The Colony Structure and Population Biology of Invasive Ants

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Abstract: *Ants are among the most widespread and damaging of introduced species. Many invasive ants share a suite of characteristics that facilitate their introduction, establishment, and subsequent range expansion. One feature of particular importance is the ability to form numerically large, ecologically dominant colonies. We review the population biology of invasive ants, focusing on the role of sociality and colony structure in their success. Specifically, we considered different hypotheses that have been proposed for the observed transitions in social structure of the two most well-studied ant invaders, the Argentine ant (*Linepithema humile*) and the red imported fire ant (*Solenopsis invicta*). In both species, genetic changes during or subsequent to introduction have led to alterations in social behavior and colony structure; these, in turn, have promoted the invasive success of introduced populations. Although many other invasive ant species appear to have similar forms of social organization, little is known about the basic population biology of these species.*

Estructura de una Colonia y Biología Poblacional de Hormigas Invasoras

Resumen: *Las hormigas se encuentran entre las especies introducidas más ampliamente distribuidas y dañinas. Muchas hormigas invasoras comparten un conjunto de características que facilitan su introducción, establecimiento y posterior rango de expansión. Una característica de importancia particular es la capacidad de formar colonias numéricamente grandes y ecológicamente dominantes. Llevamos a cabo una revisión bibliográfica de la biología poblacional de las hormigas invasoras, enfocándonos en el papel de la sociabilidad en la estructura de la colonia y su éxito. Consideramos específicamente diferentes hipótesis que se han propuesto para las transiciones observadas en la estructura social de las dos hormigas invasoras mejor estudiadas, la hormiga Argentina (*Linepithema humile*) y la hormiga de fuego importada (*Solenopsis invicta*). En ambas especies, los cambios genéticos que ocurrieron durante o después de la introducción han llevado a alteraciones de la conducta social y la estructura de la colonia, las cuales, a su vez, ha promovido el éxito de invasión de las poblaciones introducidas. A pesar de que muchas otras especies de hormigas invasoras parecen tener formas similares de organización social, se conoce poco de la biología poblacional básica de estas especies.*

Introduction

One of the fundamental truths of invasion biology is that the difficulty of controlling an introduced species after it has become widely established far exceeds the difficulty of eradication soon after introduction. Consequently, a primary goal of invasion biology is to construct a predic-tive framework for the prevention of invasions (Lodge 1993; Vermeij 1996). Although priority should be given to the immediate eradication of newly established populations, invading species can remain undetected for long periods of time and once discovered are often difficult to control. In these situations, an understanding of the population biology of invading species can guide con-

trol strategies and illuminate the characteristics responsible for the invader's success, ultimately leading to a policy of vigilance and prevention rather than containment and control. For example, determining whether future outbreaks of the Mediterranean fruit fly (*Ceratitis capitata*) in California are likely to arise from a preexisting population or from a completely new introduction (Davies et al. 1999) may determine whether emphasis is placed on quarantine or attempts at eradication.

One goal of this review is to emphasize that native and introduced populations of invasive species often possess pronounced differences in their basic population biology. Recently, studies examining populations of invasive ants in their native and introduced ranges have revealed dramatic changes in behavior, social organization, reproductive biology, and population genetics that occurred during or subsequent to introduction (Ross et al. 1996; Tsutsui et al. 2000). Moreover, the altered state of introduced populations has been considered a standard for many studies of the basic biology of social insects. When we assume that the biology of an introduced population is representative of the species as a whole, we risk constructing elaborate theories to explain phenomena that potentially arose from perturbations associated with the introduction and establishment of new populations outside their native range (Steneck & Carlton 2001).

Ants are conspicuous and influential members of many terrestrial ecosystems (Hölldobler & Wilson 1990). Their success is due in large part to their elaborate, highly developed social structures, which allow thousands or even millions of individuals to function together in a cooperative and coordinated manner (Wilson 1971). Ants are also among the most damaging invasive species (Williams 1994; Moller 1996). For example, the costs associated with the invasion of the red imported fire ant (*Solenopsis invicta*) in the United States have been estimated at $1 billion per year (Pimentel et al. 2000). Recent work suggests that the success of invasive ants may stem from changes in colony structure during or following introduction: a transition from small, family-based, territorial colonies into spatially vast and numerically dense "supercolonies." Thus, the cooperation that promotes the success of social insects generally appears to be exaggerated in many invasive ants. This link between the success of invasive ants and the modification of their social structure provides an opportunity for integrated studies of genetics, behavior, and ecology to contribute to a critical issue in conservation biology. Moreover, because the social structure of invasive ants is a product of both adaptive evolution prior to introduction and novel changes that may have occurred during introduction, studies of both native and introduced populations are likely to yield many insights into the determinants of their success.

