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Nest-mate recognition and the effect of distance from the nest on the aggressive behaviour of *Camponotus chilensis* (Hymenoptera: Formicidae)

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Summary

Nest-mate recognition and territorial behaviour in ants are widely studied phenomena. However, few studies have analysed, under field conditions, how nest-mate recognition varies with distance from the resident's colony. In a natural population of *Camponotus chilensis* in central Chile, we studied nest-mate recognition and spatial variation in aggressive behaviour. *C. chilensis* individuals were able to discriminate nest-mates from intruders, showing no aggression toward nest companions, while aggressiveness toward allo-colonial con-specifics decreased significantly with distance. Further, the overall number of interactions and the aggressiveness of the resident ants were significantly greater at 25 cm from their colony than at further distances. Given that antennation behaviour is regularly present at all distances from the nest, it seems to entail information acquisition. Biting and intruder-dragging, the most conspicuous aggressive displays, were mainly observed at distances close to the resident colony. Other behaviours such as threatening with open mandibles, ventral bending of the gaster, and backward-movement, were observed at all distances, and they seem to represent the first signs of intruder rejection.

Keywords: ant recognition, *Camponotus chilensis*, territoriality.

Introduction

Nest-mate recognition is a widely studied phenomenon in Hymenoptera species (i.e., Gamboa et al., 1986, for social wasps; Page et al., 1991, for

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honeybees; Jaisson, 1991, for ants and social wasps). In ants specifically, it is well recognized the capability to discriminate between individuals that belong to their colony from those that do not (Hölldobler & Wilson, 1990; Jaisson, 1991; Bourke & Franks, 1995; Stuart & Herbers, 2000; Hernández et al., 2002). Furthermore, this capability seems to be influenced by both kinship and coexistence relationships (e.g., habituation and dear-enemy phenomena) between individuals of different colonies. Pirk et al. (2001) found that, in *Formica pratensis*, aggression is positively correlated with both genetic distances between allo-colonial individuals and geographic distances between their nests. In addition, in some ant species, interactions between neighbouring nests show less aggressiveness than interactions with more distant nests (i.e., dear-enemy phenomenon; see Heinze et al., 1996; Langen et al., 2000).

Aggression level does not only depend on relative distance between nests, but also on the absolute distance of the tested ant from its home colony. Generally, the level of aggressiveness performed by the resident ant is greater than that performed by the intruder (Mayade et al., 1993; Mercier et al., 1997; Cammaerts & Cammaerts, 1998), suggesting that the context where encounters occur play a fundamental role (see Sakata & Katayama, 2001; Buczkowski & Silverman, 2005 for context-dependent nest-mate discrimination). Several laboratory studies have found that ant's aggressiveness diminishes with the distance from the colony entrance. For example, Mayade et al. (1993) could distinguish two kinds of spatial areas outside the nest of *Cataglyphis cursor*. They identified an area located nearby the colony's entrance, where resident ants are considerably more aggressive than intruders, and a second area, located at further distance from the nest, where resident ants show lower aggressiveness than at the nest entrance. Accordingly, the observed level of aggressiveness agrees with different marking modes found in the environment surrounding the colony, such as the territorial and home-range marking modes proposed by Hölldobler & Wilson (1990).

Notwithstanding the insight obtained from this kind of laboratory studies, few studies have analysed how aggressiveness varies with distance from the nest under natural field conditions. Because field conditions impose several uncontrolled sources of variation, it is relevant to assess if behavioural patterns observed under controlled laboratory conditions also occur under natural field conditions. In this vein, in a recent field study on the desert ant *Cataglyphis fortis*, Knaden & Wehner (2003) studied the influence of the ant's distance from the nest on the ant's level of aggressiveness, in dyadic

encounters between con-specifics belonging to different colonies. Knaden & Wehner captured ants at different distances from their natural nest, transferred them to an experimental set-up, and assessed their encounters in an experimental arena. They observed that the level of aggression was significantly higher in ants captured closer to their nests.

