



## Behavioral and genetic differentiation between native and introduced populations of the Argentine ant

Andrew V. Suarez\*, Neil D. Tsutsui, David A. Holway & Ted J. Case

*Department of Biology 0116, University of California at San Diego, La Jolla, CA 92093-0116, USA;*

*\*Author for correspondence (e-mail: asuarez@biomail.ucsd.edu; fax: +1-619-534-7108)*

Received 9 June 1998; accepted in revised form 22 February 1999

**Key words:** Argentine ant, biological invasions, competition, invasive ants, *Linepithema humile*, microsatellites, nestmate recognition, population bottleneck, unicoloniality

### Abstract

In this paper, we examine the hypothesis that reduced intraspecific aggression underlies the competitive prowess of Argentine ants in their introduced range. Specifically, we test three predictions of this hypothesis by comparing the genetic diversity, behavior, and ecology of Argentine ants in their native range to introduced populations. Differences between native and introduced populations of Argentine ants were consistent with our predictions. Introduced populations of the Argentine ant appear to have experienced a population bottleneck at the time of introduction, as evidenced by much reduced variation in polymorphic microsatellite DNA markers. Intraspecific aggression was rare in introduced populations but was common in native populations. Finally, in contrast to the Argentine ant's ecological dominance throughout its introduced range, it did not appear dominant in the native ant assemblages studied in Argentina. Together these results identify a possible mechanism for the widespread success of the Argentine ant in its introduced range.

### Introduction

Despite the widespread problems associated with biological invasions, the proximate causes differentiating invasion success and failure remain poorly understood even in some of the most economically important examples. Developing a better understanding of the mechanistic underpinnings behind a particular invader's success is important for three reasons. First, the success of effective control strategies often hinges upon a detailed understanding of the factors governing the establishment and spread of introduced species. Second, a knowledge of the mechanisms responsible for invasion success may clarify the importance of different biotic interactions as determinants of community structure. Finally, the introduction and subsequent isolation of a population can lead to short-term evolutionary changes, providing a model to study fundamental mechanisms underlying evolutionary processes such as founder effects, genetic erosion, and speciation.

Studies that compare the ecology of invasive species between their introduced and native ranges can be particularly insightful. For example, invasive species may thrive in their introduced range due to the absence of competitors, predators, parasites, or diseases that help regulate populations in the native range (Elton 1958; Orians 1986; Pimm 1991; Porter et al. 1997). This type of biotic release can increase colonization success and subsequent rate of spread. The biology of invasive species might also differ between the native and introduced ranges due to genetic changes associated with small population sizes at the time of introduction (Ross and Keller 1995; Ross et al. 1996). Such genetic changes may, in turn, lead to changes in behavior, physiology, and morphology that can further influence invasion success. While the native ranges of invasive species are often surveyed for appropriate biological control agents (e.g., Orr et al. 1995, 1997) or to investigate genetic processes (Berlocher 1984; Ross et al. 1993; Eckert et al. 1996), few studies attempt to

compare the ecology or behavior of invasive species between their introduced and native ranges. Such studies offer great promise to elucidate the causal mechanisms promoting the success of an invasive species.

Ants are renowned for their invasive capabilities and many 'tramp' species have become established worldwide (Vinson 1986; Hölldobler and Wilson 1990; Vander Meer et al. 1990; Williams 1994). Such species include the red imported fire ant (*Solenopsis invicta*), the little fire ant (*Wasmannia auropunctata*), the big-headed ant (*Pheidole megacephala*), and the Argentine ant (*Linepithema humile*, formerly *Iridomyrmex humilis*). The consequences of these invasions are important and varied. For example, invasive ants often reduce native ant diversity (Clark et al. 1982; Ward 1987; Porter and Savignano 1990). Since ants are important scavengers and predators, and commonly participate in mutualisms (Hölldobler and Wilson 1990), changes to native ant communities may cascade to other taxa and trophic levels. For example, in the fynbos of South Africa, plants that require native harvester ants to disperse their seeds suffered reduced recruitment in areas where Argentine ants displaced native ants (Bond and Slingsby 1984). Additionally, in the Hawaiian islands, which lack native ants, the introduction of the Argentine ant has resulted in reductions in the native arthropod fauna (Cole et al. 1992). There is also a growing body of literature suggesting that exotic ants impact vertebrates (Mount 1981; Allen et al. 1995; Suarez et al. 1999).

In this study, we compare the biology of the Argentine ant (*Linepithema humile*) between portions of its native range (Buenos Aires Province, Argentina) and introduced ranges (Chile and California, USA) in an effort to clarify the underlying basis of this invasion. Native to South America, Argentine ants have been introduced widely and are most successful in Mediterranean climates (Passera 1994). Throughout their introduced range, Argentine ants competitively displace other ants (Newell and Barber 1913; Crowell 1968; Erickson 1971; Tremper 1976; Bond and Slingsby 1984; Majer 1994; Cammel et al. 1996). Moreover, Argentine ants are an important agricultural and urban pest (Newell and Barber 1913; Smith 1936; Knight and Rust 1990). Despite the widespread problems associated with Argentine ant invasions throughout their introduced range, little is known about the ecology of this species in its native range.