The ecological causes and consequences of ant invasions are reviewed in detail elsewhere (Holway et al. 2002), and much attention has been paid to the effects of invasive ants on invaded habitats (Williams 1994; Wojcik et al. 2001). Here we examine the population biology of invasive ants, focusing on the role of sociality and colony structure in their success. We consider different hypotheses that have been proposed for the observed transitions in social structure of the two most well-studied ant invaders, and we propose mechanisms to explain the maintenance and elaboration of these modified colony structures in introduced populations. Finally, we consider the stability of these social structures over evolutionary time spans and examine some of the features that may limit the long-term persistence of invasive ants.

Characteristics of Invasive Ants

Many species of "tramp" ants have become established outside their native ranges as a result of human-mediated transportation (Williams 1994; McGlynn 1999). A subset of these ants is considered invasive, spreading into natural areas and displacing native species through predation and competition (Passera 1994; McGlynn 1999).

Many invasive ants share a suite of characteristics that facilitate their introduction to new environments, permit the establishment of viable populations, and promote their spread (Hölldobler & Wilson 1977; Passera 1994; Moller 1996). These include general nesting and dietary requirements, polygyny, colony reproduction by budding, and reduced intraspecific aggression (Holway et al. 2002). For example, polygyny (the presence of more than one reproductive queen within a colony) can increase both the rate of colony growth (Vargo & Fletcher 1989) and the chance that a reproductive queen will be present in transported propagules. Similarly, colony budding, in which one or several queens leave their natal colony with a group of workers to establish a new nest nearby (Wilson 1971), can promote the movement of nest fragments into vehicles of transport. Argentine ants (*Linepithema humile*), for example, routinely move their nests closer to resources (Holway & Case 2000) or to more abiotically suitable sites (Markin 1970). This peripatetic lifestyle facilitates the rapid colonization of items such as potted plants or refuse, which may then be distributed by humans. One notable exception to this pattern is the monogyne form of *S. invicta*, in which colony reproduction occurs by winged dispersal of queens, who independently found new colonies that each possess only a single queen (Markin et al. 1972).

The successful establishment of new colonies may be accomplished by relatively small propagules. Laboratory experiments show that colony fragments of both the Argentine ant and the big-headed ant (*Pheidole megacephala*) can grow quickly when initiated by a single queen with as few as 10 workers (Chang 1985; Hee et al. 2000). The minimum requirements for the establishment of a new population may be even lower. In Argentine ants,

workers can direct the development of diploid eggs into reproductive females, and queens can produce haploid (male) eggs throughout the year (Passera et al. 1988). Thus, new populations could potentially arise from a small, queenless group of workers with a mixture of haploid and diploid brood (Aron 2001). Experiments confirming that small propagules can successfully establish new colonies in the field have not yet been performed.

Although some of these characteristics also occur in many noninvasive ants (e.g., polygyny, generalist diet), unicoloniality is disproportionately common in highly invasive species (Wilson 1971; Passera 1994). Unicoloniality is characterized by the formation of widespread colonies with numerous separate but interconnected nests, each containing many queens. Individuals within these nests behave amicably toward individuals from other nests in the same colony (or "supercolony"). This cooperation over large spatial areas (sometimes hundreds of kilometers) contrasts with the territoriality that typifies many noninvasive, multicolonial ants (Hölldobler & Wilson 1990). In the absence of the costs associated with intraspecific aggression and territoriality, unicolonial ants can direct more resources toward colony growth, foraging, resource defense, and interspecific competition (Holway et al. 1998). Worker densities in introduced populations of invasive ants are often greater than those of all native ants combined in uninvaded areas (Porter & Savignano 1990; Human & Gordon 1997; Holway 1998; Hoffmann et al. 1999). Thus, unicolonial invaders can prevail in competitive interactions with native species via numerical superiority (Human & Gordon 1996; Holway 1999; Morrison 2000; Holway & Case 2001). Most invasive ant species are polygynous and have reduced nestmate discriminatory abilities in their introduced range (Hölldobler & Wilson 1990; Passera 1994; Holway et al. 2002), including North America's two most damaging species, the Argentine ant and the polygyne form of the red imported fire ant.

The Argentine Ant

The Argentine ant is native to northern Argentina, southern Brazil, Uruguay, and Paraguay (Suarez et al. 2001; Tsutsui et al. 2001) and was first recorded in North America by E. Foster in 1891 (Foster 1908). Spreading primarily via human-mediated transport, the Argentine ant is now found on six continents and numerous oceanic islands (Suarez et al. 2001).

