

## Research article

# Absence of aggression but not nestmate recognition in an Australian population of the Argentine ant *Linepithema humile*

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**Abstract.** Intraspecific aggression is rare within introduced populations of the Argentine ant *Linepithema humile*, and colonies exhibit a structure known as unicoloniality, in which aggression among nests is atypical. We document a similar form of colony structure in an introduced population of Argentine ants in Victoria, Australia, in which aggression is extremely rare among nests ranging over hundreds of kilometres. However, using a highly sensitive behavioural bioassay we found that workers display subtle differences in their behaviour towards non-nestmates and nestmates. In particular, non-nestmates consistently engage in antennating behaviour with greater frequency than nestmates, perhaps providing a mechanism for homogenization of nest odour. Further, we found that non-nestmates at seaport sites (where populations may derive from multiple introductions) antennate each other with greater frequency than their counterparts from non-seaport sites. These data suggest that the Victorian population of *L. humile* may comprise multiple independent introductions.

**Keywords:** Nestmate recognition, introduced species, invasions, unicolonial, supercolony.

## Introduction

Social insects minimize the misdirection of resources and maintain the integrity of nests by distinguishing precisely between individuals from their own nests and conspecific

intruders attempting to exploit the nest's resources. Consequently, natural selection has favoured the evolution of highly developed recognition systems, usually in the form of an odour covering the insect's cuticle (e.g. Lahav et al., 1999; Thomas et al., 1999; Wagner et al., 2000). This odour regulates a diverse array of behaviours from cooperation with nestmates to aggression and nest defence towards alien conspecifics (e.g. Crozier, 1987).

Traditionally, nestmate recognition has been assessed using behavioural assays, in which solitary or groups of workers from different nests are placed into a neutral arena and the ensuing behaviour recorded (e.g., Ichinose, 1991; Heinze et al., 1996; Lahav et al., 2001). Participants are deemed nestmates if they do not engage in any obvious aggressive behaviour, and aggression between workers from different nests is used to indicate that individuals are not nestmates (Roulston et al., 2003; but see van Wilgenburg et al., 2007). However, a lack of aggression between individuals that do not apparently derive from the same nest does not necessarily imply a lack of nestmate recognition. Rather, this perceived lack of recognition may simply reflect the sensitivity of the bioassay or the method used for analysis (Breed and Bennet, 1987; Roulston et al., 2003). For example, most researchers record a range of behaviours from bioassays, but these behaviours are then generally processed into a single number or index that represents a level of aggressiveness in the experimental trial (Roulston et al., 2003). Using a single aggression index may conceal subtle behavioural differences between treatments.

Some ant species exhibit an extraordinary social structure known as unicoloniality, in which populations comprise expansive supercolonies, and aggression between non-nestmates within a supercolony is rare (e.g.

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Chapuisat et al., 2005). This lack of aggression between non-nestmates is thought to be a key attribute in the success of invasive ants, a group that commonly exhibits this form of colony structure (Holway et al., 2002). The colony structure of the Argentine ant *Linepithema humile* is arguably the most extensively studied among these introduced invasive species (Holway et al., 1998; Tsutsui et al., 2000; Giraud et al., 2002). The Argentine ant has been introduced widely throughout temperate regions of the world and although it is multi-colonial in its native range (Tsutsui et al., 2003, but see Pedersen et al., 2006), introduced populations in California (Holway et al., 1998; Tsutsui et al., 2003), Europe (Giraud et al., 2002) and New Zealand (Corin et al., 2007) are primarily unicolonial. Two explanations attempt to account for unicolonality in introduced populations of *L. humile*, and while they differ in the underlying mechanisms (see Starks, 2003 for review), both essentially agree that these populations are characterised by a lower discriminatory ability among workers (Tsutsui et al., 2003; Giraud et al., 2002).

