POPULATION ECOLOGY

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Colony-structure variation and interspecific competitive ability in the invasive Argentine ant

Abstract The success of some invasive species may depend on phenotypic changes that occur following introduction. In Argentine ants (*Linepithema humile*) introduced populations typically lack intraspecific aggression, but native populations display such behavior commonly. We employ three approaches to examine how this behavioral shift might influence interspecific competitive ability. In a laboratory experiment, we reared colonies of *Forelius mccooki* with pairs of Argentine ant colonies that either did or did not exhibit intraspecific aggression. *F. mccooki* reared with intraspecifically non-aggressive pairs of Argentine ants produced fewer eggs, foraged less actively, and supported fewer living workers than those reared with intraspecifically aggressive pairs. At natural contact zones between competing colonies of *L. humile* and *F. mccooki*, the introduction of experimental Argentine ant colonies that fought with conspecific field colonies caused *L. humile* to abandon baits in the presence of *F. mccooki*, whereas the introduction of colonies that did not fight with field colonies of Argentine ants resulted in *L. humile* retaining possession of baits. Additional evidence for the potential importance of colony-structure variation comes from the Argentine ant's native range. At a site along the Rio de la Plata in Argentina, we found an inverse relationship between ant richness and density of *L. humile* (apparently a function of local differences in colony structure) in two different years of sampling.

Keywords Aggression · Biological invasion · Interspecific competition · Intraspecific competition · *Linepithema humile*

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Introduction

Attempts to understand the success of invasive species increasingly involve experimental approaches (D'Antonio 1993; Petren and Case 1996) and comparisons of native and introduced populations (Callaway and Aschehoug 2000; Lohrer et al. 2000). Less progress has been made integrating phenotypic variation into experimental studies aimed at uncovering the causes of invasion success. Although introduced species can undergo rapid morphological changes in new environments (Huey et al. 2000; Mooney and Cleland 2000), the ways in which phenotypic shifts contribute to the colonization ability, establishment, and spread of invasive species remain incompletely known.

Argentine ants (*Linepithema humile*) invade ecosystems in many parts of the world (Suarez et al. 2001) where they cause a variety of ecological effects (Bond and Slingsby 1984; Ward 1987; Cole et al. 1992; Suarez and Case 2002). Though multiple factors no doubt contribute to their success (Human and Gordon 1996; Holway 1999; Holway et al. 2002a), this species is of interest because, like the red imported fire ant (*Solenopsis invicta*) (Ross et al. 1996), native and introduced populations differ markedly. In its introduced range, populations of *L. humile* are unicolonial. As a result, introduced populations of Argentine ants typically form expansive supercolonies within which intraspecific aggression is absent (Newell and Barber 1913; Passera 1994; Way et al. 1997; Tsutsui et al. 2000; Giraud et al. 2002). Such supercolonies may extend for many kilometers (Tsutsui et al. 2000; Giraud et al. 2002), and historical reports document their existence from shortly after the introduction of the species (Newell and Barber 1913). Native populations from Argentina, in contrast, are much less unicolonial. Colonies there often occupy multiple nests, but intraspecific aggression commonly occurs over short (<100 m) spatial scales (Tsutsui et al. 2000). Colony structure varies somewhat in both ranges. In the introduced range, although intraspecific aggression is typically absent, at least four mutually antagonistic supercolonies are presently known from

California (Suarez et al. 2002) and two from southern Europe (Giraud et al. 2002). In the native range we have identified two locations where intraspecific aggression was absent among nests as far as 600–1,000 m apart (Tsutsui et al. 2000).