Throughout their introduced range Argentine ants are highly unicolonial (Newell & Barber 1913; Markin 1970; Keller & Passera 1989; Way et al. 1997; Suarez et al. 1999; Tsutsui et al. 2000; Giraud et al. 2002) and can attain remarkably high densities. For example, in an early attempt to eradicate Argentine ants from a 19-acre (7.7-ha) orange grove in Louisiana, Horton (1918) reported trapping an astounding

1.3 million queens in artificial nest boxes over the course of 1 year. Including workers and brood, the total volume of Argentine ants collected was over 1000 gallons (Horton 1918). Although a single "supercolony" occupies virtually the entire Californian range (Tsutsui et al. 2000), close examination has revealed several smaller "secondary" colonies (Holway et al. 1998; Tsutsui & Case 2001). The secondary colonies are spatially restricted, aggressive toward one another and toward the large supercolony, genetically distinct from one another and the large supercolony, and may be the result of separate introductions or genetic drift (Suarez et al. 1999; Tsutsui et al. 2001).

Native populations of Argentine ants differ from populations in the introduced range. In their native range, Argentine ant colonies typically consist of multiple nests occupying relatively small territories that are aggressively defended against other colonies although larger colonies (spanning hundreds of meters) can be found (Suarez et al. 1999; Tsutsui et al. 2000). Thus, a more multicolonial colony structure appears to be the ancestral state for Argentine ants, with extreme unicoloniality having arisen during or shortly after introduction. In their native range, Argentine ants also occur in sympatry with many other ant species (Suarez et al. 1999). These observations are consistent with the experimental evidence for a causal link between the loss of intraspecific aggression in introduced populations and the ability of Argentine ants to displace native ants via numerical superiority (Holway et al. 1998; Holway & Case 2001).

Native and introduced populations of Argentine ants also differ in patterns of genetic diversity (Krieger & Keller 1999; Suarez et al. 1999; Tsutsui et al. 2000; Tsutsui & Case 2001; Giraud et al. 2002). Population genetic studies using microsatellite markers have shown that introduced populations in California possess only about 50% of the alleles and one-third the expected heterozygosity of native populations (Tsutsui et al. 2000). Additionally, introduced populations in California are genetically homogeneous over large distances (up to 1000 km), whereas native populations possess genetic structure over tens to hundreds of meters (Tsutsui & Case 2001). Thus, patterns of genetic structure mirror patterns of colony structure in both ranges, suggesting that the behavioral boundaries of colonies have a genetic basis (Tsutsui et al. 2000). This is supported by the observation that in both ranges there is a significant negative relationship between the genetic similarity of nests and the degree of intraspecific aggression that they display toward one another (Tsutsui et al. 2000).

Relatedness and Unicoloniality in the Argentine Ant

Most species of ants possess kin-based social structures in which colony mates are more closely related to one another than they are to individuals from foreign colonies. Consequently, understanding of social behavior in these

species is often advanced by knowledge of the kinship within and among colonies. In monogyne colonies with singly mated queens, workers are full sisters (related by 0.75 because ants are haplodiploid). More intricate colony structures produce more complex patterns of relatedness within colonies. When many reproductive queens are present in the same colony or when queens mate with multiple males, the number of genetic lineages within a colony increases and the relatedness of colony mates decreases (Keller 1993), provided that there is not substantial inbreeding. However, estimates of relatedness from genetic data are typically calculated relative to a reference population—as allele sharing among members of a group relative to allele sharing between group members and the population at large (Queller & Goodnight 1989)—rather than from pedigree analyses. Therefore, as genetic differentiation increases within a population, estimates of relatedness within colonies also increase, and vice versa (Pamilo 1989; Ross 2001).

The behavior of invasive social insects, however, may be better explained by the relatedness *perceived* by the interacting individuals (Tsutsui & Case 2001). When social behaviors evolve in the native range of a species, genetic similarity may be used by individuals to precisely distinguish between colony mates and individuals from foreign colonies (Hepper 1991). Under these conditions, a recognition system may evolve in which cooperative social behavior is displayed only toward individuals who fall within a fixed range of genetic similarity (Reeve 1989). In ants, this type of recognition appears to be mediated by cuticular hydrocarbon-based odor cues (Vander Meer & Morel 1998; Suarez et al. 2002). Invasive species, however, frequently experience genetic changes during introduction, as population bottlenecks and founder effects reduce genetic diversity and increase the genetic similarity of descendant populations. As a result, genetic similarity and relatedness become decoupled, and cooperative behaviors may be displayed toward individuals who are genetically similar but distantly related (Tsutsui & Case 2001).

