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Original Article

# Temporary social parasitism in the ant *Strumigenys mutica*: colony composition and behavioral interactions with host species *Strumigenys solifontis* and *Strumigenys lewisi*

Riou Mizuno, Kunio Sadahiro, Ryota Hosokawa, Shogo Makita, Hiroki Matsumura,
Chung-Chi Lin & Fuminori Ito

**Abstract**

Temporary social parasitism is the most common type among four types of social parasitism and is known from more than 200 ant species. Queens of temporary social parasites invade a host ant colony, kill the host queen, and use the host workers as a workforce during the colony founding stage. In our study, we collected seven mixed colonies consisting of a *Strumigenys mutica* queen and its host species: Two included a queen of *S. mutica* and host workers, five included queens and workers of *S. mutica* and host workers. In contrast, we also found 14 mature pure *S. mutica* colonies which included a *S. mutica* queen and *S. mutica* workers. The pure colonies were extremely large (max. approx. 5000 workers per colony) compared with other species of this genus. Additionally, *S. mutica* queens had more ovarioles (10 - 17 in total) than those of other *Strumigenys* species. Associated with this, the abdomen of *S. mutica* queens were physogastric with developing ovaries. Behavioral observation of two mixed colonies revealed that *S. mutica* was highly integrated with their host ants. The foragers of captive *S. mutica* colonies hunted diverse soil arthropods but struggled to catch springtails, unlike congeneric species. The fact that workers collect food and care for brood is in line with temporary social parasitism but not with other types of social parasitism. Therefore, we confirmed that the rare species *S. mutica* is a temporary social parasite of other *Strumigenys* species such as *S. lewisi* and *S. solifontis*. Overall, we conclude that *S. mutica* is a temporary social parasite, showing a novel life history compared with other *Strumigenys* ants. Our study sheds light on how social parasitism can change the life history of an ant.

**Key words:** *Pyramica*, *Kydris*, host record, colony composition, physogastrism, foraging, life history, Hymenoptera, Formicidae.

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*Riou Mizuno (contact author), Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology Graduate University, Onna, Okinawa 904-0495, Japan; Faculty of Agriculture, Kagawa University, Ikenobe, Miki, Kagawa 761-0795, Japan. ORCID number: 0000-0002-7196-0194. E-mail: m.riou112@gmail.com*

*Kunio Sadahiro, Ryota Hosokawa, Shogo Makita, Hiroki Matsumura & Fuminori Ito, Faculty of Agriculture, Kagawa University, Ikenobe, Miki, Kagawa 761-0795, Japan.*

*Chung-Chi Lin, Department of Biology, National Changhua University of Education, Changhua 50007, Taiwan.*

## Introduction

Social parasitism, the exploitation of a society by another species, is found in wasps, bees, and is especially diverse in ants (Forel 1874, Wilson 1975). Among ants, social parasitism is divided into four types: (1) temporary social parasitism, in which a founding queen invades a host colony, replaces the host queen, and uses the host workers as laborers in the period following colony founding; (2) dulosis, in which workers invade the nests of other species and bring worker pupae of the host species back to the nest to be used as colony workforce; (3) inquilinism, in which the parasite usually lacks the worker caste and only reproductive individuals invade the host colony and are completely dependent on its resources; and (4) xenobiosis, in which a colony lives inside the nest of another species (compound nesting) and sometimes steals food resources (Hölldobler & Wilson 1990, Buschinger 2009, De La Mora & al. 2020, Rabeling 2020). The systematic distribution of social parasitism among ants is skewed: In particular, temporary social parasitism is mainly known in the Palearctic genera of subfamily Formicinae (e.g., *Formica*: Wheeler 1910, Borowiec & al. 2021; *Lasius*: Wilson 1955). Unlike in the Formicinae, social parasitism is relatively rare in another major ant subfamily, the Myrmicinae, with only a handful of species reported to exhibit this behavior (*Aphaenogaster*: Dennis 1938; *Myrmica*: Masuko & Terayama 2002; *Solenopsis*: Deyrup & Prusak 2008; and *Tetramorium*: Wagner & al. 2021). This phylogenetic skew in distribution may reflect evolutionary trends in social parasitism, highlighting the importance of describing social parasitism syndromes and their natural history in a wider range of taxa (Buschinger 2009).

*Strumigenys* Smith, 1860 is a highly diverse myrmicine genus consisting of 881 extant species (Bolton 2025). There is broad variation in mandible morphology in this genus as many species have trap-jaw mandibles which can close extremely fast via latch-spring mechanism, and others have normal, gripping mandibles (Booher & al. 2021). Even though many studies have investigated the biology and evolution of *Strumigenys* species over the past 80 years (e.g., Wesson 1936, Brown & Wilson 1959, Masuko 1984, Dejean 1986), further accumulation of natural history observations is needed to fully understand the biology of this hyper-diverse genus. Although they are speciose, only a few social parasites have been reported in this genus. A handful of species are thought to be inquilines of other *Strumigenys* (Deyrup & Cover 1998, Booher 2021), but direct evidence is lacking except for two worker-less inquiline species: the African *Strumigenys inquilina* (Bolton, 1983) and the Australian *Strumigenys xenos* Brown, 1955.

The *Strumigenys mutica* group (= former genus *Kydris*, Bolton 2000) includes six species: *S. erynnes* (Bolton, 2000), *S. media* (Wilson & Brown, 1956), *S. mutica* (Brown, 1949), *S. takasago* (Terayama & al., 1995), *S. tathula* (Bolton, 2000), and *S. yaleogyna* (Wilson & Brown, 1956). They are distributed from Asia to Oceania, except for two species that occur in the Malagasy region (*S. erynnes* and *S. tathula*: Janicki & al. 2016; Guénard & al. 2017; https://antmaps.org/, accessed on 13 August 2024). At least four species in this group (*S. erynnes*, *S. media*, *S. mutica*, and *S. tathula*) were confirmed as grip-jaw species without power amplification (Booher & al. 2021). Among the *S. mutica* group, *S. yaleogyna*, which occurs in Papua New Guinea, has an unusual lifestyle: It has an extremely large colony size for the genus *Strumigenys* and lives in mixed nests with its host species *S. loriae* Emery, 1897. Wilson and Brown (1956) concluded *S. yaleogyna* as a unique inquiline species parasitizes on *S. loriae*. Based on their observation, the largest mixed colony consisted of 1622 host (*S. loriae*) workers, 16 host queens, 1170 parasite (*S. yaleogyna*) workers, and four parasite queens (Wilson & Brown 1956). In the same study, the authors reported that *S. media* was collected from an *S. loriae* colony, but they did not collect any queens of *S. loriae* nor *S. media*. Except for these species, there is almost no natural history information on the *S. mutica* group.

