

# The invasive Argentine ant *Linepithema humile* (Hymenoptera: Formicidae) in Northern California reserves: from foraging behavior to local spread

Deborah M. GORDON & Nicole E. HELLER



## Abstract

We review the results from a 20-year study of the spread of the invasive Argentine ant, *Linepithema humile* (MAYR, 1868), in a reserve in Northern California. Ecological studies show that Argentine ants disrupt native ant communities. The best predictor of Argentine ant distribution is proximity to human disturbance, because buildings and irrigation provide water in the dry season and warm, dry refuges during the rainy season. Our studies of the effects of habitat and climatic factors suggest that human disturbance promotes spread, while lack of rainfall and interactions with native species, especially the native winter ant, *Prenolepis imparis* (SAY, 1836), slows spread in areas further from human disturbance. Genetic and behavioral studies indicate that seasonally polydomous colonies span 300 - 600 m<sup>2</sup> in the summer when they are most dispersed, and contract to one or a few large nests in the winter. There is no evidence of mixing between nests of different colonies. Studies of foraging behavior show that searching behavior adjusts to local density, that arriving first at a food resource provides an advantage over native species, and that recruitment to food occurs from nearby existing trails rather than from more distant nests. We continue to monitor the spread and impact of the Argentine ant at Jasper Ridge Biological Preserve in collaboration with citizen scientists. We are investigating how Argentine ants modify and expand their trail networks, the interactions that allow the winter ant to displace Argentine ants, and the role of human disturbance on the impact of Argentine and other invasive ants in native communities.

**Key words:** Colony structure, drought, long-term ecological research, invasion, review.

Myrmecol. News 19: 103-110

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 14 June 2013; revision received 3 October 2013; accepted 3 October 2013

Subject Editor: Philip J. Lester

Deborah M. Gordon (contact author), Department of Biology, Stanford University, Stanford CA 94305-5020, USA.

E-mail: dmgordon@stanford.edu

Nicole E. Heller, Nicholas School of the Environment, Duke University, Durham, NC 27708, USA.

## Introduction

The invasive Argentine ant, *Linepithema humile* (MAYR, 1868), is widespread in developed areas worldwide, where there is a Mediterranean climate of wet winters without heavy frost, and hot, dry summers. We have reached the 20<sup>th</sup> anniversary of our twice-yearly survey of the distribution of Argentine and native ants in Jasper Ridge Biological Preserve, a 481-hectare reserve near Stanford University in Northern California. This anniversary seems an appropriate time to summarize what we have learned from this study, and from our other work on the behavior, population genetics and interspecific interactions of this species. Here we outline our main findings. This is not a review of the literature on Argentine ants. Instead we outline our results so far on the factors that influence the rate of spread of the ants in natural and developed areas, on colony structure, and how the foraging behavior of Argentine ants, and interaction with other species, combine to determine Argentine distributions in one region of their exotic range. Pdf files of the articles cited here are available on request from D. Gordon.

## Factors that determine spread

We have monitored the spread of the Argentine ant (Fig. 1) in the Jasper Ridge Biological Preserve (JRBP) for 20 years.

Twice a year, in late summer (September) and late spring (April - May), we record the incidence of ant species at about 265 sites, spaced at least 100 m apart.

Over the course of 20 years, the Argentine ant spread rapidly into the reserve from surrounding residential areas. For the past 8 - 10 years, the spread of the Argentine ants has slowed. Figure 2 shows the incidence of Argentine ants in the reserve over the course of the study. Our studies of the effects of habitat and climatic factors suggest that human disturbance at the edges of the reserve promotes spread, while drought and interactions with native species, especially the native ant, *Prenolepis imparis* (SAY, 1836), has slowed spread in areas further from human disturbance.

The presence of Argentine ants leads to changes in the distribution of other ant species. Such effects have been widely documented throughout the world (e.g., BOND & SLINGSBY 1984, WARD 1987, HOLWAY & al. 2002). Our study shows that over 20 years, Argentine ants tend to disrupt local arthropod (HUMAN & GORDON 1996, 1997) and native ant communities (SANDERS & al. 2001, HELLER & al. 2008a, FITZGERALD & GORDON 2012). Associations among native ant species shift once Argentine ants appear, so that the assembly of ant communities is more random

once the Argentine ants become established (SANDERS & al. 2003).

We have examined in several studies how the spread of Argentine ants depends on local habitat conditions, on rainfall, and on the distribution of other ant species (HUMAN & al. 1998, HELLER & al. 2008a, FITZGERALD & GORDON 2012, FITZGERALD & al. 2012). We have considered many different factors, and consistently find that the most important predictors of the spread of the Argentine ant are distance to development and rainfall, which promote its spread, and the presence of the native winter ant *Prenolepis imparis*, which limits its spread. These three factors – human disturbance, rainfall, and the presence of *P. imparis* – all interact with each other.