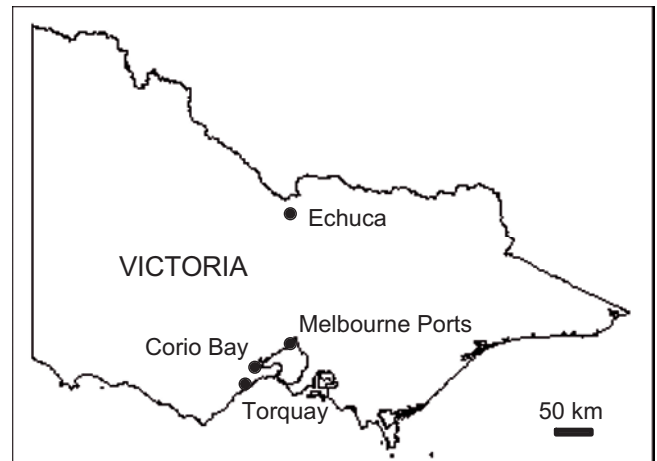
Despite the low level of aggression observed in introduced populations of Argentine ants, the local mixing of individuals among nests still influences the colony structure of unicolonial populations (Ingram and Gordon, 2003). For example, there can be subtle genetic differences within a unicolonial population, with neighbouring nests typically more closely related than nests from different locations (Ingram and Gordon, 2003). This substructure most likely reflects the short distances moved by dispersing queens and workers (Ingram and Gordon, 2003). Furthermore, multiple introductions of Argentine ants into the same area from different geographic sources will further influence the local colony structure (Tsutsui et al., 2001). For example, nests located within the vicinity of commercial, international seaports may derive from nests transported from a variety of geographically separate locations, whereas nests located in areas further inland are more likely to have derived from a single source that became established by slow nest expansion (i.e. 'budding') or human mediated dispersal (Holway, 1994; Tsutsui et al., 2001; Holway et al., 2002; Ingram, 2002; Ingram and Gordon, 2003).

Here, we use behavioural bioassays to determine whether an Australian population of *L. humile* forms a supercolony. Furthermore, we use highly sensitive bioassays to determine whether there are subtle behavioural differences in the interactions between nestmates and non-nestmates. Finally, we use these behavioural data to explore possible differences between populations that may differ in the frequency of independent introductions from multiple geographic sources. Specifically, we investigate whether workers display a stronger behavioural response to non-nestmates than to nestmates in populations located at commercial seaport sites compared with populations at non-seaport sites.

## Methods

### Sampling field populations

Four sites, each located in an urban area, were selected within the geographic range of introduced populations of *L. humile* in Victoria, Australia (Fig. 1). Two sites, Melbourne Ports and Corio Bay (Geelong), are commercial, international seaports and therefore likely to be primary sites of introduction of *L. humile* that may derive from populations from around the globe. The other two sites are Torquay, a coastal town, and Echuca, an inland town: Argentine ants in these sites are likely to have been introduced through local transportation during the establishment of human developments. The distance between the four sites ranges between 30 and 250 km (see Fig. 1).



**Figure 1.** The geographic location of the two seaport sites, Melbourne Ports and Corio Bay (Geelong), and the two non-seaport sites (Torquay and Echuca) within Victoria, Australia. Scale bar indicates 50 km.

Five nests were selected at each site, with the distance between nests within sites ranging from four to seven kilometres. The nests were located in highly modified urban habitats, including pedestrian pathways adjoining suburban streets, small urban parks and private ornamental gardens. We selected nests from a variety of habitats within each site in order to minimise any consistent between-site differences in nest habitat.

Within-site bioassays included combinations of workers from different nests (replicates), resulting in a total of 39 within-site combinations of nests (one replicate was lost). Between-site bioassays involved two nests from Melbourne Ports trialled against two nests at each of the other locations (Corio Bay, Echuca and Torquay), and two nests from Corio Bay trialled against two nests from each of the non-seaport locations (Echuca and Torquay), resulting in a total of 20 between-site combinations (replicates). Additional between-site bioassays were not logistically possible.

### Behavioural bioassays

We quantified behavioural differences between nestmates and non-nestmates using five-on-five behavioural bioassays, which provide more consistent results compared with one-on-one and colony-level interactions (Roulston et al., 2003). Five-on-five bioassays involve ten individuals and thus provide data on the interactions between both nestmates and non-nestmates. Bioassays were conducted in the laboratory, from late December 2003 to early April 2004; the choice of nest comparisons was randomised across this time period, removing any potential 'seasonal' effects.

