ASIAN MYRMECOLOGY — Volume 18, e018007, 2025
ISSN 1985-1944 | eISSN: 2462-2362 DOI: 10.20362/am.018007

Reproduction by ergatoid queens in the Oriental myrmicine ant *Acanthomyrmex concavus*, from Sabah, Borneo, with notes on their ecology and behavior

Hayato Shinohara[1*], Sze Huei Yek[2], Hiroki Matsumura[1], Hiroki Kawaoka[3],
Adam Khalife[1], Hajime Sasaki[1] and Fuminori Ito[1]

[1]Faculty of Agriculture, Kagawa University, Ikenobe, Miki, Kagawa 761-0795, Japan
[2]Institute for Tropical Biology & Conservation, University Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia
[3]Kita-ku, Okayama-shi, Okayama-prefecture, Japan

[*]Corresponding author: giru0609@gmail.com

ABSTRACT. Most *Acanthomyrmex* ants have a granivorous diet, supplemented with other invertebrates and sugars. They are characterized by dimorphic workers, with major workers having substantially larger head width than minor workers. In this study, we investigated the colony composition and behavioral characteristics of both the queen and worker castes in *Acanthomyrmex concavus* Moffett, 1986, collected in Sabah, Borneo Island, Malaysia. All colonies had one or two ergatoid queens that exhibited an intermediate morphology between major and minor workers. Colony size was small, ranging from nine to thirty-seven minor and one to three major workers. Consistent with other species of *Acanthomyrmex, A. concavus* fed on tiny seeds (*Ficus* and *Oxalis*), and major workers played a crucial role in seed cracking. We discuss the possible selective pressures linking granivory to ergatoid queen evolution in this genus, where more than half of the species have ergatoid queens.

Keywords	Formicidae, ergatoid queen, dependent colony founding, seed eating
Citation	Hayato Shinohara, Sze Huei Yek, Hiroki Matsumura, Hiroki Kawaoka, Adam Khalife, Hajime Sasaki & Fuminori Ito (2025). Reproduction by ergatoid queens in the Oriental myrmicine ant *Acanthomyrmex concavus*, from Sabah, Borneo, with notes on their ecology and behavior. Asian Myrmecology 18: e018007
Copyright	This article is distributed under a Creative Commons Attribution License CCBY4.0
Communicating Editor	Adam Cronin
ESM	Electronic supplementary information for this article can be downloaded from the Asian Myrmecology website

INTRODUCTION

Most ant queens have wings and can fly away for mating and colony foundation. However, in at least 50 different genera, permanently flightless reproductive castes (ergatoid queens, brachypterous queens, and gamergates) have evolved independently (Peeters 2012). Permanently wingless queens, ergatoid (worker-like) queens are defined as wingless reproductives that differ morphologically from workers (Wheeler 1917; Peeters 2012). These queens typically possess a mesosoma similar in structure to that of workers, but with a larger abdomen, developed ovaries, and a spermatheca (Peeters 2012). Ergatoid queens have evolved independently in a variety of ant lineages, resulting in considerable diversity in their morphology and life history traits (Peeters & Ito 2001; Peeters 2012). Ergatoid queens typically disperse on foot with other workers via dependent colony founding (DCF) strategies such as fission or budding (Peeters 2012; Cronin et al. 2013). This short-distance dispersal mechanism can lead to geographical isolation and speciation, which suggests that wing loss in queens has significant evolutionary implications (Peeters & Adams 2016).

The Oriental endemic genus *Acanthomyrmex* includes 19 described species (Bolton 2024), of which four are known to possess only ergatoid queens, while another four have both alate and ergatoid queens (Yamada et al. 2018; Jaitrong & Asanok 2019). Additionally, Yamada et al. (2018) inferred that ergatoid queens may also exist in five other species based on morphological characteristics, suggesting that ergatoid queens are prevalent in this genus. However, knowledge of queen morphology in most species of *Acanthomyrmex* is still incomplete.

Furthermore, workers in this genus exhibit a spectacular polymorphism: while minor workers take care of most tasks, major workers have enormous heads and are believed to play important roles in colony defense, seed grinding, and food storage (Moffett 1985; Buschinger & Maschwitz 1998; Terayama et al. 1998; Gobin & Ito 2000, 2003; Eguchi et al. 2008). However, behavioral studies have been limited to only a few species, and comparative studies based on a broader range of species are needed.

Acamthomyrmex concavus Moffett, 1986, has wingless females that show intermediate phenotypes between major and minor workers. Winged queens have never been found in this species, and Yamada et al. (2018) suggested the possibility of ergatoid queen reproduction. However, the presence or absence of sperm in spermathecae has not been assessed in these intermediate phenotypes. In this study, we report observations on colony structure, morphological comparisons between castes, and behavioral characteristics of intermediate phenotypes and major workers from *A. concavus* colonies collected from Sabah, Malaysian Borneo.

