COLONY COMPOSITION OF TWO MALAYSIAN PONERINE ANTS, *PLATYTHYREA TRICUSPIDATA* AND *P. QUADRIDENTA*: SEXUAL REPRODUCTION BY WORKERS AND PRODUCTION OF QUEENS (HYMENOPTERA: FORMICIDAE)

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Abstract

Colonies of ponerine ants *Platythyrea quadridenta* and *P. tricuspidata* were collected in the rainforest of West Malaysia. Two colonies of *P. tricuspidata* were composed only of workers, and three and eight workers were inseminated per colony, respectively. However, active ovaries were found in one of the three, and two of the eight mated workers. *P. quadridenta* also exhibited sexual reproduction by workers, and there were many sterile mated workers. The two largest colonies of *P. quadridenta* produced alate queens. The significance of queen production and worker sexual reproduction are discussed.

Introduction

Morphological differentiation associated with division of reproductive efforts between queens and workers is an important characteristic in the reproductive structure of ant colonies (Hölldobler and Wilson 1990). In the subfamily Ponerinae, however, considerable variation in reproductive structure has been reported in recent years (Peeters 1993). For instance, several species lack morphological queens and mated workers lay eggs instead (Peeters 1991). Such queenless reproduction has been reported in 10 genera belonging to the four tribes Amblyoponini, Ectatommini, Platythyreini, and Ponerini (Peeters 1991; Ito 1991). In addition, Sommer and Hölldobler (1992) have found unexpected variation of

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reproductive division of labour in *Pachycondyla tridentata*, in which mated queens and mated workers exist together and both lay eggs. Reproduction by both queens and workers is also reported in *Platythyrea arnoldi* (Villet 1993) and *Harpegnathos saltator* (Peeters pers comm.). These species are good experimental subjects for understanding the evolution of morphological castes and their roles in the social organization and colony life-pattern of ants.

In West Malaysia, I studied colony composition of two *Platythyrea* species (Ponerinae: Platythyreini) and found sexual reproduction by workers in *Platythyrea quadridenta* and *P. tricuspidata*, as well as production of queens in the former species. In this paper, I present information on colony composition and reproductive condition of queens and workers in these two species.

Methods

Colonies were collected in Ulu Gombak Forest Reserve (350m elevation, 3° 19' latitude, 101° 43' longitude) near Kuala Lumpur, West Malaysia, from the end of dry season (July) to the rainy season (October), in 1992. Colony composition was assessed just after collection and all individuals were dissected under a binocular microscope to check reproductive condition. Head width (outerorbital distance), pronotum width, width of IVth abdominal segment and petiole width of several individuals was measured using an ocular micrometer on a binocular microscope.

Results

Both species nested in dead branches or large logs on the ground of rainforests. These ants run very rapidly when their nests are disturbed so that it was very difficult to capture all individuals. Therefore, complete collections were made only of two colonies of *Platythyrea tricuspidata* (colony code, Pt-1 and 2) and 14 colonies of *P. quadridenta* (Pq-1 to 14).

Platythyrea tricuspidata

Both *P. tricuspidata* colonies were small (Table 1) and contained neither queens, nor queen pupae. All workers had three ovarioles in each ovary and a spermatheca. Three and eight work-

Table 1. Colony composition of *Platythyrea tricuspidata* (Pt-1,2) and *P. quadridenta* (Pq-1–14) collected in West Malaysia.* Number of mated workers having active ovaries was shown in parentheses. Only one dealated queen was mated and had active ovaries. **Not counted just after sampling.

