ASIAN MYRMECOLOGY Volume 10, e010007, 2018
ISSN 1985-1944 | eISSN: 2462-2362 © Fuminori Ito, Weeyawat Jaitrong, Rosli Hashim and Riou Mizuno DOI: 10.20362/am.010007

Colony composition, brood production and caste dimorphism in two species of the doryline genus *Lioponera* in the Oriental tropics (Formicidae: Dorylinae)

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ABSTRACT. Recent phylogenetic research indicates that the true army ants (e.g. *Aenictus, Dorylus, Eciton, Neivamyrmex*) belong to the subfamily Dorylinae, together with several non-army ant genera such as *Cerapachys, Yunodorylus, Lioponera* and *Ooceraea.* Thus, comparative studies among doryline genera are very important for understanding the biological characteristics of true army ants. We investigated colony composition of two species of the *Lioponera suscitata* group in the field and in the laboratory in Indonesia, Malaysia, and Thailand. In both species, queens were alates, and queen-worker dimorphism in body size was weak. Two queenright colonies of *L. suscitata* were monogynous, with 14 and 40 workers each, and one orphan colony had 30 workers. The colony of *Lioponera* sp. collected in Thailand had two queens and 12 workers. Colonies of both species included all developmental stages of brood. In the laboratory, the queen of *Lioponera suscitata* continuously laid eggs, and the captive colony always had all developmental stages of brood. This shows that reproduction in these two species is non-phasic.

Keywords: army ant, caste dimorphism, myrmecophagy, phasic colony cycles

INTRODUCTION

The true army ants such as *Aenictus, Dorylus* and *Eciton* show remarkable characteristics among ants including huge colonies, well-organized mass foraging, remarkable caste dimorphism and nomadism. (Gotwald 1995; Kronauer 2009; Schneirla 1971). Because these ants are predators, their role in terrestrial ecosystems is very important, especially in tropical ecosystems where they are abundant (Gotwald 1995). Recent phylogenetic analysis revealed that the true army ants belong to the subfamily Dorylinae, together with several non-army ant genera that had previously been assigned to a separate subfamily, the Cerapachyinae (Borowiec 2017; Brady et al. 2014). Thus, the biological knowledge of doryline genera is undoubtedly important for under-

standing the evolution of army ant behaviour. Unfortunately, most species in these non-army ant genera are uncommon, and therefore our knowledge is limited to a few doryline genera.

In this paper, we document colony composition of the *Lioponera suscitata* group in the field and brood development of a colony of *L. suscitata* (Viehmeyer 1913) under laboratory conditions. Our data are obtained from only four colonies of two species. Although one of the authors (FI) has spent a lot of time in the Oriental tropics for ant collection since 1990, we found *L. suscitata* in the field only three times. This suggests that the species is rare and difficult to collect. Thus, we report preliminary data on the reproductive system in this species group.

MATERIALS AND METHODS

Lioponera suscitata was described based on specimens from Celebes, Indonesia, as a member of *Phyracaces* (Viehmeyer 1913). According to Brown (1975), specimens collected in Pahan, Malay Peninsula, have a broader head than Celebes specimens, but he suggested that these ants may belong to *L. suscitata*. Body size and morphological characteristics of our specimens collected in Indonesia and Malaysia seem to agree well with the specimens from Pahan described by Brown (1975). Therefore, in this paper, we treat this species as *L. suscitata.* Specimens collected in Thailand are very similar to *L. suscitata*, however, the colour of the legs is different, and overall body size is smaller, thus we refer to them as *Lioponera* sp. 1. Voucher specimens were deposited in Bogor Zoological Museum, Thailand Natural History Museum, and University of Malaya.

Colony composition was assessed in Ulu Gombak, Peninsular Malaysia, and Gunung Halimun, West Java, Indonesia, in 1998 and 1999, and Koh Kood Island, Thailand in 2016. From three colonies of *L. suscitata* a total of four queens (including alates) and ten workers were dissected to examine ovariole numbers and the presence or absence of a spermatheca. Maximum head width and maximum width of the IVth abdominal segment were measured for three queens and 25 workers under a binocular microscope. For *Lioponera* sp. 1, one queen and one worker were dissected. Body size of two queens and 10 workers was measured as mentioned above.

