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BEHAVIORAL NOTES AND REDESCRIPTION OF THE SOCIALLY PARASITIC ANT *MYRMICA LUTEOLA* (HYMENOPTERA: FORMICIDAE)

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Abstract.—We detail behavior for the queen of the socially parasitic ant *Myrmica luteola* Kupyanskaya, and describe the worker, queen, and male. In the laboratory, a *M. luteola* queen actively invaded a nest of *Manica yessensis* and consistently rubbed against *M. yessensis* workers. Further, morphological characteristics that often occur in socially parasitic ants, i.e., short tibial spurs and ventral lobes on the petiole and post-petiole, occur in the queen and workers of *M. luteola*. The queen is also characterized by a small size (smaller than the worker) and greatly reduced propodeal spines. The observed behavior and morphology strongly suggest that *Myrmica luteola* is a temporary social parasite.

Key words: *Myrmica luteola*, *Manica yessensis*, Formicidae, Hymenoptera, social parasite, Japan.

The ant genus *Myrmica* Latreille (Myrmicinae) consists of approximately 130 species that are distributed mostly in the Palearctic and Nearctic Regions (Radchenko, pers. comm.). Bolton (1988) reexamined three related genera of social parasite ants, *Paramyrmica* Cole, *Sommimyrma* Menozzi and *Sifolinia* Emery, and considered all three genera to be junior synonyms of *Myrmica*. Consequently, *Myrmica* now contains 15 species of social parasites; most of these species are workerless (Bolton, 1988). Thus far, all of these social parasites are only known to inhabit nests of congeneric species.

Kupyanskaya (1990) described *Myrmica luteola* from the Primirski Region of eastern Russia. This ant was recently confirmed to be conspecific with the ant from Japan known as *Myrmica* sp. 5 (see Onoyama and Sonobe, 1992) (Terayama and Onoyama, unpubl.). However, detailed descriptions of the queen and male are lacking (but see Radchenko, 1995), and little is known about the biology of this species. During an ecological study of *Manica yessensis* on Mt. Fuji, Japan, the senior author (KM) found a dealated queen of *Myrmica*, which appeared to be living in a nest of *M. yessensis*. The junior author (MT) later identified this queen as *M. luteola*. The genus *Manica* Jurine, which is closely related to *Myrmica*, contains two Old World species and four New World species (Bolton, 1995). One of these species, *M. parasitica*, is thought to be a parasite of *M. bradleyi* (Creighton, 1934; Wheeler and Wheeler, 1968, 1970). Therefore, our collection appears to be the first record of a mixed colony between *Myrmica* and *Manica*. Moreover, laboratory observations of queen behavior and morphological characteristics (see below) indicate that *M. luteola*

is a social parasite. This paper notes behavior of the queen and provides descriptions of the worker, queen and male.

MATERIALS AND METHODS

Behavioral observations. We excavated a nest of *Manica yessensis* on 8 September 1990, and collected 1,375 workers, 98 alate queens, 217 males, 27 worker pupae, 676 larvae, 3 eggs, and one *M. luteola* queen. Failure to collect the *M. yessensis* queen and reappearance of many nest openings during the following year indicated that we collected only part of the colony. All ants were transferred to a laboratory nest, at which time the queen of *M. luteola* was spotted among the *M. yessensis* workers. At that time, we removed the *M. luteola* queen and placed her in an artificial nest that was maintained at room temperature. The queen remained alone and unfed over a period of about one month in order to determine if she could rear workers in the absence of host workers. The queen did not lay any eggs during this period, so on 7 October, we reintroduced the queen into a nest containing part of the original host colony (40 workers, 16 larvae and 1 worker prepupa). This nest consisted of a 9 cm plastic petri dish with a moist plaster floor and a small exit hole, and was maintained at room temperature. This dish was placed in a container (27 × 20 × 4.5 cm) that served as a foraging arena. Behavior of the ants was observed visually and with a swing arm stereomicroscope, and recorded on a tape recorder.