Kubota & Terayama (1982) suggested that *Strumigenys mutica* is a social parasite of other *Strumigenys*, based on the collection record of one colony composed of a queen of *S. mutica* and workers of a long trap-jaw species (*S. lewisi* Cameron, 1886 or *S. kumadori* Yoshimura & Onoyama, 2007). More recently, Wang & al. (2021) provided an image of a mixed colony featuring a queen and workers of *S. mutica* alongside workers of *S. solifontis* Brown, 1949. However, knowledge about the social parasitism, ecology, and behavior of *S. mutica* is still lacking. In this study, we describe the composition of both mixed and pure colonies of *S. mutica*, present the findings of behavioral observations on mixed colonies, and measure caste dimorphism in external morphology and female reproductive organs. Describing the natural history of this *Strumigenys* species illustrates its specialized traits and contributes to a better understanding of the life-history diversity and evolution of this hyper-diverse ant genus.

## Material and methods

### Field collection, colony composition, and caste dimorphism

Twenty-eight colonies of *Strumigenys mutica* were collected in Japan, Indonesia, and Taiwan between 1985 and 2022 (Tab. 1; Tab. S1, as digital supplementary material to this article, at the journal's web pages). All the species in this study were identified by a key by Terayama & al. (2014). The colonies were found nesting in rotting logs or under stones on the forest floor. All colony members were collected by using a shovel, plastic bags, and an aspirator. Just after the collection, the nests were dissected in a laboratory, and their colony composition – and that of their host in mixed colonies – were recorded.

Unlike the other *Strumigenys* ants which show inconspicuous caste dimorphism, the queens of *S. mutica* are larger than their workers (see Results). Caste difference in external and internal morphology was quantified by comparison of head width and ovaries. The maximum head width of workers (n = 129) and newly emerged gynes (n = 16) in a collected pure *S. mutica* colony (colony MS22-32) was measured. Images of the head of gynes and workers were taken with a digital camera (Shimadzu moticam 2000, Tokyo, Japan) connected to a binocular microscope (Olympus SZX12, Tokyo, Japan) and measured using ImageJ software version 1.52 k (open source: https://imagej.nih.gov/ij/, accessed on 30 January 2019). The distribution of head width was compared using the Welch Two Sample t-test performed by R software version 4.0.2 (R Core Team 2020).

Three dealate queens and six laboratory-emerged queens were dissected to determine the caste dimorphism in their internal reproductive organs. The other dealate and laboratory-emerged queens were not dissected. For caste comparison, five workers were dissected using the same method. Their number of ovarioles, presence of sperm in the spermatheca, and accumulation of yellow bodies were observed under a binocular microscope (Olympus SZ61).

### Prey preferences and foraging behavior

Two mixed colonies (colony code KS-Sm16-1 and MS22-2) were reared in the laboratory for about three months. The colonies were transferred to artificial nests made of a plastic box (82 × 148 × 32 mm) with a plaster floor. A smaller box with a plaster floor (35 × 35 × 15 mm) was placed in the artificial nest as a nesting chamber. The artificial nests were kept at room temperature, and the plaster floor was kept humid. Frozen and live Entomobryidae springtails were given as prey twice a week. The amount of given prey was adjusted depending on the requirements of the colonies. To study their food acceptance, freshly killed nymphs of Turkestan cockroaches (*Blatta lateralis* Walker, 1868), mealworms (larvae of *Tenebrio molitor* Linnaeus, 1758), nymphs of house crickets (*Acheta domesticus* Linnaeus, 1758), Symphyla, Isopoda, and sugar solution were offered to a mixed colony (MS22-2), and it was observed whether the ants consumed any or all of these. In order to know their relative preference for different type of prey, the following preys were given together at once (cafeteria experiment, n = 1 with the colony MS22-2): two cockroaches (body length 4 mm), two mealworms (5 mm), and two crickets (4 mm). After four hours, it was observed whether the ants took the given prey into the nest and consumed it.

The foraging behavior of these *Strumigenys mutica* workers was observed in one mixed colony (MS22-2). One *S. mutica* forager was followed for 10 minutes in the arena, and its behavior was observed using a binocular microscope (Olympus SZ61, Tokyo, Japan, attached with auxiliary lens Olympus 110AL0.5X 200, Tokyo, Japan, magnification of 3.35× to 22.5×) on a swing arm. The observation was repeated with 12 different foragers, so in total 120 minutes of observation were conducted. The following behaviors were observed: wandering, self-grooming, resting, fighting with a prey, carrying a captured prey, carrying a dead ant (nestmate), hunting-like behavior (see Results), and oral trophallaxis between foragers. The relative frequency of these behaviors was compared by pairwise comparisons of Wilcoxon rank sum test by the R function pairwise.wilcox.test. P-values were adjusted by Bonferroni method (Holm 1979), and differences were considered statistically significant when p-values were smaller than 0.05. Also, foragers had the opportunity to hunt live springtails. In addition, 14 springtail hunting events were observed outside of these 120 minutes of behavioral observation.

### Task performances of the parasites and the hosts in a mixed colony

Behavioral observations in mixed colonies (KS-Sm16-1 and MS22-2) were performed to determine the task performances between *Strumigenys mutica* and their host species *Strumigenys lewisi* or *Strumigenys solifontis*. Scan sampling of behaviors was conducted under a binocular microscope (Olympus SZ61, attached with auxiliary lens Olympus 110AL0.5X 200). In each scan session, the number of host workers and parasite workers performing the following behaviors were counted: brood care, allogrooming, trophallaxis, feeding on prey, transporting prey, transporting garbage, self-grooming, foraging, and prey retrieval. Brood care includes all the behaviors related to their brood such as grooming, feeding, and shuffling. The number of individuals performing a non-specific behavior such as resting and wandering was estimated by subtracting the number of individuals involved in the aforementioned behaviors from the total number of individuals. Scan observations were conducted 292 times for KS-Sm16-1 and 100 times for MS22-2. The observations were conducted at both daytime and nighttime, but no difference on their behavior was detected.

To compare the relative contribution of the host and parasite to each colony task, the mean frequency of each behavior was compared. The frequency of the following three behaviors was calculated using the total number of workers (host or parasite) as the denominator: foraging, prey retrieval, and self-grooming. Similarly, the frequency of five intranidal behaviors was calculated using the number of workers in the nest as the denominator: brood care, garbage transport, feeding on prey, prey transport, and non-specific behavior. The frequency of each observed behavior of host and parasite was compared by Wilcoxon rank sum test with the wilcox.test function in R.

During the observation, the direction of trophallaxis (which one is trophallactic donor or receiver) was difficult to assess. Therefore, the observed trophallaxis events between adult ants during the scan observation was analyzed independently from other behaviors. The observation data of trophallaxis were pooled into the following five combination categories: between parasite workers, between host workers, between parasite and host workers, between parasite workers and a parasite queen, and between host workers and a parasite queen. The relative frequency of trophallaxis in each combination was calculated with observed number of events denominated by the expected numbers of combination which may perform the trophallactic interaction (= expected value). The following equations show the method for calculating the frequency (Ft); trophallaxis between intra-specific workers (1), between inter-specific workers (2), and between workers and queens (3).

$$Ft = \frac{\#\text{trophallaxis events}}{\#\text{workers} \times (\#\text{workers} - 1)} \quad (1)$$

$$Ft = \frac{\#\text{trophallaxis events}}{\#\text{workers} \times \#\text{workers}} \quad (2)$$

$$Ft = \frac{\#\text{trophallaxis events}}{\#\text{workers} \times \#\text{queens}} \quad (3)$$

The frequency of each trophallaxis combination was compared by Pairwise Fisher's exact test performed by fisher.multcomp in the R package RVAideMemoire version 0.9-83-7. The p-value was adjusted using the Bonferroni method (Holm 1979), with statistical significance assessed as p-value < 0.05.

