Territoriality in a Queenless Ant, *Pristomyrmex pungens* (Hymenoptera: Myrmicinae)

Kazuki Tsuji and Yosiaki Ito

Laboratory of Applied Entomology and Nematology, Nagoya University, Chikusa-ku, Nagoya 464, Japan

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Workers of a queenless, thalytokous, worker-reproducing ant, *Pristomyrmex pungens* defend their nests, food resources (aphid colonies) and recruitment trails against workers of other conspecific colonies as well as against other ant species. The hypothesis that queens contribute colony specific odor as an intercolonial discrimination mechanism cannot apply to this species. Roles of environmental odor and genetically determined odor of workers should be evaluated in future.

INTRODUCTION

Colonies of *Pristomyrmex pungens* Mayr (Mirmicinae), a common terrestrial ant in Japan, lack a queen, and rarely produce males (*Teranishi*, 1929). A recent study (*Ito* et al., 1984) suggested that this species possibly reproduces completely thalytokously.

Nevertheless, only a few behavioral studies have been made so far on this species (*Teranishi*, 1929; *Morisita*, 1939a, b, 1941). *Morisita* (1939a, b) reported that workers of this species recruit more workers to colonies of honeydew-producing aphids on trees, and defend their foraging places against other ant species. Whether or not the shoots of plants occupied by *P. pungens* are defended against individuals of the same species belonging to other colonies is, however, not yet known. This paper reports the aggressive behavior of *P. pungens* workers toward other colony members, that is, the territoriality of this species.

MATERIALS AND METHODS

Workers belonging to the same or other colonies of *P. pungens* were released onto seedlings of a herb, *Artemisia vulgaris*, which had been occupied by a colony of *P. pungens* collecting honeydew from an aphid, *Metopeurum kuwayamae* (*Takahashi*) (Fig. 1). These workers were collected from an experimental field in Nagoya University, Furo-cho, Nagoya, and from a bush in Yagoto, Nagoya, on the day before the experiments. Workers belonging to colonies shown in Table 1, except MA-02 and MB-02, were collected in a plastic box by shaking *Artemisia vulgaris* plants, while ants of Colony MB-02

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were collected by the same method from a mulberry tree. Ants of Colony MA-02 were collected with a sucker from their recruitment band.

All the collected individuals were kept in the laboratory (25°C, 20–25 hr) before release. The ants were fed nothing, but a piece of wet absorbent cotton was offered to them in the laboratory. Individuals collected were marked with white paint (Sakura Paint Marker) on their gasters. On the day following collection, these individuals were released with tweezers or a fine brush on the top of Artemisia plants, where workers of Colony MA-01 were foraging from aphid colonies. Observations were made for 5 min after the release, and each combination was made of 10 replications except for Colony MA-01 (control). We avoided direct handling of ants as far as possible. Tweezers and brushes were kept clean.

Distribution of places where territorial defense took place was investigated by introducing alien workers at points surrounding the ‘nest’ of Colony MA-01. (This species does not make a permanent subterranean nest, but rears immatures in crevices. The colonies sometimes move to other sites. We call such a place a ‘nest’.) The points at which individuals were released were, A: foraging sites (Artemisia plants), B: trails, and C: the area around the trails and the nest (Fig. 1).

RESULTS

Figure 2 shows classification of behavioral sequences of contests when conspecific workers of the same or different colonies (‘intruders’, hereafter) were released on Artemisia plants on which workers of Colony MA-01 attended aphid colonies. Category 5 in Fig. 2 represents the strongest attack by the workers of Colony MA-01 (‘owners’, hereafter). When an intruder approached a colony of aphids, an owner which was receiving honeydew from aphids or working around the colony darted toward the intruder and bit its body. Then the other owner individuals joined in the attack. In these
cases, attacks by the owners were mainly made by biting with the mandibles, but the gaster of the owner was sometimes bent to deliver her sting to the intruder.

The intruders' responses to the attack were variable. Some of them ran away, some counterattacked with the tips of their gasters, or put their mouths to the tips of their gasters bending their bodies. The last behavior is similar to a posture of the transportee during adult transport in many ants (Wilson, 1971), and seems to be a submissive behavior. In all cases of Category 5, however, intruders were carried out by the owner down to the ground. In Category 4, the behavioral sequence was the same as Category 5 except that the intruder fell down from the plant. In Category 3, although one or some owner individuals attacked the intruder and bit her, the attacks soon ceased and were followed by gentle grooming of the intruder's body. In Category 2, the owner contacted the intruder and then groomed the latter. In Category 1, we could not see any difference in the owner's response from that seen between owner individuals.

Table 1 shows differences in responses of owners toward released individuals of the same colony and that of other colonies. When the intruder was a nestmate, most responses were those of Categories 1 to 3. But all the cases of introduction of alien workers escalated to Categories 4 or 5 within 5 min. Only in the case where individuals of the same colony were introduced did the initial attacks change to grooming (Category 3).

Table 1 shows that there were significant differences in owners' responses between cases where intruders were members of the same colony (MA-01) and where they were taken from other colonies. Although even workers of the same colony were often bitten by the owner, this might, in part, be due to the effect of handling of the introduced individuals. Despite this, however, difference in behavior toward workers of the same and different colonies was notable, suggesting that this species defends at least some foraging sites as territory against other conspecific colonies.

Table 2 shows that the marking had no influence on the intensity of attacks.

