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Colony composition and behavioral characteristics of *Myrmoteras iriodum* and *M. jaitrongi* in Ulu Gombak, Peninsular Malaysia (Hymenoptera: Formicidae)

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ABSTRACT. The colony composition and behavioral characteristics of the trap-jaw ants *Myrmoteras iriodum* and *M. jaitrongi* were studied in Ulu Gombak, Peninsular Malaysia. The following colony characteristics were common in both species: (1) Colony size was remarkably small, less than 10 workers on average with one mated dealate queen. Alate sexuals were produced in colonies with less than 10 workers. (2) Queens had a total of four ovarioles per individual (2+2) while workers had two (1+1). (3) Body size difference between queens and workers was not conspicuous: head width of queens was just 1.1 times bigger than that of workers. (4) Worker body size in small colonies was not significantly different from that in large colonies. (5) Virgin queens showed worker-like behavior. Finally, a solitary queen of *M. iriodum* that was kept in the laboratory showed non-claustral colony foundation. After producing five workers, an alate queen emerged.

Keywords: caste dimorphism, non-claustral colony foundation, ovary

INTRODUCTION

The genus *Myrmoteras*, which comprises ca 40 species, is endemic to the Asian tropics (Bui *et al.* 2013; Bolton 2016; antmaps.org 2017). The members of the genus have very elongate trap-jaw mandibles that can open more than 280 degrees (Moffett 1986). This ant genus shows one of the most peculiar morphologies among Asian tropical ants, however, biological information is limited to a report on the behavior and ecology of *M. toro* Moffett and *M. barbouri* Creighton (Moffett 1986), a short description of colony composition of *M.* cf. *iriodum* Moffett (Buschinger & Maschwitz 1998), and a description of the exocrine glands of *M. iriodum* (Billen *et al.* 2015, 2016).

Moffett (1986) mainly studied how the ants use their peculiar long mandibles. He reported that *M. toro* and *M. barbouri* were specialized predators on small arthropods like collembolans. Details of the behavioral characteristics of the two species and interspecific behavioral differences were reported. He showed that colony size of both species was small, with less than 20 workers per colony. However, data on colony composition in his paper were limited to only one colony for each species, because both species were uncommon and therefore difficult to collect. Buschinger and Maschwitz (1998) reported that *M.* cf. *iriodum* colonies contained one dealated queen and only a very small number of workers (10~15).

Information on colony composition is one of the most important data for understanding the organization inside the ant society (Tschinkel 2010), however, getting such information for rare ant species can be very difficult. We nevertheless managed to collect a total of 16 colonies of two *Myrmoteras* species, *M. iriodum* and *M. jaitrongi* Bui *et al*. in Ulu Gombak, Peninsular Malaysia, during our long term ant research from 1992 to present. We investigated colony composition in the field as well as behavioral characteristics under laboratory conditions for three colonies. In the laboratory, we investigated the growth of a *M. iriodum* colony starting from the founding queen. Here we report on our findings on the biology of both Malaysian *Myrmoteras* species.