### Proximity to human development

The strongest predictor of Argentine ant distribution is proximity to human development. Most recently using 17 years of data from 1993 - 2009, we used logistic regression and model selection to examine the effect of distance to development (roads, buildings and landscaped areas), vegetation cover taller than 0.75 m, elevation, distance to water, temperature and rainfall, on Argentine ant distribution (FITZGERALD & al. 2012, FITZGERALD & GORDON 2012). We also investigated how the winter ant (*Prenolepis imparis*) influences the spread of Argentine ants.

The results showed that that distance to human disturbance is the best predictor of Argentine ant distribution: the ants are more likely to be established near human disturbance. The result obtained in the 2012 study from 17 years of data (FITZGERALD & al. 2012), is similar to the result from an earlier study (HUMAN & al. 1998) reporting on the first four years of data (1993 - 1996). In the 1998 study we examined the effects of distance to water, elevation, insolation, and distance to human disturbance. That first study also showed that distance to the edge of the reserve, and thus to human disturbance, best predicted Argentine ant distribution.

The topography of the Jasper Ridge reserve led us to consider the possibility of an interaction of the effects of elevation and human development (FITZGERALD & GORDON 2012). The Jasper Ridge reserve contains a large ridge down the middle of the reserve. The reserve is surrounded by human development, mostly houses with irrigated landscaping, and also some irrigated agricultural areas. As a result of the ridge in the center and the human development at the edges, the effects in Jasper Ridge of distance to human disturbance could be confounded with the effects of elevation. To take this into account, we examined the distribution of Argentine ants in two other reserves in Northern California, near JRBP, in which elevation was not associated with distance to the edge of the reserve (FITZGERALD & GORDON 2012). The results were the same as those from JRBP: Argentine ants are most often found near human disturbance. It appears that the ants can persist about 500 m from the nearest buildings, but then, in the absence of buildings, the native ants predominate.

The association of Argentine ants and human habitation is common in its exotic range (e.g., WARD 1987, CARPINTERO & al. 2003). The distance that Argentine ants can spread into undisturbed areas from human development probably varies with climatic and environmental conditions. Water availability limits Argentine ants in natural areas



Fig. 1: The Argentine ant, *Linepithema humile*. Photograph by Dan Quinn.

(WARD 1987, MENKE & HOLWAY 2006). In wet years, the ants can penetrate farther into reserves than in dry years (DIGIROLAMO & FOX 2006, BOLGER 2007). BOLGER (2007) found that Argentine ants were abundant in an arid coastal sage scrub reserve in Southern California within about 250 meters of human development, and that they did not have an impact on native ants farther from urban edges. WARD (1987) found that in north central California, which experiences extreme dry, hot summers, Argentine ants were restricted to riparian habitat with permanent water flows. In cooler, wetter climates, such as in parts of Hawaii, ants may persist further from human development (KRUSHELNYCKY & al. 2005).

The association between Argentine ants and human development occurs because buildings provide refuges from unfavorable conditions, and because the irrigation associated with landscaping and agriculture provide water. Argentine ants come inside buildings to take refuge from cold and flooding in the winter, and to find water in the summer. We tested how the presence of Argentine ants inside buildings is related to weather conditions (GORDON & al. 2001). We asked 68 households in the San Francisco Bay Area, in Northern California, to evaluate weekly the abundance of ants in their house or apartment. We continued this for 18 months. The results were clear, and the variation was surprisingly low: ants were likely to come in every home when it was cold and wet in the winter, and, to a lesser extent, when it was hot and dry at the end of the summer. A model based on temperature and rainfall was sufficient to predict ant abundance inside homes. On a week-