Around 50 workers from each nest were collected from foraging trails using an aspirator, and then transported to the laboratory in 70 ml plastic vials. The workers from each nest were separated into two similar sized groups and placed into 100 ml vials that were coated with fluon to prevent ants from escaping. The ants in one container were painted on the abdomen with a yellow spot, using a single-bristled paintbrush and non-toxic Aquacryl™ paint. Thus, each nest contributed both painted and unpainted ants. The workers remained in the holding container for four hours between collection and when the bioassay commenced, and all bioassays were conducted in the mid to late afternoon.

The procedure for the behavioural bioassay involved introducing five painted ants from one nest and five unpainted ants from another into a 10 cm diameter arena with Fluon lined inner walls to prevent the ants from escaping. Painted workers were always introduced into the arena first, thereby controlling for any order of introduction effects, and then left for one minute to acclimatize before the unpainted ants were introduced. All ten ants were left, unrestrained, for a further one-minute to acclimatize before behavioural observations commenced. Behavioural interactions between ants were observed for ten 30 s periods, each interspersed with a 30 s non-observation period, thereby providing information on any changes in behaviour during the course of a ten minute trial. Three categories of behavioural interactions between workers were observed: i) *antennating* – a brief or prolonged ( $\leq 1-4$  s) contact between ants, in which the antenna of each ant touches the antenna or body of the other; ii) *allogrooming* – antennating for  $> 5$  s, which also involves one ant grooming the other, using mouth parts; iii) *aggression* – pulling or biting an ant, which results in injury, dismemberment or death. We recorded the frequency of interactions between all combinations of ants (i.e., painted versus unpainted, painted versus painted and unpainted versus unpainted) during the bioassays, excluding those interactions in which one ant investigated the paint spot on another ant.

The behavioural bioassay was repeated four times for each pair of nests, using naïve ants for each repeated trial. The nest from which painted ants were used was alternated to control for any influence painting the ants may have had on their behaviour. The arena was wiped with 70% ethanol between trials to remove traces of alarm pheromones.

#### Statistical analysis

For each nest pair combination, we summed the count of each behaviour category within a trial separately for interactions involving nestmates and those involving non-nestmates. We then calculated, separately for nestmates and non-nestmates, the average of each behavioural category across the four repeated trials; this average value constituted the independent value (replicate) for statistical analysis.

The sources of variation in the workers' behaviour were investigated using t-tests (for pooled data) and repeated-measures ANOVA, with nest location (seaport or non-seaport sites) as the main effect and interacting participants (non-nestmates or nestmates) as the repeated measure. We used a repeated measures model because we could not assume that, within a trial, the behaviour of nestmates was independent of the behaviour of non-nestmates, and *vice versa*.

The influence of nest location on antennating behaviour was investigated using repeated-measures ANOVA (as above). For this analysis, data from bioassays conducted between nest pairs within seaport sites ( $n = 19$ ) and within non-seaport sites ( $n = 20$ ) were pooled. We investigated the rate at which antennating behaviour changed during the course of a bioassay ( $\delta_{\text{ant}}$ ) by calculating the slope ( $\beta$ ) from the linear regression of the frequency of antennating at each time interval against the duration of the bioassay. For each trial, we calculated  $\beta$  separately for the interactions involving non-nestmates and nestmates. We then calculated a value  $\delta_{\text{ant}}$ , which was the average  $\beta$  from the regression curves of the four repeated trials for each nest combination. The sources of variation in  $\delta_{\text{ant}}$  were examined using planned comparisons (t-tests).

Data were log transformed to achieve normality where necessary, and analysed using SYSTAT 10. Presented means and standard errors were calculated from estimates generated by the models.

## Results

### *Recognition behaviour between nestmates and non-nestmates*

While aggression between individuals was observed, it was extremely rare – totalling less than four isolated incidents between pairs of workers – and was never consistently observed between nest pairs. Indeed, the frequency of aggressive behaviour was too low for any meaningful statistical analyses, and was not considered further.

In general, workers spent most of their time investigating workers from a different nest: combining data across all sites, non-nestmates consistently engaged in more antennating behaviour ( $t = 9.119$ ,  $P < 0.001$ ,  $n = 59$ ) and more allogrooming ( $t = 4.806$ ,  $P < 0.001$ ,  $n = 59$ ) than nest mates. However, the frequency of allogrooming was very low, and this behaviour was not further analysed.

