Invasion of Four Argentine Ant Supercolonies into Kobe Port, Japan: Their Distributions and Effects on Indigenous Ants (Hymenoptera: Formicidae)

by

Eiriki Sunamura¹, Koji Nishisue, Mamoru Terayama & Sadahiro Tatsuki



ABSTRACT

The presence and distribution of four antagonistic Argentine ant supercolonies within closed areas in Kobe Port, Hyogo Prefecture, Japan, were revealed. Three of them had already caused severe reduction of ant species richness, whereas one coexisted with many indigenous ant species. We detected two contact zones of Argentine ant supercolonies, where indigenous ants occurred. Studies in these contact zones would provide insight into the hypothesis that lack of intraspecific aggression is responsible for the displacement of indigenous ants by Argentine ants, although the competitive ability of one supercolony described above must be carefully examined.

Key words: Argentine ant, *Linepithema humile*, supercolony, contact zone, biological invasion, competition

¹Corresponding author: Graduate School of Agricultural and Life Sciences, The University of Tokyo, Yayoi, Bunkyo-ku, Tokyo 113-8657, JAPAN email: eirikisunamura@yahoo.com

INTRODUCTION

The Argentine ant, Linepithema humile, is native to South America, but has invaded many areas worldwide and has caused a broad range of economical and ecological damage (Suarez et al. 2001, Wild 2004). Of the ecological damage Argentine ants cause, displacement of almost all indigenous ant species is one of the most notable (Holway et al. 2002). Previous studies have suggested that the numerical advantage gained by unicoloniality is a key attribute responsible for the ecological dominance of Argentine ants in the invaded areas (Holway et al. 1998, Holway 1999). Argentine ants in an invaded area typically form a unicolonial social structure, called a supercolony, within which workers and reproductive castes can move freely among interconnected nests (Suarez et al. 1999, Giraud et al. 2002). For example, there are no behavioral boundaries (aggression) within the Argentine ant supercolonies in California and southern Europe, which extend over thousands of kilometers. In contrast to the Argentine ants and some other invasive ant species, most ant species are multicolonial, with aggression among non-nestmate conspecifics commonly observed (Hölldobler & Wilson 1990, Holway et al. 2002). Formation of a supercolony reduces the cost associated with territorial defense and enables Argentine ants to attain high worker density (Holway et al. 1998).

In contrast to Argentine ants in the invaded area, Argentine ants in the native area coexist with many other ant species (Suarez et al. 1999). In addition, Argentine ants in the native area appear to be more or less multicolonial, with aggressive behavior commonly observed over small spatial scales. These findings led to the idea that the difference in the ecological dominance of Argentine ants between invaded and native areas stems from variation in social structure. Based on this hypothesis, one might expect indigenous ants of the invaded area to coexist with Argentine ants in the contact zones of Argentine ant supercolonies, where intraspecific aggression of Argentine ants does occur (Thomas et al. 2006).

However, recent studies have revealed that Argentine ants in the native area often form supercolonies, and the only difference between the Argentine ant supercolonies in invaded and native areas is that supercolonies are several orders of magnitude smaller (25-1900 m) in the native area (Heller 2004, Pedersen *et al.* 2006). Furthermore, many ant species coexist with Argentine ants within the boundaries of Argentine ant supercolonies in the native area, where Argentine ant

density exceeded that of the invaded area in California, suggesting that the difference in species coexistence between the invaded and native area may not be due to the social structure of Argentine ants (Heller 2004). These findings shed light on the possibility that indigenous ants of the invaded area might not be able to endure Argentine ant infestation even in the contact zones of Argentine ant supercolonies.

To date, whether indigenous ants of the invaded area occur in the contact zones has not been studied, probably because locating the contact zone itself is difficult. Only recently have several contact zones become the focus of studies and located (Jaquiéry et al. 2005, Thomas et al. 2006). If indigenous ants occur in these contact zones, studies on competition between indigenous ants and Argentine ants would provide insight into the hypothesis that unicoloