ASIAN MYRMECOLOGY Volume 3, 39–44, 2010
ISSN 1985-1944 © FUMINORI ITO

Gamergate reproduction without queens in the ponerine ant *Pachycondyla* (=*Bothroponera*) *tesseronoda* (Emery, 1877) in southern India (Hymenoptera: Formicidae)

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ABSTRACT. The colony composition of the ponerine ant *Pachycondyla* (=*Bothroponera*) *tesseronoda* was studied in Mudigere, southern India. The colonies (n = 9) each consisted of 102 ($\pm$ SD 28) workers on average, without morphologically distinctive queens. Instead, one to eight gamergates (inseminated and egg-laying workers) per colony reproduced. Virgin workers developed oocytes, but most of these seem to have degenerated before maturation. Experimental removal of gamergates resulted in oviposition by virgin workers, suggesting that the presence of gamergates affects oocyte maturation in virgin workers, although the mechanisms remain unknown.

Keywords: ant, *Bothroponera*, gamergate, *Pachycondyla*, reproduction

INTRODUCTION

Colonies of most ant species consist of two morphologically distinct female castes: queens that can be inseminated and lay eggs, and workers that cannot mate with males and that are sterile in general. However, more than 100 species of poneroid (subfamilies Amblyoponinae and Ponerinae) and ectatommine ants show sexual reproduction by workers (Peeters & Ito 2001). Such mated and egg-laying workers are called "gamergates". Some species with gamergates have lost morphologically distinctive queens, while other species reproduce by both gamergates and queens (Ito & Ohkawara 1994; Peeters & Ito 2001). The number of reproductive females varies among species with gamergates. For instance, among gamergate species without queens, *Diacamma* spp., *Pachycondyla* (=*Bothroponera*) *sublaevis* (Emery), *P.* (=*B.*) *kruegeri* Forel, *Streblognathus aetiopianus* (Smith), and *Dinoponera* spp. always have one gamergate per colony (single-gamergate species), while several gamergates are found in colonies of *Rhytidoponera* spp., *Pachycondyla* (=*Ophthalmopone*) *berthoudi* (Forel) and *Amblyopone reclinata* Mayr (multiple-gamergate species) (Ward 1983; Peeters & Crewe 1985; Wildman & Crewe 1988; Ito 1993a; Paiva & Brandao 1995; Monnin & Peeters 1998, 2008). In one Indonesian *Pachycondyla* (=*Bothroponera*) sp. in which there were several mated workers per colony, Ito (1993b) investigated the fertility of these and found functional monogyny, with always a single gamergate.

To understand the diversity of social organization, comparative studies of the biology of several species in these subfamilies are undoubtedly important. In this paper, I will give information on nest structure and colony composition of the Indian ponerine ant *Pachycondyla* (=*Bothroponera*) *tesseronoda* (Emery, 1877). In addition, I examined the effects of gamergates on ovarian development of virgin workers. The orientation and recruitment behaviour

of this species collected in Sri Lanka has been reported (e.g., Maschwitz *et al.* 1974; Jessen & Maschwitz 1986), but no information on their colony structure has been available to date.

MATERIALS AND METHODS

Nine colonies of *Pachycondyla tesseronoda* were collected in Mudigere, Karnataka, southern India in the rainy season during mid-August, 1990. Workers of six colonies (Colonies B, D, E, G, H and I) were dissected under a microscope to check for insemination (the presence of sperm in the spermathecae) and for ovarian development. The ovarian condition of workers was classified into the following three developmental classes according to the presence or absence of mature oocytes or chorionated eggs and to size of oocytes relative to the adjacent nurse cells: Class I, all oocytes smaller than the nurse cells; Class II, one or more developed oocytes present and bigger than the nurse cells but no mature oocytes or chorionated eggs; and Class III, chorionated eggs and/or mature oocytes found. The other three colonies were kept in the laboratory using artificial nests. The bottom of each nest box was covered with plaster, and brood chambers were excavated in the plaster floor. The chambers were covered with glass plates. To know the effects of the presence of gamergates on ovarian development of virgin workers, two colonies (Colonies A and C) were divided into five and seven subcolonies respectively, and kept in the laboratory for three weeks. Then, all workers were dissected to check their reproductive condition. One colony (Colony F) was used for casual observation of behaviour after individual marking by enamel paint. After observation, all individuals were dissected to check their reproductive condition. The length and width of 20 eggs found in Colony E were measured under a light microscope. The maximum head width of all gamergates (n = 31), and of ten randomly selected virgin workers in each of the eight colonies containing gamergates (n = 80), was measured under a dissecting microscope.

RESULTS

1. Nest structure and colony composition

Pachycondyla tesseronoda colonies were collected by digging ground in open grassland. Nest structure was very simple. The entrance was usually located at the base of unidentified grass tussocks. A single unbranched shaft, which connected with four to six chambers, went down almost vertically to a depth of 30 to 50 cm. The size of chambers was ca. 18 cm x 10 cm with 2 cm height.