MATERIALS AND METHODS

Myrmoteras iriodum and *M. jaitrongi* belong to the subgenus *Myrmoteras*, which is characterized by a pair of long trigger hairs between the mandibles. Complete colonies, that usually nest under stones in the forest floor, were collected in Ulu Gombak (3°19'N; 101°45'E; 250 m a.s.l.), Selangor, Peninsular Malaysia between 1992 and 2016. Colony composition was examined just after sampling. Some queens and workers were dissected under a binocular microscope to check their reproductive condition (the number of ovarioles for both queens and workers, the presence or absence of sperm in spermathecae and ovary development for queens). A colony of *M. iriodum* (colony code FI13-24) was kept in the laboratory (24°C, 12L12D) in an artificial nest measuring 9.5 x 6.2 x 2.8 cm which contained a small box (3.6 x 3.6 x 1.4 cm) as a nest chamber. The floor of both the chamber and foraging arena was made by plaster of Paris in order to keep the humidity sufficiently high. Springtails, small termite nymphs, small nymphs of the myrmecophilous cricket *Myrmecophilus formosanus*, and small nymphs of *Gryllus bimaculatus* were given as prey. All queens (one mated dealate, three virgin dealate, and one virgin alate) and six workers of the colony were marked individually by applying a Mitsubishi enamel paint mark dorsally on their thorax, and their behavior was observed by scan sampling for 100 times under a binocular microscope. The behavior of all adult individuals was recorded. The interval of the sampling was ca 5 to 10 min., and sampling was replicated 10 to 15 times/day during one week. The following behaviors were recorded: foraging outside the nest chamber, nest maintenance, egg care, larval care, pupal care, self-grooming, allo-grooming, offering regurgitation, receiving regurgitation, feeding on solid prey, resting, and wandering. Nest maintenance behavior indicated that workers brought small particles of soil or plaster to the edge of the nest chamber. During regurgitation, receiving individuals slightly vibrated their abdomen. The similarity of the frequency of these behaviors among individuals was examined by a cluster analysis (Ward method, JMP Ver. 5.0). By using similar artificial nests, we also kept two colonies (FI11-23, and FI16-42) of *M. jaitrongi*, and their behavior was also observed but without quantitative methods. In one colony of *M. jaitrongi* (FI16- 42), an alate queen shed her wings in the artificial nest. To compare behavioral characteristics between both species, the behavior of mated and virgin queens in this colony was observed for 8 hours. One founding queen of *M. iriodum* collected in the field was kept in an incubator (26°C, 12L:12D) in the laboratory, and colony growth was observed for ca one year. Head width of seven queens and 27 workers of *M. iriodum* and 8 queens and 23 workers of *M. jaitrongi* was measured using an ocular micrometer attached to a binocular microscope.

RESULTS

Colony composition

The number of workers per colony in both species was small, on average ($\pm$ SD) 8.2 $\pm$ 7.1 in *M. iriodum* (N = 11), and 9.2 $\pm$ 4.4 in *M. jaitrongi* (N = 5) (Table 1). The maximum number was 22 in *M. iriodum* and 16 in *M. jaitrongi*. In all colonies of the two species, the number of mated and egg-laying dealated queens was only one, indicating that these species are monogynous. Two colonies of *M. iriodum* had two dealated queens, however, one of the two was virgin. New sexuals were produced even in the small colonies with only four workers both in *M. iriodum* and *M. jaitrongi*. In the two species, both alate and dealate queens had four ovarioles/individual (2+2) while workers had two ovarioles/individual (1+1). Body size was similar for queens and workers, although queens had a slightly larger head (*M. iriodum*: queens, head width 1.25 $\pm$ SD 0.05 mm, n = 8, workers, 1.19 $\pm$ SD 0.05 mm, n = 25, Welch test, t = -2.68, df = 11.54, p = 0.021; *M. jaitrongi*, queens, 1.07 $\pm$ SD 0.04 mm, n = 6, workers 0.99 $\pm$ SD 0.04 mm, n = 23, Welch test, t = -3.57, df = 27, p = 0.0013), and a well-developed thorax (Fig. 1). The pronotum of the *Myrmoteras* queens was normally developed, in contrast to the reduced pronotum in queens of other formicine ants. Workers were monomorphic. In *M. iriodum*, body size variation of workers among colonies was small. Workers in four small colonies with less than five workers had a mean head width of 1.17 $\pm$ SD 0.07 mm (n = 8), while workers of the largest colonies have a head width of 1.19 $\pm$ SD 0.03 mm (Welch test, t = -1.06, df = 8.8, P = 0.32, Fig. 2). In *M. jaitrongi*, too, worker head width in the smallest colony (colony size = 4 workers, head width = 1.0 + SD 0.02 mm) was not different from workers of the largest colonies (colony size = 16 workers, 0.97 + SD 0.03, Welch test, t = 2.16, df = 10, P = 0.06, Fig. 2).

Table 1. Colony composition of *Myrmoteras iriodum* and *M. jaitrongi* collected in Ulu Gombak. * numbers in parentheses indicate the number of virgin dealated queens.

