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Raiding behavior of the Japanese slave-making ant *Polyergus samurai*

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Summary

Raiding behavior of the Japanese slave-making ant *Polyergus samurai* was investigated in the field. Raiding trips occurred from early June to early September. A raiding column of several hundreds workers would rush into a target nest and rob mainly worker pupae of the host species, *Formica (Serviformica) japonica.* Most trips occurred on sunny days. Air temperature, soil temperature, relative humidity, and radiation energy at the ground surface were significantly different between days with and without raiding trips. Nuptial flights occurred on hot, sunny days, and most *Polyergus* colonies released alates simultaneously. Behaviors of newly mated queens are also provided and are compared with other *Polyergus* species.

Introduction

Approximately 180 of 8800 living ant species are known as social parasite that depend on workers of other species to rear their own brood (Hölldobler and Wilson 1990). Among these, slave-making (= dulosis) is a parasitic way of life in which dulotic species rob broods of other species and make them rear slave-makers broods (Wilson 1971). Raiding trips of slave-making ants have been well known since the previous century because of their spectacularity (Huber 1810; cited in Hölldobler and Wilson 1990).

Dulosis occurs in two phylogenetically distinct lineages of ants: the subfamilies Myrmicinae and Formicinae (Hölldobler and Wilson 1990). In Myrmicinae species, dulosis has been found in the two tribes, Leptothoracini and Tetramorini. Leptothoracini ants are tiny and easy to rear, thus their raiding behavior has been studied in detail in laboratories (Stuart and Alloway 1983). For the Formicinae species, however, most behavioral information is based on field observations (see also Kwait and Topoff 1984).

All five species of the genus *Polyergus* are obligately dulotic and cannot live without slaves because of their specialization in parasitic life (Hölldobler and

Wilson 1990). Ecological and behavioral data has been reported for all five species of *Polyergus*, including *P. rufescens* in Europe (Czechowski 1975, Mori et al. 1991) and *P. luciaus* (Kwait and Topoff 1983, 1984, Marlin 1968, 1969, 1971, Talbot 1967, 1968, Trager and Johnson 1985, Vargo and Gibbs 1987) and *P. breviceps* in the United States (Wheeler 1916, Topoff 1985, Topoff and Greenberg 1988, Topoff et al 1984, 1985a, b, c, 1987, 1988, 1989). However, far less is known about the Japanese species, *P. samurai*, although some preliminary reports exist (Sakagami and Hayashida 1962, Yasuno 1964). For example, in a recent paper, Mori et al. (1991) noted that, "Considerably less is knwon about *P. samurai*, since the information about this species is limited to the research by Sakagami and Hayashida (1962) and Yasuno (1964)." In addition, population studies for *Polyergus* with data from multiple colonies have not yet been conducted. Thus, detailed studies on the ecology and behavior of *P. samurai* are important for studies, comparing the raiding habits of *Polyergus*.

In this paper, we describe the typical raiding behavior of *P. samurai* based on a large number of observations of multiple colonies. The annual life cycle of *P. samurai* and its host *Formica japonica* was investigated to determine the factors affecting the duration of the raiding season. Mating behavior is also described and compared with other *Polyergus* species.

Materials and methods

Polyergus samurai is a slave-making ant found in Japan (Yano 1911). As in the other *Polyergus* species. *P. samurai* is highly specialized in a dulotic way of life and conducts raiding trips on *Formica japonica* nests during the summer (Yasuno 1964). The study site was an area of ca. 2.3 ha (150 × 150 m) located in the Ecology Park of the Natural History Museum and Institute, Chiba, Japan. On 10 April 1992, nest entrances of *F. japonica* were covered with a light-brown tile plate (15 × 20 cm) to locate nests of *P. samurai*. A total of 160 *Formica* nests were found and covered. The conditions under each plate were then photographed once a week. Most nests made a large chamber under the plate, and *Formica* workers carried much of the brood to the chamber. Thus, seasonal changes in brood production could be estimated from the photographs. In addition, when *Polyergus* workers were found under the nest plate, the nest was considered a *Polyergus* colony. By this method, 6 *Polyergus* colonies were found in the study area before the beginning of the raiding season. An additional six *Polyergus* colonies were found later, both inside and outside the study area. To describe a general raiding pattern of *P. samurai,* the results presented in this paper are based on the observations of all 12 colonies. Intercolonial differences in raiding activity will be analyzed in detail elsewhere (Hasegawa and Yamaguchi in prep.).

