Genetics and Behavior of a Colonizing Species: The Invasive Argentine Ant

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abstract: Baker and Stebbins's 1965 book *The Genetics of Colonizing Species* aimed to draw together scientists from a variety of disciplines to provide a conceptual framework for the study of species introductions. A goal of their volume was to examine how studies on biological invasions could be used to provide insight into basic research questions as well as to develop practical strategies for control. In this article, we attempt to follow the goals of Baker and Stebbins by reviewing work on the genetics and behavior of a widespread colonizing species, the Argentine ant (*Linepithema humile*). Specifically, we examine the evolutionary changes that have taken place as a result of this species being introduced into new environments and synthesize recent research on Argentine ants from the perspective of population genetics, recognition systems, and the mechanisms that may underlie their ecological success.

Keywords: biological invasions, colony structure, *Linepithema humile*, supercolony, unicoloniality.

These transplantations of species have, in effect, been a series of experiments in evolution. As such, they are potentially much more informative than most laboratory experimental work, since they have faced the introduced species, not with some simple defined change in selective conditions, but with a whole new ecological system in which the species has to find a place for itself. (C. H. Waddington in Baker and Stebbins 1965; introduction to the symposium, p. 1)

A goal of Baker and Stebbins's (1965) edited volume on species introductions was to bring together research on

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the "kinds of evolutionary change that take place when organisms are introduced into new territories" (preface, p. vii). The volume targeted scientists from a variety of backgrounds, from population geneticists to practitioners of purely applied branches of ecology, such as biological control. As the above Waddington quote suggests, studies on the ecology and evolution of introduced species are important not only from an applied perspective—research on species introductions also can provide insight into natural processes that would ordinarily take prohibitively long periods of time to study and that occur over spatial scales that would be unfeasible or unethical to recreate using traditional channels of experimentation (Diamond and Case 1986). Understanding the ecological and evolutionary consequences of invasions has become increasingly important because the economic and ecological fallout of species introductions continues at accelerating rates (Cohen and Carlton 1998; Mack et al. 2000; Pimentel et al. 2000).

Social insects rank among the most widespread and damaging of social organisms (Lowe et al. 2000). Well-known examples include the red imported fire ant (*Solenopsis invicta*), the Argentine ant (*Linepithema humile*), Africanized "killer" bees (*Apis mellifera scutellata*), the German yellowjacket (*Vespula germanica*), and the Formosan subterranean termite (*Coptotermes formosanus*). The cooperation of many individuals as a single eusocial superorganism is generally believed to underlie the ecological success of social insects (Wilson 1971; Hölldobler and Wilson 1990). Social insects possess complex and occasionally unusual modes of social organization that are strongly influenced by genetic relationships within and among groups. However, invasive social insects sometimes display even more extreme forms of sociality, including geographically expansive colonies with many reproductive queens and large worker forces that can dominate ecosystems in their introduced range (Chapman and Bourke 2001; Holway et al. 2002). Consequently, several widely introduced species have become emerging model systems for genetics, behavioral ecology, and invasion biology.

In this article, we integrate previous work with new

analyses of the genetics and behavior of a widespread colonizing species, the Argentine ant (*L. humile*). We attempt to follow the goals of Baker and Stebbins (1965) in that we examine the evolutionary changes that have taken place as a result of this species being introduced into new environments. Like many invaders, Argentine ants are ecologically quite different between native and introduced populations; while they typically coexist with other ants in species-rich communities in their native Argentina, they displace nearly all other ants in areas where they invade. Moreover, changes in social structure between native and introduced populations have been implicated in the Argentine ant's success. Throughout this article, we examine differences in colony size, behavior, and genetic structure between native and introduced populations, and we consider how these disparities may contribute to ecological success. We discuss this research from a variety of perspectives, including issues relating to invasion history, population genetics, colony structure, recognition systems, and the ecology of invading organisms. We conclude by suggesting areas for future study.

Origin and Spread

> That Argentina is its native home is also borne out by the fact that it does not appear to be generally a pest of importance in that country. (Newell and Barber 1913, p. 11)

Studies that compare native and introduced populations of invasive species are of paramount importance for testing hypotheses that relate to evolutionary changes experienced by invaders. A starting point of such research is the identification of native range localities that are the likely sources of introduced populations. Historically, scientists relied on museum records, range maps, morphological comparisons, and established trading routes. But for many widely introduced species, inadequate information on their distribution, a lack of taxonomic resources, and a long history of human association have obscured their geographic origins. However, with the development of molecular tools, this task has become easier and more precise.

The first records of introduced populations of Argentine ants come from the late nineteenth century in Madeira, Portugal, and the southeastern United States (Suarez et al. 2001; Wetterer and Wetterer 2006). In the United States, Argentine ants were first detected in 1891 by citizen scientist Ed Foster near the wharves of New Orleans, Louisiana (Newell 1908; Barber 1916). Brazil was believed to be the most likely source because of the importation of Brazilian coffee and sugar cane to the southeastern United States in the late 1800s (Newell 1908; Woodworth 1908). Difficulty in identifying the native range of the Argentine ant was compounded by a number of factors, foremost

among them the absence of a comprehensive taxonomic study of the genus. Many *Linepithema* species occur in close proximity in South America, and their morphological similarity has caused confusion. These issues were recently resolved by a thorough revision of the genus (Wild 2007) and a careful description of the taxonomy and distribution of *Linepithema humile* (Wild 2004). The native range of the Argentine ant is now known to include northern Argentina and surrounding portions of Uruguay, Paraguay, and southern Brazil.