The loss of intraspecific aggression in introduced populations of Argentine ants might contribute to their success as invaders (Newell and Barber 1913; Pontin 1963; Hölldobler and Wilson 1977). Intraspecific aggression and territoriality, for example, can restrict colony size and growth. In a laboratory experiment that paired Argentine ant colonies together that either fought or did not fight, aggressive pairs produced 75% as much brood and supported 50% as many workers after 70 days compared to non-aggressive pairs (Holway et al. 1998). Such reductions could decrease interspecific competitive ability because numerical advantages over native ants appear key to the Argentine ant's competitive strength (Tremper 1976; Holway 1999; Holway and Case 2001). The loss of intraspecific aggression might also facilitate supercolony movement. Argentine ants opportunistically exploit ephemeral nest sites and are unusual among social insects in the extent to which their colonies expand and contract seasonally and relocate in response to changes in the physical environment (Newell and Barber 1913; Markin 1968, 1970; Gordon et al. 2001). Such flexibility could increase a colony's ability to withstand physical disturbances or to exploit patchy resources (Newell and Barber 1913; Holway and Case 2000; Silverman and Nsimba 2000), but the putative advantages of such plasticity would seem to diminish if adjacent nests fought with one another.

In this study we examine the role of variation in colony structure as a factor contributing to the Argentine ant's interspecific competitive ability. The most convincing test of the potential importance of the loss of intraspecific aggression would be a population-level manipulation of the presence or absence of territoriality. Because such a large-scale experiment is currently unfeasible, we adopt three complementary approaches. First, we conducted a laboratory experiment that matched pairs of experimental *L. humile* colonies that either did or did not exhibit aggression toward each other against experimental colonies of *Forelius mccooki*. Second, at multiple contact zones between established colonies of *L. humile* and *F. mccooki*, we introduced experimental *L. humile* colonies that either did or did not fight with conspecific field colonies to test how intraspecific aggression in this species affects its ability to retain food resources in the face of interspecific competition. Lastly, if the loss of intraspecific aggression in *L. humile* increases interspecific competitive ability, we reasoned that areas in which intraspecific aggression is absent would support a lower diversity and abundance of other ant species compared to areas where intraspecific aggression is more pronounced. We tested this hypothesis by taking advantage of a case of natural variation in colony structure in the Argentine ant's native range. Taken together, these experimental and observational approaches represent a unique attempt to test

experimentally how behavioral variation might be linked to invasion success.

Materials and methods

Laboratory experiment

We collected material for experimental colonies of *Forelius mccooki* in May 2001 from the University of California Elliot Chaparral Reserve, San Diego Co. (Fig. 1). We constructed 12 experimental colonies each consisting of 3 queens, approximately 750 workers, and about 100 pieces of mixed brood. Each experimental colony occupied a plastic nest container (30 cm ×14 cm ×8 cm) lined with Fluon and Tanglefoot to prevent ants from escaping. Each nest container contained 3 nest chambers (16 mm ×150 mm glass test tubes) half full of water and stopped with cotton; we covered nest chambers with aluminum foil to keep them dark. Colonies were reared in the laboratory for about a month prior to the start of the experiment.

We chose *F. mccooki* as an interspecific competitor for several reasons. First, *Forelius* and *Linepithema* both form polygynous, polydomous colonies and have small, monomorphic workers. (In terms of wet mass *F. mccooki* workers are approximately 67% as large as *L. humile* workers.) Second, like the Argentine ant, *Forelius* is an aggressive and proficient competitor, using a combination of chemical defensive compounds and efficient recruitment in competition with other ants (Hölldobler 1982; Van Zee et al. 1997). Lastly, *F. mccooki* colonies are easily maintained in the laboratory, appear to adjust normally to artificial environments, and experience only small amounts of worker mortality when cultivated in the absence of Argentine ants (Holway and Case 2001; Holway et al. 2002b).

In June 2001 we collected material for experimental colonies of Argentine ants from seven locations in southwestern California (Fig. 1). All collecting sites were in riparian woodlands except for La Jolla (a suburban site) and Lake Skinner (a recreational campground). These seven sites are currently occupied by four supercolonies: one that appears to extend throughout coastal California (Tsutsui et al. 2000) and three that exhibit localized distributions (Fig. 1; Suarez et al. 2002). Nests from different supercolonies fight aggressively with one another, while intraspecific aggression is absent among nests from the same supercolony (Holway et al. 1998; Tsutsui et al. 2000; Suarez et al. 2002). After
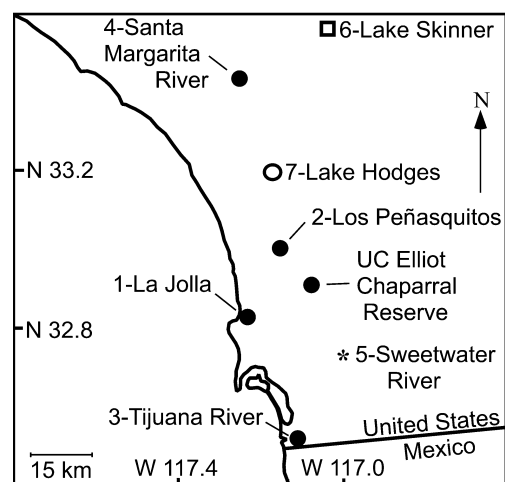

