ORIGINAL ARTICLE

Colony composition and behavioral characteristics of the myrmicine ant, *Aphaenogaster rugulosa*, an endemic species to Yonagunijima Island, the westernmost point of Japan (Hymenoptera: Formicidae)

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ABSTRACT Colony composition and behavioral characteristics of the myrmicine ant, *Aphaenogaster rugulosa*, a species endemic to Yonagunijima Island, were investigated. Colonies nested in rotten woods fallen on the forest floor. All queenright colonies (N=42) were monogynous with one dealate queen. The average colony size in worker number was $140.5 \pm \text{SD } 94.9$. Under laboratory conditions, workers and larvae fed on both fresh and dried insect preys. The workers used a kind of tool to transport diluted sugar water to the nest chamber. They dropped pine needles and trashes into the diluted sugar water and then transported the food-soaked materials back into the nest chamber, where nest members then sucked on the materials inside the nest chamber. Trophic eggs were laid by the workers, the majority of which were given to the larvae. The queens also fed on trophic eggs as well as insect preys. The workers under an orphan condition laid reproductive eggs that grew up to be males.

Key words: colony composition, tool use, queen behavior, trophic egg, worker reproduction

INTRODUCTION

The myrmicine ant genus *Aphaenogaster* is distributed in the temperate to tropical zones throughout the world, and comprises 210 valid species (Bolton 2021). So far, the biology of this ant genus has been mainly studied in temperate species (e.g., Mizutani and Imamura 1980, Higashi et al. 1987, Richards 2009, Lubertazzi 2012, Bednar et al. 2013, Caut et al. 2013, Thomas et al. 2016), whereas in tropical and subtropical regions, the biology of only a limited number of species has been studied, e.g., a description of the colony composition of six Thai species (Aupanun et al. 2018), the nest structure of three species in Florida (Tschinkel 2011), and the natural history of the Malagasy species (Dittmann et al. 2014, Csösz et al. 2021). Thirteen species of *Aphaenogaster* are distributed in the Nansei Islands of southern Japan (Terayama et al. 2014), most of which show a distribution limited to one or a few islands. This distribution patterns renders these ants as interesting materials for biogeographical research. However, the biology of all these species has not been studied. On Yonagunijima Island, the westernmost point of Japan, we have noticed that the endemic species *Aphaenogaster rugulosa*, so far found only on this island, is

very common, so we investigated the biological characteristics of this species.

In this paper, we focused on colony composition, caste difference in body size and ovaries, prey utilization inside the nest chamber, trophic egg production by workers under a queenright condition, and male production by workers under an orphan condition. Data on colony composition and caste difference in body size and ovaries are important for understanding the organization of an ant society (Tschinkel 2010, Peeters and Ito 2015). Prey utilization among nest members seems to vary among species. For example, the queens of some formicoid ants such as *Technomyrmex brunneus* and *Anoplolepis gracilipes* never feed on solid prey; they exclusively consume trophic eggs and/or oral trophallaxis from workers (Yamauchi et al. 1991, Lee et al. 2017). In contrast, the queens of many poneroid ants directly feed on solid prey (Ito et al. 2020). Even though knowledge of prey utilization among nest members is still limited in ants, it may show the degree of caste specialization. Trophic eggs are non-viable and morphologically distinct from reproductive eggs, and serve a nutritive function in a highly diverse range of animals including ants (Passera et al. 1968, Crespi 1992, Gobin et al. 1998). In *Aphaenogaster japonica*, Iwanishi et al. (2003) reported

that workers lay trophic eggs under a queenright condition but switch to reproductive egg production under a queenless condition. We investigated whether workers of *A. rugulosa* show a similar behavior to those of *A. japonica*. In addition, we briefly describe tool use by *A. rugulosa*. Notably, tool use for foraging is known in at least seven species of *Aphaenogaster* (Fellers and Fellers 1976, Tanaka and Ono 1978, Banschbach et al. 2006, Maák et al. 2017, Módra et al. 2021). Workers of *A. rugulosa* also showed behavior similar to that reported in other species of *Aphaenogaster*.