The colonies consisted of 102 workers on average, and several broods (Table 1) without morphologically distinct queens or queen pupae. All workers had 4+4 ovarioles and a spermatheca. Colony A had no mated workers, but the other colonies had 1–8 inseminated workers (Table 2). All inseminated workers had 0–2 mature oocytes and/or chorionated eggs and dense accumulations of yellow bodies in their ovaries. This suggests that all mated workers were laying eggs, thus were gamergates. In contrast, virgin workers had no mature oocytes or chorionated eggs in their ovaries; however several workers each had 2 or 3 developing oocytes in the ovaries (Class II). The developing oocytes in virgin workers were always abnormally rounded, which might indicate degeneration, and their yellow bodies were tiny, suggesting the virgin workers were sterile. In the laboratory, I often observed virgin workers laid a white fluid as has been reported for some formicoxenine ants (e.g., Heinze & Smith 1990), which was fed upon by the workers.

Egg size was large, with 1.6 $\pm$ SD 0.06 mm length and 0.46 $\pm$ 0.02 mm width (n = 20). Body size variation of workers was relatively small (Fig. 1) and no difference in head width of virgin workers was found among the eight colonies (ANOVA, $F_{7, 72} = 1.27$, $P = .28$). Gamergates and virgin workers did not differ in head width (gamergates 1.62 $\pm$ 0.04 mm; virgins 1.63 $\pm$ 0.04 mm, t-test, $t_{109} = -1.29$, $P = .2$).

Table 1. Demographic characteristics of the Indian *Pachycondyla tesseronoda* colonies collected in Mudigere, southern India.

Colony Code	Workers	Males	Cocoons	Larvae	Eggs
A	100	0	21	13	6
B	94	0	13	10	6
C	120	25	—	—	—
D	71	0	19	35	17
E	153	0	31	17	20
F	70	0	—	—	—
G	117	0	8	17	8
H	107	0	20	6	9
I	82	0	20	6	9
Mean ±SD	101.8 ±28				

—, not counted

Table 2. Reproductive status of workers in nine colonies listed in Table 1. The ovarian condition of the workers in two colonies (A and C) used for the isolation experiment is shown in Table 3. Colony F was used for casual observation.

			Mated workers			Virgin workers			
			Ovary development				Ovary development		
Code	No. workers dissected (%)	No. workers (%)	I	II	III	No. workers	I	II	III
A	83(83)	0(0)	—	—	—	83	—	—	—
B	98(95.9)	8(8.2)	0	0	8	90	13	77	0
C	113(94.2)	4(3.5)	—	—	—	109	—	—	—
D	39(54.9)	1(2.6)	0	0	1	38	6	32	0
E	130(85)	8(6.2)	0	0	8	122	6	116	0
F	47(67.1)	3(6.4)	—	—	—	44	—	—	—
G	53(45.3)	1(1.2)	0	0	1	52	11	41	0
H	52(48.5)	2(3.8)	0	0	2	50	6	44	0
I	67(81.7)	4(6.0)	0	0	4	63	8	56	0

—, not examined

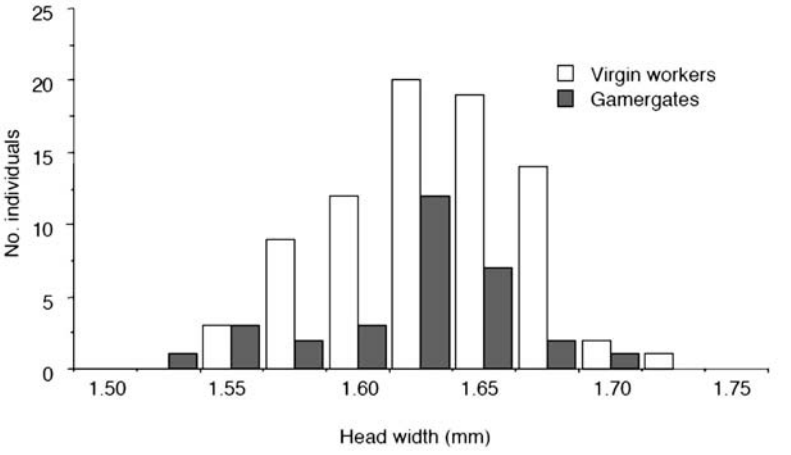

Fig 1. Head width distribution of gamergates and virgin workers in *Pachycondyla tesseronoda.*

2. Effects of gamergates on ovarian development of virgin workers

In the case of multiple-gamergate species, making gamergate-less colonies in the laboratory is often difficult, because gamergates are indistinguishable from virgin workers in their external morphology. Fortunately, by random splitting of two wild-collected colonies, I was able to make nine subcolonies without gamergates, as well as three with gamergates. As shown in Table 3, none of the virgin workers in the presence of gamergates had mature oocytes in their ovaries while, in the subcolonies without gamergates, after three weeks, three of 149 virgin workers had mature oocytes and a few of the virgin workers with Class II ovaries had normally developing oocytes. In fact, virgin workers laid eggs in 6 of 9 gamergate-less subcolonies. Unfortunately, behavioural interactions among virgin workers under orphan conditions could not be observed.

