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Colony composition and behaviour of a queen and workers in the Oriental ectatommine ant *Gnamptogenys cribrata* (Emery) 1900 in West Java, Indonesia

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Abstract. We describe colony composition and reproductive and behavioural characteristics of *Gnamptogenys cribrata*. Colonies are monogynous, composed of one dealate queen and an average of 27 workers. This species shows the unusually low number of two ovarioles (1 – 1) in both queens and workers. The queen shows larval hemolymph feeding. Workers laid two distinctive types of egg depending on social environment: in the presence of a queen workers laid small trophic eggs which were not eaten by the queen. In the queenless condition, workers laid eggs that looked similar to a queen's egg, but did not develop into a larva.

Keywords: ants, *Gnamptogenys*, larval haemolymph feeding, ovary

INTRODUCTION

The ectatommine ant genus *Gnamptogenys* is widely distributed through tropical and subtropical areas, but biological information is limited, because most *Gnamptogenys* species inhabit forests and are not common (Lattke 2004). In the Oriental tropics and Australia, 49 species of *Gnamptogenys* are known (Lattke 2004); however, detailed studies of biology have been undertaken only for *G. menadensis* and *G. bicolor* (e.g. Gobin *et al.* 1998a,b, 2001; Aikawa *et al.* 2002 ; Tanigawa *et al.* 2002). In the New World, 80 species are described (Lattke *et al.* 2007), and biology of *G. ingeborgae*, *G. horni*, *G. moelleri* and *G. striatula* has been studied (e.g. Brown, 1992; Pratt 1994; Blatrix & Jaisson 2000, 2001; Cogni & Oliveira 2004; Lommelen *et al.* 2006, 2008). These reports indicate that colony structure varies among species: gamergates, ergatoid queens and alate queens are found in this genus. Thus, comparative study of biology in this genus is important for understanding the diversity of social structure in ants. Body size of workers also varies greatly among species. For example in the Oriental tropics, *G. gastroideia* is the largest species with an average head width of 1.58 mm, and head width of most species ranges between 0.9 and 1.4 mm (e.g. *G. binghamii*, *G. bicolor*, *G. costata*, *G. menadensis*, *G. paso*, *G. posteropsis*) (Ito & Gobin, unpublished). The head width of *G. cribrata* is 0.51 mm, which is the smallest among our *Gnamptogenys* collection. Comparable smaller species are *G. chapmani* (0.66 mm) and *G. laevior* (0.76 mm). In our experience, colony collection of such small *Gnamptogenys* species is not easy. We found six colonies of *G. cribrata* (Emery, 1900) (=*Gnamptogenys dammermani* (Wheeler, 1924), synonymised in Lattke (2004)) in the Bogor Botanical Gardens, West Java, Indonesia, during 13 annual surveys of ants from 1990 to 2003. Apart from taxonomic records, the only published data on this rare species concerns morphological and

histological observations on subepithelial glands (Gobin *et al.* 2003). Here we present biological notes on this small species of *Gnamptogenys*.

MATERIALS AND METHODS

Colonies were collected in the Bogor Botanic Gardens (Kebun Raya Bogor), West Java, Indonesia from 1992 to 2002. Adult composition was recorded just after sampling, and all queens and several workers were dissected under a binocular microscope to check the number of ovarioles, mating status, presence or absence of yellow bodies, and ovary development. Maximum width of head and fourth abdominal segment of alate queens ($n = 2$) and workers ($n = 15$) in colony FI93-212 (an orphan colony), and of a dealate queen in FI93-71, were measured under a binocular microscope. One colony (FI02-97) was kept in an artificial nest (10.0 x 6.2 x 2.7 cm) placed in an incubator (25°C, 14L10D). The bottom of nest box was covered with plaster and a brood chamber (ca. 3.0 x 3.0 x 0.3 cm) was excavated in the plaster floor. The chamber was covered with glass plates. Mealworms and cricket larvae were given as prey. Behaviour of queen and workers was observed for a total of 435 min. under a binocular microscope.