To examine the reproductive cycle, one colony collected in Halimun (FI98-411, containing one queen and 14 workers) was kept in the laboratory for 4 months and brood composition of the colony was checked one to three times per week. For comparison of the colony cycle, one colony of another non-army ant doryline *Parasyscia* collected in Ulu Gombak (sp. 1 of FI, colony code FI99-63, composed of one queen and 13 workers) was also kept under the same laboratory conditions, and brood composition was recorded as for *L. suscitata*. The colonies were kept in artificial nests (20.8 x 14.6 x 5.6 cm) under constant temperature (26 ºC) and day-length (12L 12d). The bottom of each nest box was covered with plaster and a small box to act as brood chamber (ca. 6.8 x 3.9 x 1.5 cm) was placed on the plaster floor. The chamber was also layered by plaster. Larvae and/or pupae of *Pheidole* spp. and/or *Brachyponera* spp. were given as prey. To study prey specialization, termites, mealworms and crickets were also given.

RESULTS

Three complete colonies of *L. suscitata* were collected in the field from dead twigs fallen on the ground (Table 1). Two queenright colonies of *L. suscitata* contained one dealate queen, 14 and 40 workers each, and all immature stages. One orphan colony of *L. suscitata* with 30 workers had no eggs but a few larvae and several cocoons, which contained various pupal stages from prepupae to mature blackish workers, males and alate queens. The one colony from Thailand (RM-156) was found in a rotten log on the ground. It contained two dealate queens, 12 workers and also several broods of all developmental stages. One of the two queens of *Lioponera* sp. 1 was mated but the other died prior to dissection.

In *L. suscitata,* the head width of the queens was slightly but significantly larger than that of workers (queen head width 1.20 $\pm$ 0.02 mm, worker head width 1.13 $\pm$ 0.025 mm, Welch Two-sample t-test, t = 16.5, df = 2.15, P =

Table 1. Colony composition of *Lioponera suscitata* group.

Colony code	Locality	Number of Individuals					
		Dealate queens	Males	Workers	Cocoons	Larvae	Eggs
L. suscitata							
FI99-87	Ulu Gombak	1	1	40	20	15	10
FI99-129	Ulu Gombak	0	0	30	22	3	0
FI98-411	Gn Halimun	1	0	14	2	2	8
Lioponera sp. 1							
RM-156	Koh Kood Is.	2	0	12	4	7	4

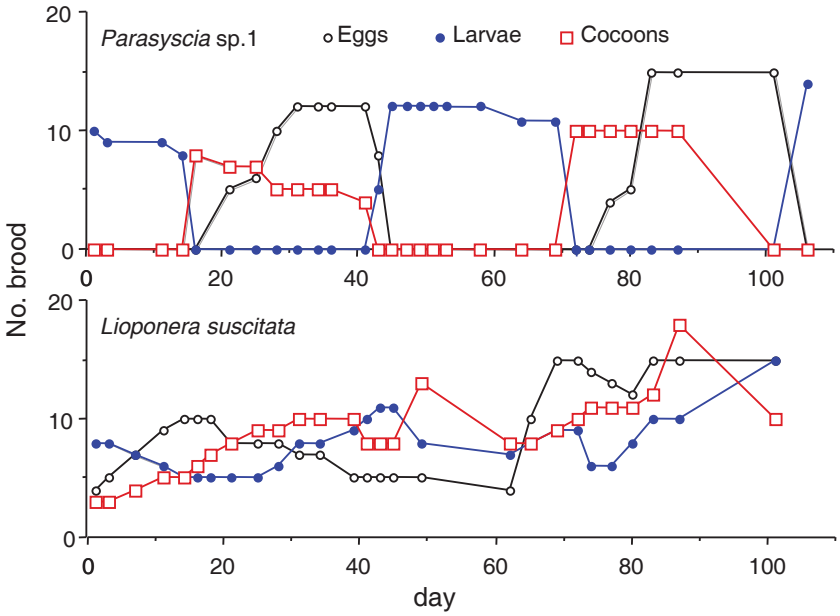

Fig. 1. Change of brood composition in *Lioponera suscitata* and *Parasyscia* sp. 1 under laboratory conditions.