MATERIALS AND METHODS

Acanthomyrmex concavus is endemic to Malaysian Borneo and has only been collected in Sarawak and Sabah. We collected a total of five *A. concavus* colonies from decaying wood on the forest floor in Kawang Forest Reserve in Sabah, Malaysian Borneo (N 5°46’42.276”; E 116°2’18.024”), in November 2023 and March 2024. After collection, colony composition was recorded, and colonies were housed in plaster nests (100×65×28mm) with nest chambers (36×36×14mm), and fed with small pieces of mealworms, cockroaches and plant seeds (genus *Ficus* and *Oxalis*) every two to three days. *Ficus* and *Oxalis* seeds are both oval, with a diameter of about 0.8 mm and 1 mm, respectively. The behavior of two intermediate phenotype females (colonies HK23-01 and HS23-104) was observed under a stereo microscope (Olympus SZ61, Japan) in one-hour sessions (eight hours during daytime and two hours in the evening on 22-23 November and 18-20 December 2023) for a total of ten hours (five for each individual). Subsequently, behavior of intermediate phenotypes in the absence of major workers was observed in colony HK23-01 for ten one-hour sessions (seven hours during daytime and three hours in the evening on 8, 10, 11, 13-14 October 2024) for a total of ten hours. Following a similar protocol, the behavior of four major workers (one from colony HK23-01, three from HS23-104) was observed for a total of twenty one-hour sessions (eighteen during daytime and two in the evening on November 22-23 and December 18- 20 2023). During each session, we recorded the frequency and time spent performing the following behaviors: resting, moving, brood care, self-grooming, feeding, allo-grooming, seed cracking, egg-laying, prey dissection. In addition, the behaviour of minor workers was recorded alongside that of the major workers when minor workers approached major workers during the observation period (colonies HK23-01 and HS23-104), with particular attention to whether they attempted seed cracking or prey dissection. After the observations, individuals from all castes were dissected to check insemination status, assess ovarian development, and determine the presence of corpora lutea (three intermediate phenotypes : HS23-104 (1), MH216 (1), FI24-77 (1); six major workers: HK23-01 (1), HS23-104 (3), MH216 (1), FI24-77 (1); and twenty-three minor workers: HK23-01 (5), HS23-104 (12), MH216 (3), FI24-77 (3). Morphological measurements were conducted using the image processing software ImageJ (four intermediate phenotype specimens, six major workers, and twenty minor workers), following Yamada et al. (2018). Specimen photographs were taken with a Sony α6300 camera connected to an Olympus MVX10 microscope, and depth stacking was performed using Zerene Stacker (Version 1.04). The presence of ocelli and wings in the intermediate phenotypes was investigated with a JCM-7000 scanning electron microscope (JEOL, Japan) at 15.0 kV. Abbreviations used for measurements and indices are as follows, according to Yamada et al. (2018). To indicate size differences among castes clearly, MW (Mesosoma width), ATW (Abdominal tergum IV width), and ATL (Abdominal tergum IV length) were measured.

HL	Head length: maximal length of cranium (head capsule) in full-face view, measured from transverse line spanning the anterior most points of clypeus to that of posterior most points of cranium.
HW	Head width: maximal width of cranium in full-face view (excluding eyes).
EL	Eye length: diameter of major axis of eye in lateral view.
SL	Scape length: maximum length of antennal scape excluding basal condylar bulb.
ML	Mesosoma length: minimum length between posteroventral corner of pronotum and posterodorsal margin of propodeal spiracle in lateral view.
MW	Mesosoma width: maximal width of mesosoma in dorsal view (excluding spines).
ATW	Abdominal tergum IV width: maximum width of fourth abdominal tergum with anterior, posterior, and lateral borders in same plane of focus.
ATL	Abdominal tergum IV length: maximum length of fourth abdominal tergum measured with anterior and posterior margins in same plane of focus.
PnSL	Pronotal spine length: length of pronotal spine, measured from posterobasalmost point to apex of spine in lateral view.
PdSL	Propodeal spine length: minimum length between posterodorsal margin of propodeal spiracle and apex of spine.
CI	Cephalic index: HW/HL × 100.
EI	Eye index: EL/HW × 100.
SI	Scape index: SL/HW × 100.
PnSI	Pronotal spine index: PnSL/ML × 100 (for minor)
PdSI	Propodeal spine index: PdSL/ML × 100 (for female).
PI	Petiolar index: PL/PH × 100.
PPI	Postpetiolar index: PPL/PPH × 100.

To compare the morphological differences among castes, we performed Kruskal-Wallis tests followed by post-hoc Wilcoxon rank-sum tests. The p-values were adjusted using the Bonferroni correction to account for the potential increase in error due to multiple pairwise comparisons. All analyses were done using R 4.3.2 (R Core Team, 2023) and the RStudio interface (RStudio Team, 2023).

RESULTS

Colony composition

All colonies nested in decaying wood under the accumulation of fallen leaves on the forest floor. Composition of the collected colonies is summarized in Table 1. Colonies included 2.2 ± 0.7 (mean ± SD, n = 5) major workers, 26.6 ± 10.8 minor workers, and little brood (pupae: 0-2; larvae: 0-16; eggs: 0-9). Four colonies had one intermediate phenotype (HK23-01, HS23-104, MH216, and F124-77) whereas one colony had two (FI24-76). No plant seeds were found in any of the five nests. The intermediate phenotypes were wingless and intermediate in size between major and minor workers. All dissected intermediate phenotypes (n = 3) had numerous corpora lutea, a sperm-filled spermatheca, and four ovarioles (2-2), and hence can be considered ergatoid queens (Fig. 1). Majors (n = 6) and minors (n = 23) always had two ovarioles (1-1) and no spermatheca. The ovariole of the ergatoid queen contained a bean-shaped mature oocyte corresponding to a reproductive egg, whereas the oocytes of major workers appeared more granular and less organized. However, all dissected major workers (n = 6) exhibited clearly swollen ovaries with a small number of corpora lutea and visible signs of trophic egg production. In contrast, minor workers (n = 23) showed little to no ovarian development. This qualitative difference was consistently observed across all colonies examined. Colony FI24-76 produced two new ergatoid queens after the death of the two original ergatoid queens (Fig. 2).