Throughout their introduced range, Argentine ants are unicolonial, that is, they maintain expansive supercolonies in which intraspecific aggression is largely

absent (Hölldobler and Wilson 1977). In such supercolonies, behavioral boundaries are weak to non-existent, and queens and workers move freely among spatially separate nests (Newell and Barber 1913; Markin 1968, 1970). Uniclonality contrasts with multicoloniality, the colony structure exhibited by most ants, which is characterized by well-developed nestmate recognition and intense intraspecific aggression (Hölldobler and Wilson 1990; Bourke and Franks 1995). The lack of nestmate recognition, typical of unicolonial species, might have several causes. First, unicolonial species, including the Argentine ant, are highly polygynous (nests contain many queens). The higher genetic variability present in polygynous colonies may reduce the efficiency of nestmate recognition systems, particularly if these abilities derive from genetically-based odors (Hölldobler and Michener 1980; Keller and Passera 1989; Bourke and Franks 1995). Second, the effectiveness of a recognition system may be further compromised by a loss of genetic variation. For example, a genetic bottleneck following introduction and establishment would result in genetic homogenization across spatially separate nests, which could further impair recognition abilities. Polygynous species, that have to contend with a variety of genetically based odors within the colony, may be particularly sensitive to this loss of genetic diversity.

The lack of intraspecific aggression, typical of unicolonial populations of the Argentine ant, may underlie its strong competitive ability. The competitive prowess of this species probably results from several consequences of its unusual colony structure which include large colony size and the maintenance of multiple nests, both of which may contribute to the high exploitative and interference abilities of this species (Human and Gordon 1996; Holway 1999).

We hypothesize that the Argentine ant's strong competitive ability in its introduced range might have resulted from changes in its social structure following introduction. We ask the following: (1) Have Argentine ants gone through a genetic bottleneck in their introduced range? (2) Do patterns of nest-mate recognition differ between the native and introduced ranges? (3) Are Argentine ants less dominant members of ant communities in their native range? We evaluated these questions in the following way. First, we used microsatellite DNA markers to examine genetic diversity between native and introduced populations. We predict reduced levels of genetic variation in introduced populations, consistent with a population bottleneck at the time of introduction. Second, we predict that

Argentine ants exhibit a higher frequency of intraspecific aggression in their native range relative to that typical of introduced populations. Finally, we predict that if intraspecific aggression is more common in the native range, the interspecific competitive ability of the Argentine ant will be reduced. As a consequence, Argentine ants should coexist with numerous species of ants in their native range and not be as numerically dominant as they are in their introduced range.

## Methods

### *Study areas*

*Native range.* Within their native range in Buenos Aires Province, Argentina, we surveyed ants at three sites located along a gradient of disturbance: Reserva Otamendi (Otamendi), Reserva Ecológica Costanera Sur (Costanera Sur), and urban parks in metropolitan Buenos Aires (Figure 1). Otamendi is a rural ecological reserve located approximately 55 km NW of Buenos Aires and includes a variety of habitats such as grasslands, seasonal wetlands, and riparian woodlands. Costanera Sur, located within the city of Buenos Aires, contains restored freshwater marsh and riparian woodlands in a variety of successional stages; this reserve is bordered on three sides by the city (urban parks and docks) and one side by the Rio de la Plata. Lastly, we surveyed two urban parks within Buenos Aires (Plaza Capaña del Desierto and a park located one block north of the intersection of Ave. Del Libertador and Ave. Carlos F. Melo). Both parks contained well-watered lawns planted with a variety of ornamental trees. We conducted research in Argentina in December 1997 (the austral summer).

*Introduced range.* We investigated aspects of the biology of Argentine ants in two widely separate portions of their introduced range: California and central Chile (Figure 1). Both central Chile and California were used to compare differences between introduced and native populations in intraspecific aggression, however, only sites in California were used for comparison of genetic variation and ant community composition. In Chile, we collected Argentine ants from Santiago and cities along the Pacific coast including Valparaiso, Viña del Mar, Quintero and Puchuncavi (Figure 1) primarily in urban areas, matorral, and *Eucalyptus* woodland. We conducted research in Chile in early December 1997. In southern California, Argentine ants were collected

for aggression assays and genetic analysis between November 1996 and March 1997 from the University of California at San Diego (UCSD) and Encinitas in San Diego County and Temecula in southern Riverside County (Figure 1), primarily in urban areas and coastal scrub habitats where they are common (Suarez et al. 1998). Using baits and pitfall traps, we compared ant communities in areas with and without Argentine ants in three habitat types in California: coastal sage scrub (Rice Canyon; sampled June 1997) and chamise chaparral (Elliot Reserve; sampled August 1996) in San Diego County (Suarez et al. (1998) for full description of study areas) and riparian woodland in Yolo County (sampled July 1996; see Holway (1998a, 1999) for a full description of study areas).

### *Genetic differentiation among introduced and native populations*

We compared overall genetic variation between ants from Argentina and California using microsatellite molecular markers. A small-insert partial genomic library was constructed using DNA extracted from worker brood collected on the campus of UCSD. DNA was extracted from this material using a QIAamp Tissue Kit (Qiagen). Twenty-five  $\mu\text{g}$  of this DNA was digested overnight with Eco R1 and Bam H1, and the entire sample was electrophoresed on a 1.0% agarose gel. Digested DNA, 300 to 700 base pairs in size, was cut out of the gel and purified using a Bio101 GeneClean kit. This DNA was then ligated into Eco R1/Bam H1-digested pBluescript II. The ligation products were electroporated into Stratagene SURE electroporation-competant cells. This library was then grown and hybridized to nylon transfer membranes using standard techniques (Sambrook et al. 1987). These membranes were then screened with P-32 end-labeled oligonucleotide repeats for clones containing microsatellites. Plasmids from positive colonies were sequenced, and primer sets were designed from the regions flanking the microsatellites. These microsatellites were then screened for polymorphism via polymerase chain reaction (PCR) of genomic DNA from individual ants collected from populations in Argentina and from introduced populations in California. Three polymorphic microsatellites were cloned and used to calculate heterozygosity. Ten Argentine ant workers were genotyped from each of 13 nests in Argentina (7 from Otamendi, 6 from Costanera Sur) and 16 nests in California (8 from UCSD, 8 from Encinitas).