Estimates of relatedness within introduced Argentine ant colonies are low or not significantly different from zero when calculated relative to other introduced populations (Fig. 1; Krieger & Keller 2000; Tsutsui & Case 2001). In contrast, relatedness within introduced colonies dramatically increases when calculated relative to native populations (Fig. 1; Tsutsui & Case 2001). Although relatedness calculated in this way deviates from the traditional definition of relatedness, it demonstrates how bottlenecks can increase genetic similarity within groups relative to the conditions under which the social structure evolved (Pamilo 1989).

Overall, the differences in genetic diversity and genetic structure between the two ranges have produced radically different social contexts for Argentine ants. In their native range, Argentine ants probably evolved in
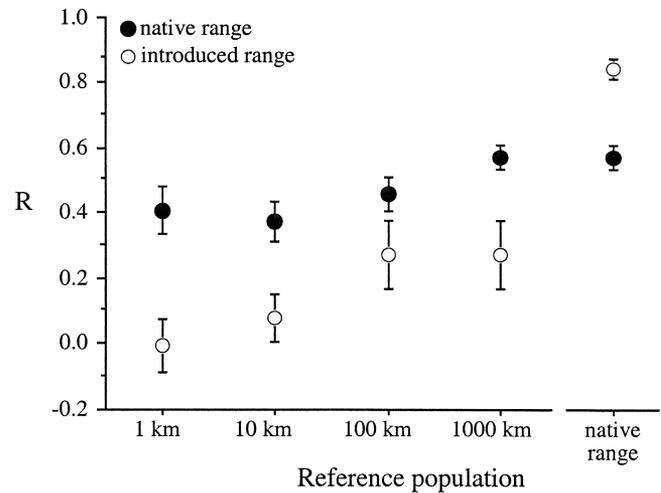

Figure 1. Mean relatedness (R) within colonies of the Argentine ant in the native and introduced ranges (±SE; modified from Fig. 5 of Tsutsui & Case 2001). The x-axis labels indicate the reference population used for estimation of R. Estimates of relatedness on the left (1 km, 10 km, 100 km, and 1000 km) were calculated with data from the same range for each colony as a reference (e.g., introduced range was used as a reference for relatedness within introduced colonies). Estimates of relatedness on the far right (native range) were calculated with all data from native populations as the reference population for both native and introduced colonies.

habitats containing many genetically diverse and differentiated colonies. In this environment, they could use cues that reflect genetic similarity to reliably distinguish colony mates from foreign individuals. In the introduced range, however, individuals using the same recognition system would be unable to distinguish colony members from nonmembers because genetic differences of equivalent magnitude are unlikely to exist. Thus, from the perspective of an Argentine ant in the introduced range, the overwhelming majority of conspecifics encountered appear to be relatives and are treated with the camaraderie typically reserved for colony mates.

Loss of Genetic Diversity in Argentine Ants: Other Factors

Two features of the Argentine ant's behavior may reduce genetic diversity to a level below that caused by a single bottleneck or series of bottlenecks: queen execution and selection against genetically different groups. Each year, Argentine ant workers in the introduced range kill up to 90% of the queens in their colony (Markin 1970; Keller et al. 1989). This behavior has been considered a puzzle

(Hamilton 1972) because it eliminates as much as 8% of the colony biomass, exacting a large cost in terms of the resources used to produce the executed queens and the lost potential for colony growth (Keller et al. 1989). Interestingly, queen execution occurs just prior to the production of new reproductives (Markin 1970; Keller et al. 1989). It has been suggested that queen execution releases the surviving queens from pheromonal inhibition and increases the amount of food available to larvae, thus facilitating the production of reproductives (Keller et al. 1989). However, a more ultimate explanation may be that this behavior increases within-colony relatedness (and genetic similarity) subsequent to queen execution, promoting social cohesion within Argentine ant colonies.

A similar phenomenon, known as *cyclical oligogyny*, occurs in some swarm-founding epiponine wasps (Queller et al. 1993; Henshaw et al. 2000). In these species, new colonies are initiated by groups of queens and workers, but through time the number of queens diminishes to one (or a few) as a result of death, dispersal, or conversion to nonreproductives. The production of new colonies, which involves the birth of new queens and swarming, occurs only after the queen number has been reduced. Each generation, this bottleneck increases the relatedness of colony members and produces conditions that favor the formation of cooperative social groups (Queller et al. 1993; Hastings et al. 1998; Henshaw et al. 2000).

