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Colony composition, prey preference and behavioral characteristics of *Leptanilla kubotai* (Hymenoptera: Formicidae: Leptanillinae)

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ABSTRACT. Leptanilline ants are cryptic, and our comprehension of their natural history remains incomplete. We collected one colony of *Leptanilla kubotai* in October 2023 and investigated the colony composition and behavioral characteristics of this rare species. The nest of *Leptanilla kubotai* was situated 15 cm deep in the soil and contained one dichthadiiform queen, 453 workers, and 663 larvae. The queen had 88 ovarioles, while the workers had no ovaries. Workers were specialized predators of geophilomorph centipedes, and promptly recruited nestmates upon encounter with a prey. Larvae showed remarkable mobility, associated with unique morphological features: a ventral hooked claw on their prothorax and a row of teeth on the external margin of their mandibles. The queen and workers performed larval hemolymph feeding and likely rely on larvae for nutrition in the absence of prey. We compare these findings to other Leptanillinae and discuss the specialization of *Leptanilla* for a subterranean lifestyle.

Keywords *Leptanilla*, larval hemolymph feeding, natural history, larval mobility

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INTRODUCTION

The ant subfamily Leptanillinae, consisting of the three genera *Leptanilla*, *Opamyrma*, and *Protanilla* (Griebenow 2024), is sister to nearly the whole remainder of the Formicidae (Brady et al. 2006; Kück et al. 2011; Branstetter et al. 2017; Borowiec et al. 2019; Romiguier et al. 2022). Therefore, biological information of Leptanillinae is crucial for understanding the evolution and diversity of ants. However, most species are cryptic, tiny and hypogaeic, hence whole colonies are rarely collected. So far, the natural history of the subfamily is only known from a handful of species including *Leptanilla japonica* (Masuko 1989, 1990), *L. clypeata* (Ito & Yamane 2020), *Opamyrma hungvuong* (Yamada et al. 2023), *Protanilla lini* (Yamamuro 2018) and *P. wallacei* (Ito et al. 2021). These reports and other fragmentary observations indicate that colony structure as well as hunting and feeding behavior vary among the three genera. All species of *Leptanilla* studied so far have dichthadiiform queens, while *Opamyrma* and all but one *Protanilla* have alate queens (Yamada et al. 2023; Man et al. 2017; Hsu et al. 2017; Baroni Urbani & de Andrade

2006). In addition, *Leptanilla* and *Opamyrma* are specialized predators of geophilomorph centipedes, while prey specialization seems to vary among *Protanilla* species (Ito et al. 2021; Yamada et al. 2023; Yamamuro 2018). Adult *Leptanilla* feed on the hemolymph of larvae from their own colony through specialized "taps". Larval hemolymph feeding (LHF) was observed directly in *L. japonica* and *L. clypeata* (Ito & Yamane 2020; Masuko 1989, 1990) and is implied by the presence of taps in the larvae of several other *Leptanilla* spp. (Barandica et al. 1994; Wheeler 1928; Wheeler & Wheeler 1965). In contrast, neither this structure nor LHF has been observed in *Opamyrma* and *Protanilla* (Ito et al. 2021; Yamada et al, 2023; Yamamuro 2018). Direct behavioral observations of Leptanillinae species remain scarce, though desperately needed to describe the biology of this early ant lineage.

Leptanilla kubotai Baroni Urbani, 1977, is the largest species of *Leptanilla* in Japan: body length of workers and queens is 1.6 mm and 2.6 mm, respectively (Baroni Urbani 1997; Terayama & Kinomura 2015). So far, this species has exclusively been collected in Shikoku Island, western Japan, and its biology remains unstudied. We collected one whole colony of *L. kubotai* at Cape Ashizuri-misaki, Tosashimizu-shi, Kochi Prefecture, Japan. This article presents the colony composition, prey preference, and characteristics of the dichthadiiform queen, workers, and larvae.

MATERIALS AND METHODS

Colony collection

The *L. kubotai* colony was collected by the first author on 28 October 2023, in a broad-leaved forest at Cape Ashizuri-misaki, Tosashimizu-shi, Kochi Prefecture, Japan (32.73°N, 133.01°E). The colony and surrounding soil were excavated and brought to the laboratory. On the next day, we carefully extracted workers, queen, and brood from the soil and counted their numbers.