Colony code	Dealate queens	Workers	Alate queens	Males
M. iriodum				
FI13-26	1	1	0	0
FI99-380	1	1	0	0
FI13-74	1	3	0	0
FI11-8	1	4	0	4
FI98-181	1	5	0	0
FI13-24	1	6	1	0
FI04-80	1	8	1	0
FI13-72	1	9	1	0
FI98-182	1 + (1)*	10	3	0
FI98-96	1 + (1)*	22	0	12
FI92MG-265	1	22	2	0
M. jaitrongi				
FI92MG-27	1	4	0	1
FI11-23	1	7	0	0
FI92MG-411	1	9	0	1
FI16-42	1	10	1	0
FI92MG-19	1	16	0	0

Colony development of *M. iriodum* under laboratory condition

The first worker emerged 11 months after we collected the founding queen. The queen frequently foraged, and hunted for prey before the emergence of workers. During this solitary period, she produced brood, although a few cocoons disappeared. We do not know whether the long duration for the production of the first worker is the normal condition or an artifact due to the laboratory condition. Three months after the emergence of the first worker, the colony grew up to 5 workers, at that stage also the first alate queen was produced. As in field colonies, the first worker was not nanitic (head width 1.16 mm), although it was slightly smaller than the workers in the largest field-collected colony (head width 1.19 ± SD 0.03 mm).

Behavioral characteristics

The following behaviors were observed for foraging, prey feeding, brood care and oviposition:

Foraging and contact with prey: Workers of the two species as well as virgin queens of *M. iriodum* kept their mandibles fully opened (ca. 280 degrees) most of the time they spent in the foraging arena. When they encountered prey animals, they slowly approached them. If prey animals moved fast, the workers and virgin queens chased the prey a bit but usually gave up. When they could be sufficiently close to have the prey within reach of the tips of the trigger hairs, they strike the prey by very quickly snapping the elongate mandibles. Closing the mandibles was powerful enough to kill the soft body arthropods they hunt for. When hunting for prey, workers never used formic acid, although they do possess a functional venom gland as is typical for formicine ants (Billen *et al*., 2015). When offered small (body length ca. 0.4 mm) and large springtails (ca. 1.3 mm) simultaneously, the ants preferred to attack the smaller prey. Beside springtails, they also attack young termite nymphs and small cricket nymphs. Foraging workers and virgin queens licked diluted sugar water in the foraging arena.

Prey feeding: Foraging ants brought prey items back to the nest chamber, and began to masticate prey by holding it between the tips of the mandibles. During prey mastication, workers and queens crossed the mandibles repeatedly, and sometimes adjusted the position of prey with their forelegs. They often fed on the masticated prey by bringing it with their forelegs to the mouthparts. After the foragers had fed on the prey they retrieved, they passed the masticated prey on to the larvae, fellow workers or both virgin and reproductive queens. When prey size was large, a few ants cooperatively masticated it. The queens and workers often fed on the masticated prey that was placed on the larval mouthparts. Inside the nest chamber, stomodeal trophallaxis among female individuals was often observed. Mated queens frequently received trophallaxis from workers, however, prey feeding as mentioned above was also observed (Fig. 3). These behavioral characteristics of foraging and feeding were common in both species. In *M. jaitrongi,* oophagy was observed once. In this case, a worker picked up an egg from the nest floor, and destroyed it with the mandible tips. The queen nearby the worker immediately picked up the damaged egg, and fed on it.

Brood care: Larvae and pupae were scattered on the nest floor in both species. No clusters of eggs and microlarvae were found in the artificial nest of *M. iriodum*, but *M. jaitrongi* made a few egg clusters with microlarvae. The reproductive queen rarely showed brood care, except for egg care just after oviposition. In *M. iriodum*, workers and dealated virgin queens often inserted their mandibles between the nest floor and larvae, opening the mandibles ca. 30 degrees and then quickly closed them, this behavior was repeated a few times. The function of this behavior, however, was unclear. In *M. jaitrongi*, such behavior was never observed.

Oviposition: Egg-laying by the queens was observed only once in each species. In both species, the queen bent her abdomen forward underneath the thorax and extruded an egg from the tip of the abdomen. The egg was picked up by the queen herself with the mandibles. Worker egg-laying was observed once in *M. jaitrongi*. Egg-laying behavior was similar to queens, but as soon as the egg emerged from the abdominal tip, it was immediately eaten by the worker that had laid the egg.

Fig. 1. A founding colony of *Myrmoteras iriodum*. Note that body size of the first worker (W1) was not nanitic, but was similar in size to the founding queen (Q). W2: the second worker just after emergence from cocoon.