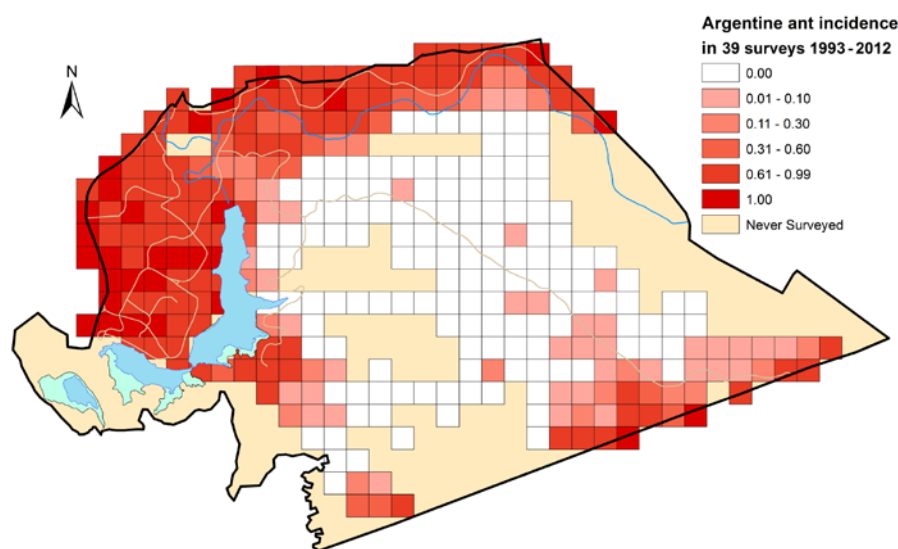


Fig. 2: Argentine ant distribution in Jasper Ridge Biological Preserve, 1993 - 2012. The color at each site represents the proportion of times Argentine ant has been detected at that site out of 39 surveys conducted every spring and autumn, from spring 1993 to spring 2013. Each square is one hectare. The Preserve is surrounded by residential and agricultural development.

to-week scale, not only did ants come in to most homes at the same time – they also left at the same time.

The finding that throughout the region, Argentine ants tend to leave buildings at the same time, when conditions outside become favorable again, has implications for pesticide use. This result suggests that pesticides are not especially effective against this species, when small groups of workers and queens can temporarily move inside a building, even if pesticides do reach the local queens the colony, with other nests and other queens, is not destroyed. Thus pesticides may do more harm, by disseminating toxic chemicals, than benefit in eliminating ants. Regardless of pesticide use, when the weather improves, the ants will leave buildings and return to nest outdoors.

### Rainfall

Over the course of 20 years, the invasion of JRBP has slowed down. Since 2001, few new sites have been invaded (HELLER & al. 2008a). This slowdown is due to the limits of abiotic conditions (they only invade so far from urban edges into wildlands; BOLGER 2007, FITZGERALD & GORDON 2012), and also may be affected by climatic changes in the region, including a drought since about 2002. At JRBP, the distribution of Argentine ants increases after summers (May - September) in which there is even a small amount of rainfall (HELLER & al. 2008a). The positive effect of rainfall on Argentine ant spread is consistent with the finding that ant distributions are higher near human disturbance (WARD 1987, BOLGER 2007), because human disturbance also provides water. In the area around JRBP, disturbed areas offer water used as irrigation for lawns and gardens, and water is available inside homes and buildings.

The effect of rainfall on the spread of Argentine ants suggests that in the long term, the distribution of Argentine ants in natural areas will be strongly influenced by climate change. Drought conditions have deepened in the western US over the past ten to 15 years. If this trend continues this may limit the spread and impact of the Argentine ant in this area and other areas experiencing warming and drying trends (ROURA-PASCUAL & al. 2004).

### Interaction with the native winter ant, *Prenolepis imparis*

As the Argentine ant invasion has slowed down, the distribution of the native winter ant (*Prenolepis imparis*) has

increased (FITZGERALD & al. 2012). Argentine ants are less likely to colonize areas where the winter ant persists. The winter ant, like the Argentine ant, feeds from the honeydew of scale insects in trees and shrubs, such as coyote brush (*Baccharis pilularis*). The interaction between Argentine and winter ants is influenced by the Argentine ants' dependence on human disturbance. Close to disturbed areas, where the Argentine ant populations thrive and so propagule pressure is high, winter ants retreat from areas occupied by Argentine ants. Further from disturbed areas, where Argentine ant populations are less successful and propagule pressure is lower, the winter ants are much more likely to coexist with or displace Argentine ants. This trend is especially true in densely forested areas, which are apparently more favorable for winter ants than for Argentine ants because winter ants are more active at cooler temperatures. Thus winter ants were more likely to resist or prevent the spread of Argentine ants in sites with high vegetation cover and shade, and less likely in sunnier grassland mixed shrubland sites near human disturbance.

We found that *Prenolepis imparis* secretes a defensive chemical from the Dufour's gland that kills Argentine ants on contact (SORRELLS & al. 2011). The winter ants are most likely to deploy this weapon when close to their own nest, suggesting that they use it defensively but not necessarily to deter Argentine ants at food resources. Other unpublished work by K. Fitzgerald suggests that winter ants are able to oust Argentine ants from trees when foragers of both species collect honeydew from scale insects in the same tree. Further work is needed to learn how Argentine ants partition resources with this native species. It would be very interesting to learn if in other places where the Argentine ant is established, and there are native species that actively resist (e.g., BLIGHT & al. 2010), if all such species have any behavioral or ecological characteristics in common.

Access to buildings and to water provided by irrigation promote Argentine ant populations and their spread into natural areas. Their effect on native ant populations is the result of local interactions and competition for resources between Argentine ants and other species. To understand these interactions, we have examined Argentine ant population biology, especially how populations grow, and their foraging behavior.

## Colony structure

The first step in understanding the population biology and foraging behavior of Argentine ants is to determine what is a colony and how the ants colonize new areas.