From June 1, *Polyergus* colonies were visited after 12:00 each day every 20 min. When raiding activity was observed, the observation was continued to the end of the raiding trips on that day. The following data were recorded: number of raiders in a raiding trip, location of raided *Formica* nests, distance between the *Polyergus* nest and the raided *Formica* nest, number of robbed brood, starting time of raiding trips, time of arrival of the first raider to the raided nest and returning time of the first

raider to onw nest. Ants were counted by hand-held counters and the distance between two nests was measured along the course traveled by the raiding party.

Weather conditions were recorded with an automatic climate monitoring system at Ecology Park. The sensor of the monitoring system was about 100 m from the study fields. Air temperature at 1 m above ground (AT, °C), relative humidity (RH, %), soil temperature at a depth of 10 cm (ST, °C), atmospheric pressure (AP, hPa), and radiation energy at the ground surface (RE, MJm^{-2}) were recorded at 1-min intervals. We used climatic data at 14:00 for RH and AP. The maximum AT and ST from 12:00 to 17:00 in each day were used for temperature data. For RE, a cumulative value from 12:00 to 17:00 was used. Qualitative weather conditions were described as follows: sunny – days with sunshine in the afternoon: cloudy – days with no sunshine in the afternoon: and rainy – days with raindrops in the afternoon. Unless otherwise mentioned, means are given with ± S.D.

Results

Description of a typical raiding trip

In 1992, raiding trips occurred from June 3 to September 3 (Fig. 1). A total of 297 trips were observed during this period. Based on these observations a typical raiding trip of *P. samurai* is described.

Raiding activity began with the departure of scouts from their natal nest. Until the appearance of scouts on the ground, *Polyergus* nests cannot be discriminated from true *Formica* nests. A few hours after 12:00 (generally 13:00–16:30), a scout appeared from the nest entrance and walked around it. Shortly after, the scout moved away from the natal nest, and, in many cases, several scouts left independently in various directions. About half an hour later, the scout quickly ran back to the nest and entered the nest entrance. After a few min, many *Polyergus* workers poured out from the nest entrance and ran around within a ca. 30-cm radius from the nest. At this time, many individuals showed characteristic behavior: A running worker stopped suddenly, then strongly bent her gaster and quickly rubbed the tips of her legs to the terminal part of the abdomen. This behavior seemed to mark her

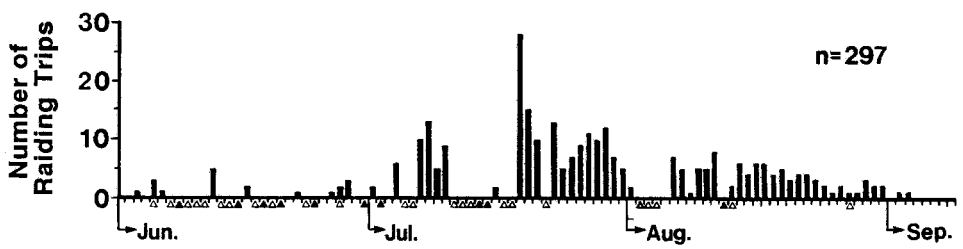

Figure 1. Occurrence of raiding trips of *P. samurai* in the Ecology Park in 1992. Raiding trips conducted by all 12 colonies in a day are combined. Open and closed triangles represent cloudy and rainy days, respectively. Days without triangles are sunny

legs with some secretion from the abdomen. However, the behavior was completed within only a few sec, and we could not confirm the precise location where the tips of the legs were rubbed. A few minutes later, a raiding swarm started in the direction from which the scout returned. Although many workers ran back and forth, the swarm as a whole advanced slowly forward. Typical raiding swarms contained several hundred *Polyergus* workers and were 20–30 cm wide and 2– 3 m long. Location of the scout in raiding trips was not determined in this study. Shortly before arriving at the target *Formica* nest, the front of the swarm stopped suddenly, and the swarm spread into a circle-like shape with a ca. 50-cm radius. *Polyergus* workers then searched for the entrances of the target nest, and, when they found one, they rushed into it. About 1 min later, the first raider left the nest with booty and ran back to her own nest. During the attack, workers of the target *Formica* nest showed almost no resistance. Returning raiders traced back the same route of the outward trip. The speed of the return trip was much faster than that of the attacking trip (see next section). Returning raiders entered their own nest with the booty, and a raiding trip ended with arrival of the last returning raider.