Laboratory rearing

The colony was kept in a 14 cm x 10 cm x 5.5 cm plastic container as the outer frame (hereafter called foraging arena) and an 8.5 cm x 5.5 cm x 1.5 cm plastic container as the brood chamber. The inner walls of the outer frame were coated with Fluon to prevent ants from escaping. The floor of the rearing container was covered with plaster mixed with activated charcoal powder. The nest was kept in an incubator maintained at 26°C from 30 October 2023 to 12 December 2023. Worker specimens are deposited at the Laboratory of Entomology, Faculty of Agriculture, Kagawa University. Specimen pictures and additional data were uploaded to a public repository:10.5281/zenodo.14744518.

To determine prey preference, we first fed the colony a variety of small soil invertebrates as follows: geophilomorph centipedes, lithobiomorph centipedes (~5mm long), Diplura (~5mm long), Entomobryidae (~1mm long), *Porcellio* sp. woodlice (~5mm long), Opisthopora (~5mm long) and larvae of *Carebara yamatonis* (~1mm long). Each invertebrate was given three times, and the behavioral response of foraging workers was recorded. As only geophilomorphs were accepted as prey, the colony was subsequently fed with live geophilomorphs of various sizes.

Behavioral observations

Queen behavior was observed under a stereo microscope (Olympus SZ61, Japan) in 30-minute observation sessions (eighteen during daytime and three during nighttime between November 1 and 21) for a total of 10.5 hours. During each session, we recorded the frequency and time spent performing the following behaviors: resting, walking, LHF, allo-grooming, self-grooming, and defecating. The foraging and feeding behavior of workers were observed using a digital video camera (Nikon Digital Sight 1000, Japan) connected to a stereo microscope (Nikon SMZ1270, Japan). Five observations were performed during the day and one at night between November 1 and 16. After the behavioral observations, the queen and 10 workers were dissected under a binocular microscope to investigate their reproductive status.

Scanning electron microscopy (SEM) of larvae

Five larvae were dehydrated using a graded ethanol series (70%, 80%, 90%, and 100%), then ethanol was replaced with t-butyl alcohol before vacuum freeze drying and sublimation. SEM images of larvae were taken using a JCM-7000 scanning electron microscope (JEOL, Japan) at 15.0 kV.

Fig. 1. Larval pile in the artificial nest of *Leptanilla kubotai*. The pile was approximately 2 cm wide. The queen can be seen standing on it at the top-center of the picture.

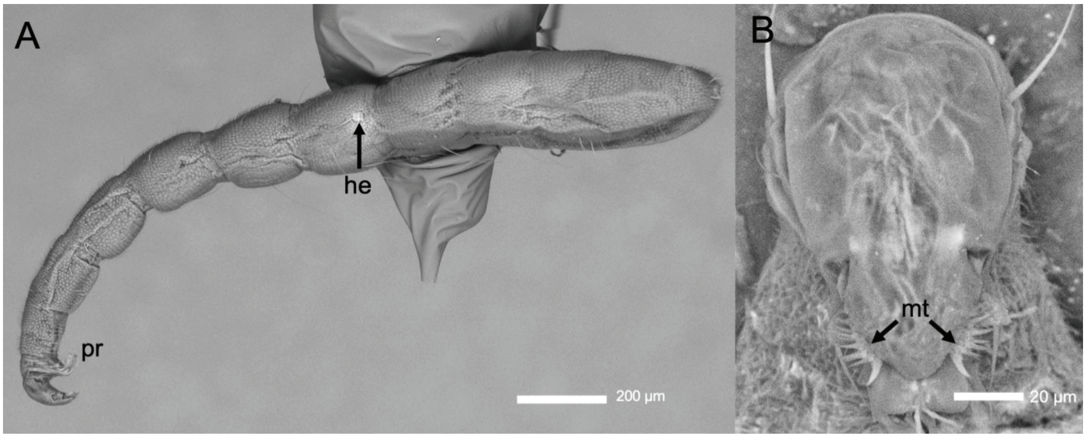

Fig. 2. SEM pictures of a *L. kubotai* larva in lateral view (A) and front view (B). pr = prothorax; he = hemolymph tap; mt = mandible teeth.

Fig. 3. Larval hemolymph feeding (LHF) performed by a worker.

Fig. 4. Picture of the *Leptanilla kubotai* queen resting. The queen's gaster was raised almost vertically.