Figure 1. Map of study areas within the native (Argentina) and introduced (central Chile and California, USA) ranges of the Argentine ant. Study sites are shown as dark circles within insets. Introduced and native areas are similar in latitude.

Expected heterozygosity is defined as the heterozygosity that would be obtained if the populations were in Hardy-Weinberg equilibrium. We calculated unbiased estimates of expected heterozygosity (Nei 1987) and compared differences between introduced and native populations using a permutation test based on Monte Carlo randomizations (T. Price, unpublished program).

#### *Geographic variation in intraspecific aggression*

To examine patterns of intraspecific aggression in the Argentine ant's native and introduced ranges, we developed a simple assay to quantify the relative aggression between workers from spatially separate nests. Argentine ants were collected with an aspirator directly from trails leaving the nest entrance. We assessed

aggression by placing one ant from each of two colonies into a 2-dram glass vial and scoring their interactions for five minutes. The vials were coated with fluon to prevent the ants from climbing the sides. Interactions between the ants were scored as follows: 0 = ignore, 1 = touch, 2 = avoid, 3 = aggression, and 4 = fighting. Ignores were contacts between individuals in which neither ant showed any interest (i.e., no antennation or aggression) and included contacts in which ants walked over one another without hesitation. If a contact included antennation, a touch was recorded. Avoids were contacts that resulted in one or both of the ants retreating in opposite directions. Aggression consisted of head biting, leg biting, leg pulling, or charging. Fighting included prolonged aggression between individuals and often consisted of one or both ants locking

their mandibles onto a body part of the other, carrying the other with its mandibles, or grappling. Between five and ten trials were repeated for each colony pair. The highest escalation score for each trial was averaged across trials within each colony pair; this average was used in the analyses.

The aggression assays were used (1) to determine the overall frequency of fighting within introduced and native populations and (2) to investigate the relationship between intraspecific aggression and geographic separation of colonies. In the first analysis, 34 colony pairs were selected randomly throughout the study areas (Figure 1). Each colony was only used once to partially satisfy independence assumptions of statistical tests, while recognizing the problem posed by unicoloniality. Distances between colony pairs were similar among the three study areas (0.01 to 66 km in Argentina, 0.1 to 110 km in Chile, and 0.01 to 70 km in California). A contingency table was used to examine differences among the regions in the proportion of trials that escalated to fighting. In the second analysis, we further examined spatial patterns of intraspecific aggression. An additional 104 colony pairs were matched to determine if aggression resulted from geographic separation. In California and Argentina, we focused this increased sampling effort on areas where fighting was detected in order to delineate aggressive groups.

#### *Effects of Argentine ants on community composition*

In their introduced range, Argentine ants displace a majority of native ant species. To determine whether Argentine ants dominate ant communities in their native range, we used a combination of visual surveys, pitfall traps, and baits to estimate overall species richness at three sites along a gradient of disturbance in Argentina. Visual surveys involved overturning objects, examining vegetation, and searching for colonies and foraging trails along the ground. Visual surveys were the exclusive means of surveying urban sites due to the limitations of working in highly populated areas. We conducted pitfall trap and bait transects at both Otamendi and Costanera Sur. At each site, 14 pitfall traps were placed 50 m apart in a linear transect. Each trap consisted of a 50 ml centrifuge tube buried flush with the ground and filled with a mixture of water and detergent. Traps were collected after 1.5 days. We also placed 14 baits, each consisting of 2.5 g of tuna, along the same linear transects used for

pitfall trapping. Bait stations were offset from pitfall traps by 20 m so as to not influence each other. At each bait, we recorded the abundance of each species present every fifteen minutes for two hours.

To assess differences in the degree to which Argentine ants dominate ant communities in their native and introduced range, we compared the results of the surveys in Argentina to surveys conducted in three different invaded habitats in California. We pitfall-trapped Elliot Reserve, Rice Canyon and Putah Creek but placed baits only at the Elliot Reserve and Putah Creek. We placed pitfall traps perpendicular to invasion fronts of Argentine ants within each of the three habitat types. Exact methods for the pitfall traps surveys were different from those used in Argentina; details may be found in Suarez et al. (1998) for the Elliot Reserve and Rice Canyon, and in Holway (1998a) for Putah Creek. At both the Elliot Reserve and Putah Creek, we placed bait transects at invasion fronts in areas where Argentine ants and native ants foraged together. Seventeen baits were placed 10 m apart within the Elliot Reserve, and 16 baits were placed 4 m apart at each of five sites along Putah Creek.

Ants were identified to species or to morphospecies within genera for tabulating species lists. Pitfall traps and bait stations may not be independent within sites. For this reason we compared the mean difference between species richness in pitfall traps with and without Argentine ants, and the proportion of baits dominated by Argentine ants using two-sample *t*-tests. Voucher specimens of ants recorded in these surveys have been deposited in the Bohart Museum of Entomology, University of California, Davis (UCDC).