Raiding characteristics

Raiding swarms of *P. samurai* in the Ecology Park robbed several classes of *Formica* brood other than worker pupae. Reproductives (adults, pupae, and larvae), small size larvae, and callow workers were robbed as booty, although most *Polyergus* raiders returned with worker pupae. The mean number of raiders in a trip was 759.7 ± 438.3 ($N = 174$), and the average of booty obtained by a *Polyergus* colony was 358.6 ± 367.6 ($N = 200$). On average, $54.7 \pm 36.4\%$ ($N = 172$) of the raiders in a trip returned with booty. The mean speed of the outward trips was 95.6 ± 45.2 cm/min ($N = 126$), whereas the mean returning speed was 162.3 ± 108.5 cm/min ($N = 141$) and significantly faster than the outward speed (Mann-Whitney's U test, $z = -8.648$, $P < 0.0001$). The average distance between a *Polyergus* nest and the raided nest and the average duration of a raiding trip were 12.5 ± 7.6 m ($N = 249$) and 26.3 ± 15.3 min ($N = 121$), respectively. Duration of a raiding trip was strongly correlated with the distance between the *Polyergus* nest and the target nest ($r = 0.758$, $N = 120$, $P < 0.0001$).

Weather conditions and occurrence of raiding trips

Figure 1 shows the occurrence of raiding trips of *P. samurai* in the Ecology Park in 1992. Raiding trips occurred from June 3 to September 3, but most frequently in late July. In central Japan, early June to mid-July is a long rainy season, which ended on 18 July in 1992. Qualitative weather conditions are also shown in Figure 1. Most raiding trips occurred on days with sunshine. Only 4 of the 56 days with trips were cloudy days. Raiding trips did not occur on rainy days. In Table 1, the average weather factors are shown relative to the occurrence of raiding. AT, RH, ST, and RE were significantly different between days with raiding trips and days without.

Table 1. Averages of climatic factors in days with or without raiding trips of *P. samurai* in the Ecology Park. Maximum air temperature at 1 m above the ground (AT) and maximum soil temperature at a depth of 10 cm (ST) from 12:00 to 17:00, relative humidity (RH) and atmospheric pressure (AP) at 14:00, and cumulative radiation energy from 12:00 to 17:00 were measured. The average ± S.D. are shown, and differences between two categories were compared with Mann-Whitney's *U* test

	AT (°C)	RH (%)	ST (°C)	AP (hPa)	RE (MJm^{-2})	N
Days with raids	30.4±3.0	60.8±7.7	29.4±3.0	1009.5±4.3	8.6±2.0	56
without raids	25.4±3.6	66.6±16.4	25.5±3.3	1009.7±5.5	5.5±2.6	41
Significance of difference	$P<0.001$	$P<0.03$	$P<0.001$	N.S.	$P<0.001$	

Observed patterns of raiding trips

In the Ecology Park, observed raiding trips could be classified into six patterns (Fig. 2): (1) Failure: a raiding swarm stops a raiding trip in progress and returns to its own nest without any attacks on *Formica* nests (N = 30: Fig. 2a). (2) Simple raiding: a raiding swarm attacks a single target nest only once and returns to its own nest (N = 191: Fig. 2b). (3) Continuous raiding: a raiding swarm continues past the first attack on a nest to raid a different target nest. In this case, raiders with booty from the first target nest return directly to their own nest, and only raiders without booty participate in the second raids (N = 10: Fig. 2c). (4) Split raiding: an outward raiding