Camponotus chilensis is among the most abundant and widely distributed ant species in central Chile (Snelling & Hunt, 1975). Colonies are mainly monogynic, but polygynic colonies may occur as a fusion of single ones (Eaton & Medel, 1994). This species displays aggressive behaviour when individuals confront con-specifics from other colonies and hetero-specifics (Ipinza-Regla et al., 1996; N. Velásquez, pers. obs.), although no systematic study has been previously carried out. In the present field study we examined nest-mate recognition and spatial variation in aggressive behaviour of the ant *C. chilensis* under natural conditions in a central Chilean population.

Methods

Study site

The study was carried out from November 2002 to April 2003 in Río Clarillo National Reserve, located 45 km southeast from Santiago, Chile (33°51'S, 70°29'W). Evergreen sclerophyllous woody plants and annual and perennial herbs are the main components of vegetation in the study site (Niemeyer et al., 2002; see also Gajardo, 1993 for a general description of central Chilean vegetation). The climate has a cold temperate regime with precipitation concentrated to the winter and a dry hot period of about seven months around summer.

Colony identification and delimitation of the study area

Ten colonies of *C. chilensis* were identified by means of offering a food patch containing ham bait. Worker ants were observed carrying the bait back to their nest, allowing identification of nest entrance and nest location. After this, we considered as active nests those where worker ants were actually observed going in and out of the nest entrance. The ten colonies were divided into five experimental pairs. Only reciprocal behavioural tests between individuals belonging to each colony pair were carried out (see below). Since co-existence relationships may influence the aggressiveness level of the ants, we

homogenised inter-colony distances by using nests with a distance of at least 40 m between each other. In this way, we avoided using nearby colonies, thus minimizing the probability of using ants belonging to nests that normally interact with each other (thus, reducing possible dear-enemy effects). In the field, different colonies are sometimes located at close distance between each other (the mean closest distance between two nest was 14.1 ± 2.4 m (\pm SE), $N = 25$, range 1.3-50.4 m), frequently ants from nearby colonies interact, and it is not rare to observe worker ants at distances around 15-25 m from the closest nest entrance (N. Velásquez, pers. obs.). Therefore, it is possible that a single ant can reach the nest area of a con-specific during its foraging activities.

We removed a few physical elements that could excessively obstruct the observation of ants (e.g., twigs, leaves or rocks measuring four or more centimetres) in a 1.5 m radius around the nests entrance, taking care to not disturb the ground in order to modify as least as possible the distribution of objects on the outer area of each nest. Although this procedure might have affected landmarks for ant navigation, we had to assure full view of ant movement. Three concentric circles with 25, 50 and 100 cm of radius from the nest entrance were delineated on the ground around each nest entrance to be the study zones. These concentric circles were smoothly drawn directly on the ground using a small wooden stick, and we did not draw the complete circle but used a segmented line, allowing ample space for ant movement. We did not observe any particular change in behaviour due to these marks. Previous experiments allowed us to determine that the aggressiveness displayed by resident ants in *C. chilensis* (see below) did not vary substantially beyond distances of 100 cm from the colony entrance.

Behavioural tests and selection of individuals

For each nest, we monitored the worker ants from the moment that they spontaneously left the entrance until they reached the selected study zone, i.e., when a focal individual reached the 25, 50, or 100 cm mark from the nest entrance (see above). Target individuals were selected when an ant spontaneously reached a selected distance during their foraging trips while carrying no load. For each experimental trial, when a target ant reached the selected distance it was trapped in a transparent plastic tube, the experimental arena. This arena consisted of a plastic cylinder of 6 cm diameter and 8 cm length,

Table 1. Frequency of observed behaviours per minute for all studied colonies at different distances from the nest.