As in epiponine wasps, fluctuations in queen number (caused by queen execution) may increase relatedness within native Argentine ant colonies, regardless of whether the workers selectively kill queens who are less related to them. When expressed in the introduced range, this behavior could increase within-colony genetic similarity and thus create conditions that further support the expression of cooperative or altruistic behavior. The potential role of queen execution in reducing genetic diversity and promoting unicoloniality in Argentine ants remains wholly unexplored, to the extent that it is unknown whether this phenomenon occurs in the native range.

Existing populations of Argentine ants in the introduced range may also prevent the establishment of subsequent introductions. If Argentine ants use genetic cues for colony-mate recognition (Tsutsui et al. 2000; Suarez et al. 2002), introduced ants that are genetically different from established populations will likely be exterminated by the preexisting supercolony, thus eliminating potential sources of genetic diversity. If this occurs, the unicoloniality that typifies introduced populations may be both a cause and an effect of reduced genetic diversity.

Similarly, intraspecific aggression, if directed toward genetically different individuals (or individuals from genetically different colonies), can create an opportunity for frequency-dependent selection to operate (Tsutsui et al., in press). Because colonies that possess higher levels of genetic diversity are more likely to possess recognition phenotypes (e.g., odor cues) considered foreign by others and rejected (Getz 1982; Crozier 1986), aggression between colonies may be directional with respect to levels of genetic diversity. Moreover, because attackers can inflict preemptive damage upon their opponent, they may experience heightened survival or reduced physical damage relative to their victims. When less genetically diverse colonies attack more genetically diverse colonies and individual attackers prevail more often, behaviorally mediated, positive frequency-dependant selection can arise (Tsutsui et al., in press). Such selection would promote the loss of genetic diversity through time in introduced populations. Studies that closely examine the role of differential genetic diversity in colony-mate recognition and the relationship between genetic identity and intraspecific aggression at both the individual and colony levels will clarify the selective forces that may influence colony structure in invasive ants.

The Red Imported Fire Ant

Solenopsis invicta is native to many of the same regions in South America as the Argentine ant (Buren 1972; Ross & Trager 1990) and has invaded North American habitats in the southeastern United States, coastal California, and Puerto Rico (Taber 2000). The rate of range expansion for Argentine ants and fire ants (*Solenopsis* spp.) throughout North America is remarkably similar (Fig. 2), despite pronounced differences in their modes of dispersal (DeHeer et al. 1999; Holway & Suarez 1999). As with the Argentine ant, genetic changes resulting from the red imported fire ant's introduction to new environments, coupled with an escape from natural enemies, has led to important changes in social structure that influence its success as an invader.

Solenopsis invicta possesses two social forms, one characterized by colonies that contain a single queen (monogyne) and another that, like that of the Argentine ant, is polygynous. Both forms are successful invaders of North America, suggesting that their invasiveness does not arise from polygyny alone. The queens and workers of the two forms are phenotypically different (Greenberg et al. 1985; Keller & Ross 1993), and the two forms are partially reproductively isolated in the introduced range (Shoemaker & Ross 1996; Ross et al. 1999). Monogyne colonies are multicolonial, with workers displaying high levels of aggression toward individuals from other colonies. In contrast, in the polygyne form aggression among colonies is reduced or absent (Morel et al. 1990; Obin & Vander Meer 1989).

The two forms have been found in both the native and introduced ranges, but not all parts of the two ranges contain monogyne and polygyne forms. (Jouvenaz et al.
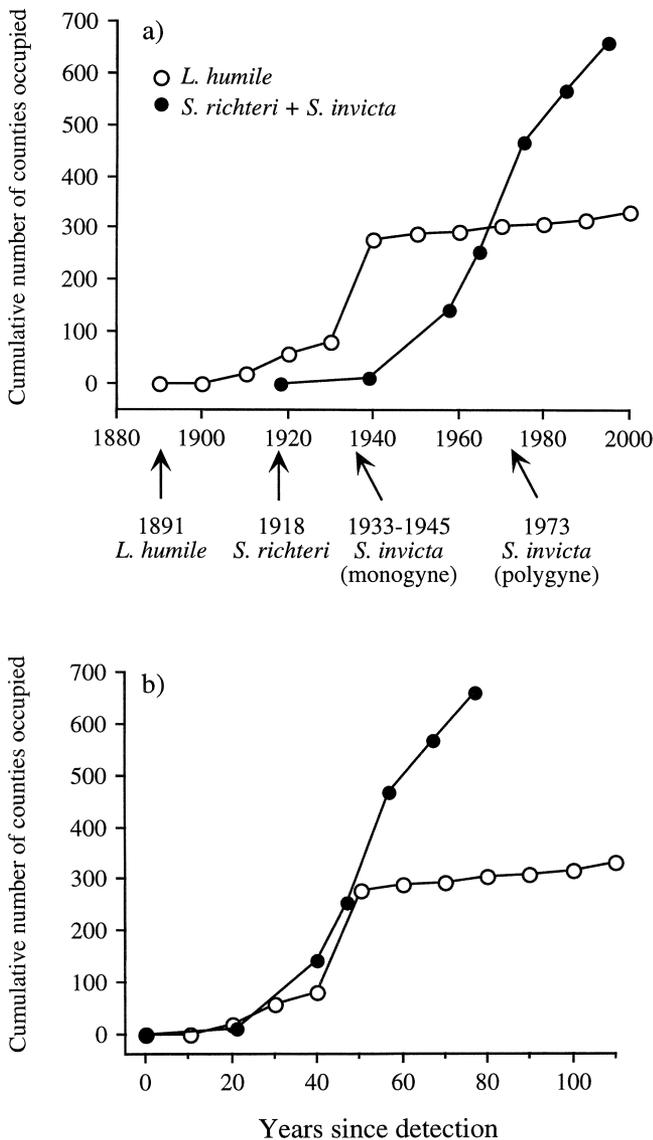
a)