Fig. 1 Map of southwestern California showing the location of eight collecting sites used in this study. *Black circles* show locations occupied by a supercolony of *L. humile* that extends into northern California (Tsutsui et al. 2000); other symbols show locations of more spatially restricted supercolonies. Sites are abbreviated by number in the text

collection, we constructed experimental colonies as for *F. mccooki*; each colony contained 3 queens, approximately 500 workers, and about 100 pieces of mixed brood. Note that experimental colonies of the two species contained an equivalent live mass of workers. We then formed unique pairings of *L. humile* colonies as follows (see Fig. 1 for the site names corresponding to each number). Aggressive pairs ($n =6$): 1 versus 5, 1 versus 6, 1 versus 7, 5 versus 6, 5 versus 7, and 6 versus 7. Non-aggressive pairs ($n =6$): 1 versus 2, 1 versus 3, 1 versus 4, 2 versus 3, 2 versus 4, and 3 versus 4. The distances separating sampling locations for aggressive and non-aggressive pairings were large and on average similar [53 ± 11 km vs 50 ± 12 km respectively (mean ±1 SE)]. Colonies were reared in the laboratory for about 2 weeks prior to the start of the experiment.

Our experimental design reflects the somewhat unusual nature of the introduced population of Argentine ants in California [Tsutsui et al. 2000; Suarez et al. 2002; see Giraud et al. (2002) for a description of a similar pattern for the introduced population in southern Europe]. Because only four supercolonies are currently known from California (Suarez et al. 2002), it was necessary to include representatives from each supercolony more than once in different pairings of experimental colonies. Since each unique pairing consisted of ants collected from geographically distant locations, however, our experimental design makes it highly unlikely that workers and queens from different experimental colonies within a pair were related by immediate descent. The large asymmetry in the size of the California supercolonies (Suarez et al. 2002) further constrained our experimental design; all of the non-aggressive pairings discussed above consisted of experimental colonies from the largest of the four supercolonies. Because the three smaller supercolonies exhibit spatially restricted distributions relative to that of the largest supercolony, we could not safely assume that samples from multiple sites within the smaller supercolonies would be unrelated by immediate descent. Since we could think of no reason why the large supercolony would consistently differ from the smaller supercolonies in its behavior towards other species of ants, we chose to sample across distance rather than supercolony identity. Nonetheless, to better justify our design, we modified an approach used by Morrison (1996) to test for gross differences in interspecific fighting ability among the different supercolonies. For each trial we placed 15 *F. mccooki* workers and 10 Argentine ant workers from one of the seven sampling sites into a petri dish (9 cm diameter) with the vertical sides covered with Fluon. After 180 min we counted the number of *F. mccooki* that appeared dead or mortally wounded (e.g., missing legs or antennae, unable to move). We conducted two sets of comparisons for this behavioral assay: (1) Argentine ant workers from colonies reared in the laboratory for 3 months (5 replicates for each sampling location), and (2) Argentine ant workers freshly collected from the field (6 replicates for each sampling location). For each set of comparisons we used a one-way ANOVA on arcsine-transformed proportions to compare Argentine ants from the four supercolonies with respect to their ability to kill or injure *F. mccooki* workers. We pooled data across the four sampling sites occupied by the big supercolony.