## **Results**

### *Genetic differentiation among introduced and native populations*

Consistent with a population bottleneck at the time of introduction, both overall allelic diversity and levels of heterozygosity were lower in introduced populations than in populations from Argentina (Table 1). At the three microsatellite loci examined, Argentine populations of *Linepithema humile* had a total of 17 alleles ( $n = 130$  workers). In contrast, only 8 alleles were present at these three loci in the introduced Californian populations, despite slightly greater sampling ( $n = 160$  workers). All 8 alleles found in California were a subset of those present in Argentina. Similarly, overall

Table 1. Number of alleles and heterozygosity for 13 nests in Argentina and 16 nests in southern California. Ten workers from each nest were genotyped at each locus.

Location	Locus	H <sub>exp</sub>	H <sub>obs</sub>	No. of alleles
Argentina	M1 (AG) <sub>9</sub>	0.617	0.308	5
	S3 (CT) <sub>11</sub>	0.381	0.227	5
	T1 (CT) <sub>23</sub>	0.764	0.362	7
California	M1	0.006	0.006	2
	S3	0.132	0.141	2
	T1	0.133	0.120	4

heterozygosity was higher in Argentina ( $H = 0.299$ ) than in California ( $H = 0.089$ ) (permutation test,  $P < 0.001$ ). The levels of heterozygosity at Otamendi and Costanera Sur were 0.227 and 0.385, respectively, whereas Californian sites were lower, at 0.117 (UCSD) and 0.060 (Encinitas) (Table 1).

#### Geographic variation in intraspecific aggression

The frequency of aggression between colonies of Argentine ants varied among the three locations (Chi-square test:  $df = 2$ ,  $\chi^2 = 18.67$ ,  $P < 0.001$ ). In Argentina, 9 of 12 trials escalated to fighting, whereas in Chile and California, 0 of 7 trials and 1 of 15 trials respectively escalated to fighting. Argentine ants fought more often in their native range than in either introduced population (Fisher's exact test: Argentina vs. California,  $df = 1$ ,  $\chi^2 = 13.349$ ,  $P < 0.001$ ; Argentina vs. Chile,  $df = 1$ ,  $\chi^2 = 9.975$ ,  $P < 0.002$ ), whereas levels of aggression were low in both portions of their introduced range (Fisher's exact test: California vs. Chile,  $df = 1$ ,  $\chi^2 = 0.489$ ,  $P = 0.484$ ). There was no significant linear relationship between escalation and distance at any of the three locations (Figure 2).

We further examined the relationship between inter-colonial aggression and geographic separation in California and Argentina between areas where fighting was detected. Over large distances ( $>500$  m), aggression among colony pairs was often absent in southern California, while in Argentina, distant colony pairs always escalated to fighting (Figure 3).

#### Effects of Argentine ants on community composition

All three study areas in Argentina contained species rich ant communities: Otamendi (32 species in 13 genera), Costanera Sur (27 species in 14 genera), and urban

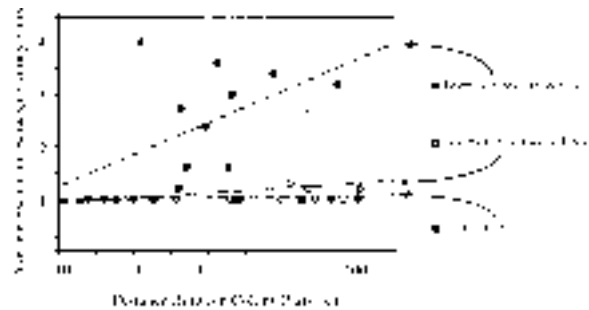
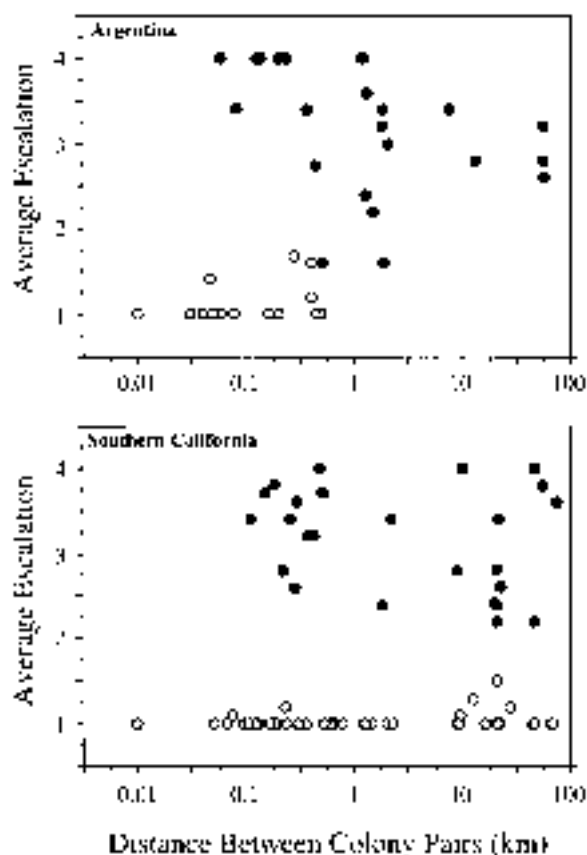


Figure 2. The relationship between intraspecific aggression and small-scale geographic distance for native (Argentina) and introduced (Chile and California) populations of the Argentine ant. The data points represent the average of each of the highest escalation values from five to ten trials between colony pairs. The regression lines shown are for illustrative purposes only (linear regressions between escalation and distance were not significant).

