested 12 behavior patterns in 333 acts (Table 1), including some associated with brood care: lick larva; antennate egg, larva or pupa; carry egg; at rest by brood; remove worker from antennating egg.

Workers of all three colonies were observed laying eggs, although not during the period of systematic tabulation of acts. Eggs of colony A (collected without the dealate queen) matured and gave rise to males. For a worker, the period from pupation to adult emergence is about one month.

Members of colony C were observed sharing food, as was also observed between the queen and larvae.

In the forest where colonies were collected, *P. crassinoda* workers were seen coming to baits solitarily and recruited by tandem running. In the laboratory, this form of recruitment was observed in colony B, initiated by mechanical stimulation when workers wandered toward colony C's nest and into its feeding arena at a time when the arena had no food in it.

The behavior "at rest in tube entrance" was recorded when a worker remained motionless inside about the outer 3 cm of a test tube with her head facing the opening.

Agonistic interactions -- grasp another ant's head with the mandibles; pressing her to the floor or to one side; biting various parts of her body; biting her gaster and rolling her onto the ground -- were observed among workers of queenless colony A, continuing for up to six minutes. These episodes apparently occurred before the appearance of new eggs in the colony, but their frequency was not recorded.

Discussion

On the whole, *P. crassinoda* shows a level of social organization similar to that of other members of its genus and subfamily. The size of its behavioral repertory -- 32 behavior patterns -- is not very different from the 42 estimated for *Ectatommoa permagnun* (Paiva & Brandão 1989) and the 35 observed (not estimated) from *Pachycondyla* (*=Neoponera*) *villosa* (Pérez-Bautista et al. 1985). These values are also close to those recorded in other subfamilies, e.g. the 38 observed from *Formica perpilosa* (Brandão 1978) and the 42 estimated for *Zacryptocerus varians* (Wilson 1976). Differences are most notable in the relative frequencies of behavior patterns. In *E. permagnun*, workers devoted 44.5% of acts to grooming, 26.5% to brood care, 10.7% to feeding and 18.7% to other activities, among which are defensive behaviors (2.4%). In contrast, *P. crassinoda* devote 17.6% of acts to grooming, 38.4% to brood care, 26.8% to feeding and 16.9% to other activities. And workers of *P. villosa* identified as specialists in brood care devote 38% and 27% of their activity to caring for eggs and larvae, respectively.

Table 1. Behavioral catalogue of *Pachycondyla crassinoda* adult females. Relative frequency (% of total acts in each caste) of behavior patterns based on 333 queen acts and 9257 worker acts from colony C.

Brood care		
. Mouth-to-mouth contact with larva	0.000	0.313
2. Lick egg	0.000	0.713
B. Lick larva	0.901	2.161
I. Lick pupa	0.000	0.238
. Antennate egg, larva or pupa	1.502	2.031
b. Carry egg	5.405	0.864
7. Carry larva or pupa	0.000	0.097
3. At rest by brood	53.453	31.976
9. Feed solid food to larva	0.000	0.151
0. Lay egg	0.901	0.000
1. Remove worker who antennates egg	0.300	0.043
Nest maintenance		
2. Handle cotton	0.000	5.941
3. Handle refuse	0.000	0.194
4. Carry refuse	0.000	0.270
5. Carry dead larva or workers	0.000	0.486
b. Lick soil	0.000	0.562
Grooming		
7. Self-grooming	5.405	13.730
B. Allo-grooming	0.601	3.021
Foraging and feeding		
9. Walk in foraging arena	0.000	3.068
0. Tandem running	0.000	0.184
. Handle food	0.000	0.043
2. Carry food to nest	0.000	0.151
3. Eat	15.916	17.976
4. Share food	11.411	4.451
5. Drink water	0.000	0.562
6. Drink honey	0.000	0.205
7. Drink fluids from dead larva or adult	0.000	0.205
Antennation		
8. Mutual antennation	0.000	1.383
Antennate another's abdomen	3.904	1.167
Others		
	0.300	0.573
0. Raise head	0.300	
0. Raise head 1. Walk while dragging abdomen	0.000	0.011

33. At rest in tube entrance	0.000	6.320
Total	100.00	100.00

As in other species of Ponerinae, queens of *P. crassinoda* perform brood-care activities. About 5.4% of their acts are carrying eggs and 0.9% licking eggs. Incomparison, Fresneau & Dupuy (1988) found somewhat higher frequencies of these behaviors, respectively 13% and 7%, in *Pachycondyla* (*=Neoponera*) *apicalis* workers. In observations of an *E. permagnun* queen, Paiva & Brandão (1989) found a much higher frequency, 59.8%, of time devoted to brood care.

The observation of worker egg laying in the three *P. crassinoda* colonies and its relationship to agonistic interactions -- physical struggles, repeatedly seen in queenless colony A -- appears to be a common phenomenon in the Ponerinae. Agonistic interactions among nestmates, which form dominance hierarchies, have been described from several species of ants and related with reproductive activity (Hölldobler & Wilson 1990), including in species of *Pachycondyla* (Oliveira & Hölldobler 1990, 1991, Ito & Higashi 1991). Observed acts of aggression between *P. crassinoda* workers suggest the existence of dominance hierarchies, as in other members of the genus, in which aggression can lead to differential egg laying.