Currently, genetic evidence shows that introduced populations of Argentine ants indeed originated in Argentina, specifically in the southern Paraná River watershed near the port city of Rosario (Tsutsui et al. 2001). Although Rosario is approximately 270 km upriver from the capital Buenos Aires, in the late nineteenth century, Rosario rivaled Buenos Aires in international shipping activity, in part because rail lines from the northern territories terminated there (Ferns 1973). Many countries in which *L. humile* established populations around this time, including Portugal (Madeira) and South Africa (Wetterer and Wetterer 2006), probably traded extensively with Argentina and neighboring countries (Ferns 1973; Randall 1978). Argentine ants are inherently slow dispersers (Holway 1998; Sanders et al. 2001), but by closely associating with humans, they spread rapidly but discontinuously throughout the twentieth century, establishing themselves in at least 23 states in the United States and 35 countries worldwide (Suarez et al. 2001; Roura-Pascual et al. 2004; Wetterer and Wetterer 2006).

In recent years, genetic tools have been used to clarify the history of Argentine ant introductions. As with other taxa, the use of mitochondrial DNA sequence data has proven useful for identifying cryptic species of *Linepithema* but has provided less resolution for reconstructing relationships among introduced populations (Tsutsui et al. 2001). Despite these limitations, genetic data coupled with interception records of ants in quarantine allowed Corin et al. (2007a) to demonstrate that Argentine ants in New Zealand probably arose from established populations in Australia. While the immediate source of most nonnative populations is probably other introduced populations, it is possible that some populations resulted from multiple introduction events from the native range. For example, some populations of *L. humile* from South Africa, Hawaii, and California are genetically distinct, in both allele identity and frequency at microsatellite loci, from other introduced populations and each other (Tsutsui et al. 2001). However, relationships among most introduced populations remain imprecisely known, and future work will benefit from the development of numerous, widely dispersed markers, such as single nucleotide polymorphisms, and studies that integrate molecular data with historical in-

formation, such as patterns of commerce and interception records (Lester 2005; Suarez et al. 2005).

Bottlenecks and Population Genetics

If a new population is founded from a preexisting one, large amounts of genetic diversity can be lost through genetic drift when a new population arises from a small number of founders (a "genetic bottleneck"), when population growth is initially slow (a "lag phase") or when population sizes remain small for long periods of time (Nei et al. 1975; Chakraborty and Nei 1977). Conversely, some introduced populations may possess higher levels of genetic diversity compared with native populations when separate introductions have occurred from multiple native populations (Kolbe et al. 2004; Lavergne and Molofsky 2007).

In Argentine ants, there is abundant evidence that introduced populations experienced a founder event. Comparisons of microsatellite loci between native and introduced populations show a reduction in allele number of at least 28% in Europe (Krieger and Keller 1999; Giraud et al. 2002), 51%–65% in California (Tsutsui et al. 2000; Buczkowski et al. 2004), 55.5% in Hawaii (Tsutsui et al. 2001), and 60% in New Zealand (Corin et al. 2007*b*; fig.

1). The number of alleles in Argentine ant populations throughout Europe, for example, could have resulted from a single founding event involving as few as 16 unrelated queens (Giraud et al. 2002). Alleles lost during introduction (i.e., those present in native populations but absent from introduced populations) are disproportionately those that occur at the lowest frequencies in the native range, as is expected from a founder event (Tsutsui and Case 2001). The introduced populations that have undergone the most severe bottlenecks (Hawaii, California, and New Zealand; fig. 1) were most likely secondary or even tertiary introductions from previously established populations in the southeastern United States (Tsutsui et al. 2001; Buczkowski et al. 2004) and Australia (Corin et al. 2007*b*), respectively.

In addition to differences in genetic diversity between native and introduced populations, the degree of population structure also differs between ranges. Compared with introduced populations, native populations of Argentine ants exhibit higher levels of genetic variation and genetic differentiation at local scales (over hundreds of meters; Tsutsui and Case 2001; Pedersen et al. 2006) and at a rangewide scale (across 1,000 km; Tsutsui and Case 2001). Although levels of genetic differentiation (F_{st}) within introduced populations can exceed zero (Tsutsui
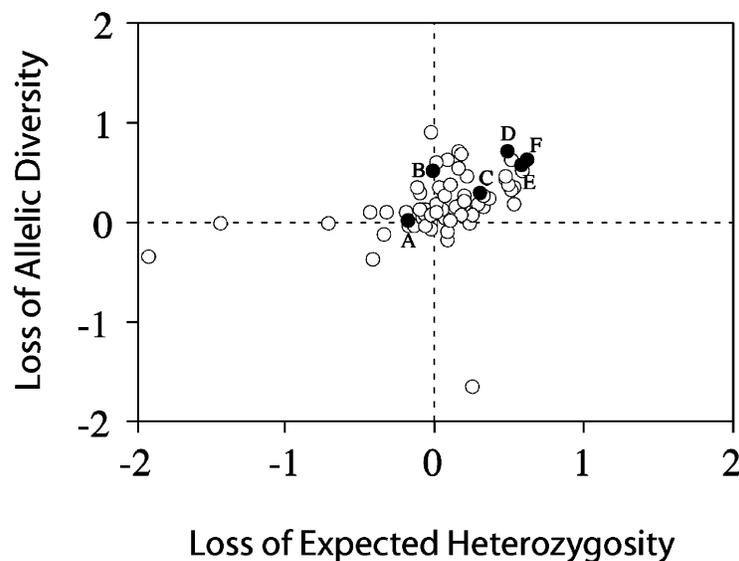