RESULTS

Colony composition

G. cribrata is a rare ant species in the Bogor Botanical Gardens. So far only six complete colonies have been collected (Table 1). During quantitative collection of ants in this garden (Ito *et al.* 2001), workers of this species were collected from only two of 118 quadrats (quadrat size: 30 cm x 30 cm) from which litter and surface soil were shifted. All colonies were collected from soil (under stones). All but one colony had only one dealate queen who mated and laid eggs. One colony had three dealate queens but only one mated and the other two were virgin. Thus, *G. cribrata* colonies are monogynous. Colony size was small with an average of 27 $\pm$ 14 (standard deviation, SD) workers (range 6 to 45). One queenright colony had a male, another had nine alate queens. These alate queens had normal wings. Number of ovarioles of both queens and workers was only two (one in each ovary). Queens had a spermatheca while we could not find a spermatheca in workers. Queens were significantly larger than workers both in head width (queens, 0.58 mm $\pm$ 0.017 SD, workers, 0.51 mm $\pm$ 0.018 SD, Mann-Whitney U-test, $Z = -2.68$, $P < 0.01$) and in abdomen width (queens, 0.59 mm $\pm$ 0.01 SD, workers, 0.48 mm $\pm$ 0.017 SD, Mann-Whitney U-test, $Z = -2.69$, $P < 0.01$)). Workers were monomorphic with small body-size variation. Egg size was 0.48 mm $\pm$ 0.03 SD in length and 0.22 mm $\pm$ 0.01 SD in width ($n = 5$).

Queen behaviour

One queen exhibited larval hemolymph feeding (LHF), as known in the congeneric *G. menadensis* (Gobin *et al.* 1998a) and in *Amblyopone silvestrii* (Masuko 1986) and *Prionopelta kraepelini* (Ito & Billen 1998). The manner of LHF is very similar to

Table 1. Colony composition of *Gnamptogenys cribrata* collected in the Bogor Botanic Gardens, West Java, Indonesia. Only queenright colonies are shown. Number in parentheses shows the number of mated queens.

Colony code	Dealate queens	Workers	Alate queens	Males
FI92-411	1 (1)	31	0	0
FI93-71	1 (1)	20	0	0
FI95-822	1 (1)	6	0	0
FI97-575	1 (1)	45	0	0
FI97-629	3 (1)	20	0	1
FI02-97	1 (1)	40	9	0

that of *P. kraepelini*. The queen of *G. cribrata* bit all parts of the body of the larvae with her mandibles, and licked hemolymph from the resulting wounds. As in *A. silvestrii* and *P. kraepelini*, larvae subjected to LHF did not die from their wounds. When *G. menadensis* was subjected to food shortage, hemolymph feeding could escalate into larval mortality (Gobin *et al.* 1998a). During 435 min. observation, we observed 10 events of LHF and 3 events of feeding on a mealworm by the queen. In total, from all observations the queen spent more time on LHF (34 min. 34 sec) than on prey feeding (20 min. 51 sec.). A feeding bout of LHF lasted on average 3 min. 27sec. (range, 1 min. 20 sec. to 6 min.), while prey feeding lasted on average 6 min. 57 sec. (range 1min. to 15 min.). This measure of prey-feeding duration is highly biased by a single feeding event that lasted 15 min. Two trophic eggs were laid by workers during observations and both were given to the larvae. The queen did not approach or eat them.

Oviposition by the queen was observed twice. The queen showed a typical egg-laying posture: she bent her abdomen underneath her thorax and extruded her sting. When the egg appeared, the queen did not pick it up with her mandibles but let it drop to the nest floor. Subsequently, a worker grasped the egg and brought it to the egg pile. Most egg care was performed by workers. Although the queen often stayed near the egg-pile, she rarely touched the eggs.

Worker behaviour

Workers foraged individually. If workers found large prey, they returned to the nest and recruited a few nestmate workers and brought back the prey to the nest co-operatively ($n = 10$). The large prey was cut into small pieces, and given to larvae. Workers and the queen sometimes picked up a piece of prey and fed on it. Workers never showed LHF (which includes pinching the larvae), but they sometimes licked larvae which were subjected to LHF by the queen.

Larvae spun cocoons before becoming prepupae as in other *Gnamptogenys* species. However, this species is exceptional as workers cut off the tip of cocoons and removed the meconium (gut purge), leaving one end of the cocoon open. This was the case in all cocoons found in the field and observed in the laboratory ($n = 20$). Naked pupae were never found in either field or laboratory.

