Nestmate Recognition and Intercolonial Aggression in the Crazy Ant, *Paratrechina longicornis* (Hymenoptera: Formicidae)

by

Say-Piau Lim[1], Alexander Shu-Chien Chong & Chow-Yang Lee[1,2]

ABSTRACT

This study focuses on two factors affecting nestmate recognition in the crazy ant, *Paratrechina longicornis* (Latreille) i.e., diet and queen dominance. Results indicated that diet affected the ability of these ants in recognizing their former nestmate, after they had been subjected to a different diet for defined periods of time. Queen dominance experiments were divided into two sections: (1) effect of the absence of queens, and (2) effect of alien queens. The role of queens in forming colonial odor in *P. longcornis* appears negligible. In addition, presence of alien queens did not have an effect on worker ants that were placed together for a period of time. No aggression was observed when these workers were reintroduced back to their former nestmates. Intercolonial aggression experiments, however did demonstrated aggression between different field-collected colonies of *P. longicornis*.

Keywords: *Paratrechina longicornis*, nestmate recognition, queen dominance, diet, intercolonial aggression.

INTRODUCTION

The importance of nestmate recognition and discrimination in social insects has been widely accepted (Holmes & Sherman 1982; Fletcher & Michener 1987; Hepper 1991; Pickett *et al.* 2000). Effective nestmate recognition is important to maintain the integrity of insect societies (Hölldobler & Wilson 1990). Nestmate recognition cues have been thoroughly investigated (Breed 1983; Hölldobler & Wilson 1990; Vander Meer & Morel, 1998) and have been determined to arise from three major sources: (1) queen dominance (Carlin & Hölldobler 1983; 1986), (2) worker-produced gestalt (Stuart 1988; Lahav *et al.* 1998) and (3) environmentally-derived factor (Obin 1986; Crosland 1989; Liang & Silverman 2000).

Chemical cues are also known to be important in nestmate recognition (Howard & Bloomquist 1982; Fletcher & Michener 1987). Recently,

[1]Urban Entomology Laboratory, Vector Control Research Unit, School of Biological Sciences, Universiti Sains Malaysia, 11800 Penang, MALAYSIA.
[2]Corresponding author. Email: chowyang@usm.my

cuticular hydrocarbons have been proven to have importance in nestmate recognition in several ant species (Lahav *et al.* 1999; Boulay *et al.* 2000; Liang & Silverman 2000; Silverman & Liang 2001). This has been shown in studies involving pure hydrocarbon fragments from *Iridomyrmex purpureus* (Thomas *et al.* 1999) and *Cataglyphis niger* (Lahav *et al.* 1999). Liang & Silverman (2000) also showed that *Linepithema humile* (that had been separated and subjected to different diets) used prey-derived hydrocarbons in recognizing and discriminating between colony and non-colony members. Besides prey, plant lipids, nesting substrates and other living substrates are also capable of contributing to cuticular hydrocarbons (Jutsum *et al.* 1979; Heinze *et al.* 1996; Singer & Espelie 1996).

Seasonal fluctuation in workers hydrocarbon profiles also suggests that environment factors, are important in determining cuticular hydrocarbon composition (Nielsen *et al.* 1999). Food quality, therefore is believed to affect nestmate recognition and intracolony aggression (Jutsum *et al.* 1979; Obin & Vander Meer 1988; Crosland 1989; Le Moli *et al.* 1992), especially hydrocarbons acquired from prey (Liang & Silverman 2000). Jutsum *et al.* (1979) also showed that workers of *Acromyrmex octospinosus* from distant colonies displayed aggression towards one another whereas those from nearby colonies did not show any form of aggression. Stuart (1987) reported similar results in the ant *Lepthotorax curvispinosus*. However, Silverman & Liang (2001) showed conclusively that aggression level in distant colonies dropped when they were fed similar diets and were provided similar nesting substrates in the lab.

There are also variations of hydrocarbon composition among the various castes within colonies (Bonavita-Cougourdan *et al.* 1993; Wagner *et al.* 1998; Kaib *et al.* 2000), or in association with reproductive status (Dahbi & Lenoir 1998a; Liebig *et al.* 2000). It has also been proven that the postpharyngeal gland acts as a reservoir to the colony's 'odor' and its contents are capable of triggering aggressive behaviors (Soroker *et al.* 1994; Hefetz *et al.* 1996).