At the start of the laboratory experiment, we randomly assigned experimental colonies of *F. mccooki* to each colony pair of *L. humile* and then connected colonies within each trio to a common foraging arena (a plastic box similar in dimensions to a nest container) via 3 m of plastic tubing (4 mm inner diameter). *Forelius* colonies were given access to the foraging arena approximately 48 h before we allowed *L. humile* colonies access to the arena. All colonies were reared on 12 h: 12 h light-dark schedule. Because *F. mccooki* prefers higher temperatures than does *L. humile* (Holway et al. 2002b), we used heat lamps (hung 0.5 m above each *F. mccooki* nest container) to elevate the local temperature of *F. mccooki* colonies to approximately 29°C during the day. The temperature for all *L. humile* all colonies was approximately 27°C during the day and 25°C at night. After the start of the experiment we placed food only in the foraging arena and fed colonies daily both crickets and a 20% solution of sucrose dissolved in water. One hour following each feeding we counted the number of workers of both species present in each foraging arena. We used these counts, averaged across sampling days, as an index of colony-level activity. After 48 days

we sacrificed all colonies and counted eggs and surviving workers. We used three response variables to describe colony performance: activity, the number of workers alive at the end of the experiment, and egg production. We used egg production instead of total brood production because, given the length of the experiment and the development time of Argentine ants, egg production provides a better measure of colony productivity during the experiment. For Argentine ants, each response variable is the summed response of each pair of experimental colonies. For each species, we used a single-factor MANOVA to test how intraspecific aggression in *L. humile* affected colony performance. To assess the individual contribution of each response variable, we used standardized canonical coefficients and univariate tests (Scheiner 2001) calculated using SYSTAT 5.0. The magnitude and sign of standardized canonical coefficients provides information on the relative contribution of each coefficient to variation in the dependent variables (Scheiner 2001).

Field experiment

We conducted a short-term introduction experiment to test how colony-structure variation in *L. humile* might influence interspecific competitive ability under field conditions. Manipulations of this sort are a useful and commonly used method to study behavioral interactions between native and introduced social insects (Roubik 1978; Schaffer et al. 1983; Human and Gordon 1996). We carried out this experiment at the University of California Elliot Chaparral Reserve from September to October 2001. At this site Argentine ants are established in a *Eucalyptus* grove bordering the reserve and meet native ants where *Eucalyptus* gives way to native chaparral, which appears to be too dry to support *L. humile*. We identified five sites (each separated by ≥300 m) where Argentine ants met *F. mccooki* along this habitat boundary. We selected only sites where we observed *L. humile* and *F. mccooki* foraging on the ground within 10 cm of one another between 0800 and 0930 hours on several different days. We focused on interactions between *L. humile* and *F. mccooki* for the reasons mentioned above (see Materials and methods: Laboratory experiment), and because no other native ants interacted in close proximity with Argentine ants at this site during the experimental period.

At each of the five *L. humile* - *F. mccooki* contact sites and over 2 consecutive days, we introduced two experimental *L. humile* colonies, one that did not fight with resident *L. humile* (day 1) and one that did (day 2). We were unable to randomize the order of our treatments because pilot experiments revealed that when aggressive colonies where introduced on day 1, established Argentine ant colonies failed to recruit the next day. Given that contact zones between *F. mccooki* and Argentine ants are difficult to locate, we were forced to present non-aggressive experimental colonies first. A possible bias that might result from this design is that field colonies of Argentine ants would become sated on the baits and lose interest in foraging on them the second day (i.e., irrespective of whether an aggressive conspecific colony was there or not). Evidence that this potential bias was unimportant comes from the pre-introduction levels of recruitment. Prior to introduction of experimental colonies, the number of resident *L. humile* present at baits did not differ between the two days of the experiment [47 ± 16 (day 1) vs 56 ± 15 (day 2) (mean ±1 SE); paired *t*-test: $t =0.932$, $P =0.404$].