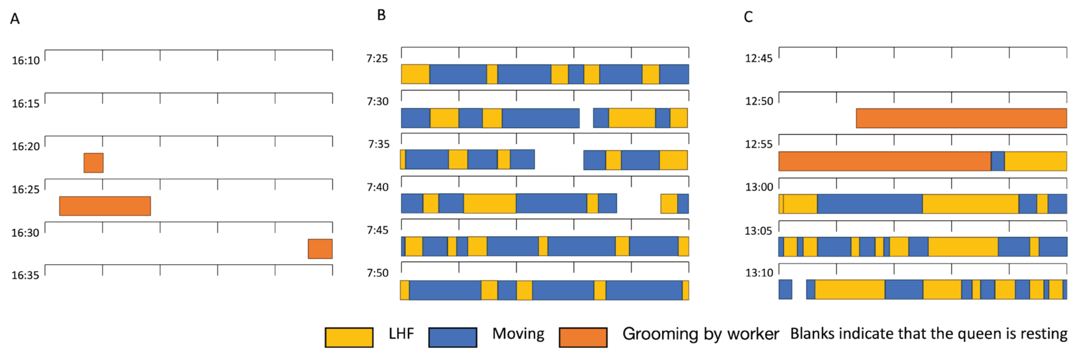

Fig. 5. 30-minute behavioral sequence of the queen of *L. kubotai* on three different days:(A) from 16:10 PM to 16:40 PM on 8 November 2023; (B) from 7:25 AM to 7:55 AM on 1 November 2023. The length of each bar indicates the duration of the behavior.

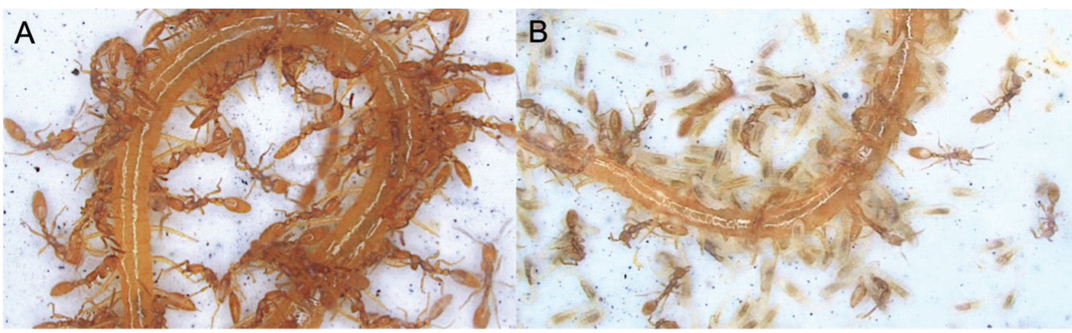

Fig. 6. (A) The geophilomorph brought into the chamber (t = 0h) and (B) the geophilomorph later (t = 1h) show that larvae were brought.

RESULTS

Nest and colony composition

The colony was situated in an irregularly shaped cavity at a depth of about 15 cm within well-compacted, moist soil. In the cavity, there was a large cluster of larvae and workers. We could not locate the queen in that cluster in the field. We examined the soil 30 cm around the nest location and collected a few additional workers. In the laboratory census, a dichthadiiform queen was found, along with 453 workers and 663 larvae. Eggs and pupae were not present.

The dissection of ten workers revealed their lack of ovaries. The queen was dissected on 12 December 2023 (the day of death). She had 88 ovarioles in total, 46 and 42 on each side, and the spermatheca was filled with sperm. Accumulation of corpora lutea was not observed.

Morphology and behavior of larvae, workers and the queen

Larvae

In the absence of prey, the larvae were gathered to form a single flat-topped pile (hereafter referred to as larval pile, Fig. 1). When larvae excreted a transparent droplet from their abdominal tip (defecation), a worker picked it up and carried it to the periphery of the pile, and discarded it on the floor (Video S1).

Electron microscopy of the lateral side of the larval body revealed that *L. kubotai* larvae have a pair of hemolymph feeding taps (Fig. 2A). These taps seemed to be clogged with hemolymph. Other morphological peculiarities of *L. kubotai* larvae are a ventral hooked claw on the prothorax and a row of teeth on the external margin of the mandibles (Fig. 2A and 2B).

Workers

When there was no prey in the foraging arena, workers rested, foraged, and cared for all other members of the colony. Resting workers remained a few millimeters to centimeters away from the larval pile.

Workers cared for other workers, larvae, and the queen as follows. Worker-to-worker allo-grooming was mostly observed at the periphery of the larval pile, where workers were also resting. On the other hand, the queen was never observed to groom workers. When workers groomed larvae, they sometimes concurrently performed LHF from hemolymph taps (Fig. 3; Video S3). When workers carried larvae, they did not use the mandibles but seemed to connect their mouthparts to the hooked claw on the larva's prothorax. Because larvae were always carried underneath the worker's body along its axis, we could not observe directly how worker mouthparts and larval claw interlocked. However, we witnessed workers attempting to connect their mouthparts to the ventral claw of larvae before carrying them. The only care given to the queen by workers was allo-grooming. Trophallaxis was never observed between any members of the colony.