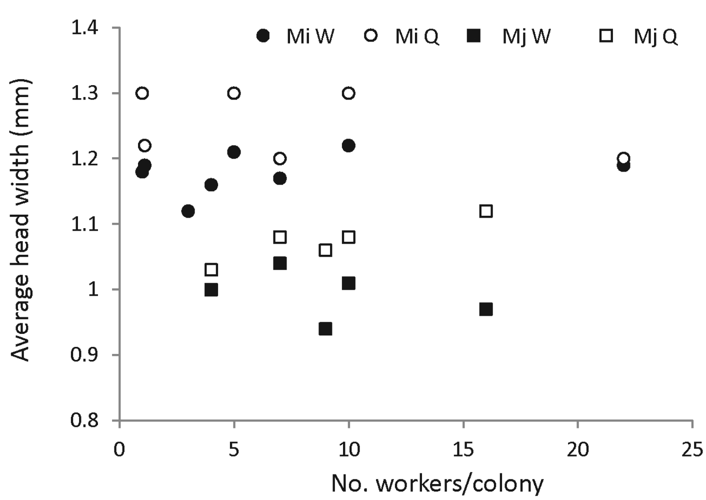

Fig. 2. Relationship between colony size and head width of queens and workers in two species of *Myrmoteras*. Mi: *M. iriodum*, Mj: *M. jaitrongi,* Q: queens, W: workers.

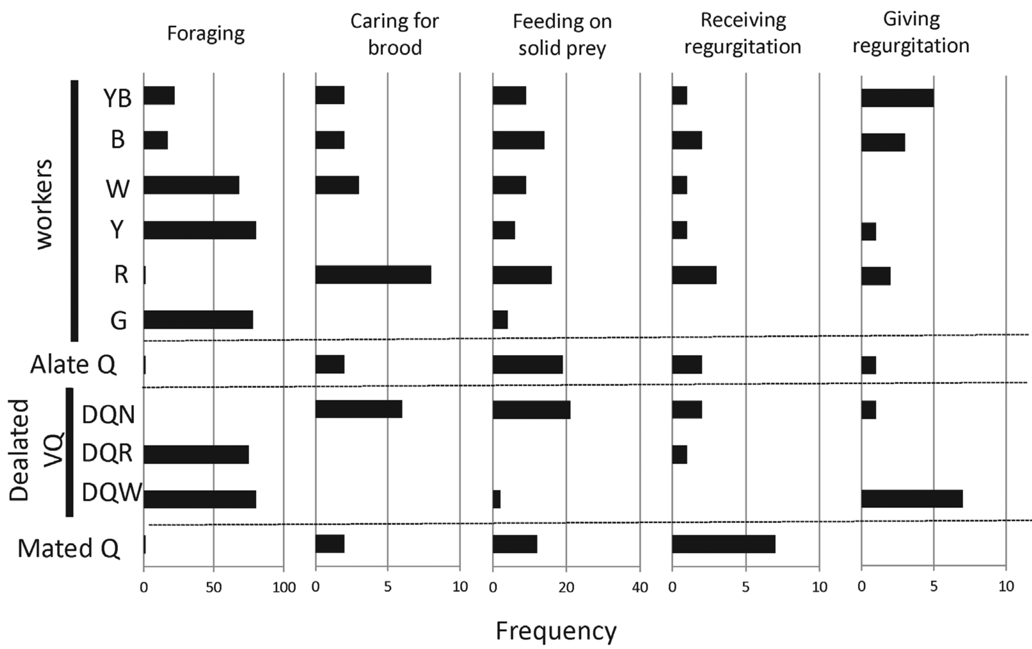

Fig. 3. Frequency of each behavior performed by a mated queen, three virgin queens, an alate queen, and six workers in a colony of *M. iriodum*. YB, B, W, Y, R, G refer to the color codes of the individually marked workers, DQN, DQR, DQW refer to the color code of the marked virgin dealated queens, VQ: virgin queen.

