

Chapter 4

THE GLOBAL EMPIRE OF AN INVASIVE ANT

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ABSTRACT

Social insects have obtained their prosperity by cooperation among individuals. This can be applied particularly to the success of invasive ants, which form unusual social structure called supercolonies, within which individuals can move freely among physically separated nests, and thereby gain high population densities to dominate indigenous ants. Native to South America, the Argentine ant *Linepithema humile* has been unintentionally introduced into many parts of the world during the last 150 years. Although it is well known that the introduced Argentine ant populations form much larger and fewer supercolonies than the native populations, the relationship among beyond-ocean populations has been poorly understood. Recent studies, however, are uncovering the behavioral, chemical and genetic relationships among introduced Argentine ant populations worldwide. Individuals from the dominant supercolonies around the world have very similar cuticular hydrocarbon profiles (nestmate recognition cue), and do not show aggressive behavior toward each other, when artificially put into contact. The supercolonies constitute the largest cooperative unit ever known. Their genetic closeness suggests a common introduction pathway. Considering historical records, descendants of the most ancient introduced population have spread to many parts of the world, without losing memory of their roots. In this article, we introduce the nestmate recognition and the mechanism of supercolony formation in invasive ants, with the global empire of Argentine ants as an example.

INTRODUCTION

Social animals have obtained their prosperity by evolving cooperative behavior among individuals. This can be applied particularly to invasive alien ants. About 150 species of ‘tramp’ ants have been brought out of their native ranges by human activities, with some becoming invasive and causing damage to ecosystems, economic resources and human well-being [McGlynn 1999]. The most damaging species are shown in Table 1. Many invasive ants, including these species, are unicolonial, and form large networks of numeral, mutually cooperative (non-aggressive) nests, called ‘supercolonies’ [Holway et al. 2002]. A mature supercolony can extend over several hundred meters, and sometimes exceeds thousands of kilometers [Tsutsui et al. 2000]. The most extreme case is the Argentine ant, which forms a intercontinental, global-scale supercolony [Sunamura et al. 2009a; van Wilgenburg et al. 2010]. Compared to native ants whose colonies are composed of one or a limited number of nests and territorial aggression among closely located nests are common, invasive ants that form supercolonies can invest more on reproduction, because of the lower cost associated with territorial aggression [Holway et al. 1998; Holway 1999]. With the numerical advantage gained by this high reproductive ability, invasive ants overwhelm native ants and almost completely displace them in the infested area [Holway et al. 2002]. The direct displacement of arthropod fauna including native ants causes indirect negative impacts on many other taxa related to them [Holway et al. 2002; Lach 2003; Ness and Bronstein 2004; Krushelnycky et al. 2005; Lach and Thomas 2008]. Sometimes the impact can be so huge that the landscape is altered. In the tropical rainforest of Christmas Island, the displacement of the red land crab by the yellow crazy ant has turned the open forest floor into a bush with a dense and diverse cover and thick litter layer [O’Dowd et al. 2003]. The high density of invasive ants also leads to serious problems for human life. Invasive ants cause agricultural damage by protecting aphids, scales and mealybugs from their natural enemies, or by stinging farmers and livestock [Wetterer and Porter 2003; Pimentel et al. 2005; Wetterer 2007; Sunamura et al. in press]. In addition, they become nuisance pests that invade structures with high frequency and sanitary pests by biting or stinging [e.g., Rhoades et al. 1971]. In one sense, “the Argentine ant megacolony is taking over the world” [Walker 2009]. In this chapter we review the nestmate recognition of invasive ants and the process of the global supercolony formation by Argentine ants.

NESTMATE RECOGNITION SYSTEM

Many ant species use cuticular hydrocarbons as nestmate recognition cue [Howard and Blomquist 2005; Markin and Drijfhout 2009]. Cuticular hydrocarbon profile (compounds and their relative abundance) differs among both species and conspecific colonies. When an individual encounters another conspecific, it detects the cuticular hydrocarbons of the opponent by its antennae, and compares the profile with the experience-based neural template of the nestmates [Ozaki et al. 2005]. When they match, the individual recognizes the opponent as a nestmate, but when they vary, it recognizes the opponent as a foreigner and runs away or attacks. All of the hydrocarbon compounds present on the ant exoskeleton are not necessarily involved in nestmate recognition, but relative proportion of multiple

components is probably important. Cuticular hydrocarbons can be derived from both genetic and environmental (e.g., diet and nest material) factors [e.g., Crosland 1989; Beye et al. 2004; Sorvari et al. 2008; van Zweden et al. 2009]. Relative contribution of genetic and environmental factors varies from species to species. Hydrocarbons are shared among colony members via grooming, and their hydrocarbon profiles become homogeneous [Soroker et al. 1994; Meskali et al. 1995]. Chemicals other than hydrocarbons may be used as nestmate recognition cue, but the knowledge is currently scarce.