Morphological data. We examined 54 individuals of *Myrmica luteola* (including paratypes). They were: Russia: 5 workers (paratypes), Primirski Region, Kedrovaya Pad', 18.ix.1973, A. N. Kupyanskaya leg. Japan: 3 queens, 3 males, 7 workers, Takane-machi, Tochigi Pref., 30.vii.1998, K. Kinomura leg.; 5 workers, Kamioka-machi, Gifu Pref., 4.x.1984, K. Yamauchi leg.; 30 workers, Mt. Fuji (1,700 m alt.), Shizuoka Pref., 18.v.-2.vi.1972, R. and F. Ishikawa leg.; 1 queen, Gotenba, Mt. Fuji (1,650 m alt.), Shizuoka Pref., 8.ix.1990, K. Masuko leg.

Myrmica mirabile is considered to be the sister species of *M. luteola*. Consequently, we also examined 3 workers of *M. mirabile* from the same nest as the holotype (Alishan, Taiwan, 21.x.1977, K. Yamauchi leg.).

The abbreviations used in this paper are:

HL, head length: maximum full face view length from the anteriormost margin of the clypeus to the occipital margin of the head.

HW, head width: maximum width of head above the dorsal extremities of compound eyes in full face view.

SL, scape length: chord length of scape excluding radicle.

FW, minimum frons width: minimum width of frons between frontal lobes.

FLW, maximum frons width: maximum width between external margins of frontal lobes.

AW, width of alitrunk: maximum width of promesonotum in dorsal view.

PH, petiole height: maximum height of petiole in lateral view, measured perpendicularly from apex of petiolar node to venter of petiole.

PW, petiole width: maximum width of petiolar node in dorsal view.

PPL, post-petiole length: maximum length of post-petiole in lateral view, measured from ventral juncture with petiole to juncture with gaster.

PPH, post-petiole height: maximum height of post-petiole in lateral view, measured

perpendicularly from apex of post-petiolar node to venter of post-petiole vertical to the longitudinal axis of petiole.

PPW, post-petiole width: maximum width of post-petiole in dorsal view.

CI, cephalic index: HW/HL × 100.

SI, scape index: SL/HW × 100.

FI, frontal index: FW/HW.

FLI, frontal lobe index: FLW/FW.

Measurements were made with a stereomicroscope at a magnification of 40× to 80×.

RESULTS

Behavioral observations. The following account summarizes the behavioral interactions between the *M. luteola* queen and *M. yessensis* workers in our laboratory colony. These observations occurred over 3 days, after which time the *M. luteola* queen died.

1. Body rubbing by the Myrmica luteola queen. We released the *M. luteola* queen into the foraging arena, where about 15 *M. yessensis* workers were foraging. Shortly after her release, the *M. luteola* queen picked up a piece of exuviae of beetle larvae, *Tribolium confusus*, which had been provided as food to the colony. Although this ecdysial skin was apparently inedible, she kept it in her mandibles for more than 30 min while walking at a rapid gait. The queen stopped all movement when she encountered a *M. yessensis* worker, whereas the worker only showed a brief antennal examination of her. After an approximately 1 hr pause in our observations, the queen was again in the foraging arena, but this time she was holding a *M. yessensis* worker by the waist (the petiole and post-petiole area) with her mandibles (Fig. 1A). The beetle exuviae had already been left in a corner of the arena. The queen hung over the worker, pointing towards the gaster of the worker, using her forelegs to alternately rub the body of the worker and her own middle- and hind legs.

We learned how this interaction was initiated by isolating the queen under a small vial cap for several minutes. We then removed the vial cap, and the queen moved into the brood chamber. She then quickly grabbed the petiolar area of the first worker that she encountered. In this posture, only the right middle- and hind legs of the queen were on the floor; the seized worker only moved its antennae. At the same time, the queen bent her gaster under the mesosoma of the worker so that she was curled around her captive. The left middle leg of the queen was curled around the juncture between the head and mesosoma of the worker. In this immobile stance, she repeatedly touched the body of the worker with her forelegs, followed by patting various parts of her own body. The worker attempted to escape, but the firm grip of the queen merely resulted in their slow rotation around the same spot. The queen released the worker after approximately 15 min, then walked around the brood chamber and seized the mesosoma of another worker. She then moved forward on the body of the worker to grip the area between the head and mesosoma (Fig. 1B). In this case, the queen held the worker, and continued her rubbing behavior for 27 min, after which time the worker was released.

