ASIAN MYRMECOLOGY — Volume 15, e015001, 2022
ISSN 1985-1944 | eISSN: 2462-2362 DOI: 10.20362/am.015001

Trophic eggs in three ponerine ant species: *Harpegnathos venator, Odontomachus simillimus and Odontoponera denticulata*

Sunittra Aupanun[1, 2], Mitsuhiro Obika[2], Riou Mizuno[2], Weeyawat Jaitrong[3], Piyawan Suttiprapan[1], Rosli Hashim[4] and Fuminori Ito[2*]

[1]Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand
[2]Faculty of Agriculture, Kagawa University, Ikenobe, Miki, Kagawa 761-0795, Japan
[3]Thailand Natural History Museum, National Science Museum, Technopolis, Khlong 5, Khlong Luang, Pathum Thani 12120, Thailand
[4] Institute of Biological Science, Faculty of Science, University of Malaya, 50603 Kuala Lumpur, Malaysia

[*]Corresponding author: ito.fuminori@kagawa-u.ac.jp

ABSTRACT. Trophic eggs in ants have been well known for a long time, however, published information of trophic eggs in poneroid ants is relatively scarce. We observed the production and fate of trophic eggs in relation to female castes and reproductive status in three species of ponerine ants in SE Asia. In all species, trophic eggs were principally offered to and eaten by reproductive females. When the trophic eggs were refused by reproductive females, other colony members fed on the trophic eggs. Reproductive females of the three species fed on both insect prey and trophic eggs, however, the proportion of time spent eating the two types of prey varied among species and also among colonies. In *Harpegnathos venator,* trophic eggs were laid by non-reproductive females including virgin workers, virgin queens, and mated but infertile workers. All trophic eggs were eaten by mated queens or gamergates (mated and egg-laying workers). The rate of trophic egg laying was as low as 0.0187 ± SD 0.0110 per individual per hour (i.e. on average one egg every two days 5 hours 29 min.). In *Odontoponera denticulata,* workers laid on average 0.0115 ± 0.009 trophic eggs per worker per hour (i.e. one egg every three days 14 hours 57 min.). All egg laying workers first brought trophic eggs to queens, but queens fed on only ca. 20% of the trophic eggs. Furthermore, queens rarely showed complete feeding. In most cases, queens ate the eggs halfway through and dumped the rest. These dumped eggs were picked up by workers, and given to larvae or eaten by workers. In *Odontomachus simillimus*, queen feeding behavior varied from insect prey to trophic eggs depending on colony growth stage. When the colony was large, workers laid trophic eggs at a low rate of 0.0035/individual/hour (i.e. one egg every 11 days 21 hours 43 min.) and most trophic eggs laid by workers were eaten by the queen.

Keywords	Feeding habit, *Harpegnathos, Odontomachus, Odontoponera,* Ponerinae, Trophic egg, Specialization
Citation	Sunittra Aupanun, Mitsuhiro Obika, Riou Mizuno, Weeyawat Jaitrong, Piyawan Suttiprapan, Rosli Hashim & Fuminori Ito (2022). Trophic eggs in three ponerine ant species: *Harpegnathos venator, Odontomachus simillimus and Odontoponera denticulata*. Asian Myrmecology 15: e015001

| **Communicating Editor** | Adam Cronin |

INTRODUCTION

Trophic eggs, found in a highly diverse range of animals, are non-viable and morphologically distinct from reproductive eggs, and serve a nutritive function (Passera et al. 1968; Crespi 1992; Gobin et al. 1998). In ants, trophic egg layers are principally workers, though dealate queens also lay trophic eggs in some species (e.g. Wardlaw & Elmes 1995). The laying of trophic eggs by dealate queens occurs more commonly during the colony founding stage in several ant species (Taki 1987; Cassill 2002). In two species of *Acanthomyrmex*, soldiers and queens lay considerable numbers of trophic eggs (Gobin & Ito 2000; Yamada et al. 2018). The main consumers also differ from species to species: trophic eggs are mainly given to the larvae in most formicoid ants, e.g. *Acanthomyrmex careoscrobis* Moffett, 1986, *Anoplolepis gracilipes* (Smith, 1857), *Aphaenogaster japonica* Forel, 1911, *Gnamptogenys menadensis* (Mayr, 1887)*, G. cribrata* (Emery, 1900), *Linepithema humile* Mayr, 1866, and *Myrmica rubra* (Linnaeus, 1758) (Brian & Rigby 1978; Bartels 1988; Gobin et al. 1998; Ito & Gobin 2008; Iwanishi et al. 2003; Lee et al. 2017), whereas most trophic eggs are eaten by queens in the ponerine ant *Neoponera apicalis* (Latreille, 1802) (Dietemann & Peeters 2000). Both workers and queens feed on trophic eggs, which are rarely given to larvae in the myrmicine ant *Leptothorax acervorum* (Fabricius, 1793) (Bourke 1991; Ito 2005). The morphological characteristics of trophic eggs are also diverse; from very soft eggs like yolky fluid in the dolichoderine genera *Dolichoderus* and *Technomyrmex* to more or less similar to normal eggs but with a thin chorion in the ectatommine ant *Gnamptogenys* spp. and the amblyoponine ant *Prionopelta kraepelini* Forel, 1905 (Torossian 1979; Yamauchi et al. 1991; Gobin et al. 1998; Ito & Gobin 2008; Ito & Billen 1998). Soft trophic eggs in dolichoderine ants are consumed in a few seconds (pers. obs.) versus ca. five to seven minutes for trophic eggs with a chorion in *P. kraepelini* (Ito & Billen 1998). Trophic eggs in ants seem to be easier to assimilate and more energetic than normal prey, however, in our knowledge, no quantitative research of such characteristics has been carried out to date.