Invasive ants may also use cuticular hydrocarbons for nestmate recognition. Direct evidence for the use of hydrocarbons has been obtained in Argentine ants [Liang and Silverman 2000], and similarity within or disparity between supercolonies have been reported in the little fire ants, garden ants and big-headed ants [Errard et al. 2005; Cremer et al. 2008; Fournier et al. 2009]. Relative influence of genetic and environmental factors to cuticular hydrocarbon profile also varies among invasive ant species. For instance, in Argentine ants and big headed ants, genetically close populations originated from single introductions maintain similar hydrocarbon profiles even after dispersing over several thousand kilometers of diverse environmental condition for decades [Tsutsui et al. 2000; Fournier et al. 2009]. This suggests that environmental factors do not strongly affect cuticular hydrocarbon profile of these species in the field. A similar pattern was reported in little fire ants which undertake clonal reproduction [Errard et al. 2005; Fournier et al. 2005]. On the contrary, in garden ants, variation in cuticular hydrocarbon profile and the resultant aggression is observed even among populations presumably originated from a common source population [Cremer et al. 2008; Ugelvig et al. 2008]. In this species, effect of environment on cuticular hydrocarbon profile may be relatively strong. In summary, an invasive ant population with lower genetic variation and lower susceptibility to environment for hydrocarbons may be able to form larger supercolonies. As a unique case, whether supercolonies are formed or not depends on a single gene or linkage group in fire ants [Keller and Ross 1998].

Table 1. Representative invasive alien ant species and the distribution. All of them but the garden ant are listed among the world's 100 worst invasive species by the IUCN (International Union for Conservation of Nature) [Lowe et al. 2000]

Argentine ant <i>Linepithema humile</i>	South America	Africa, Asia, Australia, Europe, North America, Oceanic Islands (Atlantic and Pacific)
Big-headed ant <i>Pheidole megacephala</i>	Africa or Asia?	Africa, Australia, North America, South America, Oceanic Islands (Indian and Pacific)
Garden ant <i>Lasius neglectus</i>	Middle East?	Europe
Little fire ant <i>Wasmannia auropunctata</i>	Middle and South America	Africa, Australia, North America, Oceanic Islands (Pacific)
Red imported fire ant <i>Solenopsis invicta</i>	Middle and South America	Asia, Australia, North America
Yellow crazy ant <i>Anoplolepis gracilipes</i>	Africa or Asia?	Africa, Asia, Australia, Oceanic islands (Indian and Pacific)

GLOBAL-SCALE SUPERCOLONY OF ARGENTINE ANTS

Argentine ants are native to the Parana River drainage of Argentina, Brazil, Uruguay and Paraguay [Wild 2004, 2007]. In the native habitat, frequent disturbance, namely flooding, occurs [LeBrun et al. 2007]. This might have been important for the evolution of supercolony in Argentine ants. Uniclonal species, in which queens walk out of their natal nests with workers and establish new nests, can rapidly recover from frequent disturbance and thus more adaptive to such environment than typical ant species in which new queens disperse for a long distance by nuptial flight and establish new nests without the aid of workers [Tsuji and Tsuji 1996; Nakamaru et al. 2007]. Interestingly, the native range of Argentine ants overlaps those of other invasive uniclonal ants such as *Solenopsis* fire ants and little fire ants [LeBrun et al. 2007].

With the development of human commerce, Argentine ants have been unintentionally introduced to many parts of the world during the last 150 years [Suarez et al. 2001; Wetterer et al. 2009]. Their opportunistic nesting behavior [Vega and Rust 2001] and polygyny [Keller et al. 1989] may enhance the opportunity of human-mediated dispersal of nest fragment, and the probability of inclusion of reproductive queens in it [Suarez et al. 2008]. First recorded from Madeira somewhere between 1847 and 1858, Argentine ants landed Europe (Portugal and France), North America (Louisiana and California), and Africa (South Africa) during 1890-1910, Central America (Mexico and Bermuda) and Australia (Victoria, Western Australia, New South Wales, and Tasmania) around 1940-1950, and finally Asia (Japan) in 1993 [Suarez et al. 2001; Wetterer et al. 2009]. Within each continent, country or island, Argentine ants have rapidly expanded their distribution via human-mediated jump dispersal, sometimes at a rate of > 100 km/yr [Suarez et al. 2001; Ward et al. 2005; Okaue et al. 2007; Blight et al. 2009; Pitt et al. 2009; Roura-Pascual et al. 2009], although their unaided dispersal is rather slow (colony budding on foot; <300 m/year) [Suarez et al. 2001]. Invaded areas have Mediterranean, warm or subtropical climates, similar to the native range of the species [Suarez et al. 2001; Wetterer et al. 2009]. Argentine ants mostly invade disturbed environments such as urban district and agricultural land [Holway et al. 2002], though they sometimes penetrate natural environments [e.g., Bond and Slingsby 1984; Cole et al. 1992]. Argentine ants may be well adapted to human disturbance, because they evolved in the environment with frequent disturbance [Suarez et al. 2008].