We observed 12 such aggressive interactions between the *M. luteola* queen and *M. yessensis* workers. The queen gripped the petiolar area of the *M. yessensis* worker

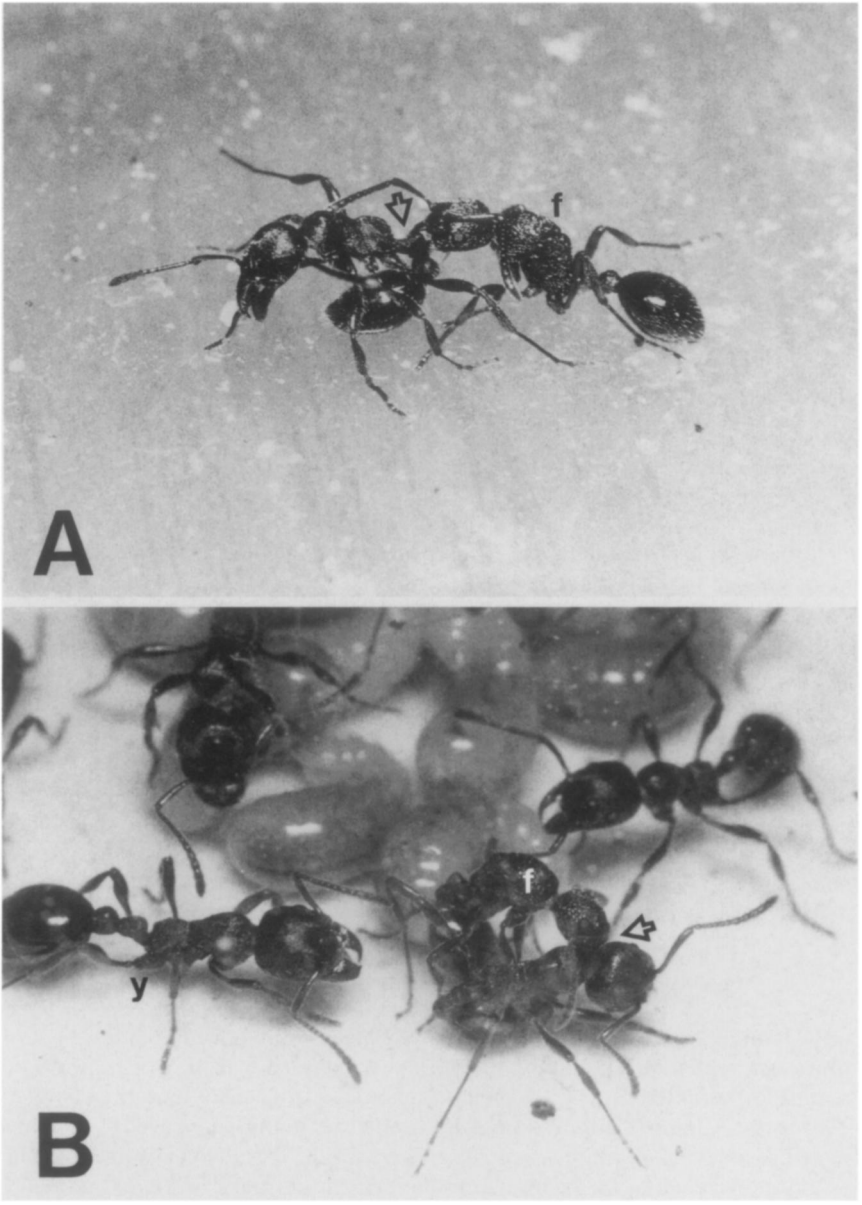


Fig. 1. A: The parasitic *Myrmica luteola* queen (f) gripping a *Manica yessensis* worker by its petiole (arrow) with her mandibles. B: *M. luteola* queen (f) holding the neck of *M. yessensis* worker with the mandibles (arrow) in the brood chamber of the host. A large *M. yessensis* worker in left (y) later removed this queen from the chamber.