b)

Years since detection

*Figure 2. Range expansion of introduced Argentine ants (*L. humile*) and fire ants (*S. invicta *and* S. richteri*) in North America: (a) time line of introduction since 1880, indicating dates of interest and (b) pattern of spread relative to the first year of detection. Data for Argentine ants were taken from Suarez et al. (2001) and A. V. Suarez (unpublished) and those for fire ants from Callcott and Collins (1996).*

1989; Porter et al. 1992; Ross et al. 1996; Porter et al. 1997). Moreover, like the Argentine ant, *S. invicta* coexists with other ant species in its native range (Fowler et al. 1990). Relatedness within polygyne *S. invicta* colonies is relatively high in native populations, but not significantly different from zero in introduced populations (Goodisman & Ross 1997; Goodisman & Ross 1998; Ross et al. 1996). As in Argentine ants, however, relatedness within introduced colonies would likely be quite high if es-

timated relative to that of native populations (Tschinkel & Nierenberg 1983; Pamilo 1989).

Solenopsis invicta has also lost genetic diversity during introduction to the United States. Although native and introduced populations do not possess significantly different H_{exp} at allozyme loci (Ross & Trager 1990; Shoemaker et al. 1992; Ross et al. 1993), introduced populations do possess fewer alleles than native populations (Ross et al. 1993; Ross et al. 1996). More recent studies using microsatellite markers show that introduced populations possess relatively high levels of genetic diversity at these loci (Krieger & Keller 1997), although introduced populations have 50% of the alleles present in native populations (Krieger et al. 1999).

Further evidence for the loss of genetic diversity in introduced *S. invicta* populations is provided by problems in some genetically based systems. For example, the loss of genetic diversity appears to have reduced variation in the sex-determining system to such a degree that diploid individuals can often be homozygous at these loci (Ross et al. 1993). Such individuals, despite being diploid, become males and are usually sterile (Krieger et al. 1999). Because sex-determination systems in Hymenoptera rely on high levels of genetic polymorphism to function correctly (Crozier 1977; Bourke & Franks 1995), they may be particularly sensitive to moderate losses of allelic diversity (Ross et al. 1993).

The Origin of Polygyny in Introduced Populations of *S. invicta*

From the perspective of invasion biology, the origin of polygyny in introduced *S. invicta* populations is of interest for at least three reasons. First, this form is more ecologically destructive than the monogyne form, displacing both native ant species and previous invaders, including the monogyne form (Porter & Savignano 1990; Greenberg et al. 1992). Second, the polygyne form of *S. invicta* was first detected in the southeastern United States some 20 years after the monogyne form was first reported (Fig. 2; Glancey et al. 1973). This has led researchers to wonder whether polygyny is a trait that arose in introduced populations subsequent to introduction, or if polygyne *S. invicta* represent additional introductions from the native range (Porter et al. 1988; Ross & Keller 1995; Tschinkel 1998). Finally, as discussed above, most invasive ants are polygynous, and the factors that have led to the origin of polygyny in *S. invicta* may be applicable to ant invaders generally.