Table 3. Reproductive status of virgin workers in twelve experimentally divided subcolonies of *Pachycondyla tesseronoda*

	Number of	Number of	Ovary development of virgin workers			Total no. eggs
Code	gamergates	workers	I	II	III	laid
A-1	0	18	5	12	1	1
A-2	0	21	3	18	0	2
A-3	0	15	1	14	0	0
A-4	0	16	2	14	0	5
A-5	0	12	5	7	0	3
C-1	1	16	1	15	0	6
C-2	1	15	1	14	0	4
C-3	2	13	8	5	0	10
C-4	0	24	16	8	0	0
C-5	0	7	3	4	0	0
C-6	0	18	0	17	1	3
C-7	0	18	2	15	1	3

DISCUSSION

The taxon *Pachycondyla* was recently revised to become a very large genus containing the former genera *Bothroponera, Brachyponera, Ectomomyrmex, Hagensia, Mesoponera, Neoponera, Ophthalmopone, Trachymesopus* etc. (Bolton 1995); however, it is possible that the current genus is a polyphyletic assemblage of taxa (Ward 2007). Thus, for discussion I compare the social characteristics of *P. tesseronoda* not only with *Pachycondyla* but also with other ponerine ants with gamergates. Among ponerine ants, gamergate reproduction has been reported in more than 30 species. Among these, queenlessness is found in *Pachycondyla* (=*Ophthalmopone*) *berthoudi*, *Pachycondyla* (=*Hagensia*) *havilandi* (Forel), *Pachycondyla (=Bothroponera) sublaevis, P. (=B.) kruegeri*, two species of African *Platythyrea*, five species of *Leptogenys*, two species of *Thaumatomyrmex*, and all species of *Diacamma*, *Dinoponera* and *Streblognathus* (Ito 1997; Monnin & Peeters 2008). In the present paper, I show gamergate reproduction without queens in Indian *Pachycondyla tesseronoda* as an additional example in the subfamily Ponerinae.

Among queenless gamergate ponerines, the number of gamergates per colony varies among species. Strictly monogynous species are common: 19 species in six genera are single-gamergate whereas four species in two genera show the multiple-gamergate condition (Monnin & Peeters 2008). In the case of *Pachycondyla tesseronoda*, 1-8 workers mated and all mated workers laid eggs. Since only about half the workers were dissected in the two colonies (D and G) in which only one gamergate was confirmed, it is possible that multiple-gamergate is the main social system in *Pachycondyla tesseronoda*. Comparative study of colony structure in gamergate species shows an interesting pattern: gamergate species with queens generally have multiple gamergates per colony while single-gamergate species always lack queens (Monnin & Peeters 2008). Based on this pattern, Monnin and Peeters (2008) hypothesised that multiple-gamergate with queens is the ancestral condition, and queen loss and single-gamergate occurred subsequently. *Pachycondyla tesseronoda* has multiple gamergates without queens, which does not change the pattern found by Monnin and Peeters (2008). However, knowledge of other ant species is still needed to test their hypothesis.

In general, colony size of multiple-gamergate species is greater than that of single-gamergate species (Monnin & Peeters 2008). Extreme examples of the latter are *P. sublaevis* in Australia and *Pachycondyla* sp. in Java, with fewer than ten workers per colony (Peeters *et al.* 1991; Ito 1993b). *Pachycondyla tesseronoda* seems to conform to this pattern: the average colony size of this species is greater than all single-gamergate species shown in Monnin and Peeters (2008) except for four species of *Diacamma*.

Inhibition in normal maturation of oocytes of virgin workers by the presence of gamergates has been shown in several single-gamergate species (Peeters & Higashi 1989; Ware *et al.* 1990; Ito & Higashi 1991; Peeters & Tsuji 1993; Monnin & Peeters 1998); however, such a phenomenon has rarely been confirmed in multiple-gamergate species, partly because complete removal of gamergates is often very difficult. Among queenless multiple-gamergate species, oviposition by virgin workers in the absence of gamergates has been experimentally demonstrated only in *P.* (=*Ophthalmopone*) *berthoudi*, *Amblyopone reclinata* and *Gnamptogenys menadensis* Mayr (Villet 1992; Ito 1993a; Gobin *et al.* 1998). This paper shows that virgin workers of *P. tesseronoda* can lay normal-sized eggs in the absence of gamergates. These observations in multiple-gamergate species without queens indicate that the presence of gamergates may somehow inhibit fertility in virgin workers, by an unknown mechanism, and that virgin-worker inhibition is a common phenomenon in queenless poneroid ants, not only in single-gamergate species.

ACKNOWLEDGEMENTS

I thank J. Billen for comments and English revision, V. V. Beravadi and his family for their kind help in colony collection, arrangement of accommodation, and great hospitality during my stay in Mudigere, C. Peeters for travelling a relay of several buses together from Bangalore to Mudigere and helpful comments on the manuscript, S. Higashi for help in laboratory experiments and financial support for my visit to India, and H. Bharti and C. Baroni Urbani for identification of species.

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