Experimental colonies used in this experiment were constructed from material collected from the same set of locations used in the laboratory experiment. Argentine ants from the University of California Elliot Chaparral Reserve do not fight with workers from the largest of the four supercolonies shown in Fig. 1 (e.g., sites 1–4). Each contact site received a unique set of experimental colonies as follows: 1 (day 1) and 7 (day 2), 1 (day 1) and 5 (day 2), 3 (day 1) and 6 (day 2), 2 (day 1) and 7 (day 2), and 3 (day 1) and 5 (day 2). Experimental colonies were each fitted with a 30 cm exit tube that remained blocked until needed.

On each day of the experiment, we placed a bait (≈1 g of apple jelly on a plastic disk 4 cm in diameter) on the ground in the vicinity

of foraging workers of both *L. humile* and *F. mccooki*. For the first few minutes of the experiment, we used an aspirator to remove *F. mccooki* from within 10 cm of the bait to increase the likelihood that Argentine ants would recruit. Thirty minutes after the first *L. humile* worker made contact with the bait, we counted the number of workers present and then introduced an experimental *L. humile* colony by unplugging its exit tube (the distal end of which was placed 10 cm from the bait) and allowing workers to leave their nest container and to explore the vicinity of the bait. After the experimental colonies were provided with access to the bait, we did not remove any *F. mccooki*. As a dependent variable we used the number of *L. humile* at the bait 30 min after experimental colonies were first introduced divided by the number present when the experimental colony was first allowed access to the bait. We used this proportion because of variation in the activity of resident *L. humile* at the five contact sites.

Pitfall trapping

To assess if colony-structure variation correlates with ant diversity and abundance, we used pitfall traps to sample ants at the Costanera Sur Ecological Reserve, Buenos Aires, Argentina (34°36′S, 58°21′W) in 2 consecutive years: January–February 2002 and February–March 2003. We chose this site for the following reasons. First, the introduced range lacks populations of Argentine ants that vary in their colony structure over small spatial scales. Second, throughout much of this reserve, *L. humile* appears more or less multicolonial, but in the southern portion intraspecific aggression is absent from an area approximately 800 m in its longest dimension (Tsutsui et al. 2000), allowing us to compare ant richness and abundance in areas with and without intraspecific aggression at the same site. We placed 10 pitfall traps in each of two areas: (1) inside the area where Argentine ants lack intraspecific aggression, and (2) outside this area but in locations with Argentine ants. Traps in the two areas were matched for habitat: open woodland adjacent to freshwater marshes. All traps were placed approximately 100 m apart. Each trap consisted of a 50 ml centrifuge tube buried flush with the ground and half-filled with a dilute solution of detergent in water. We collected traps after 2.5 days. After collection, we identified ants to species or to morphospecies within genus. For each year separately, we used a single-factor MANOVA to compare three response variables between areas located inside and outside the Costanera Sur supercolony: number of *L. humile* workers/trap, number of workers of other ants/trap, and ant species richness/trap. Individual traps are considered replicates. Only traps containing Argentine ants were used in the analysis to ensure they were placed within the foraging range of *L. humile* nests; including data from all traps does not affect patterns of significance. Measures of ant abundance were log transformed prior to analysis.

Results

Laboratory experiment

Compared to *L. humile* colony pairs that lacked intraspecific aggression, those that fought among themselves experienced reduced colony-level performance (Table 1, Fig. 2). Aggressive colony pairs, on average, foraged 55% as much during the experiment, and after 48 days, supported 52% as many workers, and produced 43% as many eggs compared to non-aggressive pairs (Fig. 2). Standardized canonical coefficients and univariate tests suggest that the three response variables contributed approximately equally to the overall effect of intraspecific competition (Table 1). All six non-aggressive pairs fused

during the experiment (i.e., queens and workers from formerly separate pairs all present together in the same nest), whereas none of the aggressive pairs fused.