MATERIALS AND METHODS

Colony collection and dissection

Colonies of *A. rugulosa* were collected on the forest floor in Yonagunijima Island (24°27'05" N, 123° 0'17" E) in March, June, September, and November from 2015 to 2020. *Aphaenogaster rugulosa* nests in dead wood or under stones. When we found the nests of *A. rugulosa* in the rotten woods, the wood pieces were brought back to the laboratory, and all individuals were carefully collected using an aspirator or a pair of forceps. Colony composition was assessed after collection. To check ovariole numbers and reproductive conditions, 8 queens and 110 workers from eight colonies collected in June 2017 and November 2019 were dissected under a binocular microscope. The head width of 69 workers in one colony and seven queens in seven colonies were measured under a binocular microscope.

Behavioral observation

Six colonies were kept at room temperature condition in a laboratory. All six colonies were monogynous with single dealate queens. The approximate number of workers in each colony when we observed behavior was as follows: 140 workers in FI17-93, 160 workers in FI17-86, 170 workers in FI20-65, 250 workers in FI15-98, 260 workers in FI19-37 and 300 workers in FI20-64. Each colony was housed in a polystyrene box (L 20.8 × W 14.6 × H 5.6 cm, or L 20.8 × W 10.6 × H 5.6 cm). Inside the box, a smaller polystyrene box (L 8.7 × W 5.7 × H 1.9 cm or L 7.5 × W 5.0 × H 1.8 cm) with an entrance hole served as a nest chamber. The bottom layer of both the chamber and the outer box was covered with plaster of Paris to maintain humidity. Freshly killed mealworms or cockroaches were given as prey two or three times per week. Diluted sugar water was put on a plastic plate set in the foraging arena.

Dried mealworms were also sometimes given to these colonies. The behavior of the queens was observed under a binocular microscope attached to a swing arm. We mainly focused on the feeding behavior of the queens, which were continuously observed for 30 min periods, and feeding behavior was recorded. Such observation was replicated 8 (4 hours) to 36 (18 hours) times per colony. For three of the six colonies, the fate of the trophic eggs laid by the workers was also noted. To observe tool-use behavior for transporting sugar water, small fragments of pine needles were put in the foraging arena of one colony. The behavior of the workers when sugar water was given was observed (n = 10 times).

Male production by the workers

To determine the ability of reproductive egg production by the workers, two queenless colonies consisting of 50 workers were made from each of three colonies. These orphan colonies were kept in an incubator under constant temperature (25 °C) and light condition (12 L:12D). Fragments of mealworms were given three times per week. Egg production and the subsequent development of brood were recorded for three months.

RESULTS

Colony composition

In total, 42 colonies were collected, of which all but one colony had one dealate queen, and the remaining colony was queenless. The number of workers/colony varied from 5 to 452, with an average of $140.5 \pm \text{SD } 94.9$ (N = 41, Fig. 1). In the field, we found an alate sexual individual in only one colony: one male in the colony that was collected in early September. The sexual production season might be July and August. The head width distribution of workers was monomorphic (Fig. 2, Shapiro-Wilk normality test, $W = 0.968$, $P = 0.288$), ranging from 0.92 to 1.24 mm (average $1.06 \pm \text{SD } 0.07$, n = 69). Head width of queens ($1.41 \pm \text{SD } 0.04$, n = 7) was markedly larger than that of the workers. All eight dissected queens were inseminated, and several mature eggs were found with dense yellow bodies. The average number of ovarioles per queen was 32 ($\pm \text{SD } 2.4$, range 28 to 34, n = 8). All but two workers had two ovarioles per worker (1-1) and two workers had three (2-1) ovarioles (n = 110). Several workers had a few developing oocytes (up to seven, Fig. 3).

Fig. 1. Frequency distribution of the number of workers in the *Aphaenogaster rugulosa* colonies.

Fig. 2. Frequency distribution of the head width of the workers and queens in *Aphaenogaster rugulosa*.

Basal oocytes seemed to be trophic eggs.