Observed Behaviour	25 cm	50 cm	100 cm
0: Antennation	1.6 ± 0.6	1.7 ± 1.0	1.4 ± 0.7
1: Threatening with open mandibles	1.1 ± 0.6	0.7 ± 0.6	0.6 ± 0.6
2: Backward-movement	0.5 ± 0.4	0.5 ± 0.7	0.5 ± 0.5
3: Ventral bending of the gaster	1.2 ± 0.7	0.6 ± 0.4	0.4 ± 0.7
4: Biting	0.6 ± 0.9	0.02 ± 0.05	0.02 ± 0.1
5: Intruder-dragging	0.05 ± 0.1	0.0 ± 0.0	0.0 ± 0.0

Values are mean ± SD. See text for details of statistic analysis.

open at both sides and with its interior wall covered with Fluon to prevent the ants from escaping. Then, a marked ant (either a nest-mate or an allo-colonial individual, see below) was also placed inside the plastic tube. This set-up allowed the encounters between ants and the continuous contact between the target ant and its territorial ground during all experimental trials. We used ants of similar size for each dyadic encounter. Ants from the target colony were considered as residents for each trial, while ants that were introduced into the arena (previously occupied by a resident ant) were considered as intruders. Only the intruder was marked because we aimed to assess the behaviour of resident ants with minimal disturbance. Thus no data on intruder behaviour was obtained. Nevertheless, both colonies of a given experimental pair were target of study, but we used different individuals of each colony as residents and intruders.

Behavioural tests were recorded on video-tape (8 mm Samsung SCW 62 NTSC camera) and behaviour displayed by the resident ant was analysed afterward in the laboratory. The different observed behaviours (OB) were classified in a scale ranging from 0 and 5 units, as used in previous studies (see Table 1; see also Carlin & Hölldobler, 1986, 1987; Hefetz et al., 1996; Errard & Hefetz, 1997; Lahav et al., 1999). The recording began when the intruder ant was introduced into the arena and ended 10 minutes later. For each selected distance, three different individuals per colony were tested. Each ant was tested only once. A control treatment consisted in confronting two worker ants belonging to the same colony at the shortest distance (25 cm from the colony entrance), testing two different pairs per colony. This treatment was carried out with the same procedures that those used for encounters between allo-colonial individuals (see below), but in this case, the

marked intruder ant was a nest-mate captured in the target nest area. Overall, we performed 90 behavioural tests and 20 control treatments. Previous observations allowed us to determinate that *C. chilensis* does not show aggressive behaviour against individuals from the same colony at any of the selected distances (see Ipinza-Regla et al., 1998 for similar results with the coexisting species *Camponotus morosus*).

For allo-colonial individuals, fifteen worker ants were captured in each colony (in a 1.5 m radius around the nest entrance). In order to be able to discriminate individuals, each allo-colonial ant was marked with an innocuous paint of a different colour. This paint did not affect the behaviour of individuals (see Torres-Contreras, 2004). This was done by putting each ant inside a glass flask, and then placed in a low temperature container (around 0-2°C) for 10 min, so its level of activity decreased significantly, allowing easy manipulation. Each intruder ant was marked with a coloured dot applied to the gaster about an hour before the tests were carried out. In the control treatment, the nest-mate ant was marked with the same paint and protocol to that used for allo-colonial individuals. After each dyadic encounter, both resident and intruder ants were executed. In this way, we assured a given ant was used only in one experimental trial.

Aggressiveness index

The frequency of each OB was determined for each treatment and an aggressiveness index (*AI*), similar to that used by Hefetz et al. (1996) and Errard & Hefetz (1997) was calculated. These studies used the duration of each behaviour in order to calculate the *AI*. In the present study, due to their short duration, we determined the frequency of the displayed behaviours. Therefore, we used the following equation to represent the *AI*:

$$AI = \sum_{i=1}^5 \frac{OB_i * F_i}{N}$$

where OB_i is the observed behaviour i , F_i is the frequency of each *OB* during 10 min of observation and N is the overall number of interactions (i.e., the sum of the frequencies of all *OBs*) observed during the recording time. Antennation ($i = 0$) was not included in this index.

