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Encounter-induced hostility to neighbors in the ant *Pristomyrmex pungens*

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Field observations have demonstrated that internest hostility is negatively correlated with the distance between nests in the Japanese queenless ant, *Pristomyrmex pungens*. This runs counter to the "dear enemy" phenomenon. This result led us to hypothesize the existence of encounter-induced hostility in *P. pungens*. We created "neighbor(s)" and "stranger(s)" by an experimental method and tested the ant's ability to discriminate the neighbors from strangers. The results indicated that the ant could distinguish the neighbors from the strangers and displayed significantly stronger hostility toward the neighbors. The recognition of neighbors was quickly established after a few encounters and was maintained for at least 10 days after the most recent encounter. Nest mates without direct encounter experience with neighbors did not show hostile behavior toward neighbors. These findings suggest that information about neighbors (probably colony odor) is not transmitted to nest mates within the colonies. Aggressiveness toward the neighbors appears to be caused and maintained on the basis of individual memories from direct contact. It may be adaptive for a species that changes nest sites frequently to discriminate strangers from neighbors and selectively attack the latter. *Key words:* aggression, ants, dear enemy effect, internest distance, learning, *Pristomyrmex pungens*, territorial behavior. *[Behav Ecol 14:713–718 (2003)]*

Many animals have been observed to defend established territories (containing food resources, nesting sites, or other resources) through fighting behaviors or threats (Wilson, 1975). The residents often behave aggressively toward intruders of the same or different species within their territory. However, conspecific neighboring individuals often react to each other less aggressively than to distant individuals once their territorial boundaries have been established (Wilson, 1975). Through such a "dear enemy" effect, residents can avoid escalated contests with neighbors through repeated encounters, or they can at least minimize the cost of fighting (Wilson, 1975). Previous studies have reported this phenomenon in many species of birds, mammals, fish, and amphibians (Ydenberg et al., 1988). It has also been detected in some ant species (Heinze et al., 1996; Jutsum et al., 1979; Langen et al., 2000; Stuart, 1987), although many ant species exhibit strongly hostile behavior toward both neighboring and distant colony members (Hölldobler and Wilson, 1990).

However, colonies of some social insect species, such as the harvester ant, *Pogonomyrmex barbatus* (Gordon, 1989) and the termite *Nasutitermes corniger* (Dunn and Messier, 1999), have been shown to react more strongly to conspecific neighboring colonies than to distant ones. These reverse dear enemy effects may occur in stable territories with greatly variable resources, in which competition may occur between neighboring colonies for the resources but little competition occurs between distant colonies (Dunn and Messier, 1999; Gordon, 1989). Workers are most likely to encounter workers of neighboring colonies near the food resources, and thus they may learn the odors of their neighbors during foraging. However, it remains to be investigated how the workers learn about neighboring colony members.

Japanese queenless ants, *Pristomyrmex pungens*, have been observed defending their nests, food resources, and recruitment trails against other conspecific colony members (Tsuji, 1988a; Tsuji and Itô, 1986). However, they do not necessarily fight with other conspecific colony members in neutral places a short distance from their nests, food resources, or recruitment trails. We observed the behavior of workers from nearby and distant colonies when they encountered one another to determine whether this territorial strategy represented a dear enemy phenomenon. Our observations demonstrated that the intensity of internest hostility was negatively correlated with the internest distance. This result suggested the presence of an underlying mechanism of encounter-induced hostility. We then experimentally created neighbors that were workers of previously encountered colonies and strangers that were workers of distant colonies that had not been encountered previously and tested for discrimination of the neighbors from the strangers.

METHODS

Pristomyrmex pungens

P. pungens inhabits areas under fallen leaves or decayed logs on forest floors in Japan. The workers can reproduce by thelytoky: females reproduce only daughters by parthenogenesis and rarely produce males (Itow et al., 1984; Mizutani, 1980; Tsuji, 1988c; Tsuji and Itô, 1986). The colonies include from thousands to hundreds of thousands of individuals. They relocate their nesting sites frequently, about once every 2 weeks during the warmer seasons (Fujita, personal communication; Tsuji, 1988b).