Table 1. Colony composition of *Acanthomyrmex concavus*. HK23-01, HS23-104, and MH216 were collected in November 2023, and FI24-76 and FI24-77 were collected in March 2024 in Kawang Forest Reserve. Numbers in parentheses indicate the number of ergatoid queens dissected.

Colony code	Ergatoid queen	Major	Minor	Egg	Larva	Pupa
HK23-01	1	1	9	7	5	1
HS23-104	1(1)	3	19	0	1	1
MH216	1(1)	3	33	9	16	2
FI24-76	2	2	37	0	4	2
FI24-77	1(1)	2	35	0	0	0

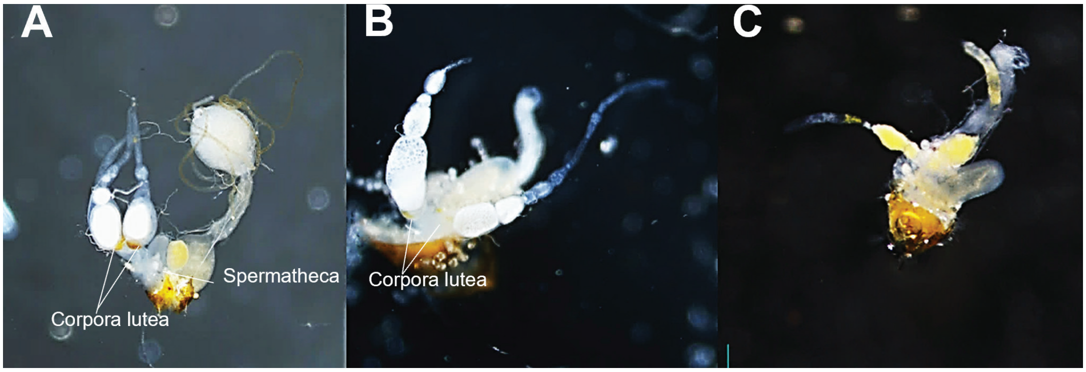

Fig. 1. Dissection pictures showing the ovaries of (A) an ergatoid queen, (B) a major worker, and (C) a minor worker. The ergatoid queen has numerous corpora lutea, a sperm-filled spermatheca, and four ovarioles. Mature oocytes are more granular and less organized in the major worker than the queen, suggesting that they are trophic eggs.

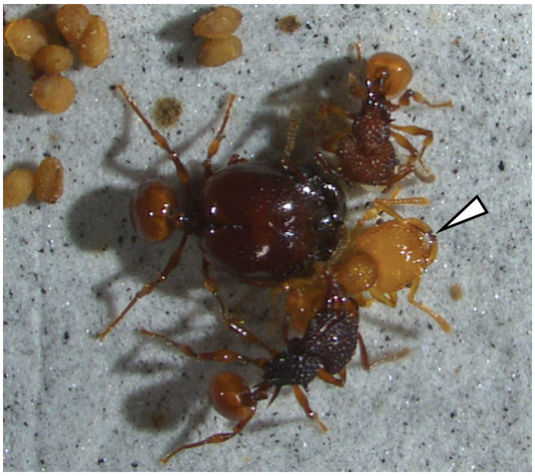

Fig. 2. Newly produced ergatoid queen in FI24-76 colony (indicated by an arrowhead) after the death of the original ergatoid queens.

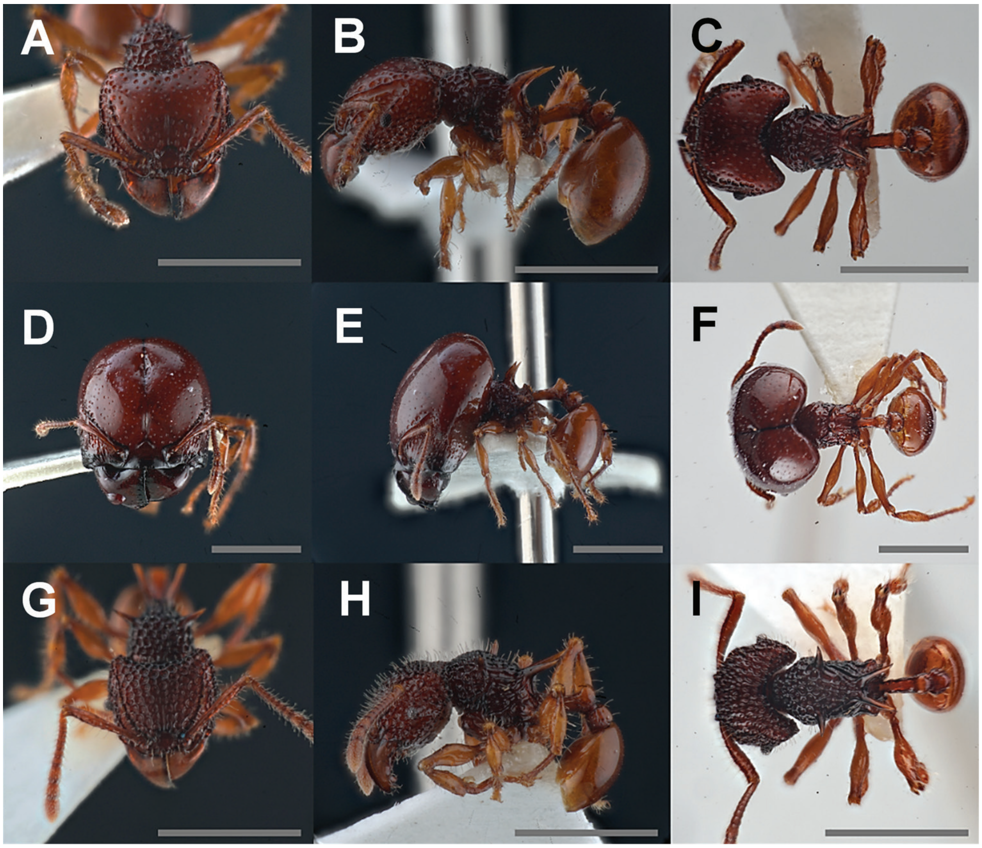

Fig. 3. Ergatoid queen (A to C), major worker (D to F), and minor worker (G to I) of *Acanthomyrmex concavus*. The scale bar indicates 1.5 mm in all images.