Statistical analysis

All analyses were performed using the Statistica software for Microsoft Windows. We used a Student *t* test in order to compare the *AI* and the overall number of interactions recorded during the encounters between individuals from the same and different colony. An analysis of covariance was carried out to determine the effect of observed behaviour and the distance from the resident colony on the frequency of the behaviour studied, with colony pair as the covariate. An ANCOVA was also used to determine the effect of distance from the resident colony over the overall number of interactions, as well as for the *AI* index (colony pair as covariate). Tukey tests were used for multiple comparisons. When necessary data were transformed to fulfill the assumptions of the test performed. Transformed data did not differ from normal distributions (Kolmogorov-Smirnov test, $p > 0.2$ for the two cases where it was used, see Results).

Results

The overall number of interactions was significantly greater in confrontations between allo-colonial individuals (mean \pm SD: 4.8 ± 1.4 ; $N = 30$) than between individuals from the same colony (1.6 ± 0.6 ; $N = 20$) (*t* test: $t_{19} = 9.091$, $p \ll 0.01$). Similarly, the *AI* was significantly higher in encounters between individuals from different colonies (1.5 ± 0.5 ; $N = 30$) compared to the encounters between individuals from the same colony (0.0 ± 0.0 ; $N = 20$) (*t* test: $t_{19} = 16.519$, $p \ll 0.01$). Worker ants from the same colony showed only antennation behaviour.

In addition, the frequency of the different observed behaviours showed significant differences, and were also at the three studied distances (see Table 1 and Table 2). Thus, the most frequent behaviours observed at 25 cm from the resident colony entrance were antennation and ventral bending of the gaster (Tukey's test: $p < 0.05$), while at 50 and 100 cm, the most frequent behaviours were antennation and threatening with open mandibles, but only antennation differed significantly from the other behaviours (Tukey's test: $p < 0.05$). Biting behaviour was significantly more frequent at 25 cm from the resident colony (Tukey's test: $p < 0.05$), while at 50 and 100 cm the frequency of this behaviour was very low. The dragging behaviour of the intruder ant only occurred at 25 cm from the resident colony entrance.

Table 2. Analysis of covariance for (A) Frequency of behaviour (on transformed data), (B) Overall number of interactions, and (C) Aggressiveness index.

Variables	Effect	df	Sum of squares	Mean square	<i>F</i>	<i>p</i> -level
A. Frequency of behaviour	Observed Behaviour (OB)	5	8.79	1.76	17.60	<0.001
	Distance	2	3.37	1.68	16.81	<0.001
	Colony pair (Covariate)	1	0.30	0.30	3.01	0.08
	Distance × OB	10	2.27	0.23	2.27	0.01
	Distance × colony pair	2	0.48	0.24	2.37	0.09
	OB × colony pair	5	4.68	0.94	9.35	<0.001
	Distance × OB × colony pair	10	0.37	0.04	0.37	0.96
	Error	504	50.47	0.1		
B. Overall number of interactions	Distance	2	1713.73	856.87	3.29	0.042
	Colony pair (Covariate)	1	1519.61	1519.61	5.84	0.018
	Distance × pair	2	276.81	138.41	0.53	0.590
	Error	84	21860.12	260.24		
C. Aggressiveness index	Distance	2	2.54	1.27	7.61	0.001
	Colony pair (Covariate)	1	0.62	0.62	3.70	0.058
	Distance × pair	2	0.27	0.13	0.80	0.453
	Error	84	13.99	0.17		

Antennation was the most frequent behaviour in all distances (Tukey's test: $p < 0.05$) (see Table 1 and Table 2).