Figure 1: Loss of genetic diversity during introduction for a variety of nonnative organisms, depicted as reduced expected heterozygosity versus reduced allelic diversity in introduced populations relative to native populations calculated as (native range−introduced range)/native range. Open circles represent data compiled by Dlugosch and Parker (2008) and Wares et al. (2005) for introduced animals, plants, and fungi. Solid circles represent introduced Argentine ant populations: *A*, North Carolina (Buczkowski et al. 2004); *B*, California (Buczkowski et al. 2004); *C*, France (Krieger and Keller 1999); *D*, Hawaii (Tsutsui et al. 2001); *E*, California (Tsutsui et al. 2000); and *F*, New Zealand (Corin et al. 2007*b*). The loss of genetic diversity in *A*, *B*, and *F* was calculated by comparing each population to the native range data of Krieger and Keller (1999) at the loci shared by both studies. Because Krieger and Keller (1999) included ants from only one colony in the native range, values for these introduced populations probably underestimate the loss of genetic diversity. For visualization, two extreme outlier points from Dlugosch and Parker (2008) were excluded.
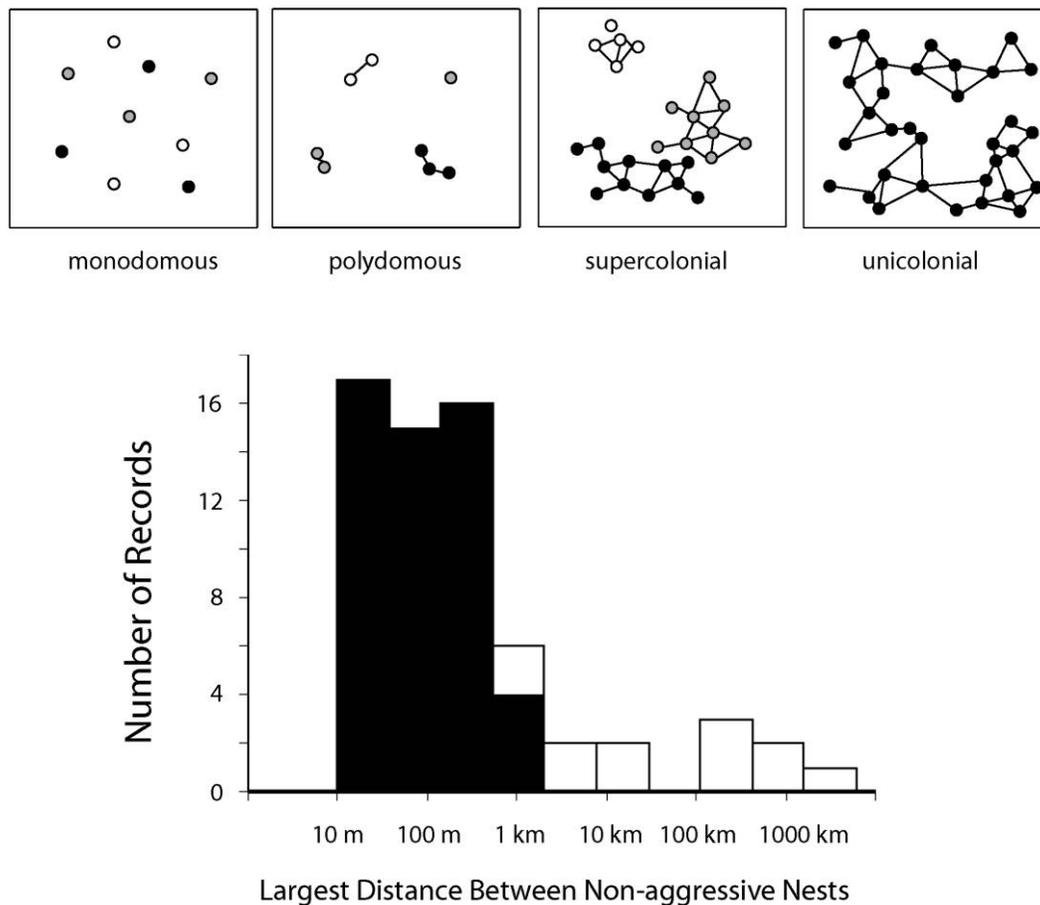
Figure 2: *Top*, four points along the multicoloniality-unicoloniality continuum. Each box represents a population within which ants compete for resources and have the potential to interbreed. Circles represent nest entrances, and lines represent the exchange of workers and resources among nests. Multicoloniality in ants occurs when each colony is territorial toward other colonies. In polydomous ants, each colony is made up of a set of neighboring nests that may exchange workers and resources. Supercolonies occur when many nests are interconnected at large enough spatial scales that interactions among members of all nests are unlikely but at small enough scales that multiple supercolonies still compete for resources and potentially interbreed. Unicoloniality describes ants (or populations of ants) where no territorial behavior (e.g., aggression) occurs among any of the nests in the entire population. *Bottom*, distribution of Argentine ant supercolony sizes in native (*solid bars*) and introduced (*open bars*) populations. Estimates of colony size are reported as the farthest distance between two nests that do not exhibit intraspecific aggression within a population or region. Native populations typically contain many supercolonies that extend for tens to hundreds of meters, while even the smallest supercolonies from introduced populations can contain nests spread out over many kilometers. Data are from Tsutsui et al. (2000), Tsutsui and Case (2001), Giraud et al. (2002), Buczkowski et al. (2004), Heller (2004), Pedersen et al. (2006), and Corin et al. (2007*b*).

and Case 2001; Giraud et al. 2002; Ingram and Gordon 2003; Corin et al. 2007*b*), these levels are far less pronounced than in native populations. Moreover, native populations show a pattern of isolation by distance, characterized by a positive relationship between spatial distance and genetic differentiation (Tsutsui and Case 2001). In contrast, introduced populations where this has been explicitly examined, in California (Tsutsui and Case 2001) and New Zealand (Corin et al. 2007*b*), show no pattern of genetic isolation by distance, even across distances exceeding 1,000 km.