Our studies examined several aspects of Argentine colony structure. Argentine ants are polydomous, and their nests are linked by trails that can last several months. Our results led us to conclude that Argentine ants have discrete, colonies, which are large and seasonally polydomous (HELLER & al. 2006). A colony occupies a cluster of a few large nests in the winter and in the summer disperses into many small, linked nests spread over a larger area.

## Genetic structure: how colonies spread to new areas

The genetic structure of the population of Argentine ant colonies at JRBP suggests that the ants do not mix freely among colonies in a population (INGRAM & GORDON 2003). We used microsatellite variation to investigate genetic differentiation among nests separated on the scale of hundreds of meters. Nests were sampled along two transects from the recent edge of the invasion back to an area in which the invasion had been well established for at least ten years, and possibly for decades. At the population scale, there was a pattern of weak genetic isolation by distance, and multi-locus genotype assignment tests revealed significant structure between subpopulations. These results show that dispersal is local and the exchange of workers among neighboring nests is limited at the scale of 100 meters. Similar *F<sub>st</sub>* values, measuring the extent of genetic differentiation, have been found in other studies at the 1 km scale (e.g., TSUTSUI & CASE 2001). Multi-locus genotype assignments are well-suited to detecting structure in recent invasions of unicolonial ants because the test does not assume equilibrium dynamics at individual loci (INGRAM & GORDON 2003).

Our results are consistent with a population structure in which worker offspring of a given set of queens within a colony do not mix freely with the workers of all neighboring colonies, due to workers walking from the nest of one colony to join a nest of another, on the scale of a few hundred meters, but instead show worker fidelity to a local area. Queens do not fly, but remain in natal nests or disperse only short distances by walking to form new nests by budding. Genetic mixing across the population of colonies, on the scale of kilometers, is driven by long-distance male flight from one colony to mate with a gyne from another. Winged males are abundant in nests in late spring, suggesting that male flights occur in early summer (MARKIN 1970).

The genetic differentiation of nests at different locations within JRBP means that the Argentine ant range spreads by short-distance budding from the edge of the invasion front. If new nests were founded from anywhere within the range, then we would not expect a pattern of differentiation. Our results, which show subtle but clear genetic differentiation, are consistent with a population that has expanded rapidly, and which maintains gene flow through male long-distance flight. This work also showed that mixing among nests decreases with time since invasion, suggesting that colony boundaries emerge over time in an invading population.

## Seasonal polydomy

Observations over three years in study plots show a clear pattern of seasonal polydomy (HELLER & GORDON 2006). Colonies coalesce into one or more winter aggregation sites from the beginning of the rainy season, in November, until the weather grows warmer in February or March. It appears that the same winter aggregation sites are used each year. Winter sites tend to be on the south side of trees in warm, sunny spots.

When the warm season begins, ants begin to disperse into separate nests, linked by trails. The colony is at its most dispersed in late summer, spanning an area of about 300 - 600 m<sup>2</sup>. It is not known how new colonies form. This is one of the most important outstanding questions for understanding the population biology of Argentine ants. One possibility consistent with our observations is that in the autumn, some queens and workers do not return to their natal winter aggregation site, and instead form a new aggregation at a new site. Another possibility is that winter aggregations split. In the spring, the new aggregations disperse to create a network of linked nests, and then those nests return to join the aggregation at the new site year after year. This would increase the spread of the population of colonies. Although males appear to fly in late June, no one has observed new nests founded by newly mated queens in that season. The budding of new colonies and mating may occur in different seasons.

## Sharing of resources within the colony

Our work suggests that resources are shared within a colony and not with neighboring colonies (HELLER & al. 2008b). We tested this using baits that contained colored dyes that were visible in the ants that fed on the bait. Baits were set out, and then we mapped the spatial distribution of labelled ants. We found labeled ants on average 10 - 30 meters from baits. The next step was to move the bait to learn whether ants recruit to the bait from the closest nests. The distribution of labelled ants did not shift when the bait was moved to the edge of a colony. This showed that the sharing of food resources was confined to a particular set of nests. Ants did not simply travel from the bait to the nearest nests; instead, they returned to the nests of their own colony. This later step was conducted over a three-month time period in the cool, rainy season (December - March). More research needs to be done to see how firm boundaries are over longer time periods and in other seasons, and how neighboring colonies interact when they meet at resources.

The evidence from both our genetic and behavior studies supports the existence of distinct colonies of groups of nests linked by trails. There is genetic substructure at a scale consistent with the scale at which nests are linked by trails and share food. This is counter to the widely suggested idea that there is indiscriminate mixing among nests of Argentine ants, and that nests are functionally part of the same colony over long distances.