0.0027). The abdomen width of the queens was significantly larger than that of workers (queen 1.30 ± 0.02 mm, worker 1.10 ± 0.025 mm, Welch Two-sample t-test, t = 12, df = 3.47, P = 0.0006). In *Lioponera* sp. 1, body size of queens was not significantly different from that of workers (queen head width 1.00 ± 0.05 mm, worker head width 1.01 ± 0.05 mm, Welch Two-sample t-test, t = 0.11631, df =1.7081, P = 0.9196; queen abdomen width 1.08 ± 0.04 mm, workers 0.99 ± 0.04 mm, Welch Two-sample t-test, t = 3.0209, df = 1.6652, P = 0.1173). In both species, the number of ovarioles of queens was 4 per individual (2-2, N = 4 in *L. suscitata,* N = 1 in *Lioponera* sp. 1) whereas workers had two ovarioles (1-1, N = 10 in *L. suscitata,* N = 1 in *L.* sp. 1). Queens had a spermatheca while we could not find a spermatheca in workers in both species.

The *L. suscitata* colony kept in the laboratory showed continuous egg-laying by the queen, and all three immature stages were always found in the nest concurrently over a four

month period (Fig. 1). The number of eggs laid per week, which was estimated from the change of brood composition, was two to six. In contrast, two clear peaks of egg numbers were found during the four month culture of *Parasyscia* sp. 1. Egg-laying by the queen was observed only during a period of larval absence. The queen laid 13 and 15 eggs in the first and second oviposition period, respectively. The interval was approximately six weeks. Both species accepted ant larvae as prey while the other insects were totally ignored.

DISCUSSION

Biological information on the non-army ant genera in Dorylinae is presently very limited in the literature. Only intensive studies of *Ooceraea biroi* (Forel 1907) exist (e.g. Ravary & Jaisson 2004). Caste dimorphism between queens and workers, in spite of being important for the understanding of social life of ants (Peeters & Ito 2015), has been rarely reported to date. The overview of queen morphology of doryline ants provided by Borowiec (2016) indicates that ergatoid queens including subdichthadiigynes are widely known in non-army ant genera, however, the caste dimorphism is not mentioned in detail. In the two species of the *L. suscitata* group that we had available in our study, body size differences between the two castes were not conspicuous. *Lioponera daikoku* Terayama 1996, also shows limited caste dimorphism in body size (Idogawa & Dobata 2018). The ovariole number of queens is four, whereas workers have two ovarioles in the two species studied in this paper. The ovariole numbers of non-army ant dorylines have been reported for *L. daikoku, Ooceraea biroi*, *Syscia humicola* (Ogata 1983), and *Zasphinctus steinheili* (Forel 1900) only (Buschinger et al. 1989; Idogawa & Dobata 2018; Masuko 2006; Ravary & Jaisson 2004). As in the *L. suscitata* group, workers of these species have two (1-1) ovarioles while ergatoid queens of *S. humicola* and alate queens of *L. daikoku* have four (2-2) (Masuko 2006; Idogawa & Dobata 2018) and ergatoid queens of *Z. steinheili* have four (2-2) to 11 (5-6) ovarioles (Buschinger et al. 1989). Four ovarioles in queens is relatively rare among Formicidae. Most poneroid queens have six or eight ovarioles/individual (Ito & Ohkawara 1994; Peeters & Ito 2015), and queens of the majority of formicoids, including doryline army ants, have more than ten ovarioles/individual (Iwata 1955; Peeters & Ito 2015). In the true army ant genera of the subfamily Dorylinae, ergatoid queens have a remarkably high number of ovarioles, e.g. about 1300/ovary in *Eciton burchellii* (Westwood 1842) (Hagan 1954), ca 500/queen in *Neivamyrmex nigrescens* (Cresson 1872) (Holliday 1904), and ca. 600/queen in *Aenictus cornutus* Forel 1900 (Ito & Jaitrong, unpubl.).