On the other hand, the distance from the resident colony had a significant effect on the overall number of interactions (see Table 2). The overall number of interactions decreased with the distance from the resident colony, being significantly different between 25 and 50 cm (Tukey's test: $p < 0.01$), and between 25 and 100 cm (Tukey's test: $p \ll 0.01$; see Figure 1). However, between 50 and 100 cm the differences were not significant (Tukey's test: $p = 0.290$). Furthermore, we found that the distance from the resident colony had a significant effect on the *AI* (see Table 2). Similarly, the *AI* decreased with the distance from the resident colony. *AI* differed significantly between 25 and 50 cm (Tukey's test: $p \ll 0.01$), and between 25 and 100 cm (Tukey's test: $p \ll 0.01$; see Figure 1), while between 50 and 100 cm no difference was detected (Tukey's test: $p = 0.441$). The colony

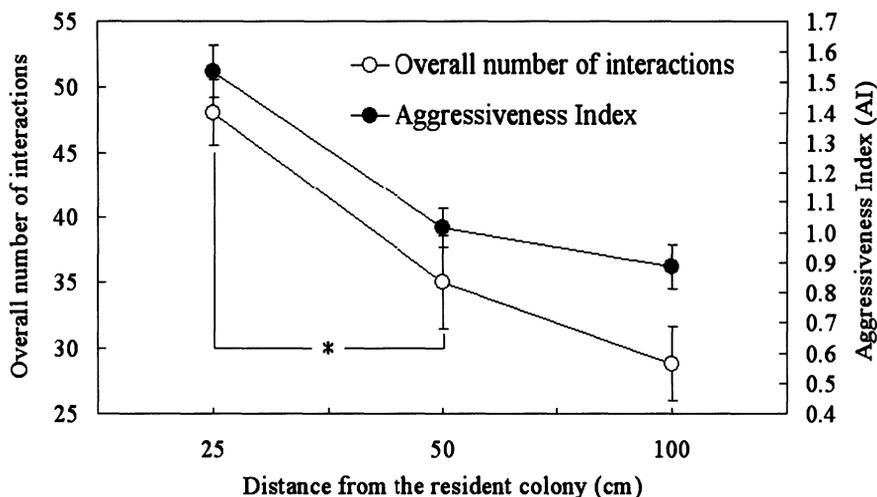


Figure 1. Overall number of interactions and the aggressiveness index (AI) as a function of the distance from the resident colony. The dots represent the mean \pm SE for all the studied distances (25, 50 and 100 cm from colony entrance). The asterisk represents significant differences. See text and Table 2 for details of statistical analysis.

pair factor considered in the analysis as covariate had a significant effect only on the overall number of interactions (Table 2), where we observed that only one pair of colonies showed a lower level of interactions.

Discussion

The results suggest that *C. chilensis* has the capability to discriminate between nest-mate and intruder individuals, performing a higher number of aggressive interactions when allo-colonial individuals are confronted. This pattern is well known in Hymenoptera, where various behavioral patterns and mechanisms have been described (e.g., Gamboa et al., 1986; Hölldobler & Wilson, 1990; Jaisson, 1991; Page et al., 1991; Bourke & Franks, 1995; Stuart & Herbers, 2000; Hernández et al., 2002).

On another hand, we observed that the behaviour that occurs with greatest frequency in all the studied distances is antennation. This suggests that more than an aggressive behaviour, antennation corresponds to a recognition behaviour used by ants in order to discriminate colony-mates from individuals of different colonies. In this vein, H. Torres-Contreras & R.A. Vásquez (unpubl.) have recently found that antennal contacts between *Camponotus*

chilensis nest-mates allow more efficient collective food exploitation. These two independent results suggest that antennation in *C. chilensis* leads to information acquisition (see also Hölldobler & Wilson, 1990). We also found that both biting and intruder-dragging occur with greater frequency at shorter distances from the nest. In fact, intruder-dragging behaviour was only observed at 25 cm from the nest entrance, suggesting that this behaviour is part of a more aggressive display and that under natural conditions it is present only in the nearby surrounding area of the resident colony. Other behaviours such as threatening with open mandibles, ventral bending of the gaster and sudden backward-movement were observed at all distances. These behaviours represent lower levels of aggressiveness and they seem to be involved in the first front of rejection displays (e.g., Lahav et al., 1999).