Colony code	Number of Individuals							
	Dealate queens	Workers	mated*	Alate queens	Males	Pupae	Larvae	Eggs
Pt-1	0	17	8(2)	0	0	-**	–	–
Pt-2	0	29	3(1)	0	0	16	13	14
Pq-1	0	2	1(1)	0	0	1	0	0
Pq-2	0	5	3(0)	0	0	2	0	0
Pq-3	0	5	3(1)	0	0	7	3	0
Pq-4	0	6	3(3)	0	0	1	4	13
Pq-5	0	10	3(2)	0	0	2	5	5
Pq-6	0	10	2(1)	0	1	8	8	1
Pq-7	0	12	2(1)	0	0	4	7	18
Pq-8	0	16	1(1)	0	0	6	19	17
Pq-9	0	19	2(2)	0	0	10	11	6
Pq-10	0	21	6(1)	0	0	7	13	13
Pq-11	0	22	0	0	0	15	14	7
Pq-12	0	33	12(3)	0	1	5	25	27
Pq-13	0	49	6(6)	8	0	19	17	11
Pq-14	2	50	4(4)	8	0	33	37	17

ers were inseminated in colonies Pt-2 and Pt-1, respectively. However, active ovaries were only found in one mated worker in Pt-2 and two mated workers in Pt-1. The other eight mated workers and all virgin workers lacked oocytes and yellow bodies in their ovaries. The body size of workers was quite uniform (Table 2) and did not differ between mated and unmated workers.

Platythyrea quadridenta

Queens occurred in only two colonies (Table 1). Worker number was 18.5 ± 15 (Mean ± SD). Number of inseminated workers was zero to twelve, representing 0 to 60% of worker population per colony. Similarly to *P. tricuspidata* colonies, 22 out of 48 mated workers (total) were sterile. Four colonies had multiple mated workers with active ovaries (=gamergates) (colony code Pq-4, 9, 13, 14). In another four colonies having multiple mated workers (colony code Pq-3, 6, 7, 10), only one gamergate was present while the other mated workers lacked developed oocytes and

Table 2. Comparison of body size between mated workers and virgin workers, and between fertile mated workers and sterile mated workers in two *Platythyrea* species. Mean ±SD was shown.

	P. tricuspidata			*P. quadridenta*					
	Virgin	Mated	P*	Virgin	Mated	P*	Mated fertile	Mated sterile	P*
No. individuals examined	15	3		11	17		4	13	
Head width	1.23 ± 0.02	1.23 ± 0.02	0.60	1.04 ± 0.02	1.04 ± 0.02	0.82	1.03 ± 0.03	1.04 ± 0.02	0.27
Pronotum width	1.03 ± 0.02	1.03 ± 0.01	0.68	0.91 ± 0.02	0.92 ± 0.01	0.20	0.93 ± 0.02	0.92 ± 0.01	0.25
Petiole width	0.69 ± 0.03	0.68 ± 0.01	0.24	0.50 ± 0.02	0.50 ± 0.02	0.62	0.50 ± 0.03	0.50 ± 0.01	0.77
Abdomen width	1.17 ± 0.02	1.17 ± 0.02	0.68	0.88 ± 0.02	0.89 ± 0.02	0.49	0.89 ± 0.01	0.89 ± 0.02	0.95