Buenos Aires (18 species in 11 genera). The Argentine ant was present in all three communities. In contrast, areas invaded by the Argentine ant in its introduced range typically contain few native ants (Erickson 1971; Tremper 1976; Ward 1987; De Kock and Giliomee 1989; Fuentes 1991; Cammel et al. 1996; Human and Gordon 1996; Suarez et al. 1998; Holway 1998a). For example, a typical urban site in southern California has, on average, three native species of ants (Suarez et al. 1998, A.V. Suarez, unpublished data). Unlike in introduced areas, where Argentine ants largely exclude native ant colonies and have a discernable front of invasion (Erickson 1971; Holway 1998b), in Argentina, we found Argentine ant nests interspersed with colonies of many other ant species.

Pitfall trap surveys demonstrated that, within sites, Argentine ants fail to reduce ant species richness in the native range (Figure 4). In addition, at both Argentina sites, pitfall traps containing Argentine ants were not localized in a particular area of the reserve but rather were widely dispersed throughout. For example, Argentine ants were captured in traps 2, 5, 8 of 14 in Otamendi and traps 3, 4, 8, 13 of 14 in Costanera Sur.

The results of the bait transects further indicate that Argentine ants do not numerically dominate ant communities in their native range. Argentine ants monopolized fewer baits at sites in their native range than they did in their introduced range in California (Figure 5). At Otamendi, Argentine ants were present at 4 of 15 baits but were only able to monopolize one. At Costanera Sur, Argentine ants were present at 5 of 15 baits but were only able to monopolize three. In contrast, at contact zones in California, where both native ants

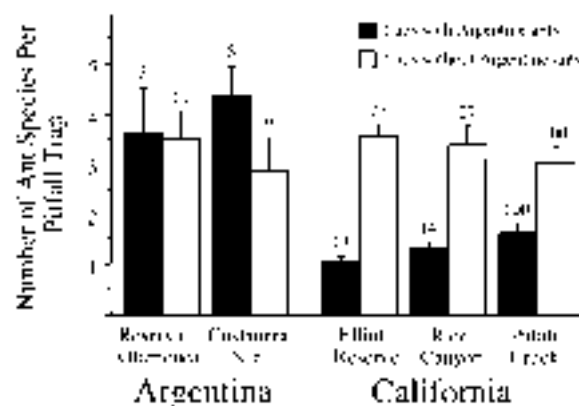


**Figure 3.** Average escalation values versus geographic separation in Argentina and California. Filled circles indicate colony pairs in which trials escalated to fighting; open circles indicate pairs in which trials did not escalate to fighting. The data points represent average highest escalation values from five to ten trials between colony pairs from areas where intraspecific aggression was detected within Argentina and California; some colonies were used more than once for these comparisons. Therefore, these points are not independent of one another. Values for Chile are not shown because intraspecific aggression was never detected there. In California, an effort was made to sample nests across supercolony boundaries. Therefore, the number of points over-represents the frequency of aggression in California.

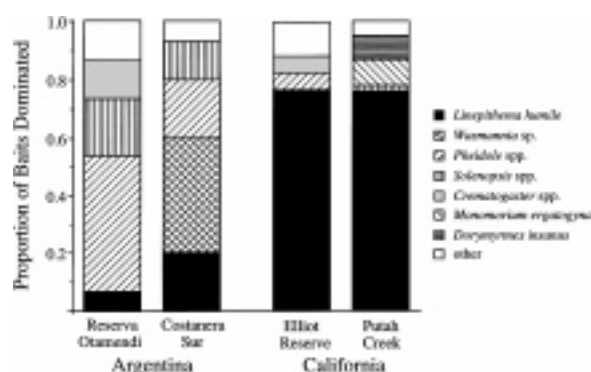
and Argentine ants had access to baits, Argentine ants excluded native ants from 76% of the baits on average (Figure 5).

## Discussion

Differences between native and introduced populations of Argentine ants were consistent with all three of our



**Figure 4.** The mean (+1 SE) number of ant species per pitfall trap for traps with and without Argentine ants in two sites in Argentina (native range) and three sites in California (introduced range). The sites in California include three habitat types: chamise chaparral (Elliot Reserve) coastal sage scrub (Rice Canyon) and riparian woodland (Putah Creek). The mean difference in the number of ant species between traps with and without Argentine ants was greater in the introduced range than it was in the native range (two-sample  $t$ -test:  $t = 4.201$ ,  $df = 3$ ,  $P = 0.0246$ ). Sample sizes indicated above each bar. The values for Putah Creek were averaged across five separate sites and are modified from Holway (1998a).



**Figure 5.** Proportion of baits dominated by different ant species or genera at two sites in Argentina (native range) and two sites in California (introduced range). Argentine ants dominated a higher proportion of baits in California than they did in Argentina (two-sample  $t$ -test:  $t = 9.433$ ,  $df = 2$ ,  $P = 0.0111$ ). The values for Putah Creek were averaged across five separate sites and are modified from Holway (1999).

predictions. Argentine ants exhibited lower heterozygosity in their introduced range in California than in their native range in Argentina. Intraspecific aggression was rare or absent within introduced populations examined. Finally, Argentine ants were not numerically dominant in the native populations studied.

Together these results identify a possible mechanism for the widespread success of the Argentine ant.

*Genetic differentiation among introduced and native populations*

We show that Argentine ants have undergone a population bottleneck at the time of introduction, and we suggest that comparative examination of population genetic structure at the levels of nest, supercolony, and range may elucidate mechanisms contributing to the extreme unicoloniality and competitive dominance seen in the introduced ranges. Ross et al. (1993) also report evidence for a genetic bottleneck in the imported fire ant, *Solenopsis invicta*, following introduction into North America.