## Results

### Colony composition and caste dimorphism

Nine collected colonies consisted of *Strumigenys mutica* and workers of long-mandibulate *Strumigenys* species (mixed colonies; Tab. 1, Fig. 1); the other nineteen collected colonies consisted only of adult ants of *S. mutica* (pure colonies; Tab. S1). The host ant species were *Strumigenys lewisi* and *Strumigenys solifontis* (Fig. 1). The host of colony FI85-1 was either *Strumigenys lewisi* or its sibling species *Strumigenys kumadori* (these species could be identified only by gynes before the worker-based key in Yoshimura & Onoyama 2007 was published). The number of *S. mutica* workers in pure colonies ranged from 194 to over 5000 workers. All pure colonies included a single *S. mutica* dealate queen (monogynous). The composition of the mixed colonies was as follows: Two colonies included only a queen of *S. mutica* and host workers, four colonies included a *S. mutica* queen with own and host workers. Only a single colony (MS22-2) included three *S. mutica* dealate queens with *S. mutica* and host workers. Two colonies (MH61 and RH-Sm17-1) were lacking any queen, possibly due to incomplete colony collection. All mixed colonies lacked the dealate host queen. It was almost impossible to identify the species of larvae in mixed colonies, but host adults emerged during laboratory rearing in a mixed colony (KS-Sm21-1), suggesting host reproductive queens had been eliminated or had died relatively recently.

In a reared mixed colony (MS22-2), a large number of *Strumigenys mutica* workers died around the 40th to 60th day (Fig. 2), but the population increased again after the rearing container was changed. After that, one queen of this colony died (66th day), while the remaining two queens survived more than half a year. Unlike the

**Fig. 1**: Mixed colony of *Strumigenys mutica* (smaller workers) and *Strumigenys solifontis* (larger workers) (colony MS22-2). Arrow shows a queen of *S. mutica* with physogastric abdomen. Scale bar = 1 mm. Photo by RM.

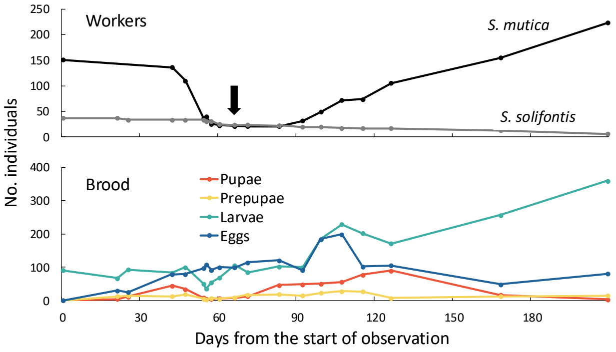

**Fig. 2**: Temporal change of colony composition during rearing of a mixed *Strumigenys* colony (MS22-2). A queen died at day 66 (shown by arrow).

**Tab. 1:** The composition of collected mixed colonies. Abbreviations: [1] Sl: *Strumigenys lewisi*; Sk: *Strumigenys kumadori*; Ss: *Strumigenys solifontis*. [2] DQ: dealate queens; W: workers; P: pupae; L: larvae; E: eggs; -, not counted. [3] Two *S. lewisi* and two *S. mutica* workers emerged from these larvae. The four remaining larvae died before pupation. [4] Two *S. mutica* workers emerged from these larvae. The three remaining larvae died before pupation. [5] The species of these larvae are unknown because the colony was not reared. [6] No host workers emerged from these larvae.

| | | | | **Colony composition[2]** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | ***S. mutica* adults** | | **Host adults** | | **Brood** | | |
| **Colony ID** | **Collected date** | **Locality** | **Host species[1]** | **DQ** | **W** | **DQ** | **W** | **P** | **L** | **E** |
| FI85-1 | 1985 | Matsue, Shimane Pref., Japan | Sl or Sk | 1 | 0 | 0 | ca. 30 | - | - | - |
| KS-Sm21-1 | 11.01.2021 | Tosashimizu, Kochi Pref., Japan | Sl | 1 | 0 | 0 | 22 | 0 | 8[3] | 0 |
| KS-Sm16-1 | 03.03.2016 | Aji, Takamatsu, Kagawa Pref., Japan | Sl | 1 | 14 | 0 | 11 | 0 | 5[4] | 0 |
| KS-Sm17-12 | 25.12.2017 | Tosashimizu, Kochi Pref., Japan | Sl | 1 | 14 | 0 | 9 | - | - | - |
| KS-Sm17-6 | 14.08.2017 | Tosashimizu, Kochi Pref., Japan | Sl | 1 | 20 | 0 | 7 | - | - | - |
| MH61 | 02.02.2022 | Kotohira Town, Kagawa Pref., Japan | Sl | 0 | 36 | 0 | 9 | 0 | 12[5] | 0 |
| KS-Sm21-5 | 13.04.2021 | Saita, Mitoyo, Kagawa Pref., Japan | Sl | 1 | 48 | 0 | 45 | - | - | - |
| MS22-2 | 30.03.2022 | Awa City, Tokushima Pref., Japan | Ss | 3 | 151 | 0 | 37 | 0 | 91[6] | 0 |
| RH-Sm17-1 | 12.08.2017 | Tsuruga, Fukui Pref., Japan | Sl | 0 | 10 | 0 | 7 | - | - | - |

**Tab. 2:** Result of dissection of nine queens. [1] DQ: dealate queen of the colony; AQ: alate queen emerged during laboratory rearing. [2] +, present; -, absent. * Number of ovarioles could only be counted for one side.

| Queen ID[1] | Colony ID | Total no. ovarioles | Sperm in spermatheca[2] | Yellow body accumulation[2] |
|---|---|---:|:---:|:---:|
| DQ1 | MS22-2 | 14 | + | + |
| DQ2 | MS22-2 | 10 | + | + |
| DQ3 | MS22-32 | 17 | + | + |
| AQ1 | MS22-32 | 13 | - | - |
| AQ2 | MS22-32 | 11 | - | - |
| AQ3 | MS22-32 | 12 | - | - |
| AQ4 | MS22-32 | 12 | - | - |
| AQ5 | MS22-32 | 13 | - | - |
| AQ6 | MS22-32 | 6* | - | - |

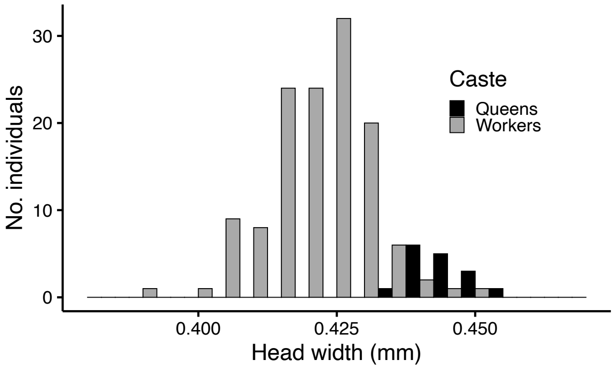

**Fig. 3:** Head width distribution of queens and workers of *Strumigenys mutica*. Queen's head width (average = 0.444 mm ± 0.005 standard deviation (SD), n = 16) was significantly wider than that of worker's (average = 0.422 mm ± 0.009 SD, n = 129, $p < 0.001$, Wilcoxon rank sum test).

parasites, the number of host (*Strumigenys solifontis*) workers decreased due to the absence of new worker emergence.