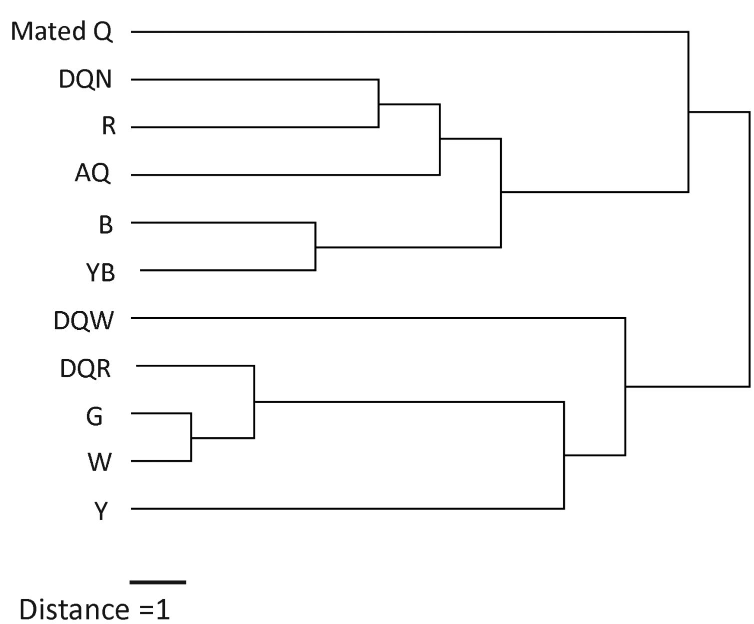

Fig. 4. Dendrogram of a cluster analysis of the behavioral profile of a mated queen, three virgin queens, an alate queen, and six workers in a colony of *M. iriodum*.

Polyethism

In *M. iriodum*, the alate queens that were produced in the laboratory colony readily dealated. As a result, we could observe the behavior of one mated queen, three virgin dealate queens, one alate queen and 6 workers. Figure 3 shows the frequency of foraging, brood care and feeding behavior. Two of the three virgin dealate queens frequently foraged in a similar way as workers, and hunted prey in the foraging arena. The behavioral similarity as examined by a cluster analysis (Ward's method) indicated that the behavior of these virgin dealate queens was similar to that of foraging workers (Fig. 4). In *M. jaitrongi,* foraging by a virgin dealate queen was never observed, however, we observed three times that she chased the springtails that entered into the nest chamber, and actually once succeeded to capture the prey inside the nest chamber.

DISCUSSION

Some notable features on the biology in *Myrmoteras* are revealed in this study. First, colony size is extremely small: colonies of both *M. iriodum* and *M. jaitrongi* contain on average less than 10 workers. To our knowledge, the colony size of these two species is among the smallest so far known for ants. Moffett (1986) reported a colony size of 22 (N = 1) and 10 workers (N =1) in *M. toro* and *M. barbouri,* respectively, while also Buschinger and Maschwitz (1998) mentioned about only 10-15 workers in colonies of *M.* cf. *iriodum*. Thus, small colony size is a common phenomenon in *Myrmoteras*. In the subfamily Formicinae, colony size is generally large with more than 100 workers (Hölldobler & Wilson 1990; Kaspari & Vargo 1995). Comparable species to *Myrmoteras* in terms of colony size are found in the subfamily Ponerinae: the Australian *Pseudoneoponera sublaevis* (Emery) (previously *Pachycondyla (=Bothroponera) sublaevis*) and the Indonesian *Pseudoneoponera insularis* (Emery) (previously *Pachycondyla (=Bothroponera)* sp.) also have small colonies with an average of 10 workers (Peeters *et al*. 1991; Ito & Higashi 1991; Ito 1993).