Although we collected only three queen-right colonies of the *Lioponera suscitata* group, the colony size of this species group is apparently small. This seems to be related to the small ovariole numbers in the queen caste. Wilson (1958) reported some biological characteristics of two species of *Lioponera*: a colony of *L. cohici* (Wilson 1957) had 80-100 workers and a colony of *L. dumbletoni* (Wilson 1957) had 200 workers. *Lioponera diakoku* has much smaller colonies with on average 13 workers (Idogawa & Dobata 2018). Among *Lioponera*, the present species group also makes smaller colonies.

The two species of the *L. suscitata* group showed non-phasic reproduction: queens laid eggs continuously and all developmental stages of brood were present in a given colony. Wilson (1958) and Idogawa and Dobata (2018) also reported such brood composition in *L. cohici*, *L. dumbletoni*, and *L. daikoku*. In L. cf. *turneri*, Hölldobler (1982) did not provide details on the reproductive cycle, however, he described that several eggs were found with large larvae in the captive colonies, indicating that this species also shows non-phasic reproduction. The other genera of non-army ant doryline species such as *Ooceraea, Parasyscia, Syscia* and *Zasphinctus* show phasic reproduction (Buschinger et al. 1989; Masuko 2006, Ravary & Jaisson 2002; Wilson 1958), where eggs are laid by queens during a very limited period, then queens stop egg-laying during the presence of larvae that show synchronized development. To date, we have collected several colonies of more than 10 species of seven genera (*Cerapachys, Chrysapace, Lioponera, Ooceraea, Parasyscia, Syscia, Yuno-*

dorylus) of non-army ant doryline species in the Southeast Asian tropics. All but the two *Lioponera suscitata* group species show phasic reproduction as shown in *Parasyscia* in this paper (Ito, unpublished). Borowiec (2016) described that the majority of non-army ant dorylines show phasic reproduction, but that three species of *Tanipone* (*T. hirsute* Bolton & Fisher 2012, *T. subpilosa* Bolton & Fisher 2012 and *T. zona* Bolton & Fisher 2012) and *Simopone* (species name was not given) are non-phasic ants, even though the data of colony composition is not shown in Borowiec (2016).

Phasic reproduction with synchronized development of brood is one of the most striking biological characteristics in the true army ant genera *Aenictus, Eciton,* and *Neivamyrmex* (Borowiec 2016; Gotwald 1995). However, its adaptive significance is still controversial. Recently Teseo and Delloro (2017) and Garnier and Kronauer (2017) discussed the adaptive significance, based on simulation models focused on foraging behavior and resource distribution. Phasic colony cycles are adaptive in species where the relative cost of foraging is high when few larvae exist, but the cost decreases as the number of larvae increases (Garnier & Kronauer 2017), especially under the condition where prey insects are difficult to be found but locally abundant (Teseo & Delloro 2017). Specialization on eusocial insects that are hard to obtain but highly abundant as prey if available is one of the possible situations for evolution of phasic reproduction (Garnier & Kronauer 2017, Teseo & Delloro 2017). *Lioponera suscitata* is a specialized ant predator but they show non-phasic reproduction, whereas the non-army ant dorylines *Cerapachys sulcinodis* Emery, 1889 and *Yunodorylus eguchii* (Borowiec 2009) are generalist predators and show phasic reproduction (Mizuno et al. in prep). Thus, ants as prey may not always fit to the prey conditions for evolution of phasic reproduction and synchronized brood development, and/or some other factors may affect this reproductive cycle. Comparative studies of several aspects of the biology of non-army ant dorylines, especially foraging behaviour and prey distribution, will provide important insights into the understanding of this derived reproductive cycle in ants.

ACKNOWLEDGEMENTS

We thank Sk. Yamane for identification of the ants, J. Billen and K. Masuko for useful comments on various earlier versions of the manuscript, D. Kronauer and an anonymous reviewer for useful comments, N. Idogawa and S. Dobata for providing us biological information of *L. daikoku*, and LIPI for permission to conduct research in Indonesia. This work was supported by grants in aid for scientific research from the Japan Society for the Promotion of Science (A 11691130; B 24405010, 14405036, 16H05769).

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