The nutritional cycle inside ant colonies can be roughly divided into three categories: feeding on solid prey, oral trophallaxis, and trophic eggs. In addition, larval hemolymph feeding is reported in amblyoponine, leptanilline, and some formicoid ants (Masuko 1996, 1989; Ito & Gobin 2009). The degree of dependence on each category varies greatly among species, and among castes. For example, in *Technomyrmex brunneus,* oral trophallaxis is lacking, and queens and larvae exclusively feed on only trophic eggs, while workers feed on insect prey (Yamauchi et al. 1992). Crespi (1992) pointed out that trophic eggs in ants are found in species that do not show trophallaxis among nestmates. This seems to be partly true, however, many exceptions exist. For example, *Anoplolepis grcilipes* and *Acanthomyrmex feroxs* show both trophic egg feeding and oral trophallaxis (Lee et al. 2017; Gobin & Ito 2000). Lack of oral trophalaxis is widespread in ponerine ants, where all members feed on solid prey, but trophic eggs are not common (see below). To understand the diversity and the significance of trophic eggs in ants, information in several ant species is indispensable.

So far, the occurrence of trophic eggs has been reported in several formicoid ants in the subfamilies Dolichoderinae, Ectatomminae, Formicinae, Myrmeciinae, and Myrmicinae (reviewed in Choe 1988; Crespi 1992; Hölldobler & Wilson 1990). Recently, trophic egg production by workers in formicoid ants has been studied by molecular analysis of ovary function of workers as a reproductive constraint (Khila & Abouheif 2008, 2010). However, data of trophic eggs in poneroid ants is relatively scarce, and has only been reported from a handful of species in five genera, e.g. *Prionopelta amabilis* Borgmeier, 1949 and *P. kraepelini* in Amblyoponinae, *Bothroponera krugeri* (Forel, 1910)*, Neoponera apicalis*, *N. obscuricornis* (Emery, 1890)*, N. vilosa* (Fabricius, 1804) and *Pachycondyla striata* Smith, 1858 in Ponerinae, and *Paraponera clavata* (Fabricius, 1775) in Paraponerinae (Hölldobler & Wilson 1986; Villet & Wildman 1991; Camargo-Mathias & Caetano 1995; Düssmann et al. 1996; Ito & Billen 1998; Dietemann & Peeters 2000; Da Silva-Melo & Giannotti 2012; Peeters 2017). During our behavioral observation of colonies of *Harpegnathos venator* (Smith, 1858), *Odontoponera denticulata* (Smith, 1858), and *Odontomachus simillimus* Smith, 1858, we discovered that trophic eggs are produced by the non-reproductive females (virgin workers, virgin queens, and infertile mated workers). The description of details of colony composition, reproductive structure, and behavioral characteristics of each species are in preparation separately. Here we report on the production and fate of trophic eggs in these species in relation to female castes and reproductive status.

MATERIALS AND METHODS

Collection of ants

Colonies of *Harpegnathos venator* were collected at two sites, Omkoi National Forest and Khoon Tuen village, Chiang Mai Province, northern Thailand between 2016 and 2018. Founding queens of *Odontoponera denticulata* were collected in May 2014, in Kamphaeng Saen, Nakhon Pathom Province, Central Thailand. A founding queen of *Odontomachus simillimus* was collected nearby the Forest Research Institute Malaysia, Kepong in December 2017. These ants were brought and maintained in the laboratory. Hereafter, as the abbreviations of *Odontoponera* and *Odontomachus,* we use *O.p.* and *O.m.*, respectively.

General methods for keeping ant colonies

Each colony was maintained in a polystyrene box in the laboratory under room temperature condition (20~ 28°C). Inside the box, a smaller polystyrene box with an entrance hole served as a nest chamber. The bottom layer of the chamber was covered with Plaster of Paris to maintain humidity. The size of the polystyrene box varied among colonies, and the box was changed from time to time to accommodate colony development.