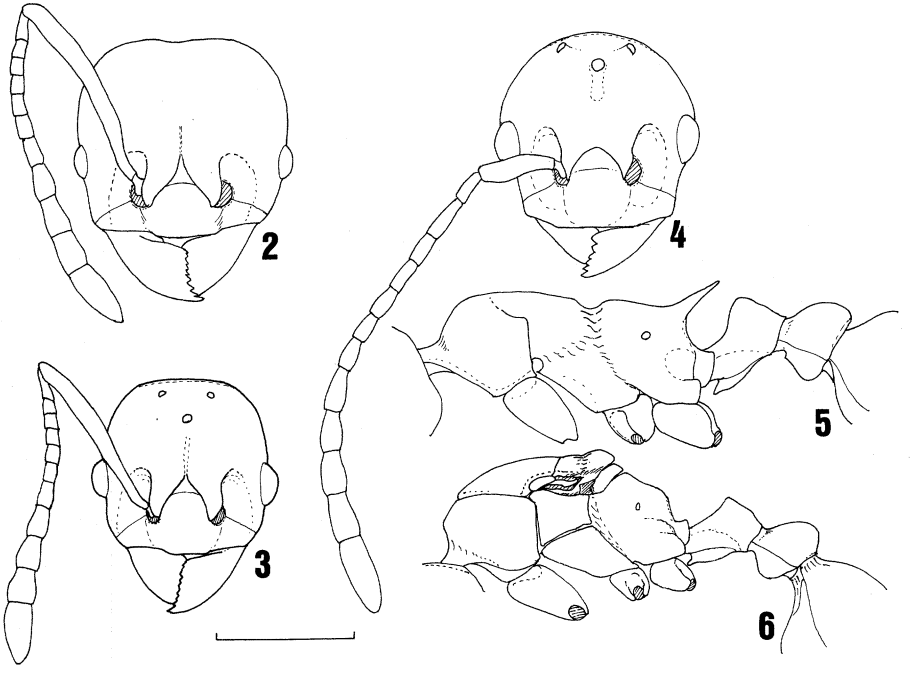
in 5 cases, the mesosoma in 2 cases (in one case the grip shifted to the juncture between the head and mesosoma, as mentioned above), the juncture between the head and mesosoma in 4 cases, and by the leg (femur) in 1 case. We recorded the approach direction for 9 of these interactions. The queen approached the *M. yessensis* workers from the front in 3 cases and from the back in 6 cases.

2. *Response of Manica yessensis workers.* To our surprise, with the exception of one individual (see below), few *M. yessensis* workers showed evident hostility to the *M. luteola* queen. For instance, even when workers gripped by the queen sometimes stridulated their gaster and directed its tip toward the queen, probably in an attempt to sting her, nearby workers only showed antennal examination or even groomed the queen. This allospecific grooming was not observed until about 5 min after the queen's intrusion, and 1 hr later, she finally received a full set of allogrooming which included cleaning of her fully opened mouthparts. The queen also groomed *M. yessensis* workers. In most cases, this grooming was quickly followed by the queen seizing the groomed worker. Thus, this behavior seems to be a maneuver of the *M. luteola* queen to obtain a captive.

The first obvious hostility toward the queen was observed 2 hr after she entered the chamber. The hostile behavior was consistently shown by one worker, who was among the largest of the workers in the colony (Fig. 1B, y). This individual seized the left antenna of the queen with her mandibles and tried to drag her out of the chamber. The queen resisted this removal and, while being dragged, she gripped another small worker by the petiole and did rubbing behavior. Finally, the queen was pulled out and released in a corner of the foraging arena. She then quickly ran back into the chamber (the worker remained in the arena) and seized another worker at the juncture between the head and mesosoma. The hostile worker then followed her into the chamber, and again caught and dragged her toward the entrance. Observations were then stopped until the next day, when the queen was found alone in the foraging arena with her left antenna heavily damaged. Later in the day, a large worker (possibly the same worker that removed the queen on the previous day) was gripping the leg of the queen and dragging her around the nest. On the next day the queen was found dead in the arena.