Experiment 1: internest distances and hostile behaviors

Collection and mapping of nesting sites

We collected 10 colonies of *P. pungens* from an experimental field at the Tokyo University of Agriculture and Technology in

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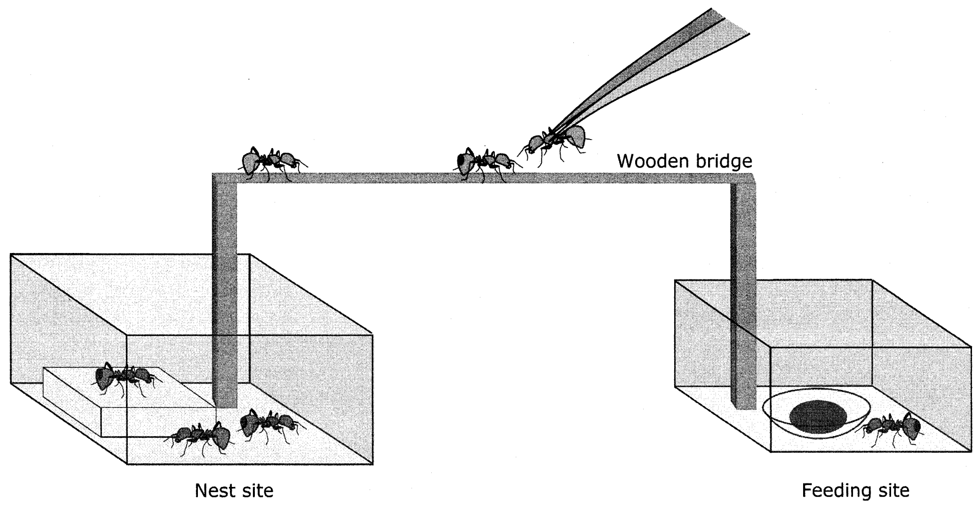

Figure 1
Experimental setup for the encounter treatment. Encounters were performed by having a strange worker come in contact with another worker on the bridge.

Fuchu, Tokyo, Japan, in August 1998, during this ant's most active season. Workers of these 10 colonies fought each other strongly when they were experimentally put on the recruitment trails of other colonies. We mapped the nesting sites of all the colonies in the experimental field to determine the distances between colonies. The collected ants were kept in plastic cases (40 cm × 30 cm × 30 cm deep) and reared at 28°C under a 16-h light and 8-h dark photoperiod. A diet of 10% honeydew and boiled egg yolk was supplied every other day.

Arena test of hostility

We picked two workers, each from a different colony, and transferred them to a Petri dish (3 cm diam, 1 cm high) and observed their behavior for 5 min (arena tests) to observe how workers react to other colony members in a neutral place away from their recruitment trail. We classified their behavior into one of the following two categories: (1) hostile behavior—either one or both of them bit their opponent; (2) nonhostile behavior—neither of them bit the other.

We observed almost all combinations of 10 colonies (43 pairs; 2 of a total of 45 possible combinations were not tested for hostile behavior because the number of collected workers in two colonies was inadequate). Five replicates were examined for each pair. The number of replicates with hostile behavior represented the hostility score for each pair. Hostility scores ranged from 0, where no hostile behavior was observed in any of the replicates, to 5, where hostile behavior was observed in all replicates. We analyzed the correlation between the hostility score and the intercolony distance by both the Spearman correlation coefficient and a randomization technique, the Mantel test ($n = 10000$; Sokal and Rohlf, 1995) to exclude effects of some colonies with generally more or less aggression. We also observed behavior between members of the same colony in control tests (five replicates for each of the colonies).

Experiment 2: encounter experiments

Collection

For the encounter experiments, we collected 11 colonies that were different from the 10 colonies for the experiment on internest distance and hostile behavior described above. Six colonies were collected in Kokubunji (original colonies A, B, D, G, H, and I), three in Mitaka (original colonies C, E, and F), and two in Fuchu (original colonies J and K), all in Tokyo prefecture, Japan. These three sites are about 3 km apart. The distances between colonies from the same site ranged from 150 to 400 m. These colonies are unlikely to have interacted with each other during the past few years because *P. pungens* relocates its nesting sites no farther than 15 m per year (Fujita Y, personal communication). Original colonies A, B, G, and J were collected in August 1999. The remainder was collected in June 2000. Each of the original colonies included about 10,000 individuals and was maintained as a stock colony for about 2 months. Groups of workers drawn from the original colonies were used in the following experiments; these groups are referred to as "experimental colonies" and labeled with the letter identifying the original colony from which they were taken.