The large difference between observed and expected heterozygosities in Argentina indicates population subdivision in the native range. In Argentine populations, expected heterozygosity ( $H_{exp}$ ) at all three loci was much higher than observed heterozygosity ( $H_{obs}$ ) (Table 1). Allele frequencies were not distributed randomly across nests; some alleles were disproportionately common in some nests while absent in others. This pattern is consistent with nest-level differentiation and concomitant reduction in  $H_{obs}$  (relative to  $H_{exp}$ ) due to the Wahlund effect. This effect was not observed in introduced populations suggesting that the genetic organization of Argentine ant social structure differs between native and introduced populations (Tsutsui et al. unpublished manuscript). This may result from the limited dispersal capabilities of Argentine ants. Argentine ant queens shed their wings within the nest and do not undergo nuptial flights, consequently colony reproduction only occurs by budding (Newell and Barber 1913; Passera and Aron 1993). Although colony reproduction occurs in the same way in California, a genetic bottleneck at the time of introduction followed by the recent range expansion throughout the introduced range is likely to have caused the reduction in genetic differentiation seen there. Since Argentine ants have been present in California for less than 100 years (Woodworth 1908), it is unlikely that there has been sufficient time for this population to have reached equilibrium. Furthermore, human-mediated dispersal is common in California where Argentine ants are overwhelmingly abundant in urban areas (Knight and Rust 1990). Their continuing spread by human commerce (particularly the transport of produce, agriculture and decorative shrubbery) may make this species less substructured in California compared to their native range.

*Geographic variation in intraspecific aggression*

The spatial scale at which intraspecific aggression was detected differed between native and introduced ranges. In Argentina, fighting was common at all spatial scales, and frequently occurred both within and among local sites. In contrast, colony pairs in southern California and Chile rarely fought, even at large distances. This suggests that Argentine ants in their introduced range behave as a single supercolony over large spatial scales (Holway et al. 1998). However, in California, aggression was detected between at least two supercolonies, implying at least some 'colony' boundaries.

Both polygyny and loss of genetic variability may influence nestmate recognition. Previous work has shown that increased polygyny in Argentine ants is associated with a reduction in the ability of workers to discriminate nestmates (Keller and Passera 1989). It is also likely that the genetic homogeneity in the introduced range might further reduce nestmate recognition by decreasing the available discriminatory cues needed to distinguish nestmates. Although nestmate recognition cues may not be exclusively genetically based, it is likely that heritable cues are involved in nestmate recognition in ants (Hölldobler and Wilson 1990). A plausible consequence of decreased nestmate recognition is the loss of intraspecific aggression, the breakdown of colony boundaries and ultimately, unicoloniality.

The loss of intraspecific aggression typical of unicolonial ants may allow these species to achieve high population densities. For example, Holway (1998b) reported that in California Argentine ant densities in invaded areas were four to ten times higher than the combined densities of native ants in paired uninvaded areas. Additional evidence that unicoloniality leads to high population densities comes from studies of the red imported fire ant, which occurs in two forms in its introduced range in the southeastern USA: a multicolonial, monogyne form and a more unicolonial, polygyne form (Ross et al. 1987). The polygyne form of *S. invicta* also attains densities exceeding those of the native ants it displaces (Porter and Savignano 1990). Moreover, the polygyne form occurs at twice the density of the monogyne form in the southeastern USA (Macom and Porter 1996). The high population densities typical of unicolonial ants may enhance their competitive ability and allow them to invade new environments successfully. Support for this idea comes from the observation that



many highly invasive ants are unicolonial to varying degrees; examples include *Wasmannia auropunctata*, *Monomorium pharaonis*, *Pheidole megacephala* and *Lasius neglectus* (Hölldobler and Wilson 1977; Van Loon et al. 1990; Passera 1994).

#### *Effects of Argentine ants on community composition*

In Argentina, the Argentine ant appears to coexist with native species in species-rich communities. Given that our sampling in Argentina was limited to only three sites and one season, additional sampling would have generated even higher estimates of species richness. These results stand in marked contrast to communities invaded by the Argentine ant in California, which typically include few native ant species and for which our sampling is more exhaustive. There are several hypotheses that may explain this difference.

First, the loss of intraspecific aggression and concomitant shift to unicoloniality may allow the Argentine ant to competitively displace a majority of native ant species throughout its introduced range. For example, Holway (1999) reported that Argentine ants were proficient at both exploitative and interference competition relative to native ant species in northern California, which were subject to a trade-off in their ability to engage in both forms of competition. The strong competitive ability of *L. humile* results from high worker densities rather than the competitive proficiency of individual workers (Tremper 1976; Holway 1999). The loss of intraspecific aggression and subsequent abandonment of territorial behavior typical of introduced populations allow worker densities to attain high levels (Holway et al. 1998). Large colony sizes, typical of unicolonial species, often play a role in determining competitive ability in ants generally (Hölldobler and Lumsden 1981; Adams 1990).

Second, like many introduced species, Argentine ants undoubtedly thrive in the absence of natural enemies. For example in Brazil, the presence of parasitic phorid flies in the genus *Pseudacteon* limit Argentine ant foraging during the day, when the flies are active, and cause Argentine ants to abandon baits (Orr and Seike 1998). The threat of parasitism by phorid flies has been implicated as a mechanism regulating the populations of other ecologically dominant ants (Feener 1981; Feener and Brown 1997). The above two hypotheses are not mutually exclusive. The loss of genetic variation and release from natural enemies may have worked

in concert to cause the observed change in colony structure between the Argentine ant's native and introduced ranges.