## Colonies within "supercolonies"

Our results on colony structure do not support the suggestion that Argentine ants are organized into very large "supercolonies". In the mid-90's the idea of the "supercolony" was introduced and quickly caught hold in the public



imagination. Bioassays showed low aggression between ants from different nests, even when the two nests were from different regions, countries or even continents (VAN WILGENBURG & al. 2010). The notion of the invasive and dominant "supercolony" was based on the idea that lack of aggression between ants of different nests corresponds to a functional connection between those nests, and that this functional connection could contribute ecological dominance and invasion success. However, aggression between Argentine ant nests is rarely observed in the field, and yet, ants from one nest do not share food with all nearby nests. Thus even ants that show no aggression still do not necessarily share resources and work together to compete. It is possible that the absence of fighting somehow promotes the sharing of resources between colonies, although this is not the case in many other species in which neighboring colonies compete for resources but rarely fight (e.g., GORDON & KULIG 1996). Other work suggests that Argentine ant supercolonies function as closed breeding units (VOGEL & al. 2009), among which males can fly and mate; thus supercolonies function as populations of colonies. Currently, there is no evidence that lack of aggression within "supercolonies", at very large scales, aids in invasion success. The number of ants that arrive at a resource is a critical factor in determining the outcome of interference and exploitative competition in Argentine ants as in many other species (GORDON 1995, HUMAN & GORDON 1999, WALTERS & MACKAY 2005). Our work suggests that the number of ants arriving at a resource reflects the size of the colony rather than the supercolony.

In our work at JRBP, we have not investigated aggressive behavior between nests from separate colonies. Aggressive behavior is a flexible trait in Argentine ants, as in other species, which varies depending on context. Many of the tests that were used to identify the boundaries of large supercolonies utilized one-one interactions in neutral arenas, and were not performed blind. When ants are introduced in groups, and in the context of nest defense, aggressive interactions are significantly more likely than when two individuals are introduced in a neutral arena (BUCKOWSKI & SILVERMAN 2005, ROULSTON & al. 2003). In addition, when tests are not performed blind, confirmation bias may affect the probability of observing aggression between nestmates (VAN WILGENBURG & ELGAR 2013). It is possible that low levels of aggression that are important in establishing colony boundaries in the field are missed by standard bioassays. Further work is needed to examine behavioral interactions between neighboring colonies in the field.

Some research shows a correlation between genetic distance, cuticular hydrocarbon distance, and aggression, such that ants that are more similar are less likely to fight (VOGEL & al. 2009, VAN WILGENBURG & al. 2010). It has been suggested that genetic diversity might be related to cuticular hydrocarbon profiles, because recognition is thought to be related to cuticular hydrocarbon profile. However, it seems unlikely that there is a very tight relation between diversity of microsatellite alleles and variation in cuticular hydrocarbon profiles. Currently no genes that influence aggressive behavior have been identified in ants, and so there is no evidence that microsatellite variation, which is thought to have little effect on phenotype itself, is associated with any other genetic variation related to aggression. Also, for

many ant species, an individual ant's hydrocarbon profile changes during its lifetime, so there must be many factors that contribute to hydrocarbon profile (STURGIS & GORDON 2012). For example, changes in hydrocarbon profile that lead to aggression can be induced in Argentine ants by changes in environmental factors such as food intake (LIANG & SILVERMAN 2000).

It has also been suggested that, if there were some correspondence between aggression and genetic variation, this could have led to the rapid evolutionary change in the aggressive behavior of Argentine ants once they reached the exotic range. However, it is not clear whether aggressive behavior differs in the native and exotic range. Argentine ant colonies in the native range of Argentina, as elsewhere, appear to show a range of colony sizes and a range of population structures, from supercolonial to multicolonial (HELLER 2004, PEDERSEN & al. 2006, VOGEL & al. 2009). Such variation in colony size and structure may reflect environmental conditions. The association in various ant species of supercolonial forms with urbanization suggests that it may be a plastic response to disturbance frequency and interspecific competition (MENKE & al. 2010).

In summary: lack of aggression between colonies does not in itself lead to any functional relation between nests. There is not yet evidence of any causal relation between genetic diversity, measured by microsatellite variation, and aggressive behavior. It is not clear whether there is any difference in aggression behavior in the exotic and native range that leads to differences in competitive abilities. A supercolony is a lineage of colonies descended from common propagules (e.g., VOGEL & al. 2010). There is no evidence for the idea that there has been evolutionary change in the aggressive behavior of Argentine ants once they expanded into the exotic range that led to the formation of functionally interacting supercolonies with novel competitive abilities.

### Foraging behavior and ecology

The behavior of Argentine ants determines their resource use and ecology (GORDON 2011). The foraging ecology of ants is the result of the collective behavior that leads the colony to find and exploit new food sources. This determines how conditions, interactions with human disturbance, and interactions with other species all influence its spread.