When we released workers of a different colony (intruders) onto the nest, or trails which had been formed on the ground or on the wall of buildings by workers of Colony

Table 1. Responses of P. pungens workers attending an aphid colony to conspecific intruders.
Numerals are frequency of each act

<table>
<thead>
<tr>
<th>Colony from which intruders were taken</th>
<th>Kind of response</th>
<th>Type I&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Type II&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(1)  (2)  (3)  (4)  (5)</td>
<td>N</td>
<td>A</td>
</tr>
<tr>
<td>MA-01&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4   6   23   4   2</td>
<td>10</td>
<td>29 c</td>
</tr>
<tr>
<td>MA-02</td>
<td>0   0   0   1   9</td>
<td>0</td>
<td>10 c</td>
</tr>
<tr>
<td>MB-01</td>
<td>0   0   0   2   8</td>
<td>0</td>
<td>10 c</td>
</tr>
<tr>
<td>MB-02</td>
<td>0   0   0   0   10</td>
<td>0</td>
<td>10 c</td>
</tr>
<tr>
<td>MB-03</td>
<td>0   0   0   2   8</td>
<td>0</td>
<td>10 c</td>
</tr>
<tr>
<td>Y-1</td>
<td>0   0   0   0   10</td>
<td>0</td>
<td>10 c</td>
</tr>
<tr>
<td>Y-2</td>
<td>0   0   0   3   7</td>
<td>0</td>
<td>10 c</td>
</tr>
</tbody>
</table>

<sup>a</sup> MA-01: Individuals of the owner colony (control).
<sup>b</sup> See Fig. 2.
<sup>c</sup> For statistical test, results were arranged in two combinations. Type I: N = Categories 1 + 2, A = Categories 3 + 4 + 5. Type II: WA = Categories 1 + 2 + 3 + 4, SA = Categories 5. Different signs (a, b) show significant differences in Fisher's exact probability test (P<.001).
Table 1. Results of test on effect of marking

<table>
<thead>
<tr>
<th>Colony of introduced individuals</th>
<th>Mark</th>
<th>Behavioral category</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>WA (1+2+3+4)</td>
</tr>
<tr>
<td>1) MA-01 (control)</td>
<td>+</td>
<td>9</td>
</tr>
<tr>
<td>2) MA-01 (control)</td>
<td>−</td>
<td>9</td>
</tr>
<tr>
<td>3) MB-01</td>
<td>+</td>
<td>2</td>
</tr>
<tr>
<td>4) MB-01</td>
<td>−</td>
<td>0</td>
</tr>
</tbody>
</table>

|                                 | SA (5)|                    |
|                                 |      | 2 a                 |
|                                 |      | 0 a                 |
|                                 |      | 8 b                 |
|                                 |      | 10 b                |

Different signs show significant difference in owner response (P<.01).

MA-01, workers of this colony always attacked the intruders. The defensive behavior seen on these occasions was similar to that seen on the *Artemisia* plants. But groups of ants on trails scattered if the observer disturbed them. When trail-ants scattered, they did not react to other ants which approached the trail. On the other hand, groups of ants attending aphid colonies were rarely scattered with slight disturbance by man.

Some ants (scouts) of Colony MA-01 were walking alone at places near their nest or trails (Fig. 1, C). The density of ants was very low here as compared with trails and foraging sites. When they met ants of another colony or another species, they usually ignored them. In only a few cases, workers of Colony MA-01 pursued conspecific aliens, and then for only a short period.

**DISCUSSION**

The nest of Colony MA-01, which was used for observation of territoriality, lay a space between the wall of a building and a sewer pipe, more than 10 m apart from other conspecific colonies. The colony used the same trails and same aphid-plants from June to October, 1984. However, the colony changed the nest site at least three times before and after the above-mentioned period. Thus, at least in this season (the major part of the reproductive season), the foraging pattern of this species might be *Öster* and *Wilson*'s (1978) Type III foraging with persistent pheromonal trails for long lasting food sources.

Results presented here show that *P. fungens* workers defended their aphid-plants and their trails from conspecific aliens; that is, this species has territoriality as do other queen-right ant species. According to the classification by *Levings* and *Traniello* (1981), the type of defence presented here is the intra- and interspecific defense of nest and persistent resources.

*Hölldobler* and *Michener* (1980) listed the following four possible mechanisms which may enable distinction of nestmates from alien workers in social insects:

1. Individuals produce discriminators which serve for individual or group recognition.
2. Individuals produce substances which are distributed among all colony members to produce a collective discriminating substance characteristic of the colony.
3. The queen produces her discriminators which are distributed to the workers to produce the colony odor.
4. Environmental odors (for example, from food and/or nest material) can be the source of colony specific discriminating substances.
However, they stressed that the 3rd mechanism, the queen odors, might be most important in higher ant species (see also HÖLDDOBLER and WILSON, 1977).

In _P. pungens_, the 1st, 2nd and 4th mechanisms are possible, but the 3rd cannot apply because this is a queenless ant. Although TERANISHI (1929) and ITOW et al. (1984) reported the existence of ergatoid-queens, the contribution of ergatoid-queens for colony odor is hardly conceivable because many colonies lack them or have many ergatoid-queens (ITOW et al., 1984). If the colony of this species is genetically uniform, as expected by ITOW et al. (1984), it may be possible there is inter-colonial discrimination by the 1st and 2nd mechanisms. To ascertain these mechanisms, estimation of intra- and intercolonial relatedness by, for example, electrophoretic patterns might be necessary.

_P. pungens_ workers carried intruders of the same species out of their foraging sites. Are they abandoned at places far from the territory, or are they eaten by members of the owner colony, or do they become colony members or slaves of the owner colony? This must be studied in future, in relation to the reproductive strategy of this species.

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REFERENCES