It is possible that a similar chain of events explains the shift in social structure and the subsequent increase in invasion success of *Solenopsis invicta*. Colony density is higher in their introduced range in the southeastern USA than in their native range in Argentina and Brazil (Porter et al. 1992, 1997). Moreover, Porter et al. (1997) suggest that their success in the introduced range is likely due to a release from natural predators and parasites. These higher colony densities may have also promoted the observed changes in social structure from the monogyne form to the polygyne form (Ross and Keller 1995; Ross et al. 1996).

#### *Implications for control*

The results of this study suggest an association between the loss of genetic variation and a reduction in intraspecific aggression in the Argentine ant. If future research substantiates a causal relationship between genetic diversity and nestmate discriminatory ability, a possible avenue for biological control could include attempts to increase genetic variation within introduced populations. For example, this could be accomplished by introducing males from genetically diverse populations, increasing the frequency of intraspecific aggression within supercolonies. Such a change could ultimately lead to a decrease in the degree of unicoloniality. However, care should be exercised before embarking upon such a course of action. Increasing genetic diversity could undermine future biological control efforts that might be able to capitalize on low levels of genetic homogeneity.

#### **Acknowledgements**

We would like to thank: Ruperta Venguet (aka 'Mima') for her generosity and hospitality in Argentina. Paula Cichero and the Administracion de Parques Nacionales for permission to work in the Argentine reserves. Sergio Rocio at Costanera Sur and park guards at Otamendi. Fred Dyer and Phil Ward for valuable discussion and insight. Phil Ward for help with ant identification. John La Bonte, Fred Dyer, Katherine Howard, Jill Shanahan, and Kevin Haight for helping with the aggression assays in southern California. Trevor Price for helpful comments and assistance with the permutation test.

This research was made possible by financial support from the United States National Science Foundation grant DEB-9610306 (to TJC), the United States Department of Agriculture NRI Competitive Grants Program 97-35302-4920 (to DAH), the National Institute of Health, CMG training grant GMO 7240 (to AVS) and the Canon National Parks Science Scholars Program (to AVS).

## References

- Adams ES (1990) Boundary disputes in the territorial ant *Azteca trigona*: effects of asymmetries in colony size. *Animal Behavior* 39: 321–328
- Allen CR, Lutz RS and Demorais S (1995) Red imported fire ant impacts on northern bobwhite populations. *Ecological Applications* 5: 632–638
- Berlocher SH (1984) Genetic changes coinciding with the colonization of California by the walnut husk fly, *Rhagoletis completa*. *Evolution* 38: 906–918
- Bond W and Slingsby P (1984) Collapse of an ant–plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology* 65: 1031–1037
- Bourke AFG and Franks NR (1995) *Social Evolution in Ants*. Princeton University Press, Princeton, NJ
- Cammel ME, Way MJ and Paiva MR (1996) Diversity and structure of ant communities associated with oak, pine, eucalyptus and arable habitats in Portugal. *Insectes Sociaux* 43: 37–46
- Clark DB, Guayasamín C, Pazmiño O, Donoso C and de Villacís YP (1982) The tramp ant *Wasmannia auropunctata*: autecology and effects on ant diversity and distribution on Santa Cruz island, Galapagos. *Biotropica* 14: 196–207
- Cole FR, Medeiros AC, Loope LL and Zuehlke WW (1992) Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology* 73: 1313–1322
- Crowell KL (1968) Rates of competitive exclusion by the Argentine ant in Bermuda. *Ecology* 49: 551–555
- De Kock AE and Giliomee JH (1989) A survey of the Argentine ant, *Iridomyrmex humilis* (Mayr), (Hymenoptera, Formicidae) in south African fynbos. *Journal of the Entomological Society of Southern Africa* 52: 157–164
- Eckert CG, Manicacci D and Barrett SCH (1996) Genetic drift and founder effect in native versus introduced populations of an invading plant, *Lythrum salicaria* (Lythraceae). *Evolution* 50: 1512–1519
- Elton CS (1958) *The Ecology of Invasions*. John Wiley, New York
- Erickson JM (1971) The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* (Mayr). *Psyche* 257–266
- Feener DH Jr (1981) Competition between ant species: outcome controlled by parasitic flies. *Science* 214: 815–817
- Feener DH Jr and Brown BV (1997) Diptera as parasitoids. *Annual Review of Entomology* 42: 73–97
- Fuentes ER (1991) Central Chile: how do introduced plants and animals fit into the landscape. In: Groves RH and Di Castri F (eds) *Biogeography of Mediterranean Invasions*, pp 43–49. Cambridge University Press, Cambridge, UK
- Hölldobler B and Lumsden CJ (1980) Territorial strategies in ants. *Science* 210: 732–739
- Hölldobler B and Michener CD (1980) Mechanisms of identification and discrimination in social Hymenoptera. In: Markl H (ed) *Evolution of Social Behavior: Hypotheses and Empirical Tests*, pp 35–37. Verlag Chemie, Weinheim
- Hölldobler B and Wilson EO (1977) The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64: 8–15
- Hölldobler B and Wilson EO (1990) *The Ants*. Belknap Press, Harvard University Press, Cambridge, MA
- Holway DA (1998a) Effects of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia* 116: 252–258
- Holway DA (1998b) Factors governing rate of invasion: a natural experiment using Argentine ants. *Oecologia* 115: 206–212
- Holway DA (1999) Competitive mechanism underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80: 238–251
- Holway DA, Suarez AV and Case TJ (1998) Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science* 282: 949–952
- Human KG and Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* 105: 405–412
- Keller L and Passera L (1989) Influence of the number of queens on nest-mate recognition and attractiveness of queens to workers in the Argentine ant, *Iridomyrmex humilis* (Mayr). *Animal Behavior* 37: 733–740
- Knight RL and Rust MK (1990) The urban ants of California with distributional notes of imported species. *Southwestern Entomologist* 15: 167–178
- Macom TE and Porter SD (1996) Comparison of polygynous and monogynous red imported fire ant (Hymenoptera: Formicidae) population densities. *Annals of the Entomological Society of America* 89: 535–543
- Majer JD (1994) Spread of Argentine ants (*Linepithema humile*), with special reference to Western Australia. In: Williams DF (ed) *Exotic Ants: Biology, Impact, and Control of Introduced Species*, pp 163–173. Westview Press, Boulder, CO
- Markin GP (1968) Nest relationship of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society* 41: 511–516
- Markin GP (1970) The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae) in southern California. *Annals of the Entomological Society of America* 63: 1238–1242
- Mount RH (1981) The red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), as a possible serious predator on some native southeastern vertebrates: direct observations and subjective impressions. *Journal of the Alabama Academy of Sciences* 52: 71–78
- Nei M (1987) *Molecular Evolutionary Genetics*. Columbia University Press, New York
- Newell W and Barber TC (1913) The Argentine ant. United States Department of Agriculture Bureau of Entomology Bulletin 122, 98 pp
- Orians GH (1986) Site characteristics favoring invasions. In: Mooney HA and Drake JA (eds) *Ecology of Biological Invasions of North America and Hawaii*, *Ecological Studies* 58, pp 133–145. Springer-Verlag, New York