The head width distribution of queens and workers is shown in Figure 3. Both head width distribution of queens and workers followed a normal distribution (queens, p = 0.87, W = 0.97; workers, p = 0.11, W = 0.98, Shapiro-Wilk normality test). The queen's head width (average = 0.444 mm ± 0.005 standard deviation (SD), range = 0.435 - 0.455 mm, n = 16) was significantly higher than that of the workers (average = 0.422 mm ± 0.009 SD, range = 0.391 - 0.452 mm, n = 129; t = 15.57, df = 29.078, $p > 0.001$, Welch Two Sample t-test). Dissected queens possessed a total of 11 to 17 ovarioles in both ovaries (Tab. 2). The queens were physogastric; their abdomen was swollen, possibly due to their developing ovaries (Fig. 1). An observed spermatheca filled with sperm was bean-shaped (width 357 × length 218 µm, DQ3 from colony MS22-32). In contrast, all dissected workers lacked ovaries (n = 5).

### Foraging behavior and prey preferences

Throughout 120 minutes of foraging observation, *Strumigenys mutica* foragers were almost always wandering restlessly around the foraging arena (Fig. 4). While wandering, they walked relatively fast, swinging the head sideways, sometimes touching the substrate with their antennae. During the observations, *S. mutica* workers seemed to be aware of a springtail moving nearby and tracked it on a short distance (less than 5 mm). A fight between *S. mutica* and springtails occurred three times when ants succeeded in capturing a springtail that accidentally stepped on the ant's head. After securing a grip between the mandibles, the ants attempted to sting the prey. One of them succeeded in stinging, but the others failed because the springtail jumped and shook off the seizing ant. In all observed springtail hunting observations including 14 events outside of the 120-minute observation, the ants always seized a springtail at the appendages (legs: n = 13; furcula: n = 3; antennae: n = 1). Only once was a forager observed to display a careful hunting behavior which resembles that of other grip-mandible *Strumigenys*

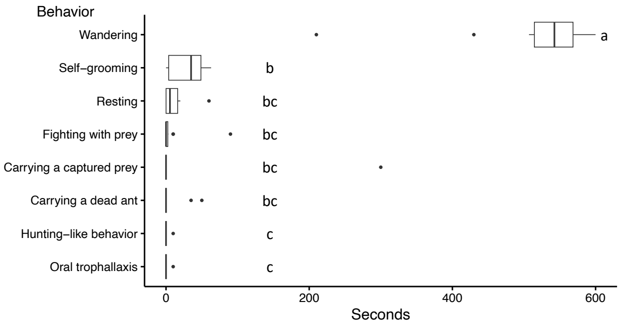

**Fig. 4**: The time-budget during the foraging observation (10 minutes * 12 workers) of the workers of *Strumigenys mutica*. Letters on the right of bars represent the results of the post-hoc pairwise comparison by Wilcoxon rank sum test. Bars sharing a letter are not significantly different ($p < 0.05$).

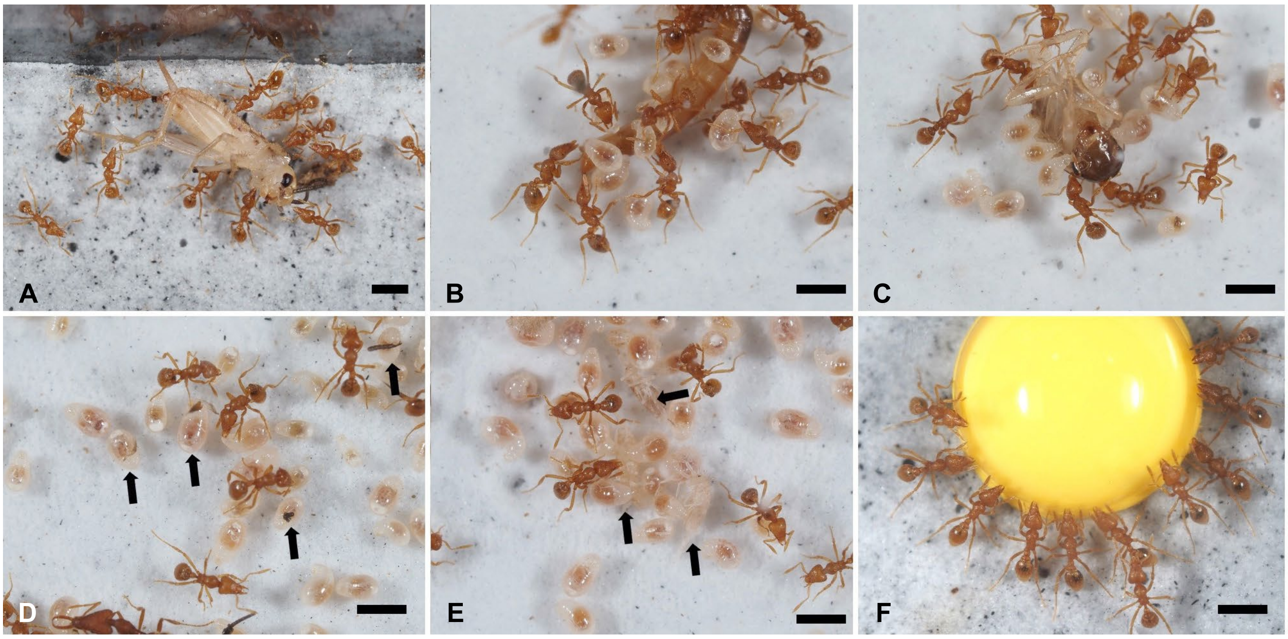

**Fig. 5**: Prey provided was cooperatively transported by *Strumigenys mutica* workers (A, killed cricket). The retrieved prey was given to the larvae by placing the larvae on the prey (B, mealworm; C, cockroach) or placed near the larval mouthparts after fragmentation (D, the larvae with prey fragment are shown by arrows). Springtails were offered to the larvae in the same manner (E). The workers also fed on sugar solution (dropped on a circular yellow plastic dish of 6 mm diameter) (F). Scale bars, 1 mm. Colony MS22-2. Photo by RM

species: The worker lowered its head with open mandibles and walked slowly. This behavior was conspicuous and clearly distinct from their "wandering" behavior, but was observed only once and lasted only for 10 seconds.