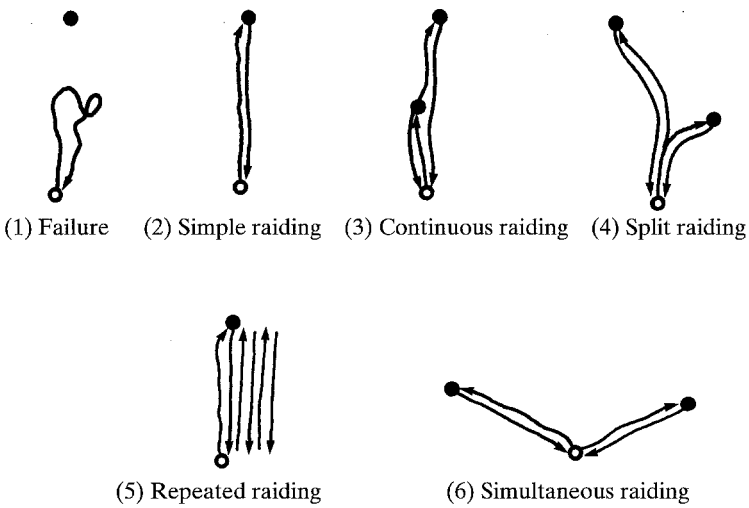

Figure 2. Observed patterns of raiding trips of *P. samurai* in the Ecology Park in 1992. O. P. *samurai* nest, ● F. *japonica*

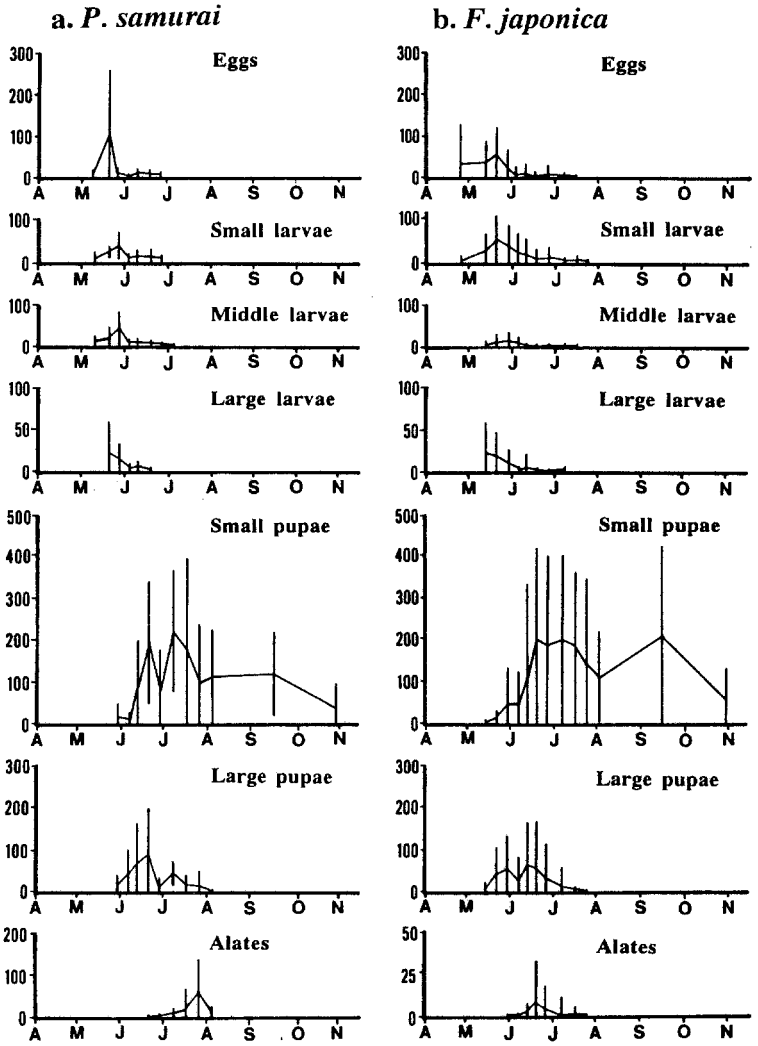

Figure 3. Seasonal production of broods in *P. samurai* (a) and its host *F. japonica* (b). The mean and S.D. are shown. Large and middle larvae are queen- and worker-destined size individuals, respectively. Small larvae are individuals that did not attain the worker-destined size. Numbers of examined colonies in each inspection are 3–6 for *P. samurai* and 9–109 for *F. japonica*

swarm splits into two different columns and the two resulting swarms each attack a different nest (N=6: Fig. 2d). (5) Repeated raiding: a raiding trip continuously repeats attack a different nest in a day (N=58: Fig. 2e). (6) Simultaneous raiding: two swarms leave simultaneously in two different directions and each attack a different target nest (N=4: Fig. 2f). On some occasions, a *Polyergus* colony showed a combination of two or three of these patterns, e.g., split raiding followed by simple raiding, etc.