The queen

The queen was usually stationary on the larval pile, with her gaster raised vertically (Fig. 4), pulsating at regular intervals of 12.47 ± 1.30 sec (N = 64) (Video S2). During the present study, she did not become physogastric and lay eggs. During the 30-minute observations, the queen was either resting (Fig. 5A), actively walking around to perform LHF (Fig. 5B), or exhibiting both behaviors (Fig. 5C). The queen performed LHF on multiple larvae for short periods. The average duration of LHF was 29 ± 34 seconds (N = 173). When the queen performed LHF, she pinched the dorsal and ventral surfaces of a larva with her mandibles and searched for the hemolymph feeding taps with her mouthparts. The queen often tightly squeezed the larvae between her mandibles.

Without being disturbed, the queen only got down from the larval pile to defecate or perform LHF. When defecating, she excreted a transparent droplet on the floor near the larval pile (N = 5). In one observation, the queen defecated while being allo-groomed by a worker, which then picked up the queen's feces from her gaster and discarded it at the edge of the brood chamber.

Prey preference test and feeding behavior

In the field, no remnants of prey were found in the nest. In the laboratory, we fed the colony a variety of small soil invertebrates. Workers did not attempt to touch, bite, or sting prey other than geophilomorph centipedes. When a geophilomorph was given, foraging workers promptly stung it. Workers came from the brood chamber in a line and also joined the hunt. For instance, on 16 November 2023, a centipede was placed in the foraging arena, where about 50 workers were foraging . The number of workers in the arena was 55 after 10 seconds, 70 after 20 seconds and 80 after 30 seconds. Workers closest to the prey started attacking, then the nearest workers - both outside and inside the brood chamber - were recruited. The first attacking workers performed antennation behavior towards the workers around, which then headed to the prey. The prey was paralyzed and transported into the brood chamber. The time before complete paralysis ranged from 25 to 65 seconds (n = 6), and the number of workers transporting prey ranged from 100 to 365 (n = 3). This variation is probably linked to the size of the prey. For instance, in the case of a ~3.5 cm long geophilomorph, 25 workers stung it until complete paralysis (it took 35 seconds from stinging by the first worker). The paralyzed centipede was carried into the brood chamber by 5 to 10 workers. Once a centipede was brought in the brood chamber, the number of workers present in the foraging arena dropped from ~50 to ~20. In the brood chamber, most workers were either eating, carrying larvae close to the prey, or caring for the larvae. Many workers also gathered around the captured centipede and chewed small wounds on its lateral intersegmental membrane (Fig. 6A). Workers first licked these wounds with their lower mouthparts and then brought larvae close to the centipede. After an hour, more than 200 larvae had been gathered near the prey (Fig. 6B), where they were observed crawling and wiggling. When the larvae found a hole in the centipede cuticle, they inserted their head into it and started feeding (Video S4). Workers and larvae exclusively fed on the soft tissues and left the hollow shriveled exoskeleton of the centipede. The larvae showed remarkable mobility, moving over 5 mm to eat prey by themselves. This mobility was only seen near a prey, otherwise larvae mostly remained immobile in the larval pile.

DISCUSSION

Nest and colony composition

The present *L. kubotai* colony was collected 15 cm deep in the soil. Terayama and Kinomura (2015) reported another *L. kubotai* colony collected from 30 cm underground beneath a large stone. Similarly, *L. japonica* was found 10 to 15 cm under the soil surface (Masuko 1990), while *L. clypeata* was found under a stone (Ito & Yamane 2020). In contrast, *L. ujjalai* and *L. belantan* colonies were collected from rotten logs (Saroj et al. 2022; Griebenow 2024).

Our colony of *L. kubotai* included 453 workers. This is a much higher number than the 92 workers collected by Terayama & Kinomura (2015) for the same species, suggesting a more mature colony. On the other hand, the estimated number of workers is 100 to 200 for *L. japonica* (Masuko 1990) and 100 for *L. clypeata* (Ito & Yamane 2020). The large colony size of *L. kubotai* may be related to the queen fecundity. Indeed, our *L. kubotai* queen had 88 ovarioles, whereas *L. japonica* had 31-32 (Masuko 1990). Since more ovarioles can produce more eggs (Gobin & Ito 2000; Peeters & Ito 2001, 2015), colony size and ovariole number are likely to be correlated. The number of ovarioles of other *Leptanilla* species remains to be investigated.

Dissection of the queen ovaries also revealed an absence of corpora lutea. Since the amount of corpora lutea is associated with egg-laying history, this observation suggests that the colony was found shortly after queen replacement. The colony was collected in late October and no larvae pupated even in laboratory conditions (i.e., until in mid December, when observations were concluded). Therefore, *L. kubotai* larvae could overwinter in the field, similarly to reported for *L. japonica* (Masuko 1990).