Compared to *F. mccooki* colonies exposed to intraspecifically aggressive pairs of *L. humile*, those exposed to
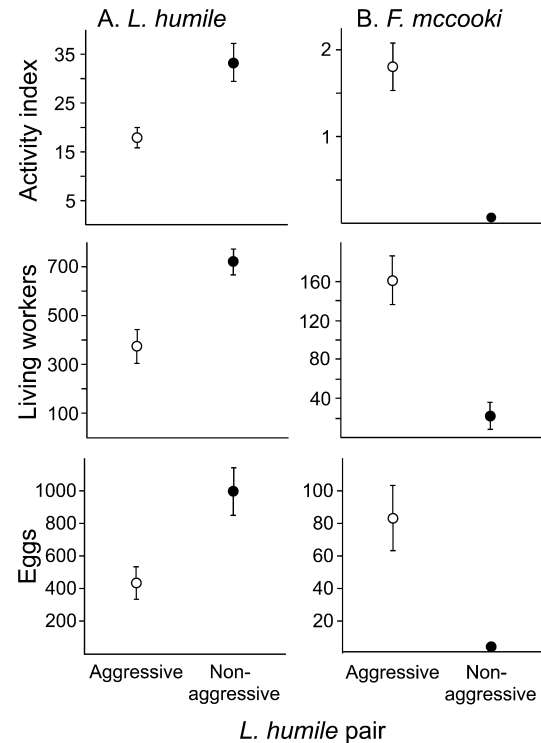

Fig. 2 Results of a laboratory experiment testing how the presence or absence of intraspecific aggression in pairs of experimental *L. humile* colonies affects three measures of colony-level performance in **A** *L. humile* and **B** *F. mccooki*. Note that for each measure of colony-level performance, scales are different for each species. All symbols = mean ±1 SE. See also Table 1

Table 1 Results of MANOVAs testing the effects of colony-structure variation in *L. humile* (intraspecific aggression present or absent) on three measures of colony-level performance in *L. humile* and *F. mccooki*

Multivariate tests

Species	df	Wilk's λ	F	P
L. humile	3, 8	0.150	15.11	0.001
F. mccooki	3, 8	0.122	19.14	0.001

Standardized canonical coefficients and univariate tests

Species	Variable	Standardized Canonical Coefficients	df	F	P
L. humile	Living workers	0.604	1, 10	19.13	0.001
	Activity index	0.806	1, 10	11.76	0.006
	Eggs	0.654	1, 10	10.55	0.009
F. mccooki	Living worker	0.102	1, 10	25.54	<0.001
	Activity index	0.878	1, 10	41.44	<0.001
	Eggs	0.594	1, 10	14.99	0.003

non-aggressive pairs experienced greatly reduced colony-level performance (Table 1, Fig. 2). Of the *F. mccooki* colonies alive at the end of the experiment, those reared with *L. humile* pairs that lacked intraspecific aggression stopped foraging and supported only 41% as many living workers and produced 15% as many eggs after 48 days compared to *F. mccooki* colonies reared with *L. humile* pairs that fought among themselves (Fig. 2). Standardized canonical coefficients and univariate tests suggest that activity contributed most strongly to the overall effect of interspecific competition. Compared to Argentine ants from aggressive pairs, those from non-aggressive pairs were present in the nest containers of *F. mccooki* during activity counts on a higher proportion of sampling days [0.73±0.12 vs 0.13±0.05 (mean ±1 SE); Mann-Whitney *U*-test: $P = 0.006$]. By the end of the experiment, four of the six *F. mccooki* colonies had been eliminated in the non-aggressive treatment, whereas aggressive pairs of *L. humile* failed to kill off any *F. mccooki* colonies. Although non-aggressive pairs of *L. humile* colonies exerted a stronger effect on *F. mccooki* colonies during the experimental period, aggressive pairs still reduced the size of *F. mccooki* colonies, on average, by 78% by the end of the experiment (Fig. 2).

There was no evidence that Argentine ant workers from the four supercolonies differed in their ability to fight against *F. mccooki* workers. Supercolony identity did not affect the ability of small groups of Argentine ants workers to kill or to injure small groups of *F. mccooki* workers [One-way ANOVA: $F_{3,31}=1.712$, $P >0.05$ (laboratory-reared Argentine ants); $F_{3,38}=0.558$, $P >0.05$ (Argentine ants freshly collected from the field)].