Prey insects given as food were as follows: Turkestan cockroach *Blatta lateralis* (Walker, 1868) for *H. venator, Reticulitermes speratus* termites (Kolbe, 1885) for *O.m. simillimus*, and several kinds of arthropods including mealworms, cockroaches, etc. for *O.p. denticulata*.

Behavioral observation

Harpegnathos venator: All individuals were marked by unique color combinations of enamel paints (Mitsubishi paint marker). As in *H. saltator* (Peeters & Hölldobler, 1995), dealate queens and mated workers can lay reproductive eggs in *H. venator*, however, most of the mated workers rarely lay reproductive eggs when the mated queens were present (Aupanun et al., submitted). Table 1 shows the composition of each colony that was observed for trophic egg laying. In FI16-120 (personal colony code), all queens were dissected immediately after collection, and the remaining individuals were kept in the laboratory for behavioral observations. This colony included five mated workers, of which two were gamergates that laid reproductive eggs (Table 1). Of the remaining three colonies, one mated queen was present in each of the colonies. In Sa18-9, no mated workers existed, and the other two colonies had two (FI16-122) and 10 mated workers (RM-562). In RM-562, one of 10 mated workers was a gamergate and both of the two mated workers in FI16-122 did not lay reproductive eggs (Table 1). For these four colonies, the behavior of all female individuals was recorded by raster scan visual sampling for 300 to 556 min per colony. This observation was made two to twelve

Table 1. Colony composition and the number of trophic eggs laid and eaten by each type of female in *Harpegnathos venator*. MQ: mated queen, VQ: virgin queen, MW: mated but non-reproductive workers, G: gamergates, VW: virgin workers, TE: trophic eggs. Mated queens and gamergates never laid trophic eggs.

Colony code	No. individuals					No. TE laid by			No. TE eaten by		Hours of observation
	MQ	VQ	MW	G	VW	VQ	MW	VW	MQ	G	
FI16-122	1	3	2	0	26	0	0	4	4	0	11
Sa18-9	1	25	0	0	20	1	0	0	1	--	5
RM-562	1	10	9	1	15	0	2	0	2	0	7
FI16-120	0	1	3	2	35	0	0	5	--	5	7
Total						1	2	9	7	5	30

Fig. 1. Gamergate of *Harpegnathos venator* feeding on a trophic egg.

months after the colonies were collected. The total number of scans was 55 to 85 per colony. During observations, if we found trophic egg laying, we followed the fate of the eggs (Table 1). After observations or death of individuals, they were dissected under a microscope to reveal their ovary development and insemination condition.

Odontoponera denticulata: Five dealate founding queens produced many workers. When colony size was ca. 80 to 1200 workers in 2016, a 30 min. observation was carried out for four to 30 times per colony. During 30 min. of observation, trophic egg laying by workers, the fate of the trophic eggs and feeding behavior of queens were recorded (Table 2). For MO15-3, the observation was focused on queen behavior for five of the total of 15 hours. During these five hours, trophic egg laying by workers was not recorded. Colony size, number of trophic eggs laid by workers, and the number of trophic eggs eaten by queens are shown in Table 2.

Odontomachus simillimus: When colony size was 65 workers (May 2019), a 30 min. observation as for *O.p. denticulata* was carried out 10 times (5 hours in total). Two months after the observation, when colony size was 130 to 140 workers, a 30 min. observation of queen behavior was carried out 40 times (20 hours in total).

RESULTS

Trophic egg laying by non-reproductive females

In three ponerine species, trophic eggs were laid by workers whereas reproductive females (mated dealate queens and gamergates) never laid trophic eggs. In *H. venator,* virgin dealate queens and infertile mated workers also laid trophic eggs. The morphology of trophic eggs and egg laying behavior were similar among the three species. Trophic eggs were more spherical than reproductive eggs, and the two types were easily discriminated in all three species. The trophic eggs were very easily flattened when held between mandibles (Fig. 1). In the process of laying eggs, the egg-layers generally bent their abdomen to a position underneath the thorax and remained in that posture until the eggs were laid. The eggs were then picked up with their mandibles. Trophic eggs were then brought to mated queens or gamergates. In *Harpegnathos venator*, 12 trophic

Table 2. Colony composition, number of trophic eggs (TE) laid by workers and that eaten by queens in *Odontoponera denticulata*. All colonies had one dealate queen. Number of workers in each colony during observation was shown.