### Priority: arriving first

Interactions between Argentine ants and other ant species are strongly influenced by priority. In bait experiments we observed how the sequence in which ants arrive at a resource determines which species persists and controls the resource (HUMAN & GORDON 1999). When Argentine ants arrive first at a resource, native ants are likely to cede the resource to the Argentine ants. However, the reverse is also true; Argentine ants that encounter another species at a bait are likely to leave and do not recruit in large numbers. Recent work suggests that priority is established very quickly, within about 20 minutes after a new resource appears (M. Vonshak & D.M. Gordon, unpubl.).

### Searching

Because priority is so important in determining which species controls a resource, the ability of Argentine ants to find new resources quickly is crucial for its success in com-

peting with other species. It seems that Argentine ants are remarkably rapid in finding new resources.

An ant colony finds new resources through collective searching behavior. How quickly resources are found depends on how well the ants cover the area in which resources could appear. GORDON (1995) investigated the searching behavior of Argentine ants in a laboratory experiment that manipulated density. Ants were allowed to enter a foraging arena from a next box. Density was altered by changing the size of the arena and the numbers of ants available to enter it.

The ants create an expandable searching network by adjusting path shape according to density. When density was high, paths became more random and thus more convoluted. When density was low, paths became straighter. This makes sense as a collective strategy for maximizing the probability that if a new resource appears, some ant will find it (ADLER & GORDON 1992). When more ants are available, the colony can afford to have each ant search more thoroughly in a small, local area, but when few ants are available, they stretch out the searching network so as to cover more ground.

### Expanding the trail network

Argentine ants search for new resources from a baseline network of established trails that link nests. Currently we are investigating how these networks are modified to incorporate new resources, and pruned when resources are no longer available. Argentine ants lay trail pheromone as they walk (GOSS & al. 1989), and their trails persist for many weeks (HELLER & GORDON 2006). An example of the consequences of this is the appearance of dead Argentine ants in the top freezer compartment of refrigerators. It seems that the ants are attracted to some odor in the rubber seal of freezers. Apparently the ants that go into the freezer lay a pheromone trail, and other ants follow them, even though the frozen ants never go back to the nest to recruit others. The trail simply leads into the freezer where the ants die. This process is clearly counter-productive with respect to freezers, but since Argentine ants are very successful, the practice of laying trail as they go probably functions well in other situations.

Recent work shows that when a new resource appears, ants are recruited from the nearby trail and not back at more distant nests (FLANAGAN & al. 2013). There must be ants that leave the trail to search for new resources, and if they find nothing, they go back to the trail. By putting out baits of sugar water with dye, we were able to see which ants had found the bait, because they were marked by the dye. Ants that found the bait went back and forth from the trail to the bait. Numbers at the bait increased very quickly, in a shorter time than it would have taken for ants to travel back to the more distant nests. Although numbers at the bait increased, the flow of ants on the trail did not. All of these results are consistent with the conclusion that new trails to resources are formed by recruitment from the trail.

However, trails formed by recruitment to food, that branch off from another trail, tend to disappear once the resource is depleted. What is required for a new trail to be established and maintained? We are currently investigating the role of food sources and nest sites in establishing new long-term trails.

### Current questions

We are continuing the survey, which is now being conducted as a Citizen-Science project at JRBP. If the current drought ends we will be in a position to learn how well the native ants, especially the winter ant, can resist the increase in Argentine ant propagule pressure associated with increased rainfall. The long-term survey also provides the opportunity to explore the impact of Argentine ants on native communities over time. There is some indication that native ant diversity is increasing in some Argentine ant invaded sites (HELLER & al. 2008a); this has been observed in other exotic ant invasions (MORRISON 2002). Long-term studies can contribute to management decisions about interventions to control invasions.

The most important outstanding question about the population biology of Argentine ants is how do new colonies form. Conditions that facilitate the formation of new colonies, perhaps by providing new sites for winter aggregations, may also promote the spread of Argentine ants.

Argentine ant colonies create a network of nests linked by trails. Shifts in this network determine where the Argentine ants are likely to find new food resources, and to establish access to scale insects. This in turn determines when the Argentine ants will take resources from, and perhaps ultimately exclude, native species. To investigate the relation between Argentine ant behavior and its ecological outcomes, we are continuing behavioral studies of colony structure and the dynamics that regulate changes in the network of trails and nests. These studies address the general question of what are the algorithms used at the local scale of interactions between ants that lead to the formation of new trails and nests, and the abandonment of others.

The interactions of Argentine ants and winter ants provide an interesting example of the gradient between competition and coexistence. We are investigating how the two species interact in particular trees and in what conditions the outcome tends to favor winter ants. It would be very interesting to learn if in other parts of the world where the Argentine ant is established there are native species that actively resist and if all such species have any behavioral or ecological characteristics in common.

### Acknowledgments

We thank the editors, anonymous reviewers and Merav Vonshak for very helpful comments on the manuscript. Many thanks to Carol Johnson for preparing Figure 2.