As a result of the cafeteria experiment, all prey items (cockroaches, mealworms, and crickets) were retrieved and consumed in a similar way within four hours (n = 1). They accepted and retrieved large, non-springtail prey items to their nest by cooperative transportation (Fig. 5A; Turkestan cockroaches: n = 8; mealworms: n = 7; house crickets: n = 7; Symphyla: n = 1). Isopods were also given but neglected (n = 2). The retrieved prey was fed to larvae by placing the larvae on the prey (Fig. 5B, C) or by placing a piece of fragmented prey near the larval mouthparts (Fig. 5D, E). The workers also eagerly licked sugar solution (Fig. 5F). The duration of feeding on sugar solution ranged from 14 seconds to 2 minutes 44 seconds (n = 8).

### Task performances between the parasites and the hosts in a mixed colony

The relative colony task performances of host and parasite workers were compared in two observed colonies (Fig. 6). The result was not always constant in both observed colonies, probably due to differences in colony condition like host species, worker population, population ratio of host and parasites, number of queens, and composition of brood. In general, the host species performed many colony tasks, though few significant differences were found between host and parasite worker behavior frequencies.

Brood care was more frequently performed by host workers, but a significant difference was observed only in larval care in one colony (MS22-2, $p = 0.005$). Foraging frequency was higher in the host workers compared with parasite workers in one colony (KS-Sm16-1, $p < 0.001$) but lower in the other one (MS22-2, $p < 0.001$). In both colonies, the frequency of grooming of parasite workers by parasite and by host workers was not significantly different ($p = 0.69$ in KS-Sm16-1; 0.74 in MS22-2). In contrast, host workers were more frequently groomed by members of their own species ($p = 0.003$ in KS-Sm16-1; $p = 0.02$ in MS22-2). Thus, while the parasites received grooming from host workers, they did not reciprocate this care.

The frequency of trophallaxis to queens was not significantly different between hosts and parasites ($p = 1$ in both colonies), but was significantly higher than that between workers of the same species both in parasites ($p = 0.005$ in KS-Sm16-1; $p < 0.001$ in MS22-2) and hosts ($p < 0.001$ in KS-Sm16-1; $p = 0.03$ in MS22-2). Trophallaxis between parasite and host workers was commonly observed, but the direction (which one is donor or receiver) could not be identified from the observation. The frequency of inter-species trophallaxis was as high as parasites' intra-species interaction in one colony (in MS22-2, $p = 1$) and that of hosts in the other colony (in KS-Sm16-1, $p = 1$). Trophallaxis between *Strumigenys mutica* queens was never observed in a polygynous colony (MS22-2). In summary, the parasites were highly integrated in the host colony; both parasite queens and workers exploited food resources from the host by inter-species trophallaxis.

Foraging frequency showed opposite results in two colonies: It was performed more frequently by hosts in one colony (KS-Sm16-1, $p < 0.001$) but by parasites in the other

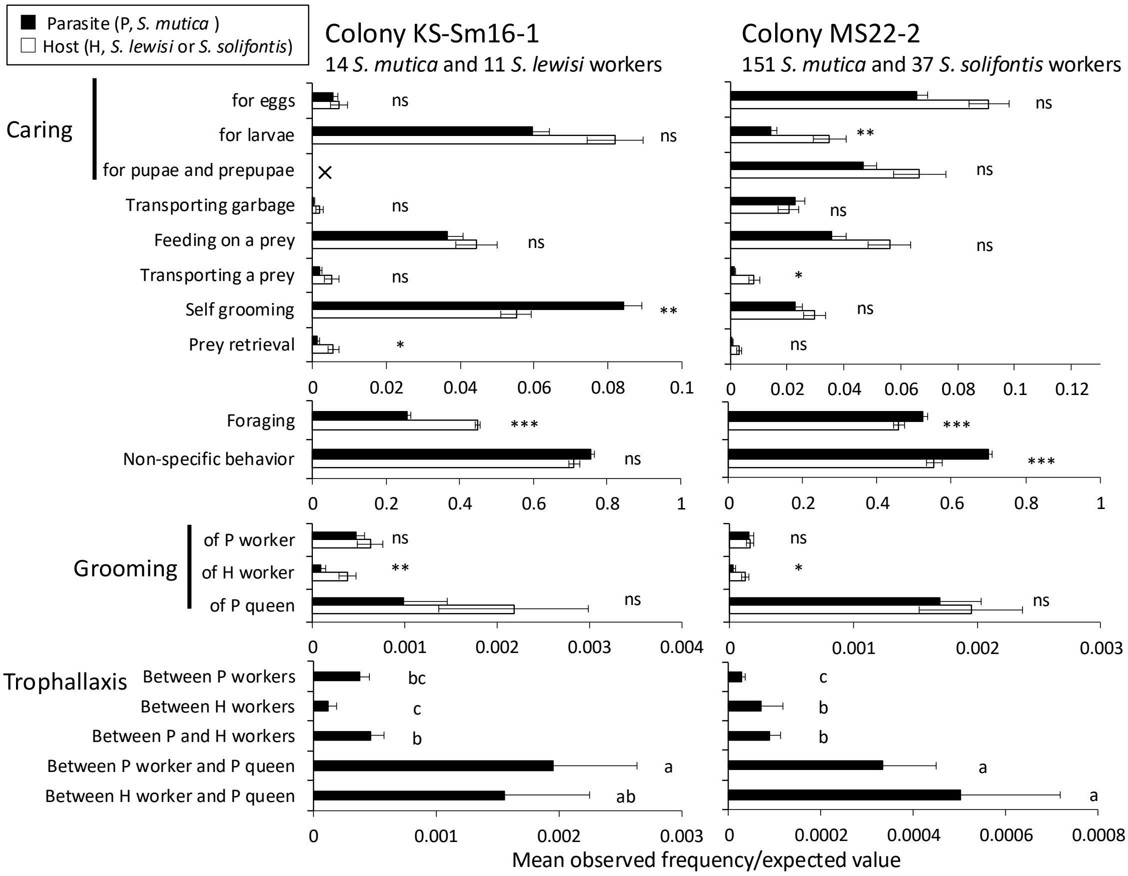

**Fig. 6**: Observed / expected frequency of each behavior in two mixed colonies. Mean frequency of performed behavior by both *Strumigenys mutica* and their host (*Strumigenys lewisi* or *Strumigenys solifontis*) workers are shown. Error bars show standard deviation. The result of Wilcoxon Rank Sum test is shown by following abbreviations; ns: $p \geq 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. ×: indicates not observed due to lacking pupa or prepupa in the colony. In the Trophallaxis section, the frequency of trophallaxis of each combination of *S. mutica* workers, queens, and host workers is shown. Letters indicate significant differences ($p < 0.05$, Fisher's exact test).

(MS22-2, $p < 0.001$). This difference might be reflecting the difference of parasite worker population per colony (11 workers in KS-Sm16-1, 151 workers in MS22-2).

During the behavioral observations, aggressive behavior between queens was observed only twice in the polygynous colony MS22-2. On the first occasion, a queen attempted to bite another queen. The second time, a queen bit an antenna of another queen, bent her abdomen, and attempted to sting.