In the introduced range, Argentine ants typically form a single large supercolony and occasional smaller supercolonies. For example, in Europe, a single supercolony is distributed over 6000 km along the Mediterranean Coast, intermingled with another smaller supercolony that extends over 700 km in eastern Spain [Giraud et al. 2002]. A third population is located in Corsica [Blight et al. 2010]. In North America, a large supercolony expands over 900 km along the coastal California, and several much smaller supercolonies are located in southern California and the southeastern U.S [Tsutsui et al. 2000; Buczkowski et al. 2004]. In western Japan, a single supercolony is expanding its distribution rapidly with human-mediated dispersal, while three other supercolonies are restricted in Kobe Port [Sunamura et al. 2007, 2009b]. In each of Australia and New Zealand, only one supercolony has been detected [Corin et al. 2007a; Suhr et al. 2009]. In contrast to the introduced range, Argentine ants are segregated into multiple, mutually incompatible supercolonies in the native range (tens to

hundreds of meters in diameters for each supercolony) [Heller 2004; Pedersen et al. 2006; Vogel et al. 2009]. In the introduced range, almost complete release from intraspecific aggression may provide Argentine ants with reproductive ability greater than that in the native range [Suarez et al. 1999; Tsutsui et al. 2000]. The notable disparity of supercolony size between introduced and native ranges may not be due to a character displacement after invasion [Pedersen et al. 2006; Vogel et al. 2009]. Rather, introduction of a limited number of native supercolonies and their expansion without significant change in nestmate recognition cue are likely to form the above distribution pattern of supercolonies in the introduced range [Helanterä et al. 2009]. Cuticular hydrocarbon of Argentine ants may not be strongly affected by environment in the field condition [Suarez et al. 2002]. Besides, genetic studies have shown that gene flow is almost or completely absent between Argentine ant supercolonies, though the mechanism is not known [Jaquiéry et al. 2005; Thomas et al. 2006; Pedersen et al. 2006]. If the loci for nestmate recognition cue are fixed for each supercolony, the lack of gene flow between supercolonies may contribute to the maintenance of unity of recognition cue within supercolonies.

Until recently, knowledge on the relationships among supercolonies around the world has been scarce. Because Argentine ants are invasive alien species, it is difficult to conduct international transportation of samples, especially live ants, through quarantine regulations. In addition, earlier genetic analysis failed to detect variation in mitochondrial DNA among Argentine ants worldwide, including the native populations [Tsutsui et al. 2001; but see Corin et al. 2007b]. Recently, however, relationships among worldwide supercolonies have been revealed. First, Wetterer and Wetterer [2006] found that the supercolony of Madeira and the largest supercolony of Europe were mutually non-aggressive. Next, Sunamura et al. [2009a, b] found that the largest supercolony of Japan has very similar cuticular hydrocarbon profile to the large supercolony of North America and Europe (at that time cuticular hydrocarbon was studied only for the populations of these regions: Liang et al. 2001; de Biseau et al. 2004). Then they transported live Argentine ants from Europe and North America internationally and conducted behavioral assays against the four Japanese supercolonies [Sunamura et al. 2009a]. As anticipated, Argentine ants from the large supercolonies of Europe and North America were mutually non-aggressive with the large supercolony of Japan. During the same period, Brandt et al. [2009] conducted global-scale microsatellite and cuticular hydrocarbon analyses of Argentine ant supercolonies. They showed that the dominant supercolonies around the world are genetically and chemically very similar, suggesting that these supercolonies originated from a common introduction pathway. Consequently, the research team conducted behavioral experiments and demonstrated lack of aggression among these supercolonies, similar to Sunamura et al. [2009a] [van Wilgenburg et al. 2010]. Furthermore, latest mitochondrial DNA analysis revealed difference of haplotypes among mutually antagonistic supercolonies but a single haplotype among the dominant supercolonies around the world [Vogel et al. 2010]. In summary, a particular supercolony is especially successful out of the native range. This supercolony is the largest cooperative unit ever known from any social insect species that exhibits intraspecific aggression. Moreover, the extent of this ant society is paralleled by human society only. This supercolony is also a very unique existence in the point that humans created it unwittingly via international trade. Then how was the intercontinental supercolony created? Wetterer and Wetterer [2006] proposed an interesting hypothesis regarding the dispersal history of the largest supercolony in Europe. Argentine ants were first discovered out of their native range on Madeira between

1847 and 1858, followed by detection in some localities in Portugal in 1890s. At that time, Madeira was an important hub for commerce between Portugal and its colonies in South America. Based on behavioral, genetic, and historical evidence, it was suggested that the European large supercolony originated in the route from South America to Portugal via Madeira, and then throughout southern Europe. The finding that the European supercolony is a part of the intercontinental supercolony gives rise to an intriguing hypothesis that descendants of the most ancient introduced population have spread to many parts of the world, without forgetting their roots [Sunamura et al. in press; van Wilgenburg et al. 2010].

If this hypothesis is correct, nestmate recognition cue of the intercontinental supercolony has not changed for more than 150 years. This constancy is worth amazing [van Wilgenburg et al. 2010]. However, at such extreme supercolony sizes, cooperative behaviors between distantly located individuals are predicted to be maladaptive and evolutionarily unstable [Helanterä et al. 2009]. The vast supercolony might differentiate into smaller ones in the evolutionary time span.

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