### References

- ADLER, F.R. & GORDON, D.M. 1992: Information collection and spread by networks of patrolling ants. – *The American Naturalist* 140: 373-400.
- BLIGHT, O., PROVOST, E., RENUCCI, M., TIRARD, A. & ORGEAS, J. 2010: A native ant armed to limit the spread of the Argentine ant. – *Biological Invasions* 12: 3785-3793.
- BOLGER, D.T. 2007: Spatial and temporal variation in the Argentine ant edge effect: Implications for the mechanism of edge limitation. – *Biological Conservation* 136: 295-305.
- BOND, W. & SLINGSBY, P. 1984: Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. – *Ecology* 65: 1031-1037.
- BUCZKOWSKI, G. & SILVERMAN, J. 2005: Context-dependent nestmate discrimination and the effect of action thresholds on

- exogenous cue recognition in the Argentine ant. – *Animal Behaviour* 69: 741-749.
- CARPINTERO, S., REYES-LÓPEZ, J. & ARIAS DE REYNA, L. 2003: Impact of human dwellings on the distribution of the exotic Argentine ant: a case study in the Doñana National Park, Spain. – *Biological Conservation* 115: 279-289.
- DIGIROLAMO, L.A. & FOX, L.R. 2006: The influence of abiotic factors and temporal variation on local invasion patterns of the Argentine ant. – *Biological Invasions* 8: 125-135.
- FITZGERALD, K. & GORDON, D.M. 2012: Effects of vegetation cover, presence of a native ant species, and human disturbance on colonization by Argentine ants. – *Conservation Biology* 26: 525-538.
- FITZGERALD, K., HELLER, N. & GORDON, D.M. 2012: Modeling the spread of the Argentine ant into natural areas: Habitat suitability and spread from neighboring sites. – *Ecological Modelling* 247: 262-272.
- FLANAGAN, T.P., PINTER-WOLLMAN, N.M., MOSES, M.E. & GORDON, D.M. 2013: Fast and flexible: Argentine ants recruit from nearby trails. – *Public Library of Science One*: 8: e70888.
- GORDON, D.M. 1995: The expandable network of ant exploration. – *Animal Behaviour* 50: 995-1007.
- GORDON, D.M. 2011: The fusion of behavioral ecology and ecology. – *Behavioral Ecology* 22: 225-230.
- GORDON, D.M. & KULIG, A.W. 1996: Founding, foraging and fighting: colony size and the spatial distribution of harvester ant nests. – *Ecology* 77: 2393-2409.
- GORDON, D.M., MOSES, L., FALKOWITZ-HALPERN, M. & WONG, E.H. 2001: Effect of weather on infestation of buildings by the invasive Argentine ant, *Linepithema humile*. – *The American Midland Naturalist* 146: 321-328.
- GOSS, S., ARON, S., DENEUBOURG, J.-L. & PASTEELS, J.M. 1989: Self-organized shortcuts in the Argentine ant. – *Naturwissenschaften* 76: 579-581.
- HELLER, N.E. 2004: Colony structure of the invasive Argentine ant in native and introduced populations. – *Insectes Sociaux* 51: 378-386.
- HELLER, N.E. & GORDON, D.M. 2006: Seasonal spatial dynamics and causes of nest movement in colonies of the invasive Argentine ant (*Linepithema humile*). – *Ecological Entomology* 31: 499-510.
- HELLER, N.E., INGRAM, K.K. & GORDON, D.M. 2008b: Nest connectivity and colony structure in unicolonial Argentine ants. – *Insectes Sociaux* 55: 397-403.
- HELLER, N.E., SANDERS, N.J. & GORDON, D.M. 2006: Linking spatial and temporal scales in the study of an Argentine ant invasion. – *Biological Invasions* 8: 501-507.
- HELLER, N.E., SANDERS, N.J., SHORS, J.W. & GORDON, D.M. 2008a: Rainfall facilitates the spread, and time alters the impact of the invasive Argentine ant. – *Oecologia* 155: 385-395.
- HOLWAY, D.A., LACH, L., SUAREZ, A.V., TSUTSUI, N.D. & CASE, T.J. 2002: The causes and consequences of ant invasions. – *Annual Review of Ecology and Systematics* 33: 181-233.
- HUMAN, K.G. & GORDON, D.M. 1996: Exploitative and interference competition between the Argentine ant and native ant species. – *Oecologia* 105: 405-412.
- HUMAN, K.G. & GORDON, D.M. 1997: Effects of Argentine ants on invertebrate biodiversity in Northern California. – *Conservation Biology* 11: 1242-1248.
- HUMAN, K.G. & GORDON, D.M. 1999: Behavioral interactions of the invasive Argentine ant with native species. – *Insectes Sociaux* 46: 159-163.