## Discussion

### Temporary social parasitism of *Strumigenys mutica*: field evidence, colony life history, colony integration, and host range

The composition of the mixed and the pure colonies of *Strumigenys mutica* suggests temporary social parasitism: One or a few queens can penetrate a colony of *Strumigenys* host species and eliminate the host queen(s) if present (this stage was suggested in the colony FI85-1 and KS-Sm21-1). Then, the production of *S. mutica* workers starts (colony KS-Sm16-1 and four other colonies) while the number of host workers slowly decreases, to the point where the colony finally consists of only *S. mutica* (19 pure colonies, Tab. S1). Also the result of our colony rearing shows a part of this process. Sexuals of *S. mutica* emerged from reared pure colonies (112 alate queens and 67 males from colony MS22-32; R. Mizuno, unpubl.; more than 200 queens and males from St_mu-01 to St_mu-05; C.-C. Lin, unpubl.). Therefore, colonies with about 1000 workers can produce sexuals and can be considered in the mature stage of colony life cycle.

Even though workerless inquilines (BROWN 1955, BOLTON 1983), compound nesting with phylogenetically distant ant species (KAUFMANN & al. 2003, YÉO & al. 2006, GRAY & al. 2018), and mixed colonies of two congeneric species (MEZGER & PFEIFFER 2008) have been reported in the genus *Strumigenys*, this study provides the first direct evidence of temporary social parasitism within this genus. Unlike the colonies of the related *Strumigenys yaleogyna* that always included both host and parasite queens (WILSON & BROWN 1956), the mixed colonies of *Strumigenys mutica* always lacked host queens. Therefore, at least two types of social parasitism (i.e., temporary social parasitism and inquilinism with worker caste) are observed in the *S. mutica* group. We cannot conclude whether the social parasitism is a common trait in this species group because there is virtually no research about the life history of the other species in the *S. mutica* species group (*S. erynnes*, *S. takasago*, *S. tathula*). WILSON & BROWN (1956) reported a mixed colony of *Strumigenys media* and their candidate host species *Strumigenys loriae*, but they did not find queens from the colony. Therefore, the argument for this colony is ambiguous; it could be a mixed-colony stage of temporary parasitism like *S. mutica*, or inquilinism with worker caste like *Strumigenys yaleogyna*. Social parasitism might be a synapomorphy in the *S. mutica* group, but the evolution of social parasitism in this group is an open question for future studies.

Although collected pure *Strumigenys mutica* colonies were monogynous, one mixed colony included multiple *S. mutica* queens (MS22-2). We observed a few aggressive interactions between the queens in this polygynous colony, and one queen died during the colony rearing. This phenomenon, with initial parasitism by multiple queens that become fewer during colony growth, resembles pleometrosis (temporary polygyny during the colony-foundation stage) in non-parasitic ant species (BERNASCONI & STRASSMANN 1999). However, more than a hundred workers also died at this time, suggesting that inadequate rearing conditions might be responsible for the queen's death. The establishing process of the mixed colony with multiple parasite queens (colony MS22-2) is unclear. One possible explanation to multiple penetration events would be that a mature *S. mutica* colony existed near the host colony. Because mature colonies of *S. mutica* are not common in the field, parasitism of the same host colony by unrelated queens is unlikely. If the success rate of parasitizing a nearby colony by walking was higher than that of a remote colony by flight, the spatial distribution of mature *S. mutica* colonies could be locally abundant. The distribution of mature colonies is essential for understanding queen dispersal, parasitism success, and the mechanisms of colony founding in this temporary social parasite.

The host populations of mixed colonies, including colonies showing early stages of parasitism, all appear to be at the low end of the colony-size distribution of the host species. The number of *Strumigenys lewisi* workers in parasitized colonies (average = 17.5 ± 13.8 SD, range 7 to 45, n = 8 colonies) was significantly lower than that in non-parasitized colonies (average = 78.0 ± 77.2 SD, range 9 to 275, n = 32 colonies; MISAKI 2016) ($p = 0.0038$, $W = 214$, Wilcoxon rank sum test). In addition, there was a positive correlation between number of queens and workers in *S. lewisi* ($S = 2080.1$, $p > 0.001$, $rho = 0.618$, Spearman's rank correlation), suggesting smaller colonies likely have fewer queens to eliminate during infiltration. Moreover, orphaned colonies often have smaller worker populations, which might be easier to infiltrate for *Strumigenys mutica* gynes without killing host queens: Queen-less colonies collected in MISAKI (2016) were the two smallest colonies among a total collected 32 colonies. Thus, it is possible that *S. mutica* gynes select or more easily infiltrate small colonies. However, if the benefit of temporary social parasitism is a jump-start to colony establishment, larger host colonies should be preferable. HUANG & DORNHAUS (2008) pointed out that temporally social parasites that utilize hosts with large colony-sizes are often phylogenetically close to their hosts, suggesting that parasites that are closely related to their hosts may be more likely to possess the invasion mechanisms required to penetrate large host colonies. All known hosts of *S. mutica* are their congeneric but phylogenetically remote species (BOOHER & al. 2021). Therefore, large host colonies might be difficult to infiltrate, and there may be a trade-off between the potential workforce and the ease of penetration for the parasite. Studying how *S. mutica* queens infiltrate the host nest and kill the queen(s) may explain why smaller colonies were selected as hosts.

Our observations showed that *Strumigenys mutica* was highly integrated with their host during the parasitic phase: The frequency of inter-species trophallaxis was similar or even higher than that of intra-species trophallaxis. Even though the number of host workers was relatively low, they still contributed substantially to colony tasks as many behavioral tasks were performed more frequently by the host workers (*Strumigenys lewisi* or *Strumigenys solifontis*). Unlike inquiline species, the workers of *S. mutica* greatly contributed to colony tasks even during the parasitic phase. The fact that they are functional is well in line with the hypothesis of temporary social parasitism.