Prey feeding behavior

The *A. rugulosa* workers took both freshly killed and dried prey insects into the nest chambers, and the feeding behavior was different towards the two types of prey. Not only the workers but also the larvae and queens immediately fed on the fresh prey. Before fragmenting the prey, the larvae were put on the prey and they started eating it (Fig. 4). The queens sometimes fed on the prey together with the larvae. The workers fed on the dried prey, and fragmented small pieces of prey were given to the larvae. The queens also fed on such dried prey, although we observed such behavior only once. In addition, the workers fed on the diluted sugar water. As reported in *A. famelica* and some other species, the *A. rugulosa* workers used a kind of tool to transport

diluted sugar water to the nest chamber (Fig. 5). They dropped pine needles into the diluted sugar water and then transported the food-soaked pine needles to the nest chamber. The nest members then sucked on the pine needles.

Trophic eggs

The workers frequently laid trophic eggs. Typical egg laying behavior is as follows: a worker bent her abdomen underneath the thorax and extruded an egg from the tip of the abdomen. The egg that appeared from the abdominal tip was picked up by the egg layer using her mandibles. The egg layer then took the trophic egg to the larvae or the queen, which fed on the eggs. When the workers give trophic eggs to the larvae, the workers keep the trophic egg between their mandibles, and hold the egg against the larval mouthparts while the larva feeds. In total, the fate of 145

Fig. 3. Frequency distribution of the number of yolky oocytes/worker in *Aphaenogaster rugulosa*.

Fig. 4. Larvae feeding on a freshly dead mealworm.

Fig. 5. Tool use for transporting sugar water. A: Workers start to feed on sugar water and put small trashes and fragments of pine leaves on the droplet. B: After 20 min. Some trashes and pine leaves were already taken back to the nest chamber. The size of the droplet decreased. C: Inside the chamber, workers sucked on the fragment of pine leaves soaked in sugar water.

Table 1. The fate of trophic eggs in three colonies of *A. rugulosa*. The number of trophic eggs eaten by queens, larvae, and unknown members is shown.

Colony code	Queens	Larvae	Unknown	Hours of observation
FI17-93	14	77	29	18
FI15-98	7	5	0	10
FI19-37	3	10	0	10

trophic eggs was observed in three colonies, of which 24 were eaten by queens, and 92 by the larvae, and the remaining 29 were kept by the workers until the end of the observation sessions (Table 1). Thus, the majority of the trophic eggs was given to the larvae.

Feeding behavior of queens

As mentioned above, the queens fed on both trophic

eggs and freshly dead prey. Oral trophallaxis was not observed. Both the frequency and time of eating prey was greater than that of trophic egg eating in three colonies, while in the remaining three colonies, trophic eggs were more frequently eaten (Fig. 6). The queens aggressively picked up trophic eggs from the workers or larvae, and on average spent $329 \pm \text{SD } 120$ sec. ($n = 18$) on eating one trophic egg. Also, the queens often picked up solid prey from the larvae and fed on it.

Male production by the workers under a queenless condition

All six orphan colonies produced one to 17 adult males, and several male pupae at three months after orphaning (Table 2).

Fig. 6. Frequency and duration for feeding on trophic eggs and insect prey by dealate queens in six colonies of *A. rugulosa*. The number of observation hours is shown in parentheses.

Table 2. Male production in orphan colonies. The number of males and each developmental stage found in each orphan colony three months after being orphaned.

Colony code	No. workers survived	Males	Male pupae	Larvae	Eggs
FI15-98-1	24	1	1	18	11
FI15-98-2	44	11	6	12	19
FI17-86-1	45	3	4	35	12
FI17-86-2	44	17	7	19	5
FI17-93-1	33	4	5	10	15
FI17-93-2	42	8	1	28	30

DISCUSSION

All but one *Aphaenogaster* species reported so far, whether temperate or tropical, nest in the soil: nests of tropical species consist of one chamber whereas temperate *Aphaenogaster* make several chambers under the ground (Aupanun et al. 2018). One exception is the Malagasy *A.*

gonacantha that often nests in hollow cavities in dead wood on or near the ground (Csösz et al. 2021). *Aphaenogaster rugulosa* nests are frequently found in rotten woods on the floor of forests. The other species endemic to Yonagunijima, *A. donan*, also nests in dead woods (Ito unpublished). Nests of both species are also found under stones, but excavating deeper soil has been rarely observed. It is unclear what ecological characteristics of ants and/or habitat are associated with such nesting habits, but it is a noteworthy characteristic of *A. rugulosa*.