Field experiment

When we introduced experimental *L. humile* colonies from the same supercolony as resident *L. humile*, workers tended to interact with one another at baits as if they were nest mates. Moreover, in all five replicates, experimental colonies evacuated their nest containers during the experiment and assimilated themselves into established recruitment trails. When we introduced experimental *L. humile* colonies from different supercolonies, workers instantly began fighting. In face of interspecific competition from *F. mccooki* and as an apparent result of intraspecific aggression, workers from aggressive *L. humile* pairings persisted at baits after 30 min to a lesser extent than did workers from non-aggressive pairings [proportion of workers remaining: 0.057±0.030 vs 0.615±0.163 (mean ±1 SE); Wilcoxon signed rank test: $P =0.043$].

Pitfall trapping in Argentina

With respect to how the presence or absence of intraspecific aggression among *L. humile* nests at Costanera Sur correlated with ant species richness and worker abundance, two different years of sampling revealed qualita-

tively similar results (Fig. 3). In 2002, traps placed where intraspecific aggression was absent captured fewer ant species, more Argentine ant workers, and fewer workers of other ant species than did traps placed in areas of high intraspecific aggression (MANOVA: Wilk's λ=0.229, $F_{3,12}=13.46$, $P <0.001$). Standardized canonical coefficients and univariate tests suggest that in 2002 differences in richness contributed most strongly to the overall effect of Argentine ant colony-structure variation [richness (standardized canonical coefficient =−0.904; univariate test: $F_{1,14}=23.90$, $P < 0.001$), Argentine ant abundance (standardized canonical coefficient =0.819; univariate test: $F_{1,14}=15.02$, $P =0.002$], and abundance of other ants (standardized canonical coefficient =−0.679; univariate test: $F_{1,14}=7.71$, $P =0.015$)].

Although sampling in 2003 was conducted slightly later in the austral summer when ant activity was lower than it was earlier in the season the previous year, overall trends appeared similar to those observed in 2002 (Fig. 3; MANOVA: Wilk's λ=0.219, $F_{3,6}=7.12$, $P=0.021$). Standardized canonical coefficients and univariate tests, however, suggest that in 2003 only differences in richness contributed significantly the overall effect of Argentine ant colony-structure variation [richness (standardized canonical coefficient =−0.963; univariate test: $F_{1,8}=21.02$, $P =0.002$), Argentine ant abundance (standardized canonical coefficient =0.552; univariate test: $F_{1,8}=2.49$, $P >0.05$), and abundance of other ants (standardized canonical coefficient =−0.640; univariate test: $F_{1,8}=3.77$, $P =>0.05$)].
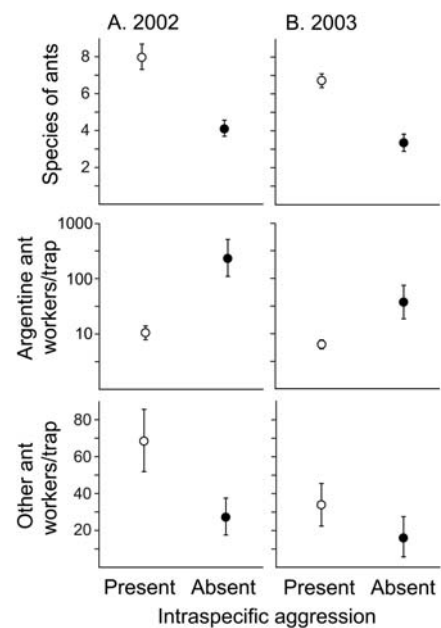

Fig. 3 Results of pitfall trap sampling at the Costanera Sur Ecological Reserve, Buenos Aires, Argentina in **A** 2002 and **B** 2003. Pitfalls were placed either inside an area where intraspecific aggression was absent or in nearby, otherwise similar areas in which *L. humile* was more multicolonial. Note that a log-scale is used to graph abundance data for *L. humile*. All symbols = mean ±1 SE