Among ants, temporally social parasitism is frequently observed in temperate regions of the northern hemisphere (e.g., *Formica* and *Lasius*) but rarely in tropical regions despite a higher species diversity (WILSON 1984, HÖLLDOBLER & WILSON 1990, BUSCHINGER 2009, GRAY & RABELING 2022). This skew is known as the "Kutter-Wilson Paradox" (RABELING & al. 2019). One of the reasons used to explain this paradox is the local abundance of their host species colonies (RABELING & al. 2019, RABELING 2020). Our colony collection showed that *Strumigenys mutica* parasitizes at least two host species (*Strumigenys lewisi* and *Strumigenys solifontis*). In addition, mixed colonies of *S. mutica* with *Strumigenys kumadori* (in Japan; K. Kinomura, pers. comm.) and *S. mutica* with *Strumigenys feae* FOREL, 1912 (in Taiwan; C.-C. Lin, pers. comm.) were collected. The distribution of these recorded host species, however, is limited: *Strumigenys lewisi* in Japan, Korea, Taiwan, China, Vietnam, and the Philippines; *S. solifontis* in Japan, Korea, and Taiwan; *S. kumadori* in Japan, Korea, China, and Taiwan; *S. feae* in Taiwan, China, Indo-China peninsular and Pakistan (GUÉNARD & al. 2017, species geographic distribution data from https://antmaps.org, accessed on 13 August 2024, including the distribution of *Strumigenys formosensis* FOREL, 1912 which was synonymized under *S. feae* by TANG & GUÉNARD 2023) although *S. mutica* is also distributed in the Sunda Islands (Japan, Korea, Taiwan, China, peninsula Malaya, Borneo, Java, and South India; GUÉNARD & al. 2017, and https://antmaps.org, accessed on 13 August 2024). We collected only a pure colony in Bogor (West Java). If *S. mutica* shows the same temporary social parasitism in Java, it might parasitize different host species. Therefore, at least five species can be hosts for *S. mutica*. This relatively wide host range of *S. mutica* might be related to their wide distribution, including tropical regions. However, no mixed colony was collected in the tropical region during this study. More host records of *S. mutica*, especially in tropical regions, are necessary to know their true host range. By contrast, *Polyrhachis lamellidens* Smith, 1874 parasitizes multiple species of *Camponotus* (Sakai 1990, Furukawa & al. 2012, Iwai & al. 2021), but their distribution range is limited to that of their single host species *Camponotus japonicus* Mayr, 1866 (Guénard & al. 2017, https://antmaps.org, accessed on 13 August 2024). Therefore, a wide host range is not always associated with a wide geographical distribution.

Interestingly, all the confirmed host records of *Strumigenys mutica* are limited to phylogenetically distant long trap-jaw species, illustrated by their prior taxonomic status: hosts as *Strumigenys* sensu stricto and parasites as *Kydris*. From this point, this host-parasite relationship might be considered as an exception of Emery's rule (Emery 1909, Buschinger 2009). *Strumigenys loriae*, the host of *Strumigenys yaleogyna*, is also a long trap-jaw species (Wilson & Brown 1956). Therefore, all the host records of the *S. mutica* group are limited to long-mandibulate *Strumigenys* so far. The reason and the significance of this association (long trap-jaw host and grip-jaw parasite) are yet to be discovered. One of the possible reasons is the colony density of species: Long-mandibulate species are more common and widespread than short-mandibulate species (e.g., Ito & al. 2001, Kitahiro & al. 2014); therefore, long-mandibulate species may be more favorable as host. The other non-exclusive explanation is that the combination of trap- and grip-jaw ants may enhance work efficiency, especially for foraging. Generally, the hunting tactics are different between trap-jaw and grip-jaw *Strumigenys*, and some long trap-jaw species prey on a wider range of arthropods than grip-jaw (Masuko 1984). Therefore, foraging by workers of both types may maximize the range of potential prey and would be successful in diverse habitats with different prey fauna. As mentioned above, the prey spectrum of *S. mutica* is wider than of other *Strumigenys* species. This may be the consequence of co-habitation with long-trap-jaw species, besides the increase in food requirements associated with the increase in colony size.

### Novel life history traits of *Strumigenys mutica* in comparison with congeneric species: large colony size, queen morphology, and predatory biology

Pure *Strumigenys mutica* colonies included a considerably larger number of workers compared with the other *Strumigenys* species: The majority of this genus has a colony size of less than 200 and rarely reaches more than 500 workers (Tab. 3). Moreover, all the collected mature colonies except for five queen-less colonies were monogynous, which suggests the high fecundity to keep the large colony size is established by queen's individual fecundity, not by the total fecundity of multiple queens.

The queens of *Strumigenys mutica* became physogastric with swollen abdomens, possibly due to their developing ovaries (Fig. 1). The head width of queens overlapped but was overall larger than that of their workers. In addition, queens of *S. mutica* possessed a high number of ovarioles (queens: 10 to 17 in total; workers: 0) showing conspicuous caste dimorphism in both external morphology and internal reproductive organs. Also, compared with other *Strumigenys* queens that commonly have only 4 ovarioles (Tab. 4; 16 other species of *Strumigenys*, F. Ito, unpubl.), the ovariole number of *S. mutica* queens are extraordinary. Related to the queen's high fecundity with many ovarioles, pure *S. mutica* colonies showed a relatively large colony size (Tab. 3). Workers of *S. mutica* lacked ovaries as in other *Strumigenys* workers (16 species of *Strumigenys*, F. Ito, unpubl.).

**Tab. 3**: List of reported colony composition of *Strumigenys* species. *Sample size (no. examined colonies) is shown in parentheses, if provided.

| Species | No. individuals per colony | | References |
|---|---|---|---|
| | **Queens** | **Workers*** | |
| **Long mandibulate** | | | |
| *Strumigenys* "br" | | 15 (1) | Kaspari & Vargo (1995) |
| *S. frivaldszkyi* | | 15 (1) | Wilson (1959) |
| *Strumigenys* "gl" | | 18 (2) | Kaspari & Vargo (1995) |
| *S. kumadori* | 1-7 | 2-187 (96) | Masuko (1999) |
| | 1-4 | 1-180 (185) | Misaki (2016) |
| *S. lewisi* | 1-21 | 9-275 (32) | Misaki (2016) |
| *Strumigenys* "lj" | | 16 (13) | Kaspari & Vargo (1995) |
| *Strumigenys* "ljls" | | 48 (2) | Kaspari & Vargo (1995) |
| *S. loriai* | | 300, 500 (2) | Wilson (1959) |