The present behavioral catalog manifests the feeding of brood with solid food, as previously notes in other Ponerinae and in many Myrmicinae (Fowler et al. 1991). However, the observation of mouth-to-mouth contact between workers and larvae suggests feeding by regurgitation (trophallaxis). This is more common in the Myrmicinae and Formicinae (Höllodler & Wilson 1990) and is presumably associated with licking salivary-gland secretions producted by larvae and workers, as is known in Myrmicinae, Formicinae, and some Ponerinae (Fowler et al. 1991).

The behavior pattern known here as "at rest in tube entrance", accounting for 6.3% of worker acts, may represent nest-entrance guarding, as is known from another *Pachycondyla* sp. (Pérez-Bautista et al. 1985) and at least one other ponerine ant, *Odontomachus chelifer* (Medeiros et al. 1992).

The behavior patterns described here indicated that *P. crassinoda* resembles other members of its subfamily in organizational pattern. We regard this species as a good candidate for future, more detailed studies of its social organization, especially with respect to a suggested dominance hierarchy among workers.

<u>Acknowledgements</u>

J.C. Simões Fontes, Harold G. Fowler, Paulo S. Oliveira, Augusto L. Henriques and Edson Frazão aided us in various phases of the study and in preparation of the manuscript. We also received valuable suggestions from an anonymous reviewer. William L. Overal gave laboratory access at the Emílio Goeldi Museum of Pará, and Samuel S. Almeida described the forest at the study site. Olivia K. de Almeida assisted in collecting the colonies, and M. Zanuto provided the tenebrionid larvae that served as food for the ants. Alda L. Henriques received a grant from CAPES Social Assistance.

References

Brandão, C.R.F. 1978. Division of labor within the worker caste of *Formica perpilosa* Wheeler (Hymenoptera: Formicidae). Psyche 85: 229-237

Fagen, R.M. & R.N. Goldman 1977. Behavioural catalogue analysis methods. Anim. Behav. 25:261-274.

Fowler, H.G., L.C. Forti, C.R.F. Brandão, J.H.C. Delabie & H.L. Vasconcelos 1991. Ecologia nutritional de formigas. Pp. 131-223 in: A.R. Panizzi & J.R.P. Parra (eds.), Ecologia Nutricional de Insetos e Suas Implicações no Manejo de Pragas. ...: Manole & CNPq.

Fresneau, D. & P. Dupuy. 1988. A study of polyethism in a ponerine ant: *Neoponera apicalis* (Hymenoptera, Formicidae). Anim. Behav. 36:1389-1399

Fresneau, D. 1984. Développement ovarien et statut social chez une fourmi primitive *Neoponera obscuricornis* Emery (Hym. Formicidae, Ponerinae. Ins. soc. 31:387-402

Hölldobler, B. & E.O. Wilson 1990. *The Ants*. Cambridge: Harvard Univ. Press 732 pp.

Ito, F. & S. Higashi. 1991. A linear dominance hierarchy regulating reproduction and polyethism the the queenless ant *Pachycondyla sublaevis*. Naturwissenschaften 78:80-82.

Kempf, W.W. 1972. Catálogo abreviado das formigas da Região Neotropical (Hym. Formicidae). Studia entomol. 15:3-344.

Lachaud, J-P. & D. Fresneau 1985. Les premières étapes de l'ontogenèse de la société chez *Ectatomma tuberculatum* et *Neoponera villosa* (Hym., Form., Ponerinae). Actes Colloq. Ins. soc. 2:195-202

Medeiros, F.N.S., L.E Lopes, P.R.S Moutinho, P.S Oliveria & B. Hölldobler 1992. Functional polygyny, agonistic interaction and reproductive dominance in the Neotropical ant *Odontomachus chelifer* (Hymenoptera, Formicidae, Ponerinae). Ethology 91:134-46.

Oliveira, P.S. & B. Hölldobler 1990.Dominance order in the ponerine ant *Pachycondyla apicalis* (Hymenoptera, Formicidae). Behav. Ecol. Sociobiol. 27:385-93.

Oliveira, P.S. & B. Hölldobler 1991. Agonistic interactions and reproductive dominance in *Pachycondyla obscuricornis* (Hymenoptera; Formicidae). Psyche 98:215-25.

Paiva, R.V.S & C.R.F. Brandão 1989. Estudos sobre a organização social de *Ectatomma permagnun* Forel, 1908 (Hymenoptera: Formicidae). Rev. bras. Biol. 49:783-92.

Pérez-Bautista, M., J.-P. Lachaud & D. Fresneau 1985. La división del trabajo en la hormiga primitiva *Neoponera villosa* (Hymenoptera: Formicidae). Fol. entomol. mex. 65:119-30.

Wilson, E.O. 1975. Sociobiology: The New Synthesis. Cambridge: Harvard Univ. Press 697 pp.

Wilson, E.O. 1976. A social ethogram of the neotropical arboreal ant *Zacryptocerus varians* (Fr. Smith). Anim. Behav. 24:354-63.

Footnotes

1. Translation by C.K. Starr of: Algumas observações sobre a organização social de *Pachycondyla crassinoda* Latreille, 1802 (Hymenoptera: Formicidae: Ponerinae). *Revista Brasileira de Entomologia* 38:605-11, 1994.

2. English abstract and keywords as in the original.