Colony code	No. workers	No. TE laid by workers	No. TE eaten by queen	Hours of observation
MO15-8	88~90	5	0	2
MO15-2	88~132	1	1	4
MO15-7	91~133	5	4	4
MO15-3	715~916	54	8	10
MO15-1	480~1280	67	13	10
Total		132	26	30

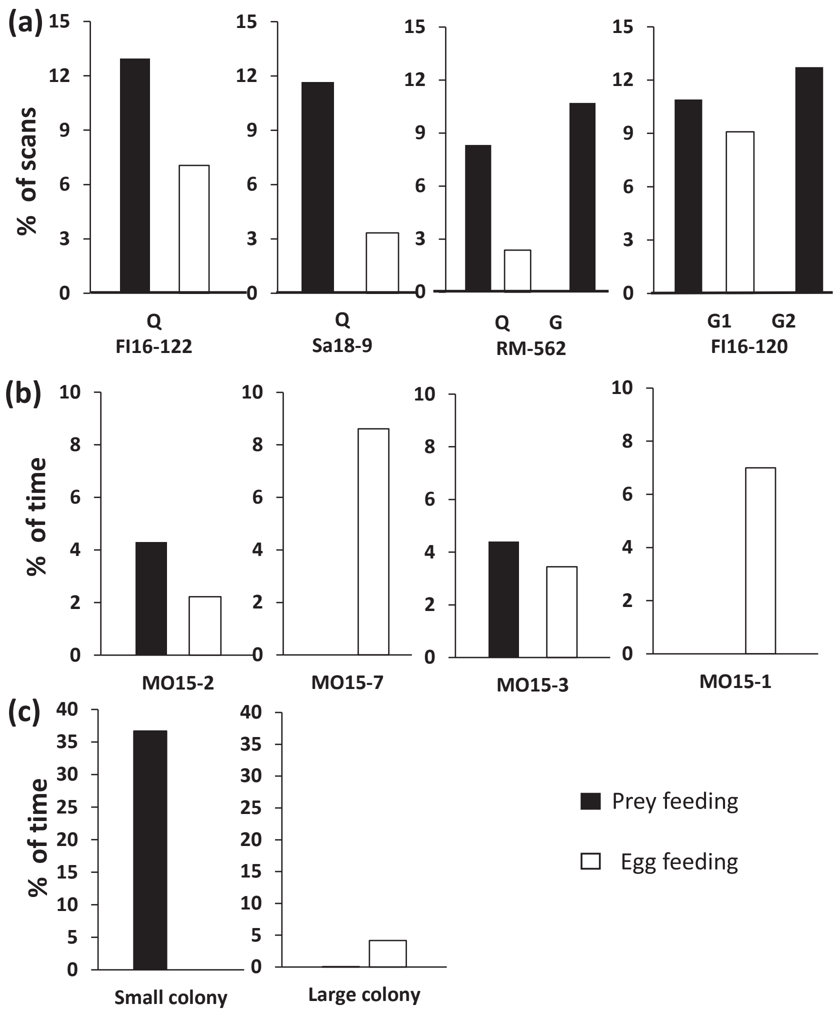

Fig. 2. Time budget of reproductive females for eating solid prey and trophic eggs. (a) dealate queens (Q) and gamergates (G) of *Harpegnathos venator*. Percentage of scans observing each behavior was shown. Total number of scans per colony was as follows: 85 times in FI16-122, 60 times in SA18-9, 84 times in RM-562, and 55 time in FI16-120. (b) dealate queens of *Odontoponera denticulata.* Duration of observation was shown in Table 2, but data of MO15-3 in this figure was based on 15 h observation (see Materials and Methods). (c) dealate queen of *Odontomachus simillimus.* Duration of observation was 5 hours for small colonies and 20 hours for large colonies.

eggs were laid during 30 h observation (Table 1). One was laid by the virgin dealate queen, two by infertile mated workers, and the remaining nine were laid by virgin workers. In five colonies of *O.p. denticulata*, 132 trophic eggs were laid by workers. In *O.m. simillimus,* no trophic eggs were observed when colony size was 65 workers, while nine trophic eggs were laid by workers during 20 h observation of a large colony with ca. 130 workers. The rate of trophic egg production per non-reproductive individual per hour was very low, 0.012 ± SD 0.0067 (N = 4 colonies) in *H. venator* (i.e. on average one egg every two days five hours 29 min.), 0.0115 ± 0.009/worker/hour (N = 5) in *O.p. denticulata* (i.e. one egg every three days 14 hours 57 min.), and 0.0035/individual/hour in the large colony of *O.m. simillimus* (i.e. one egg every 11 days 21 hours 43 min.).

Fate of trophic eggs

In *H. saltator*, mated queens and gamergates fed on all 12 trophic eggs (7 and 5 respectively). No trophic eggs were given to larvae. In the colony with one mated queen and one gamergate (RM-562), two trophic eggs were eaten by the queen, and the gamergate did not feed on any trophic eggs. In one gamergate colony (FI16-120), the two gamergates often aggressively competed for trophic eggs. The trophic egg-layers seemed to escape from the aggressive individuals, however, the trophic eggs were finally taken by the most aggressive one. In this colony, all five trophic eggs were eaten by one gamergate.

In *O.p. denticulata*, a typical sequence of trophic egg presentation was as follows: a trophic egg layer that grasped a trophic egg approached the queen, and the worker having the trophic egg stood still in front of the queen. In 25 of 132 cases, the queens were observed to aggressively confront workers, sometimes biting into their mandibles to obtain the trophic eggs. Of 25 eggs eaten by queens, two eggs were completely fed on by queens, while the remaining eggs were eaten halfway through and the rest dumped on the floor. These dumped eggs were picked up by workers, and given to larvae, or eaten by workers. The remaining 107 trophic eggs were ignored by queens, though workers brought them to queens. Consumers of trophic eggs ignored by queens were not recorded, because workers usually carried trophic eggs for a long time. Therefore, we could not follow the fate, but these were presumably eaten by larvae or workers.

In *O.m. simillimus,* all but one of the trophic eggs were eaten by the queen. The single remaining trophic egg, failing to reach the queen, was given to a larva. In this case, the worker could not physically access the queen, who was at the roof of the nest chamber.

Feeding behavior of reproductive females

Reproductive females fed not only on trophic eggs but also on solid prey in the three ponerine species. However, the time spent eating the two types of prey varied among species and with colony size. In the four colonies of *H. venator*, three mated queens and one gamergate fed on both trophic eggs and solid prey, and two gamergates fed only on solid prey. The time spent eating solid prey was longer than that eating trophic eggs in all reproductive females (Fig. 2a). The duration for eating one trophic egg was not measured exactly, but it was more than five minutes. In contrast, queens of *O.p. denticulata* in two colonies (MO15-1 and 7), exclusively fed on trophic eggs, whereas queens in two other colonies (MO15-2 and 3) spent a similar amount of time feeding on both solid prey and trophic eggs (Fig. 2b). No feeding behavior of queens was observed in the remaining colony (MO15-8). In two cases in which the whole eggs were completely consumed, queens took 10 min. 20 sec. and 11 min. 20 sec., respectively (N = 2) to do so. In cases where the eggs were partially consumed, the average time spent was 4 min. 46 sec. ± 3 min. 17 sec. SD (N = 24). In *O.m. simillimus,* feeding behavior of the queen differed according to colony developmental stage (Fig. 2c). At the time when colony size was small, the feeding on solid prey occurred 23 times, and no consumption of trophic eggs was observed in five hours of observation. When the colony size was larger (130 workers), the queen was observed to feed nine times (a total of 50 min. 25 sec.), eight of which were trophic eggs during 20 hours observation. The queen spent on average 6 min. 13 sec. (± 2 min. 4 sec. SD, N = 8) feeding on an egg. Prey feeding occurred only once, and for a duration of 40 sec. only. Thus, in the large colony, 98.7% of feeding time by the queen was spent for trophic egg feeding.

DISCUSSION

In poneroid ants, cannibalism of reproductive eggs laid by workers or queens has been reported in many species, e.g. *Diacamma* sp. aff. *indicum* Santschi, 1920*, Dinoponera quadriceps* Kempf, 1971, *Odontomachus chelifer* (Latreille, 1802), and *Stigmatomma silvestrii* Wheeler, 1928 (Medeiros et al.1992; Monnin & Peeters 1997; Kikuta & Tsuji 1999; Masuko 2003), however, as mentioned earlier, trophic egg laying is not well documented. Van Walsum et al. (1998) reported in *O.m. simillimus* that two eggs were laid by workers during 10 hours observation of a queenright colony, and these two eggs were brought to the queen who fed on them. They did not use the term "trophic eggs", but the behavior mentioned is completely consistent with trophic egg laying and subsequent behavior reported in this paper.

In this paper, we report on trophic egg production by species from three ponerine genera. In addition, workers of the ponerine ant *Cryptopone sauteri* (Wheeler, 1906) and the amblyoponine ant *Stigmatomma reclinatum* (Mayr, 1879) also lay trophic eggs (Hosokawa R, pers. comm.; Ito, unpublished). These data suggest that trophic egg production in poneroid ants may be more common than previously thought. One of the possible reasons for the lack of data on trophic egg production in this group previously may be due to its low frequency, especially in small colonies. In the three species studied in this paper, the trophic egg laying rate by a virgin individual per hour was 0.0035 to 0.012 (i.e. one egg every c.a. two to 11 days). A much lower rate (0.0017 ± 0.0058 /individual/hour, i.e. one egg every c.a. 24 days) was observed for *Neoponera apicalis* by Dietemann and Peeters (2000). Most poneroid ants have small colonies with fewer than 100 workers (Peeters & Ito 2001, 2015). If the value obtained in *N. apicalis* is applied to a colony of a given species with 100 workers, we might expect that just one or two trophic eggs would be observed during 10 hours of observations. Therefore, observation of trophic egg-laying is not easy, and obtaining quantitative data is time consuming. Actually, *N. apicalis* is a common ant and had been the subject in several studies (e.g., Fresneau & Dupuy 1988; Oliveira & Hölldobler 1990), however, the production of trophic eggs had not been reported until it was mentioned by Dietemann and Peeters (2000). A further reason for the lack of published information on trophic egg production in poneroid ants is that researchers are unlikely to report anecdotal observations of rare events.

In the three ponerine species in this study, the trophic eggs seem to be unspecialized, because time spent eating is quite long: trophic eggs were consumed in ca. 6 - 10 min. by reproductive females. Comparable data are scarce, though, Hölldobler and Wilson (1983) reported that *Oecophylla longinoda* (Latreille) queens fed on five trophic eggs during 20 min. Queens of many species of formicine ants including *Anoplolepis gracilipes* and some species of the *Prenolepis* genus group such as *Nylanderia* spp. eat trophic eggs in an instant (Lee et al. 2017; Ito et al. unpublished). Thus, trophic eggs in these three ponerine ants are not specialized for eating. This is also the case for trophic eggs of *Prionopelta kraepelini*, where the dealate queen spent six to seven min. for eating one trophic egg (Ito & Billen 1998).

In *H. venator,* trophic eggs were laid by non-reproductive females including virgin workers, infertile mated workers and virgin queens, and all trophic eggs were eaten by reproductive females (mated queens or gamergates). However, trophic eggs do not seem important as a food source for reproductive females, because the frequency of trophic egg laying is low, and both mated queens and gamergates can feed on normal insect prey. Nevertheless, it is possible that trophic eggs are significantly more valuable in terms of nutritional value and/or assimilation than normal insect prey. This is an important topic for future research. In contrast, the queen of *O.m. simillimus* in the larger colony almost exclusively fed on trophic eggs, as in *Neoponera apicalis* (Dietemann & Peeters 2000). In *O.p. denticulata,* queens fed on both trophic eggs and solid prey even in larger colonies, however, trophic eggs seem to be more common food for queens. Therefore, the significance of trophic eggs may vary among poneroid species, while also varying with colony size. A common feature of trophic eggs in poneroid ants so far reported is that the trophic eggs are mostly eaten by reproductive females, whereas larvae are the main consumer in most formicoid ants, where queens can receive nutrition via trophallaxis from workers. In the case of *O.p. denticulata,* many trophic eggs were eaten by workers and larvae, though egg laying workers first brought them to queens. Therefore, the principal consumer may be queens. One of the possible reasons why most trophic eggs were ignored by queens of *O.p. denticulata* is colony size: a large number of workers existed in the two large captive colonies where more than 80% of trophic eggs were ignored by queens. One exception in poneroid ants is known: Peeters (2017) mentioned that two trophic eggs were laid by workers in an incipient colony of *Paraponera clavata*, and both were given to larvae that fed on them very quickly. The queen of the incipient colony fed on insect prey (Peeters 2017), though the feeding habits of queens in mature colonies of *Paraponera clavata* is unknown. The difference of the main consumer of trophic eggs between poneroid and formicoid ants may relate to a morphological specialization of trophic eggs: softer, more fragile eggs in formicoid ants may be suited for larvae that have small mouthparts. Trophic eggs in ants have been known for a long time, however, the diversity and significance of trophic eggs are still not well understood. This study indicates that the nature of trophic eggs differs remarkably between poneroid and formicoid ants. Comprehensive studies including several species covering the ant phylogeny are needed for further insights into the evolution of trophic eggs.

ACKNOWLEDGEMENTS

We would like to thank all staff at Omkoi Natural Forest and Khoon Tuen Forest at Chiang Mai Province for their assistance in the field, Weetuwadee Sangtao for help in collecting the ant colonies for this study, Ryota Hosokawa for providing unpublished information of *Cryptopone sauteri,* Masaki Shiota for preliminary observation of *O.m. simillimus*, and Johan Billen, Jürgen Liebig, and an anonymous reviewer for comments and improving the English text. We also acknowledge all members of the Laboratory of Entomology, Faculty of Agriculture, Kagawa University, Japan, and the Laboratory of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, Thailand, for supporting this research. This work was supported in part by JSPS KAKENHI Grant Numbers B24405010, B16H05769 and 18K06421.

REFERENCES

Aupanun S, Jaitrong W, Suttiprapan P, Peeters C, Ito F, 2021. Nest architecture, worker reproduction, and polygyny in the ponerine ant *Harpegnathos venator*. *Insectes Sociaux*, submitted.

Bartels PJ, 1988. Reproductive caste inhibition by Argentine ant queens: new mechanisms of queen control. *Insectes Sociaux* 35: 70 – 81.

Bourke AFG, 1991. Queen behavior, reproduction and egg cannibalism in multiple-queen colonies of the ant *Leptothorax acervorum*. *Animal Behaviour* 42: 295 – 310.

Brian MV, Rigby C, 1978. The trophic eggs of *Myrmica rubra* L. *Insectes Sociaux* 25: 89 – 110.

Camargo-Mathias MI, Caetano FE, 1995. Trophic eggs in workers of *Neoponera villosa* ants (Hymenoptera: Ponerinae). *Journal of Advanced Zoology* 16: 62 – 66.

Cassill D, 2002. Brood care strategies by newly mated monogyne *Solenopsis invicta* (Hymenoptera: Formicidae) queens during colony founding. *Annals of the Entomological Society of America* 95: 208 – 212.

Choe JC, 1988. Worker reproduction and social evolution in ants (Hymenoptera: Formicidae). In: *Advances in Myrmecology* (Trager JC, ed.), Brill, Leiden, pp 163 – 187.

Crespi BJ, 1992. Cannibalism and trophic eggs in subsocial and eusocial insects. In: *Cannibalism: ecology and evolution among diverse taxa.* (Elgar MA, Crespi BJ, eds) Oxford University Pres, Oxford, pp176 – 213.

da Silva-Melo A, Giannotti E, 2012. Division of labor in *Pachycondyla striata* Fr. Smith, 1858 (Hymenoptera: Formicidae: Ponerinae). *Pscyhe* 2012: article ID 153862.

Dietemann V, Peeters C, 2000. Queen influence on the shift from trophic to reproductive eggs laid by workers of the ponerine ant *Pachycondyla apicalis*. *Insectes Sociaux* 47: 223 – 228.

Düssmann O, Peeters C, Hölldobler B, 1996. Morphology and reproductive bahavior of intercastes in the ponerine ant *Pachycondyla obscuricornis*. *Insectes Sociaux* 43: 421 – 425.

Fresneau D, Dupuy P, 1988. A study of polyethism in a ponerine ant: *Neoponera apicalis* (Hymenoptera, Formicidae). *Animal Behavior* 36: 1389 – 1399.

Gobin B, Peeters C, Billen J, 1998. Production of trophic eggs by virgin workers in the ponerine ant *Gnamptogenys menadensis. Physiological Entomology* 23: 329 – 336.

Gobin B, Ito F, 2000. Queens and major workers of *Acanthomyrmex ferox* redistribute nutrients with trophic eggs. *Naturwissenschaften* 87: 323 – 326.

Hölldobler B, Wilson EO, 1983. Queen control in colonies of weaver ants (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 76: 235 – 238.

Hölldobler B, Wilson EO, 1986. Ecology and behavior of the primitive cryptobiotic ant *Prionopelta amabilis* (Hymenoptera: Formicidar). *Insectes Sociaux* 33: 45 – 58.

Hölldobler B, Wilson EO, 1990. *The Ants.* - Belknap Press of Harvard University, Cambridge, MA, 732 pp.

Ito F, 2005. Mechanisms regulating functional monogyny in a Japanese population of *Leptothorax acervorum* (Hymenoptera, Formicidae): dominance hierarchy and preferential egg cannibalism. *Belgian Journal of Zoology* 135: 3 – 8.

Ito F, Billen J, 1998. Larval hemolymph feeding and oophagy: behavior of queen and workers in the primitive ponerine ant *Prionopelta kraepelini* (Hymenoptera, Formicidae). *Belgian Journal of Zoology* 128: 201 – 209.

Ito F, Gobin B, 2009. Colony composition and behaviour of a queen and workers in the oriental ectatommine ant *Gnamptogenys cribrata* (Emery) 1900 in West Java, Indonesia. *Asian Myrmecology* 2: 103 – 107.

Iwanishi S, Hasegawa E, Ohkawara K, 2003. Worker oviposition and policing behaviors in the myrmicine ant *Aphaenogaster smythiesi japonica* Forel. *Animal Behavior* 66: 513 – 519.

Khila A, Abouheif E, 2008. Reproductive constraint is a developmental mechanism that maintains social harmony in ants. *Proceedings of the National Academy of Sciences USA* 105: 17884 – 17889.

Khila A, Abouheif E, 2010. Evaluating the role of reproductive constraints in ant social evolution._*Philosophical Transactions of the Royal Society B* 365: 617 – 630.

Kikuta N, Tsuji K, 1999. Queen and worker policing in the monogynous and monandrous ant, *Diacamma* sp. *Behavioral Ecology and Sociobiology* 46: 180 – 189.

Lee CC, Nakao H, Teng SP, Hsu HW, Lin GL, Tay JW, Billen J, Ito F, Lee CY, Lin CC, Yang CC, 2017. Worker reproduction of the invasive yellow crazy ant *Anoplolepis gracilipes. Frontiers in Zoology*14: 24.

Masuko K, 1986. Larval hemolymph feeding: a nondestructive parental cannibalism in the primitive ant *Amblyopone silvestrii* Wheeler (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 19: 249 – 255.

Masuko K, 1989. Larval hemolymph feeding in the ant *Leptanilla japonica* by use of a specialized duct organ, the "larval hemolymph tap" (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 24: 127 – 132.

Masuko K, 2003. Larval oophagy in the ant *Amblyopone silvestrii* (Hymenoptera, Formicidae). *Insectes Sociaux* 50: 317 – 322.

Medeiros FNS, Lopes LE, Moutinho PRS, Oliveria PS, Hölldobler B, 1992. Functional polygyny, agonistic interactions and reproductive dominance in the neotropical ant *Odontomachus chelifer* (Hymenoptera, Formicidae, Ponerinae). *Ethology* 91: 134 – 146.

Monnin T, Peeters C, 1997. Cannibalism of subordinates' eggs in the monogynous queenless ant *Dinoponera quadriceps*. *Naturwissenschaften* 84: 499 – 502.

Oliveira PS, Hölldobler B, 1990. Dominance orders in the ponerine ant *Pachycondyla apicalis* (Hymenoptera, Formicidae). *Behavioral Ecology and Sociobiology* 27: 385 – 393.

Passera, L., Bitsch, J. & Bressac, C. (1968) Observations histologiques sur la formation des oeufs alimentaires et des oeufs reproducteurs chez les ouvrières de *Plagiolepis pygmaea* Latr. (Hymenoptera Formicidae). *Comptes Rendus de l'Académie des Sciences*, *Paris, Ser D*, 266: 2270 – 2272.

Peeters C, 2017. Independent colony foundation in *Paraponera clavata* (Hymenoptera, Formicidae): First workers lay trophic eggs to feed queen's larvae. *Sociobiology* 64: 417 – 422.

Peeters C, Hölldobler B, 1995. Reproductive cooperation between queens and their mated workers: the complex life history of an ant with a valuable nest. *Proceedings of the National Academy of Sciences USA* 92: 10977 – 10979.

Peeters C, Ito F, 2001. Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annual Review of Entomology* 46: 601 – 630.

Peeters C, Ito F, 2015. Wingless and dwarf workers underlie the ecological success of ants (Hymenoptera: Formicidae). *Myrmecological News* 21: 117 – 130.

Taki A, 1987. The trophic eggs of colony founding ant queens. In: *Chemistry and Biology of Social Insects* (J. Eder and H. Rembold, Eds.), Verlag J. Peperny, München, p. 268.

Torossian C, 1979. Importance quantitative des oeufs abortifs d'ouvrières dans le bilan trophique de la colonie de la fourmi *Dolichoderus quadripunctatus*. *Insectes Sociaux* 26: 295 – 299.

van Walsum E, Gobin B, Ito F, Billen J, 1998. Worker reproduction in the ponerine ant *Odontomachus simillimus* (Hymenoptera: Formicidae). *Sociobiology* 32: 427 – 440.

Villet MH, Wildman MH, 1991. Division of labour in the obligately queenless ant *Pachycondyla (= Bothroponera) krugeri* Forel 1910 (Hymenoptera Formicidae). *Tropical Zoology* 4: 233 – 250.

Wardlaw JC, Elmes GW, 1995. Trophic eggs laid by fertile *Myrmica* queens (Hymenoptera: Formicidae). *Insectes Sociaux* 42: 303 – 308.

Yamada A, Ito F, Hashim R, Eguchi K, 2018. Queen polymorphism in *Acanthomyrmex careoscrobis* Moffett, 1986 in Peninsular Malaysia (Hymenoptera: Formicidae: Myrmicinae), with descriptions of hitherto unknown female castes and males. *Asian Myrmecology* 10: 1 – 14.

Yamauchi K, Furukawa T, Kinomura K, Takamine H, Tsuji K, 1991. Secondary polygyny by inbred wingless sexuals in the dolichoderine ant *Technomyrmex albipes. Behavioral Ecology and Sociobiology* 29: 313 – 319 .

ASIAN MYRMECOLOGY
A Journal of the International Network for the Study of Asian Ants
Communicating Editor: Adam Cronin