*.t-test

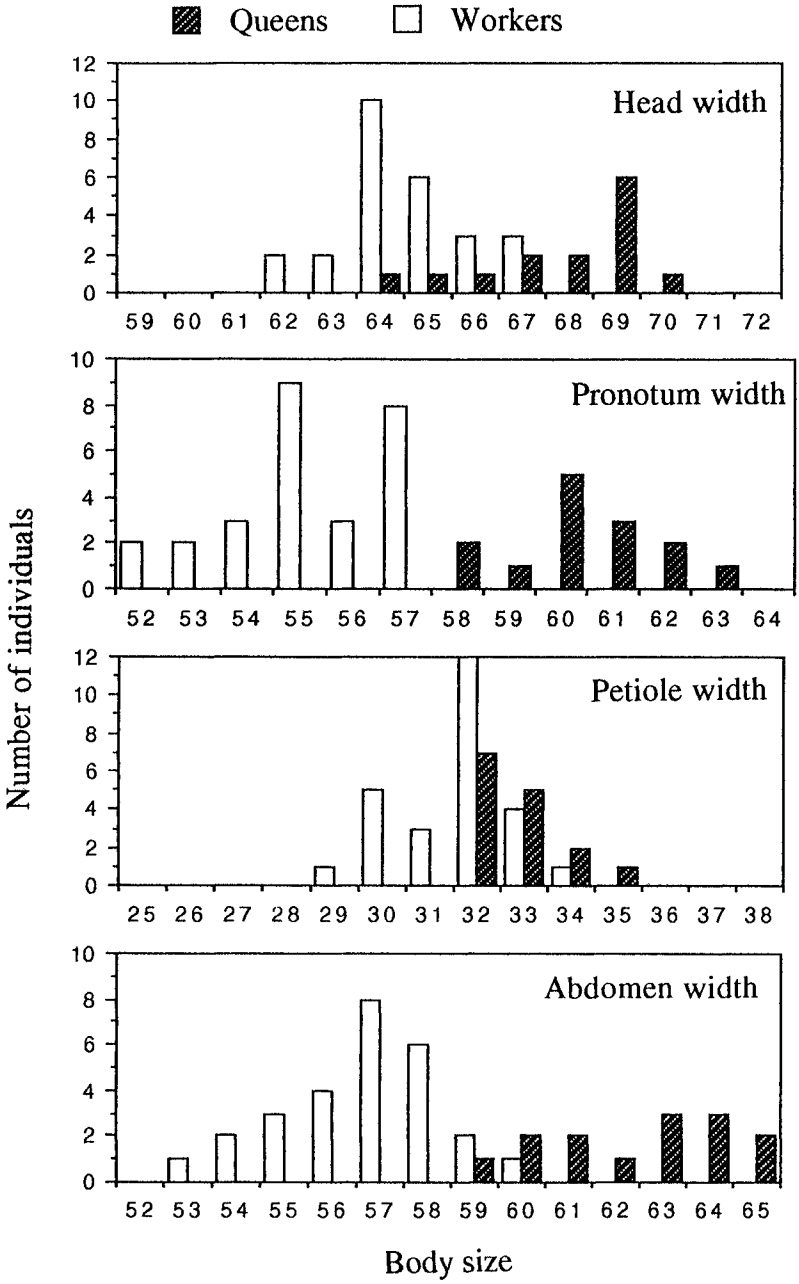
yellow bodies, indicating that these colonies were functionally monogynous. In Pq-5 and Pq-12, there were sterile mated workers, while two and three mated workers had active ovaries, respectively. In one colony (Pq-2), composed of three mated workers and two virgin workers, there were no egg laying individuals. In Pq-11, consisted entirely of virgin workers lacking visible oocytes. This suggests that colony fission had recently occurred in Pq-2 and Pq-11. In all 14 colonies, no virgin workers had visible oocytes.

Head width of workers was significantly different among five measured colonies (ANOVA, $F = 16.6$, $P = 0.0001$, $df = 4$,), however, this was not different between Pq-10 and 12 (ANOVA, $F = 3.3$, $P = 0.1$, $df = 1$,). Thus, effects of body size on reproductive conditions were examined in the two colonies (Table 2). All four measures were not different between mated workers and virgin workers, and also between gamergates and mated sterile workers (Table 2), indicating that worker body size does not affect insemination or oocyte development.

Two large colonies (Pq-13 and 14) produced alate queens, and one of these colonies contained one inseminated and dealate queen who had active ovaries. The body size of queens was significantly larger than workers in all four measures (Fig. 1). However, the size difference between the two castes in *P. quadridenta* is small relative to other ponerine ants in which queens monopolize reproduction while workers are always virgin (c.f. Ito and Ohkawara 1994). In addition, despite the queens' larger overall body size, their reproductive apparatus is almost identical to the workers: both castes had a pair of three ovarioles, and the spermathecae were about the same size.

Discussion

In the ponerine species having gamergates, the number of mated workers per colony varies greatly. For instance, in the colonies of *Diacamma* spp., *Pachycondyla sublaevis, P. krugeri* and *Streblognathus aethiopicus*, there is only one gamergate per colony and she monopolizes egg production (Peeters and Higashi 1989; Fukumoto et al. 1989; Ito and Higashi 1991; Wildman and Crewe 1988; Ware et al. 1990). Several gamergates occur in *Rhytidoponera* spp., *Ophthalmopone* spp. and *Amblyopone* sp. (Ward 1983; Peeters 1987; Peeters and Crewe 1985; Ito 1991, 1993a). Worker reproduction