Annual life cycles of the host and the parasite

Figures 3a and 3b show seasonal changes in brood production of *P. samurai* and its host *F. japonica* based on the photographic data. In all brood classes (eggs, larvae, pupae), *Formica* brood appeared about two weeks earlier than *Polyergus* brood. The start of raiding trips (June 3) coincided with the appearance of *Polyergus* pupae, and by that time most *Formica* nests had already produced pupae. However, as some *Formica* nests produced only reporductives by late June (Hasegawa and Yamaguchi, unpubl.), some raiding swarms in this season met with only reproductive pupae in target *Formica* nests. As mentioned previously, reproductive larvae, pupae, and adults were collected by some early raiding swarms, although most booty of raiding trips were worker pupae, even early in the season.

Mating flights and behavior of newly dealated queens

Nuptial flights occured on July 26 and 30 and August 6. Each day was sunny, clear, and windless. From 10:00 to 11:30, many alates appeared on the ground and ran around the nest entrances. Both sexes climbed to the tops of grass blades near the nest and flew into the sky. Mating near the nest was never observed. While mating activity continued, *Formica* workers tried to pull the *Polyergus* alates back into the nest. In the Ecology Park, seven *Polyergus* colonies, which produced reproductive pupae, released alates simultaneously on the same day.

In the afternoon of July 26, we made some behavioral observations of newly dealated queens following a nuptial flight. A total of three dealate *Polyergus* queens (probably newly dealated females) tried to enter the largest *Polyergus* nest in the Ecology Park. The first queen was accepted easily by the slave *Formica* workers and entered the nest at 15:07. The second queen was found on a grass blade near the nest at 15:15 and when pursued by a slave *Formica* worker, she fell to the ground. The fate of this queen is not known. The third queen was found on the ground near a nest entrance at 15:26. At 15:29, many *Polyergus* workers poured out from another nest entrance and ran around the nest. At this moment, the dealate queen quickly ran to the nest entrance and tried to enter it. However, a *Formica* worker found the queen and grasped her appendages, many *Formica* workers clustered around her a few seconds later. The observer (E.H.) picked up the cluster to save the queen, but found that it consisted only of *Formica* workers grasping each other's appendages. Whether the queen succeeded in entering the nest is unknown. This trouble seemed to have no effect on the raiding acitvities of resident *Polyergus* workers.

On a different occasion, we observed another kind of behavior of a dealate queen. On August 15, a raiding trip started from a *Polyergus* nest at 14:38. After the last *Polyergus* raider in the swarm left the nest (at 14:50), the observer (E.H.) noticed a dealate queen following the raiding column. She was on a grass blade above the raiding swarm and came down to the ground and traced the swarm shortly after the last *Polyergus* worker passed. The queen then ran along the side of the swarm up to the middle of the column and climbed a grass blade again. Although similar behavior was repeated during the raiding trip, the queen never made contact

with the *Polyergus* raiders. While the *Polyergus* raiders rushed into the target *Formica* nest, the queen climbed a grass blade hanging over the nest entrance. When most of the raiders had entered the target nest, the queen descended and went into the nest. She was not seen in the returning swarm.

Discussion

Duration of raiding season

Raiding trips of *P. samurai* started on June 3 in the study site, which coincided with the appearance of pupae in *Polyergus* colonies (Fig. 3a). By this time, many *Formica* nests already contained pupae (Fig. 3b). Kwait and Topoff (1984) reported that scouting activity of *P. lucidus* also started soon after the appearance of the first *Polyergus* larva in the nest. The host nests of *P. lucidus* likewise contained worker pupae by this time. Thus, *Polyergus* species seem to use the appearance of a particular stage of brood as the starting signal for the raiding season.

Mori et al. (1991) reported that the occurrence of raiding trips in *P. rufescens* correlated with air temperature. Topoff et al. (1984, 1985c) showed that *P. breviceps* used optical stimuli as location cues. There were significant differences in several climatic factors between days with and without raiding trips by *P. samurai* (Tab. 1). However, these climatic factors were strongly correlated with each other, and it is impossible to discriminate the most important factors in this study. Thus, more detailed examinations are required to elucidate cues for raiding trips in *P. samurai.*

The signal of the end of the raiding season was ambiguous in this study. As many *Formica* nests continued to produce pupae until late October, the lack of pupae in target nests is probably not the cause of the termination of raids in early September. Topoff (1985) showed that experimental overfeeding of a *P. breviceps* colony significantly reduced the frequency of raiding trips in the season. In another paper, Kwait and Topoff (1984) argued that as large proportions of robbed pupae were eaten in a laboratory *P. lucidus* colony, slave raiding in *Polyergus* species may represent a predatory behavior. If slave raids represent foraging activity in *Polyergus* colonies, the duration of the raiding season may be determined by the resource requirements of each colony. In *P. samurai*, the duration of raiding activities was markedly different between colonies (Hasegawa and Yamaguchi in prep.). Detailed analyses of the relationships between duration of raiding season, number of acquired slaves, and brood production in each colony may resolve this question.