The possibility that polygyny arose *de novo* in introduced populations was originally supported by studies of *S. invicta* in its native and introduced ranges. Following the framework proposed by Emlen (1982), this work suggests that polygyny arose in introduced populations of *S. invicta* in response to ecological constraints (Keller 1995; Ross & Keller 1995; Ross et al. 1996). Specifically,

escape from predators and parasites by fire ants in the introduced range may have allowed densities to increase (Porter et al. 1997). As a result, potential nesting sites for dispersing queens would have become rare, making independent colony founding increasingly difficult and favoring more frequent adoption of queens into established colonies (Keller 1993; Nonacs 1993). The resulting increase in within-colony genetic diversity would have led to decreased nest-mate recognition abilities, promoting even greater polygyny (Ross & Keller 1995; Ross et al. 1996).

However, several recent findings have revealed a genetic system that underlies the differences between monogyne and polygyne *S. invicta*. Queens from the two social forms typically possess different genotypes at the general protein-9 (Gp-9) allozyme locus (Ross 1997; Ross & Keller 1998; Krieger & Ross 2002). Monogyne colonies contain queens that are *BB* at Gp-9 and produce new *BB* queens that disperse and found colonies independently (Shoemaker & Ross 1996). Conversely, the queens in polygyne colonies are almost exclusively *Bb* and can produce *BB*, *Bb*, and *bb* queens. New *Bb* queens either join their natal colony or attempt to join other polygyne colonies (DeHeer et al. 1999). Any *BB* queens that attempt to join polygyne colonies or reproduce within them are killed by the *Bb* workers present in polygyne colonies (Ross & Keller 1998). Studies of queen dispersal have shown that newly produced polygyne queens with the *BB* genotype, who are doomed to execution if they remain in their natal colony or attempt to join other colonies, may attempt to found colonies independently, but with limited success (DeHeer et al. 1999). The *bb* genotype appears to be lethal in workers, and fertile *bb* queens are extremely rare (Ross 1997; but see DeHeer et al. 1999; Goodisman et al. 2000). Interestingly, polygyne colonies in the native range can possess reproductive queens that are either *BB* or *Bb* (Keller & Ross 1999). This difference between native and introduced populations could indicate the presence of other undiscovered genes or alleles that affect queen number or could be the result of a genetic bottleneck on variation at the loci involved in this process (Keller & Ross 1999; Krieger & Ross 2002).

Given the genetic basis for the alternate social forms in *S. invicta*, it is unlikely that polygyny arose in introduced populations as a result of ecological constraints alone. Instead, it appears more likely that a second introduction of *S. invicta* occurred subsequent to the establishment of monogyne *S. invicta*, during which the Gp-9 *b* allele was introduced to North American populations. This scenario provides an interesting contrast with Argentine ants. Whereas the overall loss of genetic diversity appears to have facilitated the invasive success of Argentine ants (Tsutsui et al. 2000), an increase in diversity at the Gp-9 locus in *S. invicta* may have allowed introduced populations to become polygyne, and hence more invasive.

The *Gp-9* locus has been cloned recently and shown to resemble most closely the sequence of a moth pher-

omone-binding protein (PBP), suggesting a role for Gp-9 in pheromone-mediated behaviors (Krieger & Ross 2002). Although the amino acid sequence identity between the protein encoded by Gp-9 and the moth PBP is only 26%, the Gp-9 protein possesses six cysteine residues that appear to be conserved among PBPs in general (Krieger & Ross 2002). Moreover, phylogenetic analysis has shown that other species in the genus *Solenopsis* possess an association between social form and Gp-9 that matches the patterns reported for *S. invicta* (Krieger & Ross 2002).

Other Factors Affecting Genetic Diversity in *S. invicta*

Two factors may act to increase genetic diversity in introduced populations of the more unicolonial, polygyne form of *S. invicta*: (1) gene flow from the monogyne form and (2) hybridization with the black imported fire ant, *S. richteri*. Because gene flow between the two forms occurs unidirectionally, predominantly from monogyne to polygyne via the mating of monogyne males with polygyne queens (Ross & Shoemaker 1993; Shoemaker & Ross 1996; DeHeer et al. 1999), the monogyne form may act as a reservoir of genetic diversity for the polygyne form. However, the magnitude of gene flow from monogyne colonies into polygyne colonies has not led to the genetic homogenization of the two forms (Ross et al. 1999).

Hybridization between *S. invicta* and *S. richteri* may also increase genetic diversity in *S. invicta*. Genetic studies have shown that introduced populations of these two species hybridize in the southeastern United States (Vander Meer 1985; Ross et al. 1987; Diffie et al. 1988). Moreover, gene flow between the two species is either bidirectional or predominantly from *S. richteri* into *S. invicta* (Goodisman et al. 1998).