Kaspari and Vargo (1995) demonstrated Bergman's rule of colony size in ants: colony size of tropical species ($<23.3^\circ$ latitude) is generally smaller than that of temperate species. Aupanun et al. (2018) demonstrated this trend in *Aphaenogaster*, by using the colony size data of 18 species. In their paper, the data on *A. rugulosa* was based on three colonies ($140 \pm \text{SD } 108$ workers, $N = 3$). In this study, we added 38 colonies to the data, and the average colony size ($140.5 \pm \text{SD } 94.9$) is almost the same as in the former report. Aupanun et al. (2018) treated *A. rugulosa* as

a temperate species, because Yonagunijima is located north of 23.3°. Compared with other species studied by Aupanun et al. (2018), the colony size of *A. rugulosa* is smaller than most of temperate species, while it is larger than seven of nine tropical species. Thus, *A. rugulosa* shows an intermediate colony size between tropical and temperate species of *Aphaenogaster*. As in other *Aphaenogaster* species, the colonies of *A. rugulosa* are always monogynous. In ants, polygyny has evolved many times independently: several genera contain both monogynous and polygynous species (Hölldobler and Wilson 1977). In *Aphaenogaster*, Aupanun et al. (2018) showed that all twelve species so far studied are monogynous. This is one of the important characteristics of this genus.

Queen–worker size dimorphism is notable in *A. rugulosa* as in other congeneric species. Size dimorphism is one of the important indices of degree of social evolution: ancestral ants show slight size difference between queens and workers as found in the majority of poneroid ants, whereas marked size dimorphism is found in several formicoid ants (Peeters and Ito 2015). Such size dimorphism is related to behavioral specialization of both queens and workers. Regarding feeding behavior, the queens of ancestral ants can feed on solid prey directly as shown in *Myopias conicaria* (Ito et al. 2020), whereas the queens of derived ants dependent on oral trophallaxis from workers and/or feeding on trophic eggs laid by workers. For example, in two genera of dolichoderine ants, *Dolichoderus* and *Technomyrmex*, the queens feed on trophic eggs only (Torossian 1979, Yamauchi et al. 1991). Queens of the formicine ant, *Anoplolepis gracilipes*, never feed on solid prey; instead, they feed on both trophic eggs and oral trophallaxis (Lee et al. 2017). In this respect, the feeding behavior of *A. rugulosa* queens is novel: they feed on both freshly killed insects and trophic eggs, even though they show marked size dimorphism between castes. This feeding behavior of the queens is similar to a few species of ponerine ants recently observed (Aupanun et al. 2022). The feeding behavior of the larvae also seems to be ancestral: the larvae are put on intact prey. Similar feeding behavior of larvae has been reported in *Aphaenogaster subterranea* (Buschinger 1973). In poneroid ants, larvae feed on prey insects directly, whereas formicoid larvae feed on masticated prey (Ito et al. 2017, 2020). The feeding behavior of *A. rugulosa* larvae is similar to poneroid larvae, but the *A. rugulosa* larvae often feed on trophic eggs.