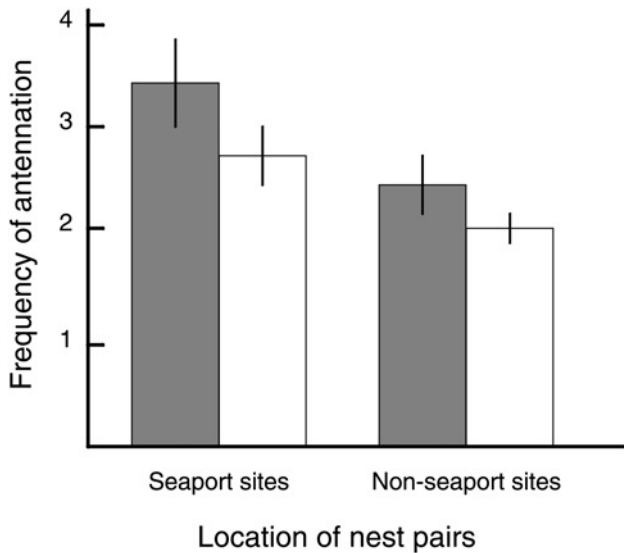
### *Influence of nest location on antennating*

Non-nestmates located in both seaport and non-seaport locations engaged in antennating behaviour more frequently than nestmates ( $F_{1,37} = 47.607$ ,  $P < 0.001$ ; Fig. 2). Furthermore, ants from nests within seaport sites exhibited antennating behaviour significantly more frequently than did ants from nests at non-seaport sites ( $F_{1,37} = 4.878$ ,  $P = 0.033$ ; Fig. 2). There was no significant interaction between the main effects and the repeated measure ( $F_{1,37} = 3.229$ ,  $P = 0.081$ ).

### *Rate of change in the frequency of antennating*

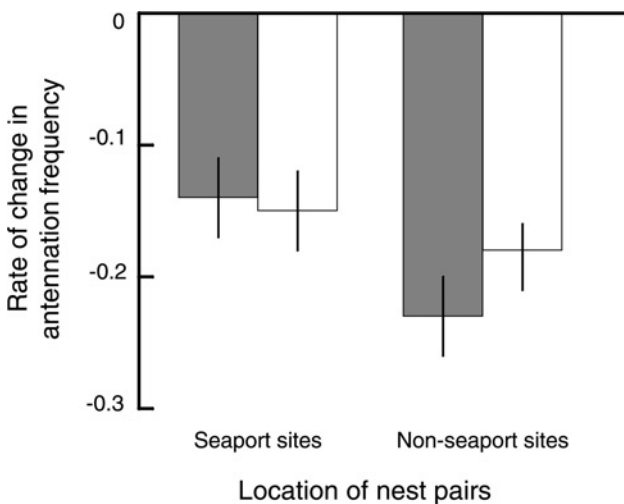
Over the course of the bioassay, there was a significant decline in the frequency of antennating both among non-nestmates ( $F_{1,8} = 28.374$ ,  $r^2 = 0.780$ ,  $P = 0.001$ ) and among nestmates ( $F_{1,8} = 47.910$ ,  $r^2 = 0.857$ ,  $P < 0.001$ ). If seaport and non-seaport sites differ in the frequency of independent introductions from multiple geographic sources, then the frequency of interactions between non-nestmates should decline more rapidly in populations located at non-seaport sites than those from commercial seaport sites (who are expected to maintain a consistently high level of behavioural interactions). Such differences are not expected for interactions involving nestmates.

These predictions were supported by the analysis of  $\delta_{\text{ant}}$  (the rate of change in antennating frequency of ants during the bioassay):  $\delta_{\text{ant}}$  among non-nestmates from non-seaport sites was greater than that of non-nestmates from seaport sites ( $t = -2.186$ ,  $P = 0.035$ ,  $df = 37$ ), but  $\delta_{\text{ant}}$  for



**Figure 2.** The mean frequency with which nestmates (open bars) and non-nestmates (closed bars) from nests within either seaport or non-seaport locations engaged in antennating behaviour. The rate represents the total number of antennating events involving all ten ants over the ten minute observation period. Error bars represent standard errors about the mean.

nestmates did not significantly differ between the two locations ( $t = -0.954$ ,  $P = 0.346$ ,  $df = 37$ ; Fig. 3). In other words, non-nestmates at non-seaport sites rapidly ceased to interact, while their counterparts from seaport sites continued to investigate each other for the duration of the bioassay.