External morphology of ergatoid queens

The external morphology of ergatoid queens was compared with that of minor and major workers (Fig. 3, Table S1 and S2). The mesosomal sclerites of ergatoid queens were completely fused without any dorsal suture or articulation, as in the workers. Major workers exhibited the largest values for all measurements expect PnSL, PdSL and PPH. Overall, ergatoid queens were more similar to minor than major workers (Fig. 4). Head size was significantly different between castes ($(HW \times HL)^{1/2}$ = 1.29 ± 0.06 mm in ergatoid queens, N = 4; 1.10 ± 0.39 mm in minor workers, N = 20; 2.39 ± 0.07 mm in major workers, N = 6; Kruskal-Wallis test, χ^2 = 20.129, df = 2, $p < 0.001$). Pairwise tests indicated that ergatoid queens had a significantly larger head than minor, but smaller head than major workers (ergatoid queen and minor workers, Wilcoxon rank sum test, W = 76, $p < 0.001$; ergatoid queen and major workers, Wilcoxon rank sum test, W = 0, p = 0.003). Ergatoid queens had a shorter mesosoma than minor and major workers (ML = 1.19 ± 0.03 mm, 1.21 ± 0.03 mm and 1.26 ± 0.04 mm, respectively). However, despite an apparent effect of castes on mesosoma length (Kruskal-Wallis test, χ^2 = 6.223, df = 2, p = 0.045), pairwise comparisons failed to reveal any significant difference (ergatoid queen and minor workers, Wilcoxon rank sum test, W = 32, p = 1; ergatoid queen and major workers, Wilcoxon rank sum test, W = 2, p = 0.19). On the other hand, mesosoma width was significantly different between castes (MW = 0.72 ± 0.03 mm for ergatoid queens, 0.79 ± 0.01 mm for major workers, 0.72 ± 0.03 mm for minor workers; Kruskal-Wallis test, χ^2 = 12.09, df = 2, p = 0.0024). Prothoracic spines were well-developed in minor workers, smaller in ergatoid queens, and lacking in major workers. Gaster size was significantly different between castes ($(ATW \times ATL)^{1/2}$= 1.18 ± 0.05 mm in ergatoid queens, N = 4; $(ATW \times ATL)^{1/2}$ = 1.20 ± 0.02 mm in major workers, N = 4; 0.86 ± 0.03 mm in minor workers, N = 19). The gaster of ergatoid queens was larger than that of the minor workers (Wilcoxon rank sum test, $W = 76$, $p < 0.001$), and approximately the same size as that of the major workers (Wilcoxon rank sum test, $W = 6$, $p = 1$) (Fig. 4B). Scanning electron microscopy of the head and thorax of ergatoid queens revealed an absence of ocelli and wings (Fig. 5).