Discussion

Numerous studies report on the unicoloniality of introduced populations of Argentine ants, but supporting evidence comes primarily from behavioral assays that involve pairs of workers from different nests (Tsutsui et al. 2000; Giraud et al. 2002). In the laboratory experiment described in this study all six pairs of *L. humile* colonies that lacked intraspecific aggression fused with one another despite that the average distance separating collecting sites exceeded 50 km. This result provides a unique colony-level illustration of the extent to which supercolonies can act in an apparently cooperative and integrated manner even across large spatial scales (see also Roulston et al. 2003). Moreover, the presence or absence of intraspecific aggression in colony pairs, both in the laboratory and in the field, agreed without exception to studies that assessed colony identity by matching pairs of workers from different nests (Tsutsui et al. 2000; Suarez et al. 2002; Tsutsui et al. 2003). Trials involving pairs of workers could potentially give a misleading impression of colony membership given that workers are divorced from their social environment, but the agreement between the two approaches justifies the use of worker-worker matches (see also Roulston et al. 2003).

The widespread loss of intraspecific aggression and the concomitant formation of supercolonies typical of introduced populations of Argentine ants appear to enhance interspecific competitive ability. In a structurally simple laboratory environment pairs of experimental *L. humile* colonies that did not fight among themselves exerted a much stronger competitive effect on experimental *F. mccooki* colonies than did intraspecifically aggressive pairs. Likewise, among competing colonies of *L. humile* and *F. mccooki* in the field, Argentine ants persisted at baits to a greater extent when colonies of non-aggressive conspecifics were introduced than when colonies of aggressive conspecifics were introduced. Both in the laboratory and in the field, interference between *L. humile* and *F. mccooki* was prominent. In the laboratory pairwise fights between workers of the two species occurred often, both in the nest containers of *F. mccooki* and in the shared foraging containers. In pairs of experimental *L. humile* colonies that did not fight with one another, Argentine ant workers were present in the nest containers of *F. mccooki* on 73% of sampling days and may have prevented *F. mccooki* from foraging. Interference competition was not a mere artifact of the laboratory environment. When they meet, established colonies of *L. humile* and *F. mccooki* often engage in lengthy colony-level skirmishes. The interference behaviors evident between these species in the field, both in natural and staged interactions, qualitatively resemble those observed in the laboratory (Holway and Case 2001).

Colony-structure variation in the Argentine ant may be an important determinant of community-level dominance. At a site in the native range of *L. humile*, we found that this species was more abundant and other ants were both less abundant and less diverse in areas where intraspecific aggression was absent than in nearby areas where intraspecific aggression was common. Although sampling was confined to one site, this finding at least suggests that the formation of large supercolonies may enhance interspecific competitive ability. Given that the success of invasive ants is sometimes attributed to competitive release (Holway et al. 2002a), the association between colony-structure variation in *L. humile* and the richness and abundance of other ants in Argentina is of interest because it argues for the importance of unicoloniality as a determinant of ecological dominance even in the absence of competitive release.

Both our laboratory and field experiments had designs that may have increased the degree of intraspecific and interspecific competition. Although the lines of evidence discussed above argue for a role of reduced intraspecific aggression in the ecological success of the Argentine ant, manipulative experiments are clearly needed to assess under more realistic circumstances the extent to which the loss of intraspecific aggression contributes to increases in colony size, colony growth and interspecific competitive ability.

This study provides experimental support for the hypothesis that the success of invasive species may hinge on phenotypic changes that occur following introduction. The importance of such changes remains a largely unexplored area of research. While some studies document invasive species undergoing morphological changes after introduction (Mooney and Cleland 2000), few link these shifts to ecological success. Chapman and Bourke (2000) review examples of apparent changes in colony organization between native and introduced populations of social insects and raise the interesting possibility that these differences might commonly influence success in novel environments. It remains an outstanding question, however, whether changes in colony structure will persist over the long term. The extreme unicoloniality observed in introduced populations of *L. humile* and those of some other invasive ants, for example, may not be evolutionarily stable (Queller and Strassman 1998). Progress in this area remains hampered in part by a lack of quantitative information concerning native populations—a deficiency that highlights the importance of comparisons between native and introduced populations (e.g., Ross et al. 1996; Porter et al. 1997; Tsutsui et al. 2000). If phenotypic shifts contribute commonly to the success of invasive species, then the task of predicting potential invaders before they become problematic becomes even more difficult.

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