Encounter procedure

We first randomly selected 1000 workers of original colony A and transferred them to the experimental cage (30 cm × 20 cm × 20 cm deep; experimental colony A) in 1999 to determine whether workers learn about the other colony members. The experimental cage was connected to the feeding site by a wooden bridge (40 cm long and 5 mm wide) over which the workers walked (Figure 1). The workers were allowed to get to the honeydew or egg yolk at the feeding site only by way of the bridge. We then picked up one worker from original colony B with forceps and held it so that it contacted a foraging worker of experimental colony A on its way to or from the nest site (encounter treatment; Figure 1). We halted the encounter treatment just before the workers started biting each other, which would have occurred within several seconds after the contact, and removed them. We changed the workers from original colony B every five encounter treatments with five different workers from experimental colony A. A total of 300 workers from experimental colony A were subjected to the encounter treatments. The encountered workers were subsequently marked with pink dots (Paint Marker, Mitsubishi Industries, Japan) on the back of their abdomens (they are hereafter referred to as "experienced workers") and returned to the experimental cage. Three hundred of the rest of the workers were picked up on the bridge and marked with blue dots (they are hereafter referred to as "nonexperienced workers") and returned to the experimental cage. The workers from original colony B used in the encounter treatments were removed and were not returned to their colony. The nest mates of encounter opponents' colonies were thereafter considered to be neighbors.

We subsequently performed 100 encounter treatments per day for the experienced workers of the experimental colony; the average number of encounters was 0.33 per individual per day. These treatments were performed every day for 7 days.

The encounter procedures were also performed with colonies B, C, D, E, and F as the territory owners and colonies A, D, G, I, and G as the opponents in 1999 and 2000 (Table 1). All of these procedures were performed about 1 month after the colonies were collected.

Arena test on hostility toward neighbors and strangers

Hostility toward neighbors. We tested the experienced workers from experimental colony A for hostile behavior toward their neighbors, original colony B, 2 h after the daily encounter treatment, using the same arena test method as the experiment of internest distances and hostile behaviors. The nonexperienced workers of experimental colony A were also tested by the same methods. Ten replicates (one worker per one replicate) were performed for both the experienced and nonexperienced workers. We examined all of the arena tests in the following blind manner. We marked 10 workers of the original colonies with the blue or pink dots 1 h before the arena tests and performed the tests in a random order that was not known by the experimenter. We removed the workers used in the arena test from both the experimental and original colonies. The tests were repeated every other day from the first to the seventh day (i.e., at the first, third, fifth and seventh day) of the encounter treatments, totaling 40 replicates (10 replicates/day $\times$ 4 days). Identical arena tests were performed with experimental colonies B, C, D, E, and F and original colonies A, D, G, I, and G as the neighbors.

Hostility toward strangers. To determine whether the experienced workers would simply be more aggressive toward members of other colonies, we carried out arena tests for the hostility toward members of other colonies that the experienced workers had never encountered (those members are hereafter referred to as "strangers") as a control test for the preceding experiment, hostility toward neighbors. We examined the hostile behavior of the experienced and nonexperienced workers of experimental colonies A, B, C, D, E, and F toward the members of original colonies E, G, E, I, G, and H as strangers. Ten replicates were performed for both the experienced and nonexperienced workers and were repeated at the third, fifth, and seventh day of the encounter treatments, totaling 30 replicates. We performed these tests at the same time (i.e., 2 h after the daily encounter treatment) and under the same conditions and the same protocol as the arena tests on the experiment of hostility toward neighbors described above.

We used logistic regression and likelihood ratio tests to compare the extent of difference between the hostility of experienced and nonexperienced workers toward neighbors with the difference between the hostility of the former and the latter toward strangers (Kasuya E, personal communication; Sokal and Rohlf, 1995).

Experiment 3: test for maintenance of hostility

In 1999 we determined whether the workers memorize their neighbors and how long they maintained their hostility toward neighbors. The experienced workers of experimental colony A were examined for hostile behavior toward the neighbor colony B every other day through arena tests for 13 days after the final encounter treatments. Neither the experienced nor nonexperienced workers used in the arena tests were returned to the experimental colonies.