| | No. individuals per colony | | |
| --- | --- | --- | --- |
| **Species** | **Queens** | **Workers*** | **References** |
| **Long mandibulate** | | | |
| *S. louisianae* | 1 | 181 (1) | Wilson (1953) |
| *S. mayri* | | 100 (1) | Wilson (1959) |
| *Strumigenys* "mi" | | 48 (30) | Kaspari & Vargo (1995) |
| *Strumigenys* "nf" | | 26 (4) | Kaspari & Vargo (1995) |
| *S. rotogenys* | 1 | 8-80 (7) | Mezger & Pfeiffer (2008) |
| *S. solifontis* | 1-14 | 1-530 (28) | Masuko (1980) |
| *Strumigenys* "wk" | | 26 (3) | Kaspari & Vargo (1995) |
| *Strumigenys* sp. | | 200 (1) | Wilson (1959) |
| *Strumigenys* sp. | | 50 (1) | Wilson (1959) |
| *Strumigenys* sp. 1 | | 80 (6) | Kaspari & Vargo (1995) |
| *Strumigenys* RMTH sp. 1 | 1 | 7 (1) | R. Mizuno, unpubl. |
| **Short mandibulate** | | | |
| *S. apalachicolensis* | | 332 < (1) | Deyrup & Lubertazzi (2001) |
| *S. arizonica* | 1-2 | ca. 30-40 | Booher (2021) |
| *S. brevisetosa* | Several | ca. 30 (1) | Wesson & Wesson (1939) |
| *S. calvus* | 1 | 72, 86 (2) | Dong & Kim (2020) |
| *S. clypeata* | | 62 (1) | Wilson (1953) |
| *S. dietrichi* | | 80 < (1) | Kennedy & Schramm (1933) |
| *S. hexamera* | 1 | 18-22 (3) | Masuko (2013) |
| | 1 | 0-48 (67) | Masuko (2023) |
| *S. membranifera* | 1 | 36 (1) | Wilson (1953) |
| | 1-14 | 5-333 (6) | Ito & al. (2010) |
| *S. leptothrix* | 1 | 179 (1) | R. Mizuno, unpubl. |
| *S. memorialis* | 1 | 54 (1) | Deyrup (1998) |
| *S. mutica* | | 1000 < (1) | Azuma (1950) |
| | | 617-5000 < (7) | present study |
| *S. pilinasis* | 1 | ca. 30 | Wesson & Wesson (1939) |
| | 1-6 | 19-111 (14) | Duffield & Alpert (2011) |
| *S. ornata* | | ca. 20 (1) | Wesson & Wesson (1939) |
| *S. pergandei* | 1 | 146 (1) | Wilson (1953) |
| | | 700 < (1) | Brown (1964) |
| *S. pulchella* | | 6-60 | Smith (1931) |
| *S. rostrata* | 1 | 45, 98 (2) | Talbot (1957) |
| | 1-24 | 14-160 (28) | Duffield & Alpert (2011) |
| *S. serrula* | 1 | 30-200 (51) | Dejean (1987) |
| *S. sydorata* | 1 | 23 (1) | Musfira & al. (2022) |
| | 1 | 35, 62 (2) | R. Mizuno, unpubl. |
| *S. talpa* | | ca. 60 (1) | Wesson & Wesson (1939) |
| *S. zeteki* | | 30 (34) | Kaspari & Vargo (1995) |
| *S.* sp. (= *Smithistruma* sp. 1) | | 57 (8) | Kaspari & Vargo (1995) |
| *S.* sp. (= *Smithistruma* sp. 2) | | 55 (3) | Kaspari & Vargo (1995) |
| *S.* sp. (= *Smithistruma* sp. 3) | | 99 (1) | Kaspari & Vargo (1995) |
| *S.* "st" (= *Smithistruma* "st") | | 26 (7) | Kaspari & Vargo (1995) |

**Tab. 4**: Survey of known queen ovariole number (total of both sides) of *Strumigenys* species.

| Species | No. ovarioles per queen (references) |
|---|---|
| *S. feae* | 4 (F. Ito, unpubl.) |
| *S. hexamera* | 2 or 4 (Masuko 2013) |
| *S. hirasimai* | 4 (F. Ito, unpubl.) |
| *S. hispida* | 4 (F. Ito, unpubl.) |
| *S. japonica* | 4 (F. Ito, unpubl.) |
| *S. kumadori* | 4 (F. Ito, unpubl.) |
| *S. leptothrix* | 4 (R. Mizuno, unpubl.) |
| *S. lewisi* | 4 (F. Ito, unpubl.) |
| *S. membranifera* | 4 (Ito & al. 2010) |
| *S. mutica* | 10 to 17 (present study) |
| *S. minutula* | 4 (F. Ito, unpubl.) |
| *S. rogeri* | 4 (Lee & al. 2018) |
| *S. solifontis* | 4 (R. Mizuno & F. Ito, unpubl.) |
| *S. strigatella* | 4 (R. Mizuno, unpubl.) |

Although many socially parasitic species have relatively small queens compared with non-parasitic congeners (Stille 1995, Wagner & al. 2021), *Strumigenys mutica* has larger queens. This might be explained by the difference of caste dimorphism and colony foundation strategy in their ancestral state. In general, the evolution of temporary parasitism can be considered as a transition of colony foundation strategy, from independent colony foundation (ICF) to the parasitism. In many temporal parasitic species (*Formica*, *Lasius*, etc.), their non-parasitic congeners establish a new colony mainly via claustral ICF (Keller & Passera 1989). They show conspicuous caste dimorphism, queens have larger bodies containing a large amount of resources (e.g., proteins, lipids) to produce their first batch of workers without needing to forage outside (Peeters & Ito 2015, Peeters 2020). In this evolutionary transition from claustral ICF to temporal parasitism, smaller queens can be selected for due to a reduction of investment in initiating the colony. In other words, the cost for claustral ICF is replaced by a parasitic strategy.

Meanwhile, *Strumigenys* show weaker caste dimorphism and semi-claustral colony foundation: The foundress queen forages and feeds the larvae (*Strumigenys* spp.: Dejean 1987; *Strumigenys membranifera* Emery, 1869: Ito & al. 2010). This strategy prevents their full morphological specialization for reproduction because worker-like morphological traits are necessary for successful foraging during the colony foundation stage (Keller & al. 2014). Therefore, in the case of *Strumigenys mutica*, the selection for reducing queen body size did not occur because queens are originally "small", or similar to worker body size. In addition, due to their parasitic life history, queens do not need to forage during colony foundation by temporary social parasitism, allowing specialization of queen morphology with respect to reproductive function and enabling rapid colony growth during the parasitic stage. So, larger body size would be preferred with capacity for larger reproductive organs. A higher ovariole number in temporary social parasitic species was also observed in *Formica*: The queens of temporary social parasitic species have a larger number of ovarioles (64 to 90 per queen in *Formica pratensis* Retzius, 1783, see Schmidt 1974; 26 to 100 in *Formica polyctena* Foerster, 1850, see Brian 1979) compared with queens of related species with independent foundation (36 to 44 in *Formica rufibarbis* Fabricius, 1793, see Hohorst 1972).

Many gripping-jaw *Strumigenys* species are specialized predators of springtails or other soil arthropods that perform specialized cautious hunting tactics (e.g., Masuko 1984, 2009a, 2009b). By contrast, *Strumigenys mutica* accepted most dead insects as prey. Also, their foraging behavior was different from that of other *Strumigenys* species (Wilson 1953, Dejean 1986, Masuko 1984). In more detail, the workers of *S. mutica* always wandered on the ground and almost never performed cautious hunting behavior. In general, foraging strategies of ants are related to their colony size: Species with smaller colony size forage as individuals or small groups, while species with larger colony size use mass recruitment, trunk trails, or group hunting (Beckers & al. 1989). Because temporary social parasitism and the queen's high fecundity allowed *S. mutica* to reach a large colony size, their foraging strategy and food preferences may be adapted to grow and maintain their colony size. However, we have no evidence suggesting the existence of nestmate recruitment nor trail pheromones.

As many reports have discussed, *Strumigenys* ants mostly share common life-history traits represented by small colony size, specialized hunting behavior, and semi-claustral colony foundation. In contrast, *Strumigenys mutica* is a temporary social parasite that shows a novel life history: specialized queen morphology, large colony size, and generalist diet. Interestingly, the life history traits of *S. mutica* resemble those of typical myrmicine ants. However, the role of social parasitism syndromes in ant evolution remains largely understudied.

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## Declaration on use of generative artificial intelligence tools

The authors declare that they did not utilize generative artificial intelligence tools in any part of the composition of this manuscript.

## Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript was written by Riou Mizuno and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

## Conflicting interest

Not applicable.

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