DESCRIPTION OF MORPHOLOGY.

Diagnosis of worker (Figs. 2, 5). Total body length 5.5–6.5 mm. Body brownish yellow, legs lighter. Head slightly (1.02–1.08 times) longer than wide, with slightly convex sides and almost straight occipital margin in full face view. Mandible with 9 or 10 teeth. Anterior margin of clypeus straight or slightly concave in the middle. Antennal scape 0.93–0.98 times as long as head width, strongly curved near the base and a little thickened at the bend, but not angled and no trace of a lobe; pedicel 2.8 times as long as wide; 1st to 6th funicular segments each slightly longer than wide; apical 4 segments forming a club. Frons wide (FI = 0.39–0.42); frontal area with dense longitudinal rugae. Eye oval, 0.20–0.27 mm in length. Promesonotum reticulate. Propodeal spines moderately long and straight. Petiole with short anterior peduncle; anterior margin slightly concave, posterior margin straight in profile; lobe-like subpetiolar process present. Post-petiole subcubical, with convex dorsal margin;



Figs. 2–6. *Myrmica luteola* Kupyanskaya, worker, queen and male. 2, Head in full face view, worker. 3, ditto, queen. 4, ditto, male. 5, alitrunk, petiole and post-petiole in profile, worker. 6, ditto, queen. Scale bar: 1 mm.

ventral lobe developed. Gaster smooth and shiny. Legs with recumbent hairs. Tibial spurs of middle- and hind legs short with reduced pectination.

Diagnosis of queen (Figs. 3, 6). Total body length 5.3–6.0 mm. Body brownish yellow, legs lighter. Head slightly (1.02–1.08 times) longer than wide, with slightly convex sides and straight or slightly convex occipital margin in full face view. Mandible with 8 or 9 teeth. Anterior margin of clypeus straight or slightly concave in the middle. Antennal scape 0.92–0.98 times as long as head width, strongly curved at base but not angled, and no trace of a lobe; pedicel 2.8 times as long as wide; 1st to 6th funicular segments each slightly longer than wide; apical 4 segments forming a club. Frons relatively wide (FI = 0.42–0.45); frontal area with dense longitudinal rugae. Compound eye convex, oval, 0.24–0.25 mm in length. Ocelli relatively small, forming an obtuse triangle. Alitrunk 1.80–1.97 times as long as high, with convex dorsal margin in profile; mesonotum longitudinally rugose and 0.73–0.79 times as wide as head width; posterolateral corner of propodeum dully angulate or round without spine. Petiole with short anterior peduncle; anterior margin slightly concave, posterior margin straight in profile; lobe-like subpetiolar process present and developed. Post-petiole with developed ventral lobe. Gaster smooth. Tibial spurs of middle- and hind legs short, with reduced pectination. Forewing 5.0–5.2 mm in length; Rs vein not reaching Rs + M; cross vein 2r interstitial with r-m.

Table 1. Measurements of *Myrmica luteola* presented as average (range). All values are in mm. See text for abbreviations.