Other Species

Although other species display the characteristics outlined above, most remain woefully understudied. Some species, such as *Pheidole megacephala*, *Wasmannia auropunctata*, and *Anoplolepis gracilipes*, are both invasive and unicolonial (Passera 1994; Hoffmann et al. 1999; Holway et al. 2002). Although the impact of these species on natural communities can be severe (Williams 1994; Hoffmann et al. 1999), much basic research comparing native and introduced populations has yet to be done. Several other species, including *Lasius neglectus*, *Monomorium pharaonis*, and *Tetramorium bicarinatum*, also appear to be unicolonial in some parts of their introduced range (Van Loon et al. 1990; Astruc et al. 2001;

Espadaler & Rey 2001). Although these species are not always considered invasive, little is known about native populations or their general ecology and social behavior. Finally, there are dozens of introduced ant species about which virtually nothing is known (McGlynn 1999). Many of these species may have the potential to become invasive, and prevention may be possible only if we are aware of their dispersal capabilities (both natural and human-mediated) and the factors that could facilitate their successful establishment and spread.

The remarkable body of literature on *S. invicta* can also be used as a framework for the study of other fire ant species, many of which possess both monogyne and polygyne forms. These include *S. xyloni* (a native North American fire ant; Summerlin 1976), the widely introduced *S. geminata* (Banks et al. 1973; Adams et al. 1976), and *S. richteri*, (Creighton 1930). Because this genus contains both invasive and noninvasive species that are both monogyne and polygyne, comparative ecological and genetic studies across species may illuminate determinants of colony structure that are relevant to *S. invicta* and other ant invaders.

Studies of the population biology of some noninvasive ants have also shown that not all unicolonial species are invaders. For example, unicoloniality in the mound-building *Formica* appears to have evolved in association with long-lived, densely inhabited habitats in which colonies occupy large, elaborate nest structures (Bourke & Franks 1995). This contrasts with the invasion of transient or disturbed habitats by invasive ants, and the tendency of some (such as the Argentine ant) to form low-cost, temporary nests.

The Future of Ant Invaders

Ultimately, the most common fate of invasive ants may be displacement by subsequent invaders. In the southeastern United States, for example, the Argentine ant appears to have been displaced throughout much of its introduced range by the black imported fire ant (*S. richteri*), and both were later displaced by *S. invicta* (Wilson 1951; Glancey et al. 1976; Taber 2000). The replacement of Argentine ants by *S. invicta* may also soon occur in California, where *S. invicta* has recently been introduced (Taber 2000). Similar patterns have been documented for other species of invasive ants in different locations, including Bermuda (Haskins & Haskins 1965) and Hawaii (Fluker & Beardsley 1970). Previous invaders are not always completely displaced by new colonists and may even promote the establishment of future exotic species through habitat alteration (Simberloff & Von Holle 1999). In extreme cases, ecosystems can be transformed into communities of exotic species, as has occurred in Hawaii, which has over 40 introduced ant species but no native ants (Reimer 1994).

Some of the features that allow invasive ants to be successful in the short term may limit their long-term persistence. Predictions from kin-selection theory suggest that unicoloniality may not be stable over evolutionary time spans. Because workers in large supercolonies may seldom interact with immediate relatives, their actions do not necessarily enhance the survival and reproduction of individuals who carry the same genes (Queller & Strassman 1998). This means the heritability of worker traits, both beneficial and deleterious, decreases under conditions of widespread, indiscriminate altruism, and selection cannot act on these traits (Queller & Strassman 1998). Over time, deleterious mutations can accumulate, adaptive traits may be lost, and selection could promote selfish or nepotistic behaviors that lead to the breakdown of unicoloniality. Additionally, if processes such as queen execution or positive frequency-dependent selection are operating in introduced populations of invasive ants, levels of genetic diversity may become so low that individual fitness is reduced or susceptibility to pathogens or parasites is increased.

Closely studying the population biology of invasive and potentially invasive ants offers much hope for understanding the mechanisms of their success and subsequently developing guidelines for prevention and control of future invasions. Examining the characteristics of known invaders will allow us to more easily identify potentially invasive species and actively limit their opportunities for establishment. Moreover, when an invader does become established, this knowledge can reveal potential vulnerabilities and provide guidance for novel attempts to undermine the social structure that allows these species to prosper. For example, because the success of many invasive species hinges on the elevated colony densities associated with unicoloniality, control strategies designed to induce intraspecific aggression in invasive ants through genetic (Suarez et al. 1999; Tsutsui et al. 2000) or chemical (Silverman & Liang 2001) manipulations warrant careful consideration. Increasing levels of intraspecific aggression in introduced populations of invasive ants may reduce their densities to the point where native species could persist in communities from which they would otherwise be displaced.

Acknowledgments

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