Table 1
Combinations of treatments in encounter experiment

Experimental colony	Neighbors	Strangers
A	B	G
B	A	J
C	H	D
D	F	E
E	I	H
F	H	I

The experiment measured hostile behavior of experienced and nonexperienced workers toward neighbors and strangers. See text for collection sites.

Experiment 4: test for learning two neighbors

We also performed the experiments on hostility induction and the arena tests with experimental colony C as the territory owner and two other original colonies, H and K, as the neighbors (Nei.-1 and Nei.-2) to determine whether workers can learn two neighbors at the same time. We performed 100 encounter treatments for each of the two opponents per day for seven days with the experienced workers of the experimental colony. Ten replicates of the arena tests for hostility toward the two neighbors were examined every other day through the encounter treatments. We also carried out arena tests for the hostility of the experienced and nonexperienced workers toward a stranger (original colony D) as a control test.

Experiment 5: test for the effect of artificial marking

We marked five workers each from original colonies A, B, D, and F with both pink and blue dots to judge the possible effect of artificial marking on hostile behavior and examined intercolony hostility by the arena test. We also tested intercolony hostility between nonmarked workers of two original colonies. Twenty replicates were performed for each treatment in this test.

RESULTS

Experiment 1: internest distances and hostile behavior

The distance between the nesting sites of the colonies ranged from 8.1 to 94.1 m, with a median distance ($\pm$ interquartile range) of 37.6 $\pm$ 29.3 m. Hostility scores between the colonies ranged from 0 to 5, with a median ($\pm$ interquartile range) of 2.0 $\pm$ 2.8. No hostile behavior was observed among nest mates of the same colonies. The hostility scores between the colonies were significantly negative correlated with the internest distances (Spearman's coefficient of rank correlation: $r_s = -0.445$, $z = -2.636$, $n = 43$, $p < .01$; Mantel test, $p < .01$; Figure 2).

Experiment 2: encounter experiments

We combined all of the data throughout the experimental period for each experimental colony because the frequencies of hostile behaviors did not differ throughout the experimental period within each treatment of each experimental colony (logistic regression test for 12 experimental treatment, ns for each case, $n = 40$ for each case).

If experienced workers were simply more motivated to be aggressive due to the encounter treatment, they would exhibit

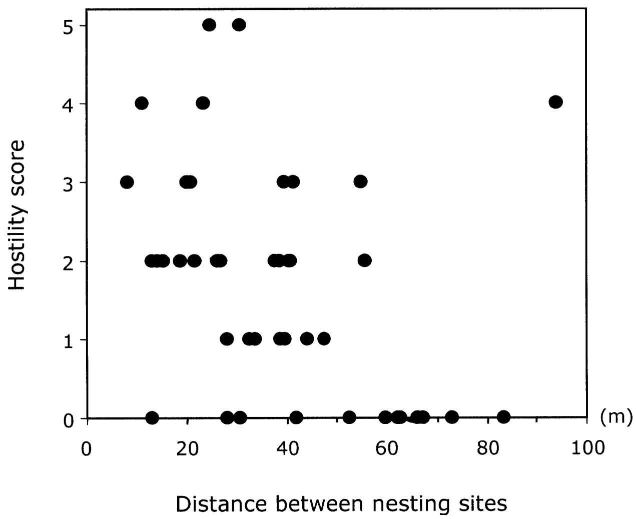

Figure 2
Hostility scores versus internest distance (n = 43). For units of hostility score, see text (experiment 1).