In this study we also found that the level of aggressiveness of worker ants of *C. chilensis* varies with the distance from the colony. The ants showed the highest levels of aggression when confronting intruders at 25 cm from the nest entry, decreasing its level of aggressiveness as the distance at which dyadic encounters occur is further away from the colony entrance. This pattern of differential aggressiveness has been described in laboratory experiments with the ants *Cataglyphis cursor* (Mayade et al., 1993), showing higher levels of aggressiveness in experimental arenas with substances extracted from the neighbouring area of the colony entrance, and lower aggressiveness in arenas with substances extracted from further away areas. This phenomenon in which the resident individual's aggressiveness decreases with distance from its nest seems to be a general pattern observed in other animals, for example, in some vertebrates (i.e., Bolyard & Rowland, 2000 for fishes; Raetti, 2000 for birds).

Furthermore, our field study of *C. chilensis* dyadic encounters, although carried out at only three different distances from the colony entrance, suggests that aggressive behaviour does not decrease uniformly with distance from the nest. The overall number of interactions followed a similar pattern. These patterns might be the result, at least partially, of the heterogeneous distribution of chemical signals in the surrounding areas of a colony, and support the different marking modes found in the area surrounding the nest, as proposed by Hölldobler & Wilson (1990).

Few previous studies have analysed how aggressiveness varies with distance from the nest under field conditions. Knaden & Wehner (2003) found that the desert ant *Cataglyphis fortis* is more aggressive when captured close

to the nest. These authors recently showed that the state of the ant's path integrator, a navigational toolkit that tells the ant how far it is away from home (Wehner & Srinivasan, 2003), is sufficient to control the level of aggression, independently of the actual presence of the nest, its odour cues, and landmark surroundings (Knaden & Wehner, 2004). Since chemical communication and the use of odorant signals are widespread in ants (Howard & Blomquist, 1982; Hölldobler & Wilson, 1990), we believe that path integration might not be the main source of information for territorial behaviour in *C. chilensis*. Thus, nest-mate recognition and territoriality in *C. chilensis* seems to rely more heavily, but probably not exclusively, on the ecological context where ants are located (rather than in the inner state of the animal), where signals are assessed from direct behavioural contacts and/or from cues or landmarks located in the landscape.

Nest-mate recognition implies the existence of a recognition mechanism. Chemical signals comprising lipids deposited on the cuticle are involved in the underlying mechanism of nest-mate recognition (Howard & Blomquist, 1982; Hölldobler & Wilson, 1990; Wagner et al., 2000). Ant colonies seem to have characteristic chemical signal(s) that ants are capable of recognising and using as a cue to elicit aggressive behavioural display when they face hetero-specifics and/or allo-colonial con-specifics (Carlin & Hölldobler, 1986, 1987; Carlin et al., 1987; Mercier et al., 1997; Lahav et al., 1999).

The present field study agrees with laboratory studies that have analysed how aggressiveness varies with distance from the nest entrance, which had found that the type and/or concentration of chemical signals deposited in the surface influence territorial behaviour. Studies in *C. cursor* show that the concentration of territorial marks is greater near the colony entrance than in foraging areas (Mayade et al., 1993). Thus, the lower aggressiveness presented by workers of *C. chilensis* at distances further than 25 cm from the colony entrance could obey to the lower concentration of territorial marks, and to the increment of home-range marks, which when are perceived by the ants would determine priorities in the activities to be executed. On the other hand, another possible explanation for the decrease in territorial behaviour with distance from the nest could lie on memory capabilities of ants. Recent findings show striking capabilities of odometric memory in *Cataglyphis* ants, which do not rely on pheromone trails to assess distance to the nest (Cheng et al., 2006). Thus, it is possible that the workers of *C. chilensis* assess the distance or time elapsed as they leave from the nest and become less aggressive

as this number increases. Future studies should focus on identifying territory limits, the precise mechanism implicated, and the influence of different ecological conditions involved in territorial and home-range behaviour.

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