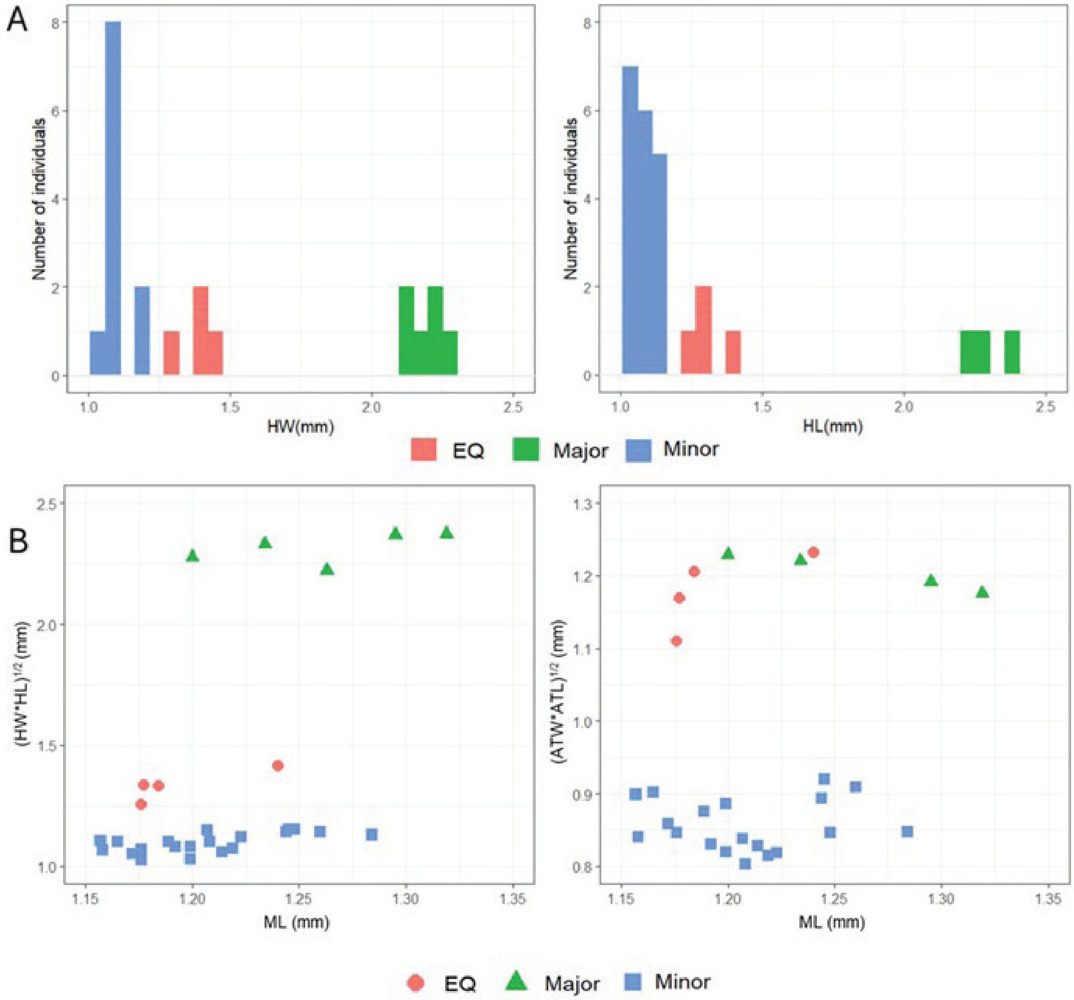

Fig. 4. (A) Distribution of head width (left) and head length (right), and (B) Head size ($(HW \times HL)^{1/2}$, left) and gaster size ($(ATW \times ATL)^{1/2}$, right) as a function of thorax length (ML) for all castes of *Acanthomyrmex concavus*. Ergatoid queens were more similar to minors than major workers.

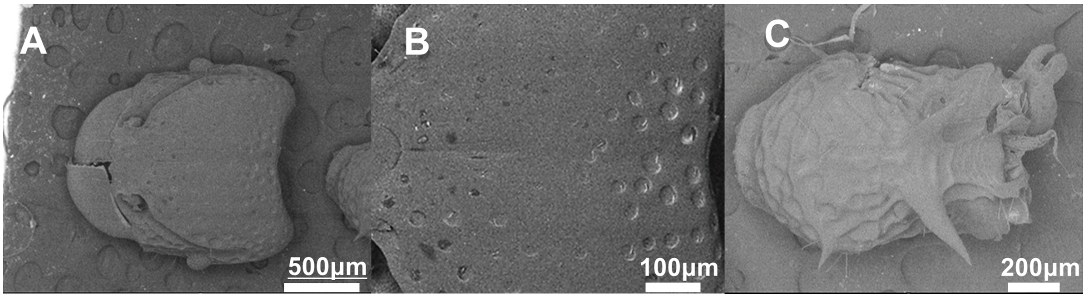

Fig. 5. SEM images of the ergatoid queen of *Acanthomyrmex concavus*. (A) Full head; (B) close-up view; (C) thorax. (A) and (B) revealed the absent of ocelli, whereas (C) revealed the absent of wings.

Fig. 6. An ergatoid queen attempting to crack an *Oxalis* seed in the absence of major workers. The ergatoid queen only successfully cracked the seed once, out of 11 trials.

Fig. 7. A major worker firmly clamping a seed (arrowhead) and squeezing it with its mandibles.

Behavior of ergatoid queens

In colonies containing both major and minor workers, the queen spent most of the time stationary and groomed herself (Fig. S1). When she was groomed by workers, both major and minor workers participated. In 20 hours of observation in two colonies (HK23-01, HS23-104), reproductive egg-laying was seen only once. No trophic egg-laying was observed. Queens directly fed on dead mealworms and cockroaches brought to the nest by minor workers, and never ate trophic eggs nor received oral trophallaxis. During the observation period, oral trophallaxis was also not observed between workers, and the colony did not feed on liquid food under laboratory conditions. Seed cracking by ergatoid queens was only observed in the absence of major workers (Fig. 6). HK23-01 was a colony that eventually consisted of only one ergatoid queen and minor workers because all major workers died during rearing. In ten hours of observation, the queen attempted seed cracking eleven times, successfully crushing a seed only once. In most cases, the ergatoid queen failed to crush a seed, then moved around the nest and tried again, repeating this cycle multiple times within an hour. The average number of seed-cracking attempts was 1.1 ± 1.5 times per hour, with a maximum of five occurrences within one hour. The duration of these events ranged from 30 to 2910 seconds. On 21 October 2024, seeds of sorrel (*Oxalis* sp.) and fig (*Ficus* sp.) were artificially cracked and provided to the HK23-01 colony, which had only one queen and three minor workers remaining, after all the brood had died and egg-laying ceased for more than three months. Within three days of receiving the seeds, the queen resumed egg-laying. By the end of the first week, the number of reproductive eggs had increased to four.

Behavior of minor and major worker

Minor workers foraged and took care of the brood. Major workers usually rested inside the nest chamber (Fig. S2), sometimes showing self and allo-grooming, and performed two remarkable behaviors: seed cracking and prey fragmentation.