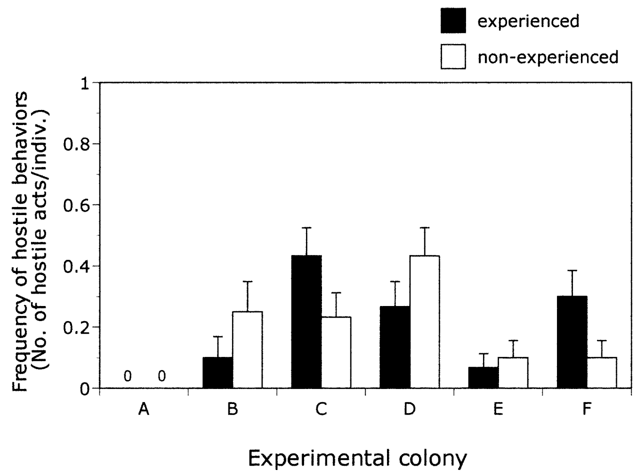

Figure 4
Frequency of hostile behavior of experienced workers (solid bars) and nonexperienced workers (open bars) of experimental colonies toward workers of stranger colonies (experiment 2); n = 30 for each experiment; bars indicates SEs.

more hostile behavior toward not only neighbors but also to strangers than nonexperienced workers. However, the extent of the difference between hostility of experienced and nonexperienced workers toward neighbors was significantly greater than that of the difference between hostility of the experienced and nonexperienced workers toward strangers (logistic regression and likelihood ratio test; $\chi^2_1 = 4.46$, $p <$ .05; Figures 3 and 4). This result indicates that the experienced workers discriminated between the workers of neighbors and strangers and exhibited more hostile behavior toward neighbors than toward strangers. A high frequency of hostile behavior toward neighbors arose at the first and third experimental days and was maintained throughout the experimental period, most notably in each of experimental colonies A, C, and D (frequency of hostile behavior of experienced workers [nonexperienced workers]; 0.3 [0.1] and 0.8 [0.1], 0.5 [0.1] and 0.4 [0.3], 0.3 [0.1] and 0.4 [0] in the first and third experimental days in experimental colonies A, C, and D, respectively).

Experiment 3: maintenance of hostility

The frequency of hostile behavior of the experienced workers was maintained at a high level 1 day after the last encounter treatment and then declined significantly after 1 day (logistic regression test, $p < .05$ in day 1 vs. each of the rest; Figure 5). However, the experienced workers exhibited a higher level of hostile behavior than nonexperienced workers from day 4 to day 10 (logistic regression test, $\chi^2_1 = 4.1$, $p < .05$). They maintained hostility at least 10 days after the last encounter treatment. The hostility score on the 13th day did not differ from that of the nonexperienced workers test on the same day (Figure 5).

Experiment 4: test for learning two neighbors

The experienced workers of experimental colony C exhibited hostile behavior toward the workers of both of the two neighbors more frequently than did nonexperienced workers (chi-square test and sequential Bonferroni test: Nei.-1,

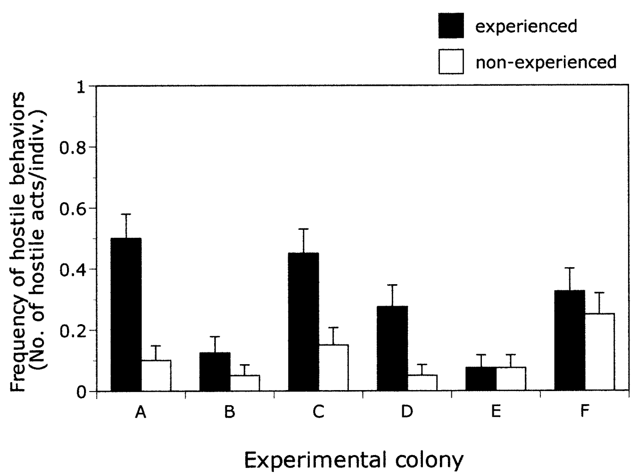

Figure 3
Frequency of hostile behavior of experienced workers (solid bars) and nonexperienced (open bars) workers of experimental colonies toward workers of neighbor colonies during the encounter treatments (experiment 2); n = 40 for each experiment; bars indicates SEs.

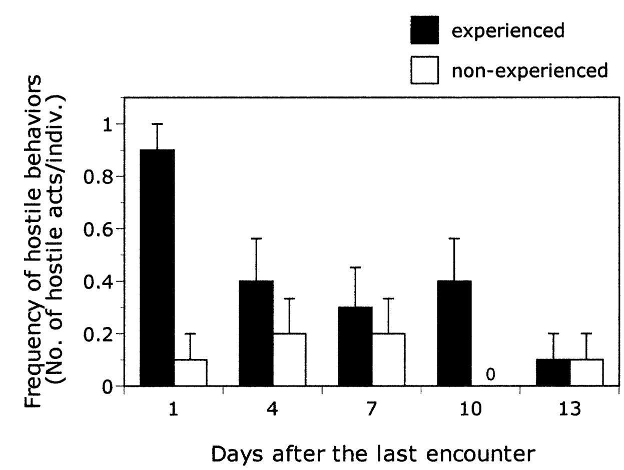

Figure 5
Frequency of hostile behavior of experienced (solid bars) and nonexperienced (open bars) workers of experimental colony A toward workers of opponent colonies after the last encounter (experiment 3); n = 10 for each day.

$\chi^2_1 = 10.59$, $p = .001$; Nei.-2, $\chi^2_1 = 4.78$, df = 1, $n = 40$, $p = .028$; Figure 6). They did not exhibit hostile behavior toward workers of a stranger colony more frequently than nonexperienced workers (chi-square test: $\chi^2_1 = 0$, df = 1, $n = 30$, ns; Figure 6). These results suggest that the experienced workers are able to simultaneously discriminate workers of two neighbors from a stranger. However, the extent of the difference between the hostility levels of experienced and nonexperienced workers toward the two neighbors was not significantly greater than the difference between hostility of experienced and nonexperienced workers toward the stranger (logistic regression and likelihood ratio test; $\chi^2_1 =$ 2.15, ns) because data from a single colony were not sufficient for this statistical analysis.

Experiment 5: test for the effect of artificial marking

There were no significant effects of artificial marking on hostility because there was no significant difference between the hostility scores of marked and unmarked ants from two original colonies (frequency of hostile behavior out of 20 replicates pooled from 2 colonies was 4 and 3 for marked and unmarked workers; Fisher's Exact test, $p = .99$, $n = 20$, ns). This held true for the experiments involving encounters between workers with pink and blue marks (Fisher's Exact test, $p = .99$, $n = 20$, ns)

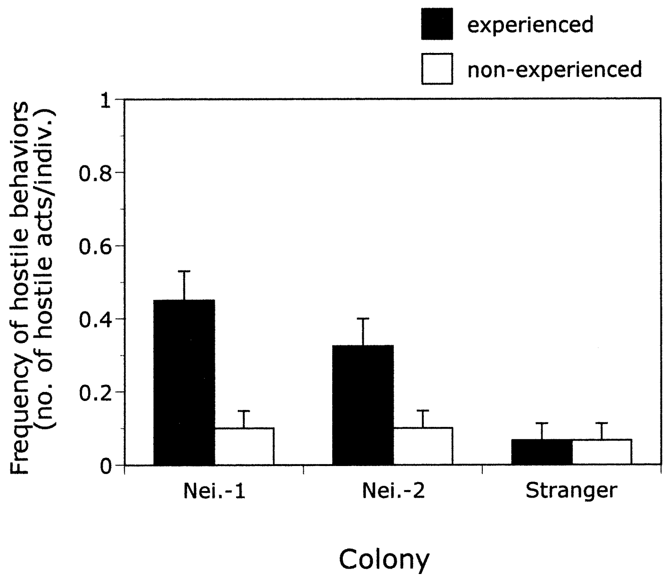

Figure 6
Frequency of hostile behavior of experienced (solid bars) and nonexperienced (open bars) workers of experimental colony C toward two neighboring colonies (Nei.-1 and Nei.-2; $n = 40$ for each experiment) and a stranger colony ($n = 30$; experiment 4).

DISCUSSION

P. pungens workers could distinguish the workers of other colonies that they had experienced, (i.e., neighbors) from workers that they had not experienced (i.e., strangers), and they became more aggressive toward neighbors (Figures 3 and 4). They exhibited hostility toward neighbors after the first experimental day, and the effect persisted over at least seven encounters. The results also indicated that they remained hostile toward workers from the familiar colonies for 10 days after the most recent encounter treatments (Figure 5). This rapid occurrence of hostility and duration of memory may be related to the ecology of *P. pungens.* The colonies of this species relocate nests, on average, every 2 weeks (Fujita, personal communication; Tsuji, 1988b). They may be required to learn about their competitors as soon as they settle at a new nesting site to effectively defend their food resources. Ten days of memory maintenance may be sufficient since they always relocate nest sites within 2 weeks.

Experienced workers can apparently learn the characteristics of two encountered colonies at the same time, although data from only one experimental colony are not sufficient for a statistical analysis (Figure 6). The ability to learn two or possibly more colonies concurrently may be necessary because colonies are likely to have several neighboring colonies in the field.

It is notable that nonexperienced workers of the experimental colonies did not show hostility toward the neighbors. This suggests that information was not transmitted from experienced workers to nonexperienced workers in the experimental colonies. Transmission of learned information among workers would probably be difficult because it would require a highly elaborate communication system, such as the dance language of honeybees (Seeley, 1997). However, huge numbers of workers are often observed in intense fights with neighboring colonies in the natural populations of this species (Tsuji and Itô, 1986). Not all recruited nest mates may learn information (probably colony odors) about neighboring colonies. The experienced workers may simply emit alarm pheromones after repeated encounters with the same neighboring colony instead of transmitting the learned information; these alarm pheromones would provoke the aggression of nest mates and probably newly recruited nest mates as well. This seemingly adaptive behavior might be regulated by simple decision-making rules of individual workers, which rely on individual memories and respond to information from their direct contacts. Our study is consistent with the idea that collective behavior in social insect colonies is based on a simple regulatory system rather than on a complex individual system (Bonabeau et al., 1997; Seeley, 1997; Tsuji et al., 1999).

This study has presented evidence demonstrating that neighboring colonies of *P. pungens* fight more aggressively with each other than with distant colonies (Figure 2). This suggests that a hostile social relationship opposite to the dear enemy relationship can occur, as is the case with the harvester ant *Pogonomyrmex barbatus* (Gordon, 1989) and the termite *Nasutitermes corniger* (Dunn and Messier, 1999). Those authors argued that the colonies would compete with their neighbors rather than strangers for the possession of newly available resources when their territories were stable but contained greatly variable resources (Dunn and Messier, 1999; Gordon, 1989). Strangers from distant colonies may be transient and will not forage within the territories of other distant colonies when the territory is stable. In contrast, neighbors are likely to frequently invade adjacent territories and therefore compete for new resources.

The colonies of *P. pungens* do not have stable territories for an extended time (Fujita, personal communication; Tsuji, 1988b) and cannot be directly compared with territorial animals that have been used to test the dear enemy hypothesis. However, the workers of *P. pungens* can learn the characteristics of neighbors and discriminate them from strangers. The learning mechanism may be similar to that of many species that exhibit the dear enemy phenomenon. Whether they exhibit hostility toward neighboring or stranger individuals may depend on both the benefit (e.g., food resource) and cost (e.g., damage from fighting) that result from competition among them.

The colonies of *P. pungens* compete with neighbors for unstable food resources, such as insect carcasses and honeydew of aphids, once they have settled at a nesting site (Tsuji, 1988b; Tsuji and Itô, 1986). Because *P. pungens* colonies recruit large numbers of workers quickly into the food area along their trail, neighbors would always be a menace to food resources (Tsuji K, personal communication). However, a single worker from a stranger colony may have simply strayed from a distant colony or be merely passing a focal colony's territory. It would therefore not benefit *P. pungens* workers to attack a separated stranger at the first encounter. Furthermore, *P. pungens* workers always scout for new food resources alone in a neutral place near their nests or trails. It could be dangerous and costly for only one forager to attack a separated stranger. Tsuji (personal communication) suggests the possibility that trail-making ant species generally show aggressive behavior toward neighbors rather than strangers.

The frequency of hostile behaviors varied among the experimental colonies (Figures 3 and 4). Workers of some colonies showed less aggressiveness than those of other colonies. This result suggests that some factors other than encounter experience, such as physiological conditions, activity of workers, age structure, or colony size, may influence whether workers exhibit hostile behavior toward members of different colonies. These factors may account for the variation in hostility that was not explained by the distance between nesting sites (Figure 2).

The present study demonstrated that workers of social insect species are able to learn and distinguish competitors from strangers, just as some birds, mammals, and other vertebrates can. *P. pungens* is thus a suitable model species for further investigating the role of individual learning and memory in the recognition mechanisms found in the adaptive behavior of animals.

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