**Figure 3.** The overall mean rate of change of antennating behaviour among nestmates (open bars) and non-nestmates (closed bars) from nests within either seaport or non-seaport locations. Larger, negative values indicate a more rapid rate of decline. Error bars represent standard errors about the mean.

## Discussion

We observed very few aggressive interactions among non-nestmates in the population of *L. humile* in Victoria, suggesting the existence of a large 'supercolony'. This colony structure is consistent with that of other introduced populations of Argentine ants in California (Tsutsui et al., 2000), Europe (Giraud et al., 2002) and New Zealand (Corin et al., 2007), each of which are characterised by an absence of aggression between non-nestmates. Nevertheless, our bioassays and analyses revealed subtle behavioural differences among workers of *L. humile* that have not been observed previously within unicolonial populations. We found that workers antennated and allogroomed non-nestmates more frequently than nestmates. These data contrast with a previous study (Giraud et al., 2002) that reports no differences in the antennating behaviour of nestmates and non-nestmates from the same supercolony. While this difference may reflect biological differences between the two populations (e.g. the density of nests and thus history of encounters between non-nestmates), it may also simply reflect a difference in the number of subjects used in each bioassay; Giraud et al. (2002) used pairs of ants while the present bioassays were 'five-on-five'.

We also found that non-nestmate workers at seaport sites investigate each other with greater frequency than non-nestmates at non-seaport sites. Further, while these behaviours declined over the course of the bioassay, the higher rate of antennating among non-nestmates at seaport sites was sustained for longer than for non-nestmate workers from non-seaport sites. The underlying causes of this difference are unknown, but may involve some process of homogenization of the odour profile of the two nests (Dahbi and Lenoir, 1998; Soroker et al., 2003), which may take longer in trials involving ants with more divergent individual hydrocarbon cues.

It seems unlikely that environmental factors alone can fully explain the higher frequency of antennating behaviour exhibited by *L. humile* workers at seaport than non-seaport sites, because our sampling method controlled for potential variation in habitat types, which may influence recognition cues (see Liang et al., 2001; Suarez et al., 2002). In particular, we were especially careful to minimise any between-site differences in nest habitat, and while we cannot discount any consistent environmental differences between port and non-port sites, such differences would require consistency among all of the nests across two sites. Instead, differences in the genetic diversity of nests at seaport and non-seaport sites may be a more likely explanation for the observed differences in antennation frequency between these sites, although this explanation requires genetic analyses. Populations at secondary sites of introduction, such as non-seaport sites, may be comparatively less genetically differentiated than seaport sites. Colony expansion in *L. humile* occurs via 'budding' (Holway, 1994), which involves small groups of queens and workers moving to a new nest site by foot

(Tsutsui et al., 2000; Ingram, 2002). Colony budding is slow and nests established away from urban areas may be less likely to survive; *L. humile* has never been recorded in undisturbed habitat in Australia, perhaps having been contained by physical conditions unsuitable for *L. humile*, in combination with strong interspecific competition from native ants that are more tolerant to hot, dry conditions (Thomas and Holway, 2005). Instead, colonization of sites far from seaports in Australia most likely occurred through human mediated transportation. It seems improbable that Argentine ant queens would reach locations distant from seaports in similar numbers and from as diverse a range of origins as those located at sites of initial introductions.

The assumption that multiple introductions have occurred at seaport sites is supported by evidence from other parts of this species' introduced range. Multiple introductions of Argentine ants are likely in Europe (Giraud et al., 2002) and North America, Hawaii and South Africa (Tsutsui et al., 2001). Furthermore, it is likely that further introductions of *L. humile* have occurred since their initial introduction into Victoria in 1939 (Heterick et al., 2000), and these subsequent introductions could have originated from a variety of sources across the globe. Clearly, it would be interesting to investigate whether the patterns described here emerge in other invasive populations.

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