Seed cracking: *Ficus* and *Oxalis* seeds were provided to five colonies. Both seed types were harvested by minor workers, retrieved from the foraging area within 30 seconds to 10 minutes. Retrieved seeds were then immediately brought into the chamber, where they were groomed briefly before being offered to major workers. Occasionally, minor workers attempted to crack seeds with their mandibles, but unsuccessfully. Upon receiving the seeds, major workers spent a lot of time licking their entire surface. Then, they clamped and squeezed them with their mandibles, and their body vibrated while cracking the seeds (Fig. 7). Once squeezed, seeds were cracked within a few seconds. Afterward, both major and minor workers licked the contents and remaining fragments of seed coat were discarded into the waste area of the chamber. Over the course of 20 hours of observation, two major workers tried to crack an *Oxalis* seed and succeeded. The time taken to crush the seeds was 720 seconds and 300 seconds. However, when *Ficus* seeds were introduced outside the observation period, seed cracking was only successful two out of five times. When seeds and mealworms were offered simultaneously, minor workers stored the seeds within their nest and consumed the mealworms. Stored seeds were occasionally consumed, but usually left untouched. On one occasion, several stored seeds germinated in the nest chamber, and the colony moved out.

Prey killing and fragmentizing behavior: During the observations, major workers were often stationary within the chamber and never foraged outside even though the chamber entrance hole was large enough for majors to go through. In contrast, minor workers engaged in hunting, but when a wounded mealworm was brought into the chamber, it was transported to a major worker that delivered the final blow by biting it. Major workers also actively participated in the fragmentation of the prey, using their mandibles and forelegs to process prey fragments into a ball. The "meatball" was then passed to either a minor worker or a larva, which consumed it entirely. It was not passed to the ergatoid queen. The consumption of a deceased minor worker was also observed. A major worker bit into the ventral side of the dead minor worker's head, and surrounding workers and larvae fed on its mouthparts. Subsequently, both major and minor workers participated in the fragmentation of the body, with the head, thorax, and abdominal cuticle being discarded, while the remaining body parts were consumed.

Trophic egg laying: During the observation period for both the queen and major workers, trophic egg laying was not observed. However, outside of the observation period, both a major and a minor worker laid a single trophic egg. Both trophic eggs were directly given to larvae by the workers. Although they could not be photographed, these two trophic eggs appeared to be smaller than reproductive eggs.

DISCUSSION

Ergatoid queen morphology in *A. concavus*

Queens of *Acanthomyrmex concavus* exhibited morphological traits that were intermediate between those of major and minor workers, but more closely resembled those of minor workers. In addition, they lacked ocelli and wings, possessed a sperm-filled spermatheca, and had completely fused mesosomal sclerites without any dorsal sutures or articulations. These results confirm that queens are ergatoid, as suggested by Yamada et al. (2018). Similar ergatoid queen phenotypes - intermediate between major and minor workers - have been reported in *A. minus* and *A. humilis* (Terayama et al. 1998; Eguchi et al. 2008). Moreover, no alate queens were observed in any of the five colonies collected, and ergatoid queens gave birth to new ergatoid queens in one colony. This suggests a possible replacement of alate queens by ergatoid queens in *A. concavus*. Ergatoid queens can be classified as either multi-purpose when produced in large numbers and capable of performing worker roles, or sole-purpose when produced in limited numbers and specialized for reproduction (Molet et al. 2009). In *A. concavus*, ergatoid queens spent most of their time stationary and did not engage in worker-like tasks. Furthermore, the number of ovarioles in ergatoid queens (four) was higher than that of workers (two), suggesting that their primary role is reproduction. However, in the absence of major workers, ergatoid queens engaged in seed cracking, indicating that they have a latent ability to perform worker tasks.

Queens of *A. concavus* had four ovarioles, which is the same to ergatoid queens of two species *A. padanensis* and *A. sulawesiensis*, and less than two other congeneric species (six for alate queens of *A. ferox* and both alate and ergatoid queens of *A. careoscrobis*) (Terayama et al. 1998; Yamada et al. 2018). In Aculeata including ants, six and eight ovarioles are widespread, and reduction from these number is not common (Iwata 1955, Ito et al. 2017). In general, ovariole numbers is the good proxy of fecundity, thus it may relate to colony size (the number of workers) (Villet et al. 1991; Peeters & Ito 2015). However, the average colony size of *A. concavus* was 26.6 ± 10.8 minor workers and 2.2 ± 0.7 major workers, which is consistent with other *Acanthomyrmex* with queens having six ovarioles (25 ± 11 minor workers and 2.6 ± 1.5 major workers for *A. ferox*, 22.6 ± 11.1 minor workers and 1.8 ± 0.9 major workers for *A. careoscrobis*; Gobin & Ito 2000; Yamada et al. 2018). For species with alate queens, the average colony size may be underestimated because colonies in the early stages of independent founding are included in the data. In contrast, *A. concavus* may exhibit DCF, in which case the average colony size could be overestimated. This discrepancy may have led to observed differences in the number of ovarioles that are not directly related to colony size.