Second, the queen of *M. iriodum* shows non-claustral colony foundation. Although we observed only one queen of *M. iriodum* under laboratory conditions, the thorax structure of queens without reduction of the pronotum is in agreement with their non-claustral colony foundation. Keller *et al*. (2014) showed that the pronotum of queens in claustral species is remarkably reduced whereas non-clasutral queens have a normally developed pronotum, because developing the pronotum is necessary to provide space for the muscles that operate head movements. A similar thorax morphology of queens was also reported in *M. insulcatum* Moffett and *M. toro* by Moffett (1985). Among the subfamily Formicinae, the majority of independent founding species show claustral colony foundation (Peeters and Ito, 2015). Known exceptions so far are a few species of *Polyrhachis* (Lenoir & Dejean 1994; Ito unpubl.), and *Cataglyphis nigra* (André) (Fridman & Avital 1983). Claustral colony foundation usually goes along with the production of nanitic workers, however, such small workers do not seem efficient for a predatory life style on live arthropods. Actually, claustral colony foundation is rarely found in ponerine ants in which the majority of species are predators, whereas it is often found in formicoid ants where omnivorous ants are common (Wilson & Nowak 2013). *Myrmoteras* ants are predators on small arthropods, therefore non-claustral colony foundation may be necessary for the production of functional workers that must be sufficiently large for predation. When handling prey, we observed the same masticatory behavior in *M. iriodum* and *M. jaitrongi*, holding the prey between the slender mandibles, as was also reported for *M. barbouri* and *M. toro* (Moffett 1985). During this peculiar behavior, secretions from the intramandibular gland, that opens all along the masticatory edge of the mandibles, may play a role (Billen *et al.* 2015).

Third, the ovariole number of queens is small with a total of just four per individual. In aculeate Hymenoptera, the majority of solitary species have six or eight ovarioles/female (Iwata 1955). In general, the number of ovarioles increases with the evolution of sociality or a parasitic life style (Iwata & Sakagami 1966). Many ponerine ants have six or eight ovarioles (Ito & Ohkawara 1994), while formicine queens generally have considerably more ovarioles (Peeters & Ito 2015). The smallest ovariole number of reproductive females so far reported is two ovarioles/queen in *Acanthomyrmex minus, Gnamptogenys cribrata,* and four species of *Probolomyrmex* (Ito 1998; Ito & Gobin 2008; Terayama *et al*. 1998), four ovarioles are found in queens of some species of the ectatommine genus *Gnamptogenys* (Ito & Gobin 2008) and several species of the myrmicine genus *Strumigenys* (Ito *et al*. 2010). To our knowledge, there are no formicine species in which queens have less than 10 ovarioles (59 species of 27 genera examined, Ito and Peeters, unpubl.).

Fourth, the behavioral specialization of queens seems weak. Virgin dealate queens of *M. iriodum* can forage in a similar way as workers, and both alate and dealate virgin queens show brood care. In *M. jaitrongi*, the virgin dealated queen never participated in foraging, however, this behavioral difference between the two species may result from differences in colony composition: the observed colony of *M. iriodum* had 6 workers, while that of *M. jaitrongi* had 11 workers. A reduction in morphological specialization, especially of the thorax structure, may make such worker-like behavior possible for queens.

The overall biological information provided here clearly indicates that the genus *Myrmoteras* is one of the most peculiar ants among the subfamily Formicinae. Small colony size, predatory life style, and less specialization of queens seem to be an ancestral condition in ants (Wheeler 1926). It would be interesting to find out whether these characteristics represent the ancestral or a derived condition in this subfamily.

Moffett (1986) reported on the behavioral characteristics of *M. barbouri* and *M. toro*, of which the former species has a pair of long setae between the mandibles as in *M. iriodum* and *M. jaitrongi*, while the latter lack such setae. *Myrmoteras barbouri* is a specialist predator on collembola, while *M. toro* can attack a broader range of small arthropods including isopods. The foraging behavior and prey preference of *M. iriodum* and *M. jaitrongi* seem similar to *M. barbouri*. Our observation of the queen and worker behavior in *M. iriodum* and *M. jaitrongi* show some differences with that of the two species that were studied by Moffett (1986). First, Moffett described that queens and larvae only feed on liquid food through trophallaxis from workers, whereas we found that the reproductive queens and larvae of *M. iriodum* and *M. jaitrongi* not only feed on liquid food from workers but also on solid prey items. Second, the condition of immatures of *M. iriodum* in the nest chamber seems different from the species studied by Moffett (1986) and *M. jaitrongi* in the present study: *M. toro* and *M. jaitrongi* make clusters of eggs and small larvae, whereas *M. iriodum* never makes such clusters inside their nest. Workers of *M. toro* often held a larva or pupa by gently gripping them between the mandibles or immobilized them with their forelegs (Moffett 1986). Such behavior was rare in the two species we studied, as larvae and pupae usually laid on the nest floor. The rareness of the representatives of this genus makes them difficult to study, however, further research is necessary for a better understanding of the behavioral diversity among *Myrmoteras*.

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