Colony Structure

Although the Argentine ant is a particularly aggressive and a hard fighter when coming into contact with most other species of ants, there is no apparent antagonism between separate colonies of its own kind. In fact, in heavily infested areas the workers and queens are so intermingled that the individuality of colonies is entirely lost sight of and all colonies appear to become part and parcel of one enormous community. (Newell and Barber 1913, p. 51)

One important element of a social insect's colony structure is the spatial arrangement of nests that a colony occupies (Hölldobler and Wilson 1990; fig. 2, *top*). In ants, colonies can occupy a single nest (monodomy) or multiple nests interconnected by worker movements (polydomy). Variation can exist among species (or populations) in the degree of polydomy. At one extreme, polydomous colonies may occupy a few nests separated by small distances, among which worker and resource exchange occurs frequently. In other species, however, the number of nests can be extremely high, with the area occupied extending over distances large enough that worker exchange is unlikely. In this latter case, the term "supercolony" is used to describe the expansive spatial scale and high nest densities observed (Pedersen et al. 2006). In polydomous species, even those that form supercolonies, territorial behavior can still exist at the scale of the population (i.e., in areas where different supercolonies come into contact). The term "unicoloniality" is reserved for the most extreme case of polydomy and refers to cases in which the entire "population consists of nests without clear colony boundaries, whose members intermix" (Bourke and Franks 1995, p. 263; fig. 2, *top*).

Argentine ants have long been cited as a classic example of a highly unicolonial species that forms populations within which intraspecific aggression is completely absent (Wilson 1971). Although Argentine ants are relatively well studied, the existence of intraspecific aggression in this species was unknown until about 10 years ago (Holway et al. 1998). Since then, intraspecific aggression has been documented in both the native and introduced ranges of Argentine ants, although it occurs at different spatial scales and frequencies in the two areas: introduced populations are almost always unicolonial, while native populations typically exhibit intraspecific aggression over distances ranging between tens and hundreds of meters. Colonies of Argentine ants in both their native and introduced ranges are highly polygynous (possessing many reproductive queens) and polydomous (Keller 1988; Tsutsui and Case 2001; Heller 2004; Pedersen et al. 2006). Moreover, colonies in the native range may be quite large, occupying constellations of nests extending across large areas. In these respects, colonies of Argentine ants in the native range may be considered "supercolonies," where supercolony is defined as a collection of nests among which there is no intraspecific aggression but that occurs over spatial scales in which direct worker interactions among all nests is unlikely or impossible (Pedersen et al. 2006). It is critical to note, however, that the formation of supercolonies is not a diagnostic feature of unicoloniality. Rather, unicoloniality pertains to situations where each population comprises one huge, widely dispersed colony (Wilson 1971). A key feature distinguishing populations of polydomous

colonies and unicolonial populations is scale—unicolonial populations are those in which all potentially interbreeding or competing colonies lack intraspecific territoriality and aggression.

In practice, multicoloniality (the existence of multiple territorial colonies in a population) and unicoloniality exist as extremes at either end of a continuum (fig. 2, *bottom*). Introduced populations of Argentine ants fall near the unicolonial end of this spectrum, whereas native populations lie somewhere in the middle, forming localized supercolonies that are, on average, considerably smaller than those in the introduced range (Tsutsui et al. 2000; Pedersen et al. 2006; fig. 2). Recent assertions that Argentine ants are unicolonial in both native and introduced populations (Heller 2004; Pedersen et al. 2006) are therefore inconsistent with the generally accepted and well-established usage of the terms multicoloniality and unicoloniality (Wilson 1971; Bourke and Franks 1995). Studies investigating native populations of Argentine ants conclusively show that, although these populations can include supercolonies, they differ from unicolonial populations in that colony boundaries and intraspecific aggression are readily detected—often over spatial scales <100 m. No known colonies in the native range approach the size of introduced supercolonies in North America (Tsutsui and Case 2001), Europe (Giraud et al. 2002), Australia (E. L. Suhr, S. W. McKechnie, and D. J. O'Dowd, unpublished manuscript), New Zealand (Corin et al. 2007b), Bermuda, or Chile (Tsutsui et al. 2000) (fig. 2, *bottom*).

While most introduced populations of Argentine ants exhibit unicoloniality, in some areas localized supercolonies have been identified. These smaller supercolonies are genetically distinct from one another, and workers from these different supercolonies display aggression when they encounter each other (Jaquiery et al. 2005; Thomas et al. 2006). To date, one such spatially restricted supercolony has been reported in Europe (Giraud et al. 2002), while several have been discovered in southern California and the southeastern United States (Suarez et al. 2002; Buczkowski et al. 2004). Because these smaller supercolonies possess unique alleles and alleles at different frequencies than those of nearby unicolonial populations (Jaquiery et al. 2005; Thomas et al. 2006), they may be the products of secondary introductions from the native range or from other introduced populations.

Relatedness and Colony-Level Genetic Variation

Relatedness is often estimated among workers of social insect colonies and is a valuable measurement used to characterize breeding systems and to infer inclusive fitness and kin selection (Pamilo and Crozier 1982; Queller 1994). Relatedness is essentially the genetic similarity among focal individuals relative to a reference population that is chosen

based on factors including both the breeding system and the potential for competition (Griffin and West 2002). In practice, care must be taken in both the estimation of relatedness coefficients and their interpretation. When relatedness is estimated using molecular markers, positive values of relatedness result when the individuals of interest share alleles more frequently than random individuals in the population at large. Although this makes intuitive sense, the choice of "the population at large" is nontrivial and strongly influences the estimates of relatedness. Various studies of relatedness within Argentine ants illustrate this problem.