- Orr MR, Seike SH, Benson WW and Gilbert LE (1995) Flies suppress fire ants. *Nature* 373: 292–293
- Orr MR, Seike SH and Gilbert LE (1997) Foraging ecology and patterns of diversification in dipteran parasitoids of fire ants in south Brazil. *Ecological Entomology* 22: 305–314
- Orr MR and Seike SH (1998) Parasitic flies (Diptera: Phoridae) alter the foraging success of Argentine ants (*Linepithema humile*) in their native habitat in Brazil. *Oecologia* 117: 420–425
- Passera L (1994) Characteristics of tramp species. In: Williams DF (ed) *Exotic Ants: Biology, Impact, and Control of Introduced Species*, pp 23–43. Westview Press, Boulder, CO
- Passera L and Aron S (1993) Social control over the survival and selection of winged virgin queens in an ant without nuptial flight, *Iridomyrmex humilis*. *Ethology* 93: 225–235
- Pimm SL (1991) *The Balance of Nature: Ecological Issues in the Conservation of Species and Communities*. University of Chicago Press, Chicago, IL
- Porter SD and Savignano DA (1990) Invasion of polygynous fire ants decimates native ants and disrupts arthropod community. *Ecology* 71: 2095–2106
- Porter SD, Fowler HG, and Mackay WP (1992) Fire ant mound densities in the United States and Brazil (Hymenoptera: Formicidae). *Journal of Economic Entomology* 85: 1154–1161
- Porter SD, Williams DF, Patterson RS and Fowler HJ (1997) Intercontinental differences in the abundance of *Solenopsis* fire ants (Hymenoptera: Formicidae): escape from natural enemies? *Ecological Entomology* 26: 373–384
- Ross KG and Keller L (1995) Ecology and evolution of social organization: insights from fire ants and other highly eusocial insects. *Annual Review of Ecology and Systematics* 26: 631–656
- Ross KG, Vargo EL and Fletcher DJC (1987) Comparative biochemical genetics of three fire ant species in North America, with special reference to the two social forms of *Solenopsis invicta* (Hymenoptera: Formicidae). *Evolution* 41: 979–990
- Ross KG, Vargo EL, Keller L and Trager JC (1993) Effect of a founder event on variation in the genetic sex-determining system of the fire ant *Solenopsis invicta*. *Genetics* 135: 843–854
- Ross KG, Vargo EL and Keller L (1996) Social evolution in a new environment: the case of introduced fire ants. *Proceedings of the National Academy of Science* 93: 3021–3025
- Sambrook J, Fritsch EF and Maniatis T (1987) *Molecular Cloning: A Laboratory Manual*, Second edition. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY
- Smith MR (1936) Distribution of the Argentine ant in the United States and suggestions for its control or eradication. United States Department of Agriculture, Circular 387. Washington, DC, 40 pp
- Suarez AV, Bolger DT and Case TJ (1998) Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology* 79: 2041–2056
- Suarez AV, Richmond JQ and Case TJ (1999) Prey selection in horned lizards following the invasion of Argentine ants in southern California. *Ecological Applications* (in press)
- Tremper BD (1976) Distribution of the Argentine ant, *Iridomyrmex humilis* Mayr, in relation to certain native ants of California: ecological, physiological, and behavioral aspects. PhD Thesis, University of California, Berkeley, CA, 260 pp
- Van Loon AJ, Boomsma JJ and Andrasfalvy A (1990) A new polygynous *Lasius* species (Hymenoptera: Formicidae) from central Europe. 1. Description and general biology. *Insectes Sociaux* 37: 348–362
- Vander Meer RK, Jaffe K and Cedeno A (eds) (1990) *Applied Myrmecology: A World Perspective*. Westview Press, Boulder, CO
- Vinson SB (ed) (1986) *Economic Impact and Control of Social Insects*. Praeger Press, New York
- Ward PS (1987) Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. *Hilgardia* 55: 1–16
- Williams DF (ed) (1994) *Exotic Ants: Biology, Impact, and Control of Introduced Species*. Westview Press, Boulder, CO, 332 pp
- Woodworth CW (1908) The Argentine ant in California. University of California Agricultural Experiment Station 38: 1–192