Seeds as an unpredictable but necessary food resource

The genus *Acanthomyrmex* is known to store plant seeds within the nest (Moffett 1985). Seed acquisition and processing may be critical for colony survival, and seed cracking is primarily performed by major workers (Moffett 1985; Buschinger & Maschwitz 1998). In the case of *A. concavus*, although no plant seeds were found in wild nests, all colonies maintained in the laboratory collected, stored, cracked and consumed seeds. In *A. ferox* and *A. careoscrobis*, the number of fig seeds stored within the nest is highly variable in the field (Gobin & Ito 2000; Yamada et al. 2018), suggesting that seed availability is unstable. Therefore, it is likely that these ants immediately engage in seed collection when an opportunity arises. In times of food scarcity, *A. ferox* can distribute nutrition via trophic eggs (Gobin & Ito 2000). In *A. concavus*, both major and minor workers were observed laying trophic eggs. As in *A. ferox* (Gobin & Ito 2000), major workers had more developed ovaries and corpora lutea than minor workers, and oocytes indicative of differentiation into trophic eggs. This suggests that major workers serve a key trophic function, acting both as seed crackers and trophic egg layers. The use of trophic eggs appears to be a common food sharing strategy within the genus *Acanthomyrmex*. When only arthropods such as mealworms were fed, queens stopped egg-laying. But in a colony without major workers, where the ergatoid queen had ceased to lay eggs, providing pre-cracked seeds led to resumption of egg laying by the ergatoid queen. Seeds are nutritionally rich, as they pack high levels of carbohydrates, lipids and proteins in their cells for germination (Bewley & Black 2014), and may thus be a compulsory food resource for *Acanthomyrmex* queens. Similarly, the genus *Proceratium* primarily feeds on arthropod eggs, but can use alternative food sources such as soil invertebrates (Brown 1957, 1980). However, when arthropod eggs are removed from the diet of laboratory colonies of *P. itoi*, workers can survive but larvae fail to develop properly and die (Shinohara, unpublished). In specialist feeders, different castes can have different needs, including energy-efficient or nutrient-rich diets for egg and larval development. The importance of seed nutrition for *Acanthomyrmex* colony growth and survival should be examined more thoroughly in the future.

Colony founding strategies in *Acanthomyrmex* and importance of the "seed mill caste" for colony survival

Independent colony founding (ICF) is characterized by long-distance dispersal of flying queens but a very low survival rate whereas in dependent colony founding (DCF), queens and workers disperse locally on foot but their survival rate is much higher (Cronin et al. 2013). Ecological conditions that reduce the survival rate of ICF queens, such as habitat patchiness, limited nest sites, harsh climates, resource limitations, and nest instability (Roff 1986; Heinze & Tsuji 1995; Zera & Denno 1997; Liebig et al. 1998), are thought to favor a shift towards DCF and ergatoid queens (Heinze & Tsuji 1995). In environments where food resources are limited, producing a few ergatoid queens with high survival rates is more adaptive than producing a large number of costly, low-survival alate queens (Bolton 1986; Buschinger & Heinze 1992; Tinaut & Heinze 1992). More than half of the known species of *Acanthomyrmex* possess ergatoid queens that coexist with or have replaced alate queens (Yamada et al. 2018). This suggests that selective pressures favoring ergatoid queens are widespread across the genus *Acanthomyrmex* and may be linked to seed stochasticity and patchiness. For example, workers of *A. ferox* are rarely seen around decaying figs on trees or the forest floor, but instead more commonly seen collecting fig seeds from bird droppings on the leaves of the understory vegetation (Ito et al. 2017). Specializing on fig seeds would restrict their habitat to forest edges and gaps in the forest where bird droppings can reach to the ground (Ito et al. 2017). Granivory may have favored the evolution of DCF and ergatoid queens. However, in several species of *Pogonomyrmex*, another granivorous ant genus, ergatoid queens have been reported to perform ICF (Johnson 2010). This genus found in the arid regions of North America, where their primary food source, seeds, is produced in relatively predictable cycles associated with seasonal rainfall, likely increasing the success rate of ICF. In contrast, *Acanthomyrmex concavus* inhabits tropical rainforests, where the availability of fig seeds is more variable (Lambert & Marshall 1991; Sakai et al. 1999; Harrison et al. 2000) and thus would be less likely to adopt an ICF strategy.

The head of alate queens of *Acanthomyrmex* is similar to that of major workers (Yamada et al. 2018), and they may perform major worker-like behavior such as seed cracking during early stage of colony growth when major workers are absent. On the other hand, major workers can be present at the start of a new colony in species with a DCF strategy, hence queens do not need a major worker-like head. As a result, minor-like or intermediate phenotypes of ergatoid queens like in *A. concavus* are viable and less costly. The presence of at least one major worker in each collected colony, and that the low seed-cracking success rate of ergatoid queens, support this hypothesis. Nonetheless, this strategy is risky and the absence of major workers can lead to the death of the colony, as the seed-cracking ability of small ergatoid queens is low. Interestingly, ergatoid queens with a major-like head are found in *A. glabfemoralis*, *A. crassispinus* and *A. careoscrobis* (Eguchi et al. 2008; Yamada et al. 2018), suggesting that different species can have different strategies to deal with the trade-off between queen production cost and seed cracking ability. Developing our understanding of the natural history of additional species is paramount for understanding the evolution and diversity of ergatoid queen morphology in *Acanthomyrmex*.

ACKNOWLEDGEMENTS

This research was permitted by an Access License issued by Sabah Biodiversity Council [ref. no. JKM/MBS.1000-2/2 JLD.17 (25) to Sze Huei Yek, and ref. no. JKM/MBS.1000-2/2 JLD.17 (27) to Fuminori Ito]. Lab behavior and ecology study were conducted at Kagawa University under the Export License [ref. no. JKM/MBS.1000-2/3 JLD.5 (58) issued to both Sze Huei Yek and Fuminori Ito]. Adam Khalife was supported by the Japanese Society for the Promotion of Science (Postdoctoral Fellowship P22761).

REFERENCES

Bewley JD, Black M, 2014. *Physiology and biochemistry of seeds in relation to germination: 1 development, germination, and growth*. Springer.

Bolton B, 1986. Apterous females and shift of dispersal strategy in the *Monomorium salomonis*-group (Hymenoptera: Formicidae). *Journal of Natural History* 20(2): 267–272.

Bolton B, 2024. AntCat.org: An online catalog of the ants of the world. Available from https://antcat.org/. Accessed on 26 November 2024.