The queen's role in generating colony odor has also been studied. However, results varied from the queen being the main source of colonial odor to it being negligible in creating the colony's odor (Hölldobler & Wilson 1990; Lenoir *et al.* 1998). Bonavita-Cougourdan *et al.* (1987) found that individual worker ant is capable of memorizing specific hydrocarbon signatures and this gives them the ability to detect and reject intruders that have signatures that differ from what is in their memory. This is achieved through antennation that is essential in ant colonies and nestmate recognition. The queen's impact on the colony odor can be seen in ant species that have high queen-worker dimorphism levels (e.g.: *Camponotus* spp.), but this effect is absent in species that have low caste dimorphism levels such as *Cataglyphis niger*. This occurrence suggests a relationship between the degree of queen-worker dimorphism and the involvement of queens in forming the colonial odor (Lenoir *et al.* 1998).

This present study was conducted to determine two factors (diet and queen dominance) affecting nestmate recognition in the crazy ant, *Paratrechina longicornis*. We also attempted to demonstrate intercolonial aggression in this species. *P. longicornis* is an emerging pest ant species in tropical and subtropical areas, particularly those that have suffered human intrusion (Trager 1984; Hölldobler & Wilson 1990; Yamauchi & Ogata 1995; Wetterer *et al.* 1999; Lee *et al.* 1999; Lee 2002).

MATERIALS AND METHODS

The *P. longicornis* used in this study were collected from the field and cultured in the lab. There were five main sites for collection: Air Itam, Batu Uban, Batu Lancang, Gelugor, and Teluk Kumbar in Penang Island, Malaysia. Sucrose (0.25 M) and insect prey (Lobster cockroach [*Nauphoeta cinerea*]) were provided *ad libitum* within the rearing tray. These trays (42.0 x 26.5 x 8.5 cm) were treated with fluon on the inner sides to prevent the ants from escaping.

Effects of Diet On Nestmate Recognition

In this study, ants from one colony were separated into two small subcolonies and provided different foods. Their acceptance or aggression towards each other was observed after a certain period of time. Each subcolony contained one queen, 140 - 160 workers, and 20-30 broods. Colonies were placed in a fluon-lined plastic container (17.8 x 12.2 x 7.3 cm). The two subcolonies were joined together using glass tubing (15 cm length x 1.5 cm inner diam.). The openings of the tubing were stuffed with cotton balls which were removed on the days of assays. Controls were fed with Lobster cockroaches in both subcolonies, while in treatment sets, one subcolony was fed with Lobster cockroaches while another one with German cockroaches (*Blattella germanica*). Sucrose (0.25 M) was provided *ad libitum* and food was changed regularly to avoid mold development. Behavioral assays were conducted at 1, 2, 3, 4, 5 and 6 weeks post-treatment. During assays, single worker ants were each taken from the two subcolonies and placed together; their behavior towards one another was observed for 5 minutes and scored according to the following behavioral indices:

0 – Antennal contact
1 – Biting
2 – Seizing of legs
3 – Seizing of antennae
4 – Stings

A total of 10 pairs were observed for both control and treatment colonies.

In addition, the cotton used to block the tubing was removed and the total number of ants that crossed between the two subcolonies within an hour was recorded.

Queen Dominance

1. Absence of queen

Four hundred workers and 80 – 100 brood were separated from parent colonies and reared without the queen under the same condition as its parent colony. Behavioral assays were conducted on the 7, 14, 28, 56, and 84th day by placing the two ex-nestmates together to observe their acceptance towards each other. Their behavior was recorded according to indices described above. A total of 20 pairs were each observed for 5 minutes.

2. Effects of An Alien Queen

Ten workers from one colony were placed together with an alien queen in a plastic cup (8.3 cm height x 7.5 cm inner diameter) and observed for 10 minutes. These behavior of the workers toward the alien queen was recorded. A total of twenty queens were tested.