Mating and behavior of newly dealated queens

Including this study, mating behavior in four of the five *Polyergus* species is known at present. Only a short report exists on the biology of *P. nigerrimus* (Marikovsky 1963). Since almost nothing is known about this species, we have excluded it from the following discussions. Mass nuptial flights are conducted by *P. rufescens* (Mori

et al. 1991), *P. samurai* (this study), and *P. lucidus* (Talbot 1968, Marlin 1971). Mating near the nest with multiple males has been reported for *P. lucidus* (Marlin 1971). However, mating on the ground was not observed in *P. rufescens* (Mori et al. 1991) and *P. samurai* (this study). Alate females of *P. breviceps* mate with a single male in a raiding swarm, then shed their wings and follow the swarm in order to enter the target *Formica* nest (Topoff and Greenberg 1988). Thus, mating systems seem to differ between the species.

Intrusions of dealate queens into host nests with raiding swarms were also observed in *P. lucidus* (Marlin 1968, Talbot 1968, Kwait and Topoff 1984). *P. rufescens* (Mori et al. 1991), and *P. samurai* (T. Sakai unpubl. and this study), although many new queens of *P. samurai* seem to intrude upon *Formica* nests independently (T. Sakai pers. com.). This presents an interesting problem. Apparently, in the case of *P. breviceps,* dealate queens within raiding swarms must be kin of raiding *Polyergus* workers. The queens of *P. rufescens* are also likely to be kin of the raiding workers because the dealate queen settled among the raided workers (Mori et al. 1991). In *P. samurai*, however, there is a possibility that dealate queens following raiding trips are not kin to raiding workers, and, if so, *P. samurai* exploits the labor force of an alien colony of the same species in addition to its interspecific parasitism on the host species. This situation has been indicated for *P. lucidus* by the paint-marking method (Kwait and Topoff 1984). Genetic analysis using allozyme polymorphism or DNA fingerprinting would better demonstrate kinship between the raiding workers and queens in *Polyergus* species.

Chemical techniques for raiding

The observations on a dealate queen that tried to enter a *Polyergus* nest are interesting from the viewpoint of chemical ecology. In the slave-making ants, raiders use chemical substances (known as propaganda substances) to disrupt the organized resistance of host species (Regnier and Wilson 1971). Confusion shown by the *Formica* workers in this study may be caused by some secretion from the *Polyergus* queen. In newly mated queens of *P. breviceps*, some chemicals from the Dufor's gland have been used at intrusion into *Formica* nests (Topoff et al 1988). In addition, *P. samurai* workers seem to chemically deceive the slave *Formica* workers by acquiring a cuticular hydrocarbon profile from the nursing slave workers (Yamaoka 1990). Detailed analysis of substances from each gland and bioassays for their functions are needed to examine the chemical technique used by *Polyergus* species.

In *P. breviceps*, raiding swarms deposit some chemical substances on the ground during outward trips and return to the nest following this trail (Topoff et al. 1984). Existence of a chemical trail has also been suggested for other *Polyergus* species (Talbot 1967, Mori et al. 1991). Until now, however, there was no description of the marking behavior in the genus *Polyergus*. In *P. samurai*, many individuals showed a characteristic behavior before starting a raiding trip, i.e., applying their tarsi to the terminal part of the abdomen. This behavior may be a way of trail marking, because raiders could trace the substance laid on the ground from the legs. However, this behavior was too rapid to determine the precise position to which tarsi were held. *Polyergus* species have a pigidial gland between the 6th and 7th abdominal tergites

(Hölldobler 1984), in addition to the poison and Dufour's glands which penetrate the anal opening. Chemical analysis of the substances from these glands is required to learn the origin and function of the trail substance of *P. samurai.* Therefore, knowledge of chemical communication techniques of the host and parasite are especially important to understand complex social interaction in host-parasite systems of ants.

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