Brown WL, 1957. Predation of arthropod eggs by the ant genera *Proceratium* and *Discothyrea*. *Psyche* 64(3): 115.

Brown WL, 1980. A remarkable new species of *Proceratium*, with dietary and other notes on the genus (Hymenoptera: Formicidae). *Psyche* 86(4): 337–346.

Buschinger A, Heinze J, 1992. Polymorphism of female reproductives in ants. In: *Biology and Evolution of Social Insects* (Billen J, ed.), Leuven University Press, Leuven, Belgium, 11–23.

Buschinger A, Maschwitz U, 1998. Die faulsten Ameisen der Welt. *Ameisenschutz aktuell* 12(4): 110–114.

Cronin AL, Molet M, Doums C, Monnin T, Peeters C, 2013. Recurrent evolution of dependent colony foundation across eusocial insects. *Annual Review of Entomology* 58: 37–55.

Eguchi K, Bui TV, Yamane S, 2008. Vietnamese species of the genus *Acanthomyrmex* Emery, 1893 – *A. humilis* sp. n. and *A. glabfemoralis* Zhou & Zheng, 1997 (Hymenoptera: Formicidae: Myrmicinae). *Myrmecological News* 11: 231–241.

Gobin B, Ito F, 2000. Queens and major workers of *Acanthomyrmex ferox* redistribute nutrients with trophic eggs. *Naturwissenschaften* 87(7): 323–326.

Gobin B, Ito F, 2003. Sumo wrestling in ants: major workers fight over male production in *Acanthomyrmex ferox*. *Naturwissenschaften* 90(7): 318–321.

Harrison RD, Yamamura N, Inoue T, 2000. Phenology of a common roadside fig in Sarawak. *Ecological Research* 15(1): 47–61.

Heinze J, Tsuji K, 1995. Ant reproductive strategies. *Researches on Population Ecology* 37(2): 135–149.

Ito F, Gobin B, Hashim R, 2017. Harvesting fig seeds from bird feces by an Oriental myrmicine ant species, *Acanthomyrmex ferox* Emery, 1893 (Hymenoptera: Formicidae). *Asian Myrmecology* 9: e009017.

Ito F, Miyazaki S, Hashim R, Billen J, 2017. Colony composition and behavioral characteristics of *Myrmoteras iriodum* and *M. jaitrongi* in Ulu Gombak, Peninsular Malaysia (Hymenoptera: Formicidae). *Asian Myrmecology* 9.009010: 1-9.

Iwata K, 1955. The comparative anatomy of the ovary in Hymenoptera. Part. I. Aculeata. *Mushi*, (29): 17-34.

Jaitrong W, Asanok L, 2019. Two new species of the ant genus *Acanthomyrmex* Emery, 1893 (Hymenoptera, Formicidae, Myrmicinae) from Thailand. *ZooKeys* 842: 113.

Johnson RA, 2010. Independent colony founding by ergatoid queens in the ant genus *Pogonomyrmex*: queen foraging provides an alternative to dependent colony founding. *Insectes Sociaux 57*: 169-176.

Lambert FR, Marshall AG, 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *Journal of Ecology* 79(3): 793–809.

Liebig J, Hölldobler B, Peeters C, 1998. Are ant workers capable of colony foundation? *Naturwissenschaften* 85: 133-135.

Moffett MF, 1985. Behavioral Notes on the Asiatic Harvesting Ants *Acanthomyrmex notabilis* and *A. ferox*. *Psyche* 92(2–3): 165–179.

Molet M, Fisher BL, Ito F, Peeters C, 2009. Shift from independent to dependent colony foundation and evolution of 'multi-purpose' ergatoid queens in *Mystrium* ants (subfamily Amblyoponinae). *Biological Journal of the Linnean Society* 98(1): 198–207.

Peeters C, 2012. Convergent evolution of wingless reproductives across all subfamilies of ants, and sporadic loss of winged queens (Hymenoptera: Formicidae). *Myrmecological News* 16: 75–91.

Peeters C, Ito F, 2001. Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annual review of entomology*, 46(1): 601-630.

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

Peeters C, Adams RMM, 2016. Uncoupling flight and reproduction in ants: Evolution of ergatoid queens in two lineages of *Megalomyrmex* (Hymenoptera: Formicidae). *Journal of Insect Science* 16(1).

R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

RStudio Team, 2023. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.

Roff DA, 1986. The evolution of wing dimorphism in insects. *Evolution* 40(5): 1009–1020.

Sakai S, Momose K, Yumoto T, Nagamitsu T, Nagamasu H, Hamid AA, 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany* 86(10): 1414–1436.

Terayama M, Ito F, Gobin B, 1998. Three new species of the genus *Acanthomyrmex* Emery (Hymenoptera: Formicidae) from Indonesia, with notes on the reproductive caste and colony composition. *Entomological Science* 1(2): 257–264.

Tinaut A, Heinze J, 1992. Wing reduction in ant queens from arid habitats. *Naturwissenschaften* 79(2): 84–85.

Villet MH, Crewe RM, Duncan FD, 1991. Evolutionary trends in the reproductive biology of ponerine ants (Hymenoptera: Formicidae). *Journal of Natural History* 25(6): 1603–1610.

Wheeler WM, 1917. The phylogenetic development of subapterous and apterous castes in the Formicidae. *Proceedings of the National Academy of Sciences*, 3(2): 109-117.

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.e010009: 1-19.

Zera AJ, Denno RF, 1997. Physiology and ecology of dispersal polymorphism in insects. *Annual review of entomology* 42: 207–230.

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