	Paratype workers (n = 5)	Workers (n = 10)	Queens (n = 3)	Males (n = 3)
HL	1.38 (1.31–1.41)	1.39 (1.26–1.50)	1.30 (1.25–1.35)	0.98 (0.98–0.99)
HW	1.33 (1.25–1.41)	1.32 (1.18–1.45)	1.24 (1.20–1.32)	0.96 (0.95–0.98)
SL	1.19 (1.13–1.21)	1.18 (1.09–1.29)	1.08 (1.06–1.10)	0.48 (0.46–0.50)
FW	0.54 (0.53–0.55)	0.54 (0.48–0.60)	0.51 (0.50–0.53)	0.25 (0.25–0.26)
FLW	0.61 (0.58–0.64)	0.60 (0.55–0.66)	0.58 (0.55–0.60)	0.41 (0.40–0.42)
AW	0.89 (0.87–0.93)	0.90 (0.86–0.94)	0.94 (0.93–0.98)	1.20 (1.18–1.23)
PH	0.47 (0.45–0.50)	0.48 (0.45–0.53)	0.56 (0.55–0.58)	0.51 (0.50–0.53)
PW	0.32 (0.31–0.35)	0.32 (0.30–0.36)	0.34 (0.33–0.36)	0.37 (0.34–0.40)
PPL	0.45 (0.43–0.46)	0.43 (0.40–0.46)	0.45 (0.44–0.45)	0.44 (0.43–0.45)
PPH	0.50 (0.49–0.52)	0.50 (0.47–0.54)	0.55 (0.53–0.56)	0.57 (0.57–0.58)
PPW	0.46 (0.45–0.48)	0.45 (0.41–0.48)	0.50 (0.48–0.51)	0.50 (0.49–0.52)
CI	96 (93–98)	95 (93–97)	95 (92–98)	98 (97–100)
SI	89 (85–91)	89 (85–92)	87 (83–90)	50 (48–53)
FI	0.40 (0.39–0.42)	0.41 (0.40–0.42)	0.44 (0.42–0.45)	0.26 (0.26–0.27)
FLI	1.14 (1.10–1.19)	1.11 (1.09–1.16)	1.09 (1.04–1.14)	1.59 (1.56–1.62)

Diagnosis of male (Fig. 4). Total body length 5.7–6.0 mm. Head and alitrunk black; gaster blackish brown; legs dark brown; mandible brown; antenna black or dark brown. Head length approximately (1.00–1.02 times) same as head width. Occipital margin convex in full face view; posterolateral corner round, not forming an angle. Mandible with 5 or 6 teeth. Antennal scape short, not reaching posterior margin of head, and its length 0.48–0.53 times head width; pedicel twice as long as wide; funicles slender, i.e., 1st funicular segment 2.7 times as long as wide and 2nd and 3rd segments 2.0 times as long as wide, respectively; apical 5 segments forming a club. Frons with longitudinal rugae. Mesonotum reticulate in most part; posterolateral corner of propodeum round or weakly angulate. Petiole reticulate, longer than high in profile. Post-petiole very weakly microreticulate, with convex ventral margin. Gaster smooth. Hind femur and tibia with recumbent straight hairs. Forewing 5.9–6.2 mm in length; Rs vein not reaching Rs + M; cross vein 2r interstitial with r-m.

Measurements. Measurements are given in Table 1.

Geographical variation. The ventral margin of the subpetiolar process is nearly straight in the paratype workers. In the Japanese specimens, this feature is convex and its anteroventral angle is well developed.

Destination of material. Five paratypes were deposited in the collection of the Department of Earth and Environmental Sciences, Faculty of Science, Kagoshima University, Kagoshima, 30 workers from the Mt. Fuji in the collection of the National Science Museum, Tokyo, and the others were deposited in the collection of the junior author.

Distribution. Far East Russia (Primirski and Sakhalin), Kurilen Islands (Kunasiri) and Japan (Hokkaido and Honshu).

Remarks. *Myrmica luteola* possesses some morphological characteristics that are common in social parasites, i.e., short tibial spurs and ventral lobes on the petiole

and post-petiole in both the worker and queen. In addition, the propodeal spines are developed only in the worker, and the queen is smaller than the worker (Table 1). In the male, the antennal scapes are short, and the 1st to 3rd funicular segments are more than twice as long as wide. All of these characteristics separate *M. luteola* from East Asian congeners. The most closely related species, *M. mirabile*, occurs in montane regions of Taiwan (Elmes and Radchenko, 1998). However, *M. mirabile* is not a social parasite.