The colony contained more larvae than workers. While a high number of larvae intuitively reflects colony growth, we believe that they also constitute a food reserve for the winter. Masuko (1990) wrote that LHF in *L. japonica* was likely an adaptation to counterbalance exclusive specialization on geophilomorph prey, which may cause occasional food shortages. *Leptanilla kubotai* showed the same diet specialization and hence may face similar starvation periods, particularly in the winter when geophilomorphs take shelter deep in the ground (Bortolin et al. 2018). Contrary to other ant workers that can use trophallaxis and trophic eggs to share nutrients, *L. kubotai* can only vampirize their own brood for nutrition. A high number of larvae - more than that of workers - means a large nutrient supply and a low destructive impact of LHF.

Larval adaptations to a specialist lifestyle

The *L. kubotai* queen exclusively fed on larval hemolymph via hemolymph taps, a behavior similar to that observed in other *Leptanilla* species (Masuko 1990). LHF from specialized hemolymph taps is only known in this genus, with the exception of *Proceratium itoi* (Masuko 1989, 1990, 2019; Ito & Yamane 2020). Structures similar to hemolymph taps have been identified in *L. charonea*, *L. escheri*, *L. revelierii*, *L. swani* and *L. zaballosi* but not in *L. judaica* (Barandica et al. 1994; Kugler 1986; Wheeler & Wheeler 1965).

In the laboratory, only geophilomorph centipedes were hunted and consumed by *L. kubotai*. The same oligophagy was reported in *L. japonica* (Masuko 1990), and *L. taiwanensis* larvae were observed feeding on a geophilomorphs in the field (Ogata et al. 1995). Feeding behavior of *L. kubotai* larvae observed in the present study was somewhat different from that reported in *L. japonica* (Masuko 1990). In *L. kubotai*, the workers first bit the integument of the centipede to make wounds and eat, then larvae were brought and used these same wounds to feed. In contrast, *L. japonica* workers immediately brought larvae to make these wounds by themselves (Masuko 1990). Morphological similarities between the larvae of both species suggest that *L. kubotai* larvae could probably make wounds on their own, but they always used those made by workers. While workers of *L. kubotai* may cut through their prey more easily than *L. japonica* in virtue of their larger body size (Baroni Urbani 1997; Richter et al. 2020), this difference in feeding behavior is intriguing.

Leptanilla kubotai larvae moved on their own to find surface openings of the centipede body. Their mobility may be increased by the ventral hooked claw on their prothorax (Fig. 2A). This morphological structure was described in *L. japonica* by Masuko (1990) who discussed its role in facilitating transportation of larvae by workers in *L. japonica*, which seems to also be the case for *L. kubotai*. We suggest that the prothoracic claw can also be used as a grappling hook to grab onto hairs or rough cuticular surface of geophilomorphs. In addition, larvae of *L. kubotai* had a row of teeth on the external margins of the mandibles, as in *L. japonica* (Fig. 2B). The function of these distinctive mandibles may not only be puncturing the centipede body (Masuko 1990) but also helping the larval head to fully penetrate into it. Overall, larvae of *L. kubotai* and *L. japonica* display morphological structures for activeness - as opposed to larval passiveness (Matte & LeBoeuf 2024) - that have not been described in *Protanilla* and *Opamyrma*, the two other genera from the same subfamily Leptanillinae, despite similar food processing habits. Larval morphology and behavior remain to be investigated more thoroughly in this subfamily.

Specialization in Leptanillinae

Comparing the life-history of *Leptanilla* with the two other leptanilline genera reveals interesting differences. On one hand, *Protanilla* nest in the soil or fallen dead branches and may have a diverse diet, at least in captivity (Billen et al. 2013; Hsu et al. 2017; Ito et al. 2021; Katayama & Tsuji 2011; Yamamuro 2018). On the other hand, all colonies of *Opamyrma hungvuong* were collected underground near tree roots and are predators of geophilomorph centipedes and Scolopendromorpha (Yamada et al. 2023). Finally, *Leptanilla* species commonly nest in the ground, have a pale flattened body without compound eyes, and all are specialist predators of geophilomorphs (Ito & Yamane 2020; Masuko 1990; Saroj et al. 2022). There seems to be a different degree of specialization of diet and foraging stratum among the three genera. While *Protanilla* and *Opamyrma* may still occasionally forage and nest above ground, *Leptanilla* seems more deeply committed to a subterranean lifestyle.

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