Queens
Workers
Head width
Pronotum width
Petiole width
Abdomen width
Number of individuals
Body size
59 60 61 62 63 64 65 66 67 68 69 70 71 72
52 53 54 55 56 57 58 59 60 61 62 63 64
25 26 27 28 29 30 31 32 33 34 35 36 37 38
52 53 54 55 56 57 58 59 60 61 62 63 64 65

in *Platythyrea* has been reported in five African species, *Platythyrea brevidentata, P. cribrinodis, P. schultzei, P. lamellosa,* and *P. arnoldi* (Villet 1990, 1992a, 1993). Except for *P. arnoldi*, colony of these species contain one gamergate. In the Oriental tropics, the social organization of *Platythyrea* species has been little studied.

In *Platythyrea tricuspidata* and *P. quadridenta*, mated workers reproduce sexually in West Malaysia. In this study, most colonies contained multiple mated workers, but only a few laid eggs in each colony. The same situation was found in an Indonesian species of *Pachycondyla* (=*Bothroponera*) (Ito 1993b). In this case, there is a dominance hierarchy through frequent aggressive antennation, in which one dominant mated worker laid eggs, while low-ranked mated workers were sterile (Ito 1993b). The mechanism regulating oviposition by mated workers in *Platythyrea tricuspidata* and *P. quadridenta* is unknown, however, dominance behaviour is a possibility. Unlike some queenless species having multiple gamergates such as *Rhytidoponera* sp. 12 (Peeters 1987), the presence of sterile mated workers in Malaysian *Platythyrea* spp. and Indonesian *Pachycondyla* (=*Bothroponera*) sp. indicates that insemination is not always associated with ovarian development, as pointed out in *Amblyopone* sp. (Ito 1993a) and *Ophthalmopone berthoudi* (Villet 1992b).

As already reported for *P. arnoldi* (Villet 1993), *P. quadridenta* produced alate queens, and one mated dealate queen was found. Queens were not discovered in the colonies of *Platythyrea tricuspidata*, but the type specimen of *P. tricuspidata* subsp. *penangensis* Wheeler, described from Penang, north Malaysia, is a dealate queen (cited in Brown 1975). Intensive collection may yet provide evidence of queen production in *P. tricuspidata.*

Queens of *P. quadridenta* were produced in only two colonies which were largest in my collected colonies. This is consistent with characteristics of sexual production in several ant species, in which small colonies produced workers only while large colonies produced queens and males (Hölldobler and Wilson 1990). Colony size may be proximate factor for queen production in *P. quadridenta.*

Fig. 1. Frequency distribution of body size in queens and workers of *Platythyrea quadridenta.* 60 = 1 mm.

Among ponerine species in which only queens reproduce sexually, queens have a wider IVth abdominal segment than workers (Ito and Ohkawara 1994). Although the number of ovarioles in queens is usually the same as in workers, the width of the spermatheca is remarkably larger in queens than in workers (Ito and Ohkawara 1994). In comparison, the dimorphism in these characters between female castes was weak in *P. quadridenta*, suggesting that reproductive specialization between the two castes is less developed. The important difference between the queens and the workers may be mode of colony proliferation: workers may found their colonies only by colonial budding while queens may be able to start their colonies by independent colony foundation, although this has not been confirmed in the field.

The significance of sexual reproduction by both queens and workers is suggested in *Rhytidoponera metallica*, in which reproduction is mostly performed by mated workers (Haskins and Wheldman 1965), although a small number of alate queens are sometimes produced. Ward (1986) reported in this ponerine ant that a dealate queen could start a new colony independently, and after the queen's death, several workers showed sexual calling behaviour under the queenless condition in the laboratory. This observation indicates that alate queens function as a dispersal form to exploit new habitat and workers function as a non-dispersing form that continues reproduction of successful colonies established in good habitats. Further investigations of the ecology of colony foundation, particularly of the demographic characteristics of colonies founded by queens independently and of colonies founded by workers cooperatively, and of mechanisms regulating queen production are necessary to further our understanding of sexual reproduction by both workers and queens in ponerine ants.

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