Trophic egg production in *Aphaenogaster* has been well studied in *A. japonica* by Iwanishi et al. (2003) who observed 9 colonies for 302 hours: of 839 trophic eggs laid by workers, 389 and 107 were given to larvae and queens,

respectively, and the remaining 278 trophic eggs were eaten by workers including egg layers. As in *A. japonica*, the main consumer of trophic eggs is larvae in *A. rugulosa*. Although the morphological characteristics of trophic eggs have not been studied in detail in this paper, the trophic eggs do not seem to be specialized as food because the queens take a relatively long time ($329 \pm \text{SD } 120$ sec.) to eat a single trophic egg. Comparable data was obtained for the ponerine ant, *Odontomachus simillimus*: the queen spent 373 sec. ($\pm \text{SD } 124$, $n = 8$) on eating a trophic egg, whereas formicine and dolichoderine queens feed on a trophic egg in a few seconds (Lee et al. 2017, Aupanun et al. 2022). This finding may mean that trophic eggs in formicine and dolichoderine ants are well specialized food. As in *A. japonica*, the *A. rugulosa* workers quickly changed from trophic egg production to reproductive egg production under an orphan condition. All orphan colonies of *A. rugulosa* produced males, whereas male production was not frequent in *A. japonica* (Iwanishi et al. 2003). It is unknown whether such a difference resulted from species difference in ovarian activity, or differences of culture methods.

“Tool use” as shown in *A. rugulosa* has been reported in at least seven other species of *Aphaenogaster* (Fellers and Fellers 1976, Tanaka and Ono 1978, Banschbach et al. 2006, Maák et al. 2017, Módra et al. 2021). Dropping small fragments of debris and soil into liquid food resources and taking the soaked trash back to the nest are regarded as efficient liquid transportation because *Aphaenogaster* workers have no social stomach unlike some other formicoid ants (Banschbach et al. 2006). Furthermore, Maák et al. (2017) showed that workers of *A. subterranea* and *A. senilis* developed a preference for tools with a good soaking capacity. In summary, the biological information provided here and in other studies shows that the genus *Aphaenogaster* has both advanced and ancestral behavioral traits. Further comparative studies of this and related genera should give an important insight into the evolution of behavioral traits in ants.