Queen experiments were extended by allowing the workers to live with an alien queen and her broods. Two replicates were performed. Behavioral assays were conducted weekly (up to 5 weeks) by placing a worker ant that had lived with an alien queen with one of its former nestmates. Their behavior towards each other was recorded.

Intercolonial aggression

This experiment was conducted by placing individual ants from different field collection sites to observe their acceptance towards one another. Five populations from different locations in Penang Island, Malaysia were used. A total of 20 pairs of ants were observed for 5 minutes for every combination. The behavioral index was used to record their behavior.

Data analysis

Data collected were subjected to Kruskal-Wallis (KW) analysis of variance, and means were separated with KW multiple comparison, or Mann-Whitney test at 95% confidence interval.

Table 1. Mean antagonistic behaviour in control & treatment after being subjected to different diets up to n^{th} days[1].

Day	Control	Treatment
7	0.00 a	0.00 a[2]
14	0.00 a	0.57 ± 0.27 a
21	0.00 a	1.17 ± 0.35 b
28	0.00 a	3.10 ± 0.44 b
35	0.00 a	2.97 ± 0.31 b
42	1.80 ± 0.80 a	2.79 ± 0.33* b

[1]All n = 30, except when indicated by *, where n = 24.
[2]Means compared by Mann-Whitney test (P < 0.05).

RESULTS AND DISCUSSION

Ants that were subjected to different diets after a certain period of time showed aggression towards one another. Means of antagonistic behavior between treatments and controls differed significantly (P < 0.05) from 21 days post-treatment onwards (Table 1). Antagonistic behavior that was shown after 21 days of separation could possibly be due to the amount of acquired prey hydrocarbon that was insufficient to affect the original cuticular hydrocarbon. Liang & Silverman (2000) demonstrated these prey-acquired hydrocarbons have similar profiles with the prey's cuticular hydrocarbon profile itself. They concluded that the acquired hydrocarbons had affected the ants' nestmate recognition ability and had led to aggressive behavior. Apparently, in *P. longicornis*, the acquired hydrocarbons will change gradually after the ants consume prey, until a level is reached where former nestmates do not recognize each other and they start to exhibit aggression.

After the barriers were removed, the number of ants that crossed the glass tubing in between subcolonies was not significantly different (P > 0.05) (Table 2) up to day-42 post-treatment. This was likely due to the total number of ants in each subcolony. Ants divide tasks such as nest tending, protection and foraging and collecting among the workers (Holldobler & Wilson 1990). When the number is small, tasks partitioning will be affected nonetheless, especially when queen and brood have been tended by a small number of workers.

For the ant, *Cataglyphis iberica*, Dahbi *et al.* (1999) showed that social isolation for eight weeks followed by reintroduction only led to increased trophallatic activities, and did not induce antagonistic behavior. This may explain the lack of aggression among worker ants in our isolation experiments. Silverman & Liang (2001) observed that *Linephithema humile*'s crossing subsided gradually in time and concluded that former

Table 2. Mean of total crossings between two subcolonies in control & treatment after being subjected to different diets up to n[th] days.

Day	Control	Treatment
7	26.00 ± 12.49 a	0.00 ± 5.86 a[2]
14	8.33 ± 2.33 a	9.00 ± 3.06 a
21	46.33 ± 15.94 a	9.67 ± 0.88 a
28	74.33 ± 31.21 a	14.33 ± 4.67 a
35	54.67 ± 14.24 a	15.67 ± 8.74 a
42	67.67 ± 30.25 a	5.50 ± 0.50* a

[1]All n = 3, except when indicated by *, where n = 2.
[2]Means compared by Mann-Whitney test ($P < 0.05$).

nestmates had not lost their ability to recognize each other due to diet partitioning.

Although our results were not entirely similar to those of Silverman & Liang (2001), it was clearly shown that ants in the treatments displayed aggression towards unfamiliar intruders and vice versa. This was seen from day-21 post-treatment in the treatment colonies and further provided evidence that former nestmates no longer recognized each other apparently after the chemical cues used in recognition had changed.

Other studies have also shown dynamic changes in cuticular hydrocarbons over time (Vander Meer *et al.* 1989; Provost *et al.* 1993). Dahbi & Lenoir's (1998a) suggested that three months were not enough to allow the cuticular hydrocarbon profiles to change significantly enough to induce antagonistic behavior. Dahbi and Lenoir (1998b) also found that hydrocarbon profile changes were more significant over a twelve-month period. These findings help to explain our results.

In the queen dominance experiment, queen removal did not appear to have an effect on nestmate recognition throughout the entire duration of the experiment (84 days). When these ants were reintroduced back to their former nestmates, only antennation was observed. Results from these experiments, however, suggest that the role of queens in forming the colonial odor is negligible. The same results were reported by Dahbi & Lenoir (1998a) where *Cataglyphis iberica* workers were isolated for three months without their queen. The only observed behavior in this experiment was increased antennal contacts when former nestmates were put together. Provost (1989) also observed similar findings in *Lepthotorax lichtenstieni* and reported that these ants only increased their antennal contact frequency after being isolated for four months without the queen.

In the alien queen experiment, workers did not accept the alien queen, but showed antagonistic behavior towards her. Among the two treatments, only one was significantly different from the control ($P < 0.01$) (Table 3). This antagonistic behavior, however, gradually decreased within 10 minutes after test initiation, and the workers started to tend the alien queen as if she were their own. Further experiments in which workers were allowed to stay with the alien queen showed that she did not affect the recognition of workers by their former nestmates. These workers only antennated with one another when they were placed together again during assays that lasted for 35 days.

Table 3. Mean antagonistic behavior of worker ants towards an alien queen.

Study sets	Mean
Control	0.00 a[1]
Treatment # 1	3.80 ± 1.37ab
Treatment # 2	6.20 ± 1.37 b

[1]mean values followed by the same letter within the same column are not significantly different ($P > 0.01$; Kruskal-Wallis multiple comparison test).

Experiments with the alien queen and workers further refuted the queen's role in forming colonial odor. Workers that stayed with the alien queen did not show any aggression towards former nestmates for a period of 35 days. In certain species such as those of the genus *Camponotus*, however, queens are believed to be the source of colonial odor (Carlin & Hölldobler 1983; 1986). Provost (1989) proved the queen's role in forming colony odor by placing her alternatively within two colonies of isolated workers (the workers were still able to recognize each other). However, Haskins & Haskins (1950) showed the opposite results where two isolated groups of ants (with and without queens) did not recognize each other after four months of separation.

Earlier, Hedges (1998) reported that it was not known if crazy ants display intercolonial aggression. Results from our intercolonial aggression experiments confirmed that this behavior occurs in *P. longicornis* (Table 4). The five different strains examined here showed antagonistic behavior towards one another in all instances. Variations in colony odor among colonies might be explained by the presence of other alternate environmental odors. In ant colonies, dynamic colonial odor is achieved through a general odor among the colony members called the *gestalt* and it is used as a reference to display amicable or aggressive behavior between nestmates (Crozier & Dix (1979). It is possible that gestalt odor influenced our results, however, further experiments are needed to confirm the main factors influencing intercolonial aggression.

Table 4. Mean intercolonial antagonistic behavior among different colonies of the crazy ants, *Paratrechina longicornis*.

Colonies	Mean[1]
Gelugor x Batu Uban	4.55 ± 0.68 a[2]
Teluk Kumbar x Batu Lancang	4.05 ± 0.63 a
Gelugor x Batu Lancang	3.65 ± 0.66 ab
Gelugor x Teluk Kumbar	3.50 ± 0.64 ab
Batu Lancang x Air Itam	3.40 ± 0.69 ab
Teluk Kumbar x Air Itam	2.80 ± 0.41 ab
Batu Uban x Batu Lancang	2.90 ± 0.53 ab
Gelugor x Air Itam	2.55 ± 0.50 abc
Batu Uban x Teluk Kumbar	2.30 ± 0.45 abc
Batu Uban x Air Itam	0.85 ± 0.35 bc
Batu Uban x Batu Uban	0.00 c

[1]n = 20
[2]Means compared by Mann-Whitney test ($P < 0.05$).

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