- HUMAN, K.G., WEISS, S., WEISS, A., SANDLER, B. & GORDON, D.M. 1998: The effect of abiotic factors on the local distribution of the invasive Argentine ant (*Linepithema humile*) and native ant species. – *Environmental Entomology* 27: 822-833.
- INGRAM, K.K. & GORDON, D.M. 2003: Genetic analysis of dispersal dynamics in an invading population of Argentine ants, *Linepithema humile*. – *Ecology* 84: 2832-2842.
- KRUSHELNYCKY, P.D., JOE, S.M., DAEHLER, C.C. & LOOPE, L.L. 2005: The role of abiotic conditions in shaping the long-term patterns of a high-elevation Argentine ant invasion. – *Diversity and Distributions* 11: 319-331.
- LIANG, D. & SILVERMAN, J. 2000: "You are what you eat": Diet modifies cuticular hydrocarbons and nestmate recognition in the Argentine ant, *Linepithema humile*. – *Naturwissenschaften* 87: 412-416.
- MARKIN, G.P. 1970: The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae), in Southern California. – *Annals of the Entomological Society of America* 63: 1238-1242.
- MENKE, S.B., BOOTH, W., DUNN, R.R., SCHAL, C., VARGO, E.L. & SILVERMAN, J. 2010: Is it easy to be urban? Convergent success in urban habitats among lineages of a widespread native ant. – *Public Library of Science One* 5: e9194.
- MENKE, S.B. & HOLWAY, D.A. 2006: Abiotic factors control invasion by Argentine ants at the community scale. – *Journal of Animal Ecology* 75: 368-376.
- MORRISON, L.W. 2002: Long-term impacts of an arthropod-community invasion by the imported fire ant, *Solenopsis invicta*. – *Ecology* 83: 2337-2345.
- PEDERSEN, J.S., KRIEGER, J.B., VOGEL, V., GIRAUD, T. & KELLER, L. 2006: Native supercolonies of unrelated individuals in the invasive Argentine ant. – *Evolution* 60: 782-791.
- ROULSTON, T.H., BUCZKOWSKI, G. & SILVERMAN, J. 2003: Nestmate discrimination in ants: effects of bioassay on aggressive behaviour. – *Insectes Sociaux* 50: 151-159.
- ROURA-PASCUAL, N., SUAREZ A.V., GÓMEZ C., PONS, P., TOUYAMA, Y., WILD, A.L. & PETERSON, A.T. 2004: Geographical potential of Argentine ants (*Linepithema humile* MAYR) in the face of global climate change. – *Proceedings of the Royal Society B-Biological Sciences* 271: 2527-2534.
- SANDERS, N.J., BARTON, K.E. & GORDON, D.M. 2001: Dynamics of the distribution and impact of the invasive Argentine ant, *Linepithema humile*, in Northern California. – *Oecologia* 127: 123-130.
- SANDERS, N.J., GOTELLI, N.J., HELLER, N.E. & GORDON, D.M. 2003: Community disassembly by an invasive ant species. – *Proceedings of the National Academy of Sciences of the United States of America* 100: 2474-2477.
- SORRELLS, T.R., KURITZKY, L.Y., KAUFMAN, P.G., FITZGERALD, K., STURGIS, S.J., CHEN, J., DIAMCO, C.A., BASURTO, K.N. & GORDON, D.M. 2011: Chemical defense by the native winter ant (*Prenolepis imparis*) against the invasive Argentine ant (*Linepithema humile*). – *Public Library of Science One* 6: e18717.
- STURGIS, S.J. & GORDON, D.M. 2012: Nestmate recognition in ants: a review. – *Myrmecological News* 16: 101-110.
- TSUTSUI, N.D. & CASE, T.J. 2001: Population genetics and colony structure of the Argentine ant (*Linepithema humile*) in its native and introduced ranges. – *Evolution* 55: 976-985.
- VAN WILGENBURG, E. & ELGAR, M.A. 2013: Confirmation bias in studies of nestmate recognition: a cautionary note for research into the behavior of animals. – *Public Library of Science One* 8: e53548.

- VAN WILGENBURG, E., TORRES, C.W. & TSUTSUI, N.D. 2010: The global expansion of a single ant supercolony. – *Evolutionary Applications* 3: 136-143.
- VOGEL, V., PEDERSEN, J.S., D'ETTORRE, P., LEHMANN, L. & KELLER, L. 2009: Dynamics and genetic structure of Argentine ant supercolonies in their native range. – *Evolution* 63: 1627-1639.
- VOGEL, V., PEDERSEN, J.S., GIRAUD, T., KRIEGER, M.J.B. & KELLER, L. 2010: The worldwide expansion of the Argentine ant. – *Diversity and Distributions* 16: 170-186.
- WALTERS, A.C. & MACKAY, D.A. 2005: Importance of large colony size for successful invasion by Argentine ants (Hymenoptera: Formicidae): Evidence for biotic resistance by native ants. – *Austral Ecology* 30: 395-406.
- WARD, P.S. 1987: Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. – *Hilgardia* 55: 1-16.