As mentioned above, workers laid trophic eggs which were smaller in size than normal eggs laid by queens. When we made an orphan colony, aggression among workers was frequently observed and one worker became dominant. Subsequently she started to lay eggs and for the following 12 weeks, an egg pile of 5-8 eggs was present in the nest chamber. However, larvae never appeared during these 3 months. Dissection after observation indicated that the only dominant worker had well-developed ovaries.

DISCUSSION

We found notable characteristics in the behaviour of *G. cribrata* even after only fragmentary observations. The *G. cribrata* queen showed LHF. This behaviour is common in the subfamily Amblyoponinae: LHF has been found in at least five amblyoponine genera (Masuko 2003). Besides the Amblyoponinae, LHF has been reported in *Leptanilla japonica* (subfamily Leptanillinae), *Calyptomyrmex* sp. (Myrmicinae), *Proceratium* spp. (Proceratiinae), *Gnamptogenys bicolor* and *G. menadensis* (Ectatomminae) (Masuko, 1986, 1989; Gobin *et al.* 1998b; Ito 2001; Aikawa *et al.* 2002). Thus in the genus *Gnamptogenys*, *G. cribrata* is the third species found to show LHF. LHF had been known to occur in specialised predators that lack regurgitation or trophic eggs: prey items of these specialist predators are often difficult to hunt. Ant colonies have to bridge periods between prey catches, which may represent an ultimate factor for the occurrence of LHF as an aberrant feeding mode (Masuko 1986, 1989). However, the three species of *Gnamptogenys* and *Prionopelta kraepelini* are exceptional as workers lay trophic eggs and prey specialisation is not found (Gobin *et al.*1998a; Ito & Billen 1998). Other important reasons might exist for the occurrence of LHF.

Workers always cut off the abdominal tip of cocoons, and removed the meconium. Such

behaviour has been also reported in *Prionopelta kraepelini* (Ito & Billen 1998), *Onychomyrmex* sp. and *Pachycondyla chinensis* (Ito, unpublished). Within the genus *Gnamptogenys*, we have never seen such cut cocoons in *G. menadensis, G. bicolor, G. striatula* or five other *Gnamptogenys* species (Ito and Gobin, unpublished). The significance of this behaviour is unknown, but it is likely a sanitary measure to ensure pupa survival. Our preliminary experiment on *P. chinensis* indicated that without the cocoon being opened and the meconium removed, the pupae died (Ito & Gobin, unpublished). Thus this behaviour is important for survival of pupae in this species. However many other ants with cocoons do not show such behaviour. The factors affecting the occurrence of cocoon cutting are still unknown.

In the queenright condition, only the queen laid reproductive eggs that she dropped to the floor. Eggs were taken to the egg-pile by workers as in *Acanthomyrmex ferox* (Gobin & Ito 2000). In an orphaned condition the dominant workers laid eggs, but eggs did not develop into larvae. In *G. menadensis*, a species with both queens and gamergates, worker-laid eggs showed similar low hatching rates until workers mated (Gobin *et al.* 1998b). The reason for such an extremely low hatching ratio of eggs laid by virgin workers in these ants is unknown; a male-killing agent, such as the bacteria *Wolbachia*, or recessive lethal alleles are possible explanations. In the case of *G. cribrata* in Bogor, infection by *Wolbachia* had not been detected (Wenseleers *et al.* 1998). Myrmecologists usually focus on egg-laying by virgin workers but rarely check the fate of eggs. In the case of two *Gnamptogenys* species, egg-laying itself does not contribute to male production in queenless colonies. The result indicates that the investigation of egg fate is necessary for understanding the real contribution to male production by virgin workers.

Finally, the remarkably small number of ovarioles in queens is notable. This is the smallest ovariole number in ant queens, matched only by a few species of *Probolomyrmex* (Ito 1998; Kikuchi & Tsuji, 2005). In ponerine and ectatommine ants, six and eight ovarioles are most common (Ito & Ohkawara 1994, Peeters 1997). Among the Oriental *Gnamptogenys*, however, only four ovarioles (2-2) in queens have been known in *G. costata, G. posteropsis* and *G. laevior* (Ito, unpublished), whereas *G. menadensis* queens have up to ten ovarioles (Gobin *et al.* 1998b). While the reasons are unknown, the variation in the number of ovarioles is one of the remarkable characteristics of the genus *Gnamptogenys*.

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