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REFERENCE

- Aupanun S, Kulsarin J, Jaitrong W, Ito F. 2018. Colony composition and nesting habits of six species of *Aphaenogaster* in Thailand (Hymenoptera: Formicidae). *Asian Myrmecology* 10: e010003 (1–8). DOI: 10.20362/am.010003.
- Aupanun S, Obika M, Mizuno R, Jaitrong W, Suttiprapan P, Hashim R, Ito F. 2022. Trophic eggs in three ponerine ant species: *Harpegnathos venator*, *Odontoponera denticulata* and *Odontomachus similis*. *Asian Myrmecology* 15: e015001.
- Banschbach VS, Brunelle A, Bartlett KM, Grivetti JY, Yeaman-Irwin R. 2006. Tool use by the forest ant *Aphaenogaster rudis*: Ecology and task allocation. *Insectes Sociaux* 53: 463–471. DOI: 10.1007/s00040-006-0897-2.
- Bednar DM, Shik JZ, Silverman J. 2013. Prey handling performance facilitates competitive dominance of an invasive over native keystone ant. *Behavioral Ecology* 24: 1312–1319. DOI: 10.1093/beheco/art069.
- Bolton B. 2021. *An online catalog of the ants of the world*. <http://antcat.org>. (Accessed October 13, 2021).
- Buschinger A. 1973. Transport und Ansetzen von Larven an Beutestücke bei der Ameise *Aphaenogaster subterranea* (Latr.) (Hym., Formicidae). *Zoologischer Anzeiger* 190: 63–66.
- Caut S, Jowers MJ, Cerdá X, Boulay RR. 2013. Questioning the mutual benefits of myrmecochory: A stable isotope-based experimental approach. *Ecological Entomology* 38: 390–399. DOI: 10.1111/een.12028.
- Crespi BJ. 1992. Cannibalism and trophic eggs in subsocial and eusocial insects. In: Elgar MA, Crespi BJ (eds) *Cannibalism: ecology and evolution among diverse taxa*. Oxford University Press, Oxford. 176–213.
- Csász S, Loss AC, Fisher BL. 2021. Taxonomic revision of the Malagasy *Aphaenogaster swammerdami* group (Hymenoptera: Formicidae). *PeerJ* 9: e10900. DOI: 10.7717/peerj.10900.
- Dittmann MT, Dammhahn M, Kappeler PM. 2014. Investigating behavior and ecology of *Aphaenogaster swammerdami* (Formicidae) in selectively logged forest: 20 years later – a happy ant? *Malagasy Nature* 8: 35–48. DOI: 10.5167/uzh-97024.
- Fellers JH, Fellers GM. 1976. Tool use in a social insect and its implications for competitive interactions. *Science* 192: 70–72. DOI: 10.1126/science.192.4234.70.
- 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. DOI: 10.1046/j.1365-3032.1998.234102.x.
- Higashi S, Hinomizu H, Nakano S, Ohtani T, Toda MJ, Yamamoto M. 1987. Dispersion patterns of ant nests in a cool-temperate woodland of northern Japan. *Research Bulletins of the College Experiment Forests Hokkaido University* 44: 603–610.
- Hölldobler B, Wilson EO. 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64: 8–15.
- 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). DOI: 10.20362/am.009010.
- Ito F, Nguyen DA, Eguchi K, Toyota A, Billen J. 2020. Colony composition, queen behavior, specialized predation on millipedes, and exocrine glands in the ponerine ant *Myopias conicara* Xu, 1998 (Hymenoptera: Formicidae). *Entomological Science* 23:142–151. DOI: 10.1111/ens.12406.
- Iwanishi S, Hasegawa E, Ohkawara K. 2003. Worker oviposition and policing behavior in the myrmicine ant *Aphaenogaster smythiesi japonica* Forel. *Animal Behaviour* 66: 513–519. DOI: 10.1006/anbe.2003.2222.
- Kaspari M, Vargo EL. 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. *The American Naturalist* 145: 611–631. DOI: 10.1086/285758.
- 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. DOI: 10.1186/s12983-017-0210-4.
- Lubertazzi D. 2012. The biology and natural history of *Aphaenogaster rudis*. *Psyche* ID 752815: 1–11. DOI: 10.1155/2012/752815.
- Maák I, Lőrinczi G, Le Quinquis P, Módra G, Bovet D, Call J, d'Ettorre P. 2017. Tool selection during foraging in two species of funnel ants. *Animal Behavior* 123: 297–216. DOI: 10.1016/j.anbehav.2016.11.005.
- Mizutani A, Imamura S. 1980. Population and nest structure in the ant *Aphaenogaster japonica* Forel in Sapporo, Japan. *Kontyu* 48: 241–247.
- Módra G, Elek MI, Lőrincz Á, Lőrinczi G. 2021. Comparison of foraging tool use in two species of myrmicine ants (Hymenoptera: Formicidae). *Insectes Sociaux* DOI: 10.1007/s00040-021-00838-0.
- 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, Ito F. 2015. Wingless and dwarf workers underlie the ecological success of ants (Hymenoptera: Formicidae). *Myrmecological News* 21: 117–130.
- Richards PJ. 2009. *Aphaenogaster* ants as bioturbators: Impacts on soil and slope processes. *Earth-Science Review* 96: 96–106. DOI: 10.1016/j.earscirev.2009.06.004.
- Tanaka T, Ono Y. 1978. The tool use by foragers of *Aphaenogaster famelica*. *Japanese Journal of Ecology* 28: 49–58. (In Japanese with English summary)
- Terayama M, Kubota S, Eguchi K. 2014. *Encyclopedia of Japanese ants*. Asakura-syoten. Tokyo.
- Thomas FJ, Auld TD, Ramp D, Kingsford RT. 2016. A switch in keystone seed-dispersing ant genera between two elevations for a myrmecochorous plant, *Acacia terminalis*. *Plos one* 11: e0157632. DOI: 10.7931/J2F18WNE.
- 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. DOI: 10.1007/BF02223549.
- Tschinkel WR. 2010. Back to basics: sociometry and sociogenesis

- of ant societies (Hymenoptera: Formicidae). *Myrmecological News* 14: 49–54.
- Tschinkel WR. 2011. The nest architecture of three species of north Florida *Aphaenogaster* ants. *Journal of Insect Science* 11: 1–30. DOI: 10.1673/031.011.10501.
- 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. DOI: 10.1007/BF00165955.