Nests of *M. luteola* are usually found under stones or around tree roots in rocky sites or partially forested areas. Nuptial flights occur from July to September in Primirski (Kupyanskaya, 1990) and from September to mid-October in Japan (Onoyama and Sonobe, 1992).

DISCUSSION

It is obvious from our laboratory observations that *Myrmica luteola* is a social parasite. By rubbing against *M. yessensis* workers, the *M. luteola* queen could transfer the odor of the host colony to her own body. In this relation, it is to be noted that the queen picked up exuviae of a beetle larva prior to entering the *M. yessensis* nest. This behavior may be significant as chemical deception against host workers in the initial stage of invasion. Rubbing alternately between the body of the host and the body of the inquiline also occurs in myrmecophilous beetles (Dettner and Liepert, 1994). Such behavior was described in detail for the beetle *Diploeciton nevermanni*, which lives in army ant nests (genus *Neivamyrmex*) (Akre and Torgerson, 1968), and also licks the body of the army ant workers. In the workerless inquiline ant *Leptothorax kutteri*, Franks et al. (1990) reported that the queens actively "groom" the queen and workers of the host ant *L. acervorum*, supposing that this activity is crucial for the parasite to obtain the host odor (but the behavioral details of the grooming, e.g., whether the parasite rubs against the body of the host were not detailed in the paper). The parasitoid wasp *Paralipsis eikoae* also displays a similar rubbing behavior (Takada and Hashimoto, 1985). The adults of this parasitoid need to acquire the odor of the ants in the genus *Lasius* before they can reach the root aphids (their host species) that are maintained inside the nest of the ants. Gas chromatography-mass spectrometry analysis demonstrated that this chemical deception results from the transfer of odor via rubbing rather than by the wasp synthesizing the odor substances (Akino and Yamaoka, 1998).

A lack of observations in the present study did not permit us to learn how *M. luteola* queens obtain nutrition from the host colony. However, our observations indicated that the queen showed a special interest in the host larvae and attached her mouthparts to their head, suggesting some involvement of the host larvae in her nutrition.

Bolton (1988) published a taxonomic revision of all known parasitic *Myrmica* species. These ants often show the parasitic syndrome, i.e., the modifications in the petiole and post-petiole and the reduction of the middle and hind tibial spurs. However, these characteristics are not limited to the parasitic species (Bolton, 1988). Even non-parasitic *Myrmica* show a series of reductions in size of the spur from large and pectinate to absent, although still the well developed pectinate spurs are most common among them. Both the worker and queen of *M. luteola* display reduced middle

and hind tibial spurs. However, it remains unclear how these morphological characteristics relate to the parasitic lifestyle. Apart from this, the queen of *M. luteola* might mimic a worker of *M. yessensis*. We assume this because the propodeal spines are lacking in both queen and worker of *M. yessensis* but the body size of *M. luteola* queen is quite similar to that of *M. yessensis* worker.

In social insects, it is a general rule that socially parasitic species are closely related to their hosts. It is known as Emery's Rule for ants (Hölldobler and Wilson, 1990; but see Ward, 1996 for an argument against this rule). All previous host records for parasitic *Myrmica* are congeners (Bolton, 1988). Also for *M. luteola*, a single individual of its dealated female was recovered from a nest of *Myrmica jessensis* on Mt. Fuji (Sakai, pers. comm.). Based on this collection, Onoyama and Sonobe (1992) supposed *M. luteola* (*Myrmica* sp. 5 in their paper) to be a temporary social parasite of *M. jessensis*. On the other hand, *Manica* has been considered to be the genus most closely related to *Myrmica*. The present discovery of *M. luteola* queen, which was most likely parasitizing a *Manica yessensis* nest, further indicates a close phylogenetic relationship between *Myrmica* and *Manica*. However, lack of observations makes it difficult to assess the degree of host specificity by queens of *M. luteola*. Additional field and laboratory observations are needed to detail the biology of *M. luteola*, which could in turn give some important clues for taxonomic reconsideration of these genera, more practically, considering *Manica* as a synonym of *Myrmica*.

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