In their introduced range, Argentine ants from the same supercolony are remarkably similar genetically (up to 90% of alleles shared at microsatellite loci; Tsutsui et al. 2000). However, estimates of relatedness among Argentine ants are often reported as not different than zero in introduced populations (Kaufmann et al. 1992; Krieger and Keller 2000; Ingram and Gordon 2003). Such low levels of relatedness have been suggested to be a problem for kin selection theory because it is difficult to reconcile how such a cooperative unit would evolve or be maintained (Queller and Strassman 1998). In these studies, however, relatedness was calculated among focal individuals relative to other individuals within the same supercolony. It is important to recognize that the altruistic behavior of Argentine ants evolved under very different conditions in their native range. In fact, if we consider how closely related introduced Argentine ants are, relative to the levels of genetic diversity and genetic differentiation that occur in the native range, the challenge that they present for kin selection disappears. That is, estimates of within-colony relatedness are extremely high within supercolonies when calculated relative to the genetic conditions under which these behaviors evolved (fig. 3; Tsutsui and Suarez 2003).

The same issue occurs within native populations if relatedness is calculated using only other nests within the same supercolony as a reference population (Pedersen et al. 2006). However, since different supercolonies probably compete for space and resources (Thomas et al. 2006), a better estimate of relatedness among workers should include members of neighboring supercolonies in the reference population. When this approach is used, estimates of relatedness among Argentine ant colony members in the native range increase substantially as well (Tsutsui and Case 2001; Pedersen et al. 2006; fig. 3). Future work will benefit from a careful examination of how relatedness is measured and what it means from both ecological and evolutionary perspectives.

In addition to differences in relatedness, there is more genetic variation within supercolonies in native populations than there is in introduced populations (fig. 4). For example, using data from seven microsatellite loci (Tsutsui
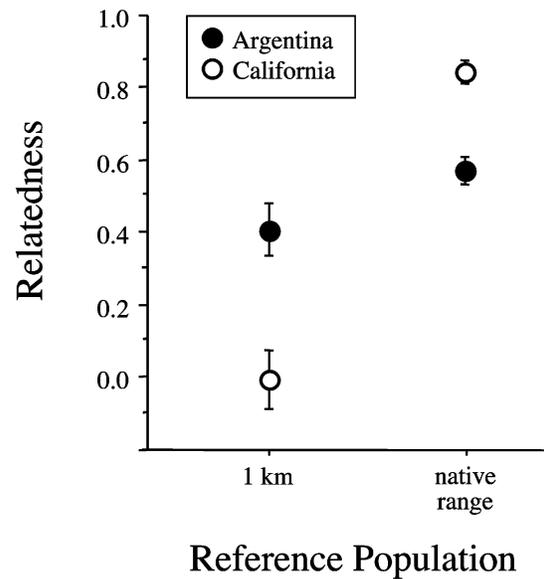

Figure 3: Estimates of relatedness (Queller and Goodnight 1989) for nestmates in Argentine ant colonies vary depending on the reference population used. For introduced populations in California (*open circles*), relatedness among nestmates is not different from zero if calculated relative to other nests in the same population (1 km). However, when calculated relative to Argentine ants from native populations, estimates of relatedness among nestmates in California approaches 0.9. In contrast, for nestmates in native populations (*solid circles*), estimates of relatedness do not change as substantially as the reference population is increased. Data are from Tsutsui and Case (2001).

et al. 2000), we constructed allele accumulation curves for supercolonies with the program EstimateS (Colwell et al. 2004; Colwell 2005). In this analysis, we included only supercolonies for which we had genotypic data for at least 20 individual worker ants. In one case, for the large supercolony that dominates California, we had data from 300 individuals. For ease of comparison with the smaller samples, we selected a random subset of 50 individuals from this supercolony for analysis. Based on asymptotic estimates of allelic diversity, within-supercolony diversity is higher in native populations relative to introduced populations (Mann-Whitney *U*-test, $P = .02$; fig. 4).

Nestmate Recognition and the Relative Roles of Genetic and Environmental Factors

A general interest in unicoloniality (Bourke and Franks 1995) and the notion that colony structure variation helps to explain ecological success in Argentine ants (Holway et al. 1998) has led to considerable research on the mechanisms of nestmate recognition. Published studies indicate that Argentine ants primarily use genetically based cues to identify colony mates, but laboratory studies demonstrate
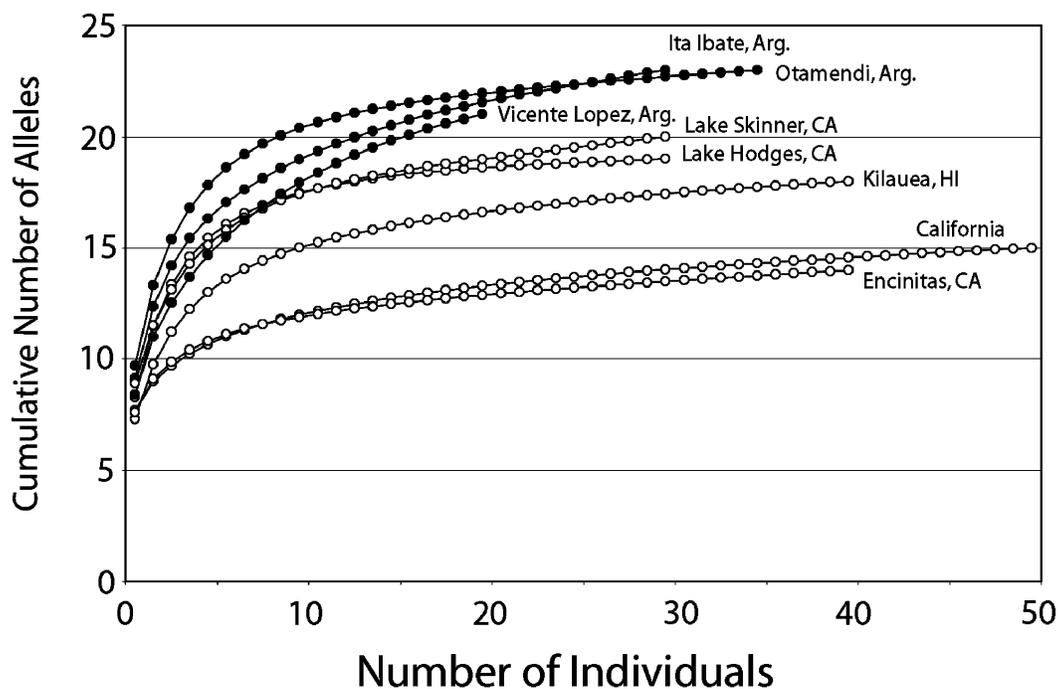
Figure 4: Allele accumulation curves for seven microsatellite loci in three native (*solid circles*) and four introduced (*open circles*) supercolonies of Argentine ants. The curve labeled "California" refers to the large unicolonial supercolony that extends throughout much of the state.

that dietary factors can also influence patterns of nestmate recognition (Liang and Silverman 2000). Additionally, when aggression occurs between ants from different colonies, the intensity of the response can be influenced by a variety of factors, including previous experience with other colonies (Thomas et al. 2006) and carbohydrate scarcity (Grover et al. 2007).

In Argentine ants, several lines of evidence point to the primacy of genetically based cues as the labels used in nestmate recognition. The high levels of intraspecific aggression observed between supercolonies in introduced and native populations are correlated with pronounced genetic differences among colonies but not with evident environmental gradients (Tsutsui and Case 2001; Jaquiery et al. 2005; Thomas et al. 2006; Pedersen et al. 2006). Moreover, two lab studies found that when experimental colonies of Argentine ants were reared on the same diet and under uniform environmental conditions, for either 12 months (Suarez et al. 2002) or 18 months (Giraud et al. 2002), the lab colonies maintained their original behavior toward each other; ants from sites that were initially aggressive remained aggressive, and ants that were nonaggressive remained nonaggressive. These lab studies indicate that homogenization of environmental cues does not reduce aggression in Argentine ants.

Genetics and behavior are also correlated with hydro-

carbon chemistry in Argentine ants. Analyses of cuticular hydrocarbon profiles of workers in the introduced range show substantial variation between supercolonies that display aggression but little variation within supercolonies (Suarez et al. 2002; Torres et al. 2007). Ants from the large supercolony in California, for example, possess similar hydrocarbon profiles despite the large geographic area and range of habitats over which they occur (Suarez et al. 2002).

Because within-colony levels of genetic diversity can affect the structure and function of recognition systems, there may be an association between the genetic diversity of Argentine ant colonies and their ability to distinguish nestmates from non-nestmates. Specifically, ants from colonies with low levels of genetic diversity would be expected to imprint on only a few hydrocarbon odors during development and thus should possess stringent recognition systems at adulthood (Tsutsui et al. 2003b; Tsutsui 2004). Similarly, ants from high-diversity colonies should possess more permissive recognition systems, as they would imprint on a broad array of odors and subsequently accept a broader suite of hydrocarbons as nestmate-specific labels (Tsutsui et al. 2003b; Tsutsui 2004). Consequently, when high-diversity colonies encounter low-diversity colonies in the field, aggression on average should be asymmetrical, with ants from the low-diversity colonies attacking more

frequently. However, interactions between high-diversity colonies, such as those in the native range, are not expected to be asymmetrically aggressive because the sets of colony labels possessed by diverse colonies are likely to be non-overlapping.

In accordance with this model, data from several supercolonies in the introduced range in the United States show that aggression is indeed asymmetrical between colony pairs, and genetic analyses suggests that this polarity is biased with respect to relative levels of genetic diversity; ants from low-diversity colonies initiate attacks against ants from high-diversity colonies more often than the reverse (Tsutsui et al. 2003b). In contrast, asymmetry in aggression among Argentine ants from different supercolonies in the native range occurs much less commonly (fig. 5), as expected, given the higher levels of within-colony genetic diversity and the greater genetic differentiation typical of native populations.

Although this evidence supports the idea that Argentine ants predominantly use genetically based cues to identify colony mates, lab studies indicate that particular prey-derived cues can also trigger aggression. In one series of studies, Liang and Silverman (2000) discovered that lab colonies of Argentine ants immediately began to attack each other after one colony was fed brown-banded cockroaches, *Supella longipalpa*. Gas chromatography/mass spectrometry (GC/MS) revealed that *S. longipalpa* hydrocarbons were present on the exoskeletons of roach-fed ants. Interestingly, when Argentine ants were fed other insects (*Musca domestica*, *Incisitermes minor*, *Zootermis nevadensis*, *Reticulotermes flavipes*, *Oncopeltus fasciatus*, *Acheta domesticus*, *Tenebrio molitor*, and *Camponotus ferrugineus*), diet-induced aggression did not occur (Liang et al. 2001). Thus, the aggressive rejection of nestmates by the Argentine ants fed *S. longipalpa* appears to be a specific response of acquiring hydrocarbons unique to a particular prey species (although low levels of aggression were also recorded in the *A. domesticus* treatment, for which the hydrocarbon profiles also overlapped those of Argentine ants).

Finally, levels of intraspecific aggression can be modulated by previous experience. In a series of studies, Thomas and colleagues (Thomas et al. 2005, 2006, 2007) showed that Argentine ant workers collected near zones of contact between supercolonies displayed higher levels of aggression toward each other compared with naive ants collected from sites away from colony boundaries. Studies using laboratory colonies showed that levels of aggression displayed by naive ants increased and that polarity in aggression disappeared after prolonged contact with ants from foreign supercolonies, even if physical contact between ants was restricted by the presence of a mesh barrier separating the colonies (Thomas et al. 2005, 2007).
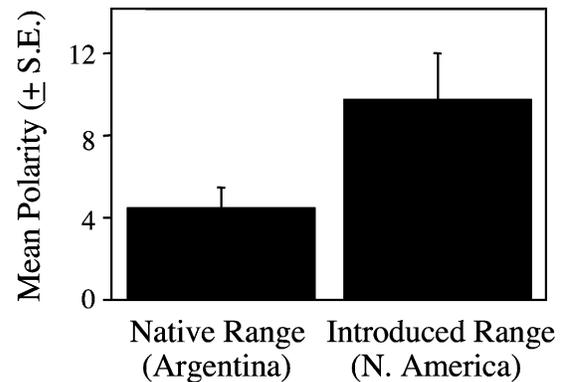

Figure 5: Mean polarity of between-colony aggression in the native (Argentina) and introduced (California) ranges of the Argentine ant. Polarity = (no. of behavioral assays initiated by the more aggressive colony + 1)/(no. of assays initiated by the less aggressive colony + 1). The mean value of this ratio across all colony pairs was 4.51 in the native range (466 behavioral assays across 20 colony pairs) and 9.68 in the introduced range (547 behavioral assays across 10 colony pairs). The aggression data for the introduced range are from Tsutsui et al. (2003b).

Thus, it appears that behavioral boundaries between supercolonies of Argentine ants can become more pronounced through time, as aggressive interactions between ants cause future interactions to be even more agonistic. This behavioral flexibility could also contribute to the lack of asymmetry in aggression seen between colonies in Argentina (fig. 5). Such plasticity is opposite the "dear-enemy" phenomenon reported for other species of ants (e.g., Langen et al. 2000), in which aggression is lower among ant colonies that frequently interact, presumably as a mechanism to reduce costs associated with frequent fighting.

Mechanisms of Ecological Success

> Probably the Argentine ant displaces other species because it lacks colonial boundaries and fights with other species. (Pontin 1963, p. 573)

A complete understanding of the causes of the Argentine ant's widespread ecological success involves a careful examination of how the phenotypic and genetic changes described above map onto patterns of ecological dominance in native and introduced populations and an evaluation of how these factors, relative to others, limit abundance. In general, multiple factors no doubt act simultaneously to increase the abundance of introduced populations. With respect to *Linepithema humile*, these factors include the following: (1) characteristics that predispose this species to tolerate (and even thrive) in environments disturbed

by humans, (2) escape from natural enemies (predators, parasites) and specialized pathogens, (3) biogeographic disparities in the importance of interspecific competition, and (4) changes in colony structure between native and introduced populations. These factors all probably play a role in the widespread success of *L. humile*, and an outstanding challenge will be to develop a more quantitative understanding of the relative importance of each factor and how they interact.

The success of certain invasive species can result in part from an evolutionary history that has included exposure and adaptation to anthropogenic disturbances. Species with little history of human contact may also become successful invaders when they have traits that predispose them to associate successfully with humans. Argentine ants lack a long history of human association, but some of their ecological and behavioral characteristics make them well suited to occupying human-modified environments. The existence of these traits appears to result from evolving in environments where physical disturbances (especially flooding) resemble those that occur commonly in urban environments. The seminomadic and decentralized nature of Argentine ant supercolonies presumably allows this species to cope with high levels of environmental instability and heterogeneity typical of human-modified environments. Moreover, the Argentine ant's opportunistic nesting behavior permits this species to occupy urban environments, buildings, orchards, and other areas that would be unsuitable to species with more restrictive nesting requirements. The tendency for Argentine ants to relocate their nests to take advantage of favorable microenvironments can bring them into association with nursery stock and other forms of human commerce, where they can then be transported long distances by jump-dispersal events (Suarez et al. 2001).

Human-mediated jump-dispersal events have given the Argentine ant the opportunity to colonize many new areas, but these events may have also contributed to the Argentine ant's success in a different way, namely, by allowing this invader to arrive in novel environments in the absence of coevolved natural enemies and pathogens. Although native populations of Argentine ants could be subject to greater levels of predation, parasitism, and infection compared with introduced populations, there are no known specialized enemies of Argentine ants and thus no information on the potential for such agents to regulate native populations. Argentine ants appear to lack host-specific phorid fly parasitoids (Orr et al. 2001) that are currently being used against populations of the red imported fire ant in the United States (Graham et al. 2003; Porter et al. 2004). Given what is known about native populations of Argentine ants in northern Argentina (Suarez et al. 1999; Tsutsui et al. 2000; Le Brun et al. 2007), it seems unlikely

at this point that a specialized and widespread predator or macroparasite/parasitoid exists that is important in regulating *L. humile* populations. Little or nothing, however, is known about the potential importance of pathogens, endosymbionts, and microparasites. The importance of such organisms should be critically evaluated. Argentine ants are host to parasitic nematodes (Markin and McCoy 1968) and at least two strains of *Wolbachia* (Tsutsui et al. 2003*a*; Reuter et al. 2005), but the ecological significance of these associations is unknown.

While no specific predators or parasites have been identified that might help to keep native populations of Argentine ants in check, interactions with other dominant ant species clearly compromise the competitive ability of *L. humile* in northern Argentina (Le Brun et al. 2007). The ant communities of the floodplain savannas and woodlands of the Paraná and Paraguay rivers, the heart of the Argentine ant's native range, are home to a number of other common and behaviorally dominant ant species that co-occur with *L. humile* and with one another. These ants include *Camponotus blandus*, *Camponotus rufipes*, and *Camponotus punctulatus* as well as several other species that are invaders themselves elsewhere in the world: *Paratrechina fulva*, *Pheidole obscurithorax*, *Solenopsis richteri*, *Solenopsis invicta*, and *Wasmannia auropunctata*. A variety of observational and experimental evidence suggests that these ants collectively present a level of interspecific competition that Argentine ants simply do not experience in their introduced range (Buren 1983; Le Brun et al. 2007). Although it is a difficult hypothesis to test, it seems likely that evolving in the intensely competitive environments of South America has contributed to the Argentine ant's highly aggressive behavior and its proficiency at resource competition. The biotic and abiotic factors that make this region of central South America a prime exporter of invasive species deserve further study, but whatever factors are involved, it seems likely that biogeographic disparities in interspecific competition play a key role in the success of *L. humile* in California (where interactions between Argentine ants and native ants are most thoroughly studied) and probably elsewhere as well.

In different parts of their introduced range, Argentine ants no doubt experience reduced levels of interspecific competition compared with levels experienced by native populations, but introduced populations also encounter reduced levels of intraspecific competition. As discussed above, native populations, compared with introduced populations, more often exhibit intraspecific aggression at spatial scales where intraspecific territoriality and competition could limit abundance (Tsutsui et al. 2000). Lab experiments illustrate that intraspecific aggression reduces colony-level competitive performance and growth (Holway et al. 1998) as well as interspecific competitive ability (Hol-

way and Suarez 2004). These experiments demonstrate in principle how the loss of intraspecific aggression could lead to increases in colony size and the formation of super-colonies, both of which would enhance interspecific competitive ability. The high levels of aggression observed in these lab experiments are not artifacts of rearing colonies in a structurally simple environment; territorial aggression under natural conditions can result in substantial mortality (Thomas et al. 2006). Intraspecific aggression might also constrain supercolony movement. As discussed above, 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 changing environmental conditions (Newell and Barber 1913; Markin and McCoy 1968, 1970). This flexibility could increase a colony's ability to withstand physical disturbances and to exploit patchy resources (Newell and Barber 1913; Holway and Case 2000; Silverman and Nsimba 2000), but the presumed advantages of such plasticity would diminish if adjacent nests fought with one another. The existence of localized supercolonies in the native range of *L. humile* does not preclude this characteristic from being important in the success of this species as an invader. Argentine ants appear more competitively dominant in areas where they form localized supercolonies in Argentina (Holway and Suarez 2004). Key unresolved questions concern the extent to which intraspecific competition limits abundance under natural conditions and how habitat structure, resource quality, colony size, and interspecific competitors affect the relative importance of conspecific territoriality as a factor limiting abundance.

Conclusions and Future Directions

Variation in colony size makes Argentine ants a fascinating model system for studies of social evolution. Three hypotheses have been proposed to explain the unicolonial social organization of introduced populations of Argentine ants: (1) a "genetic bottleneck" resulting in lower levels of genetic diversity in introduced populations relative to native populations (Tsutsui et al. 2000), (2) "genetic cleansing" of alleles at loci involved in recognition (Giraud et al. 2002; Tsutsui et al. 2003*b*), and (3) "ecological constraints" that prevent new colonies from becoming established in introduced areas where Argentine ant densities are high (Giraud et al. 2002). Our synthesis of the literature supports the hypothesis that there have been reductions in genetic diversity in introduced populations relative to native populations. In contrast, the fact that Argentine ants from introduced areas are still aggressive toward ants from genetically distinct supercolonies suggests that they have not lost this behavior through a loss of diversity at only

recognition loci (genetic cleansing) or plasticity (ecological constraints). The suggestion that Argentine ants are unicolonial in their native range is also unwarranted. Unicoloniality is a population-level phenomenon, and the presence of multiple, genetically distinct, supercolonies in native populations that compete for resources does not justify the use of unicoloniality in the native range. Moreover, relative to the unicolonial populations typical of their introduced range, supercolonies in the native range have greater levels of genetic diversity, and estimates of relatedness differ substantially between ranges. Research that explicitly tests the predictions of each of these hypotheses will enhance our understanding of the evolution of extreme unicoloniality in this system.

Although cuticular hydrocarbons appear to play a central role in nestmate recognition and are thus important in understanding the variation in colony structure seen in Argentine ants, we know little about the genetic and biochemical mechanisms underlying hydrocarbon synthesis, the processes that regulate hydrocarbon variation, or the neurobiology of hydrocarbon reception and behavioral responses. The interdisciplinary nature of these questions calls for an interdisciplinary approach to discovering answers. Clearly, behavioral ecologists and invasion biologists will need to join forces with chemists, molecular geneticists, and theoreticians if we hope to achieve a thorough understanding of this system.

Similarly, there are technical hurdles that must be cleared to advance our understanding of this invasion. For example, disentangling the Argentine ant's invasion history and the genetic underpinnings of their chemical ecology and behavior will require the development of new genetic tools. The rich (and rapidly growing) set of genetic and genomic resources that have been developed for the honeybee *Apis mellifera* (Whitfield et al. 2002, 2006; Weinstock et al. 2006) may highlight candidate genes that are important in Argentine ant behavior. Alternatively, it may be worthwhile to develop genetic tools specifically for the Argentine ant, as has been done for the red imported fire ant *Solenopsis invicta* (Wang et al. 2007). The recent rapid advances in DNA sequencing technology coupled with the growing interest in Argentine ants as an emerging model system suggest that sophisticated genetic and genomic tools for studies of Argentine ant biology may soon be available.

Other important questions will be answered only by taking a broader view. Are there long-term evolutionary constraints that limit the persistence of unicolonial species? Are there ecological or evolutionary factors that predispose some species to evolve unicoloniality? Large-scale phylogenetic and comparative analyses may answer some questions about the origins and evolution of unicoloniality generally. Although this type of colony structure is com-

mon in introduced populations of highly invasive ants, it is rare in ants generally. A thorough understanding of the origins of unicoloniality may therefore produce insights of applied importance by suggesting methods for preventing establishment and spread of invasive ants or for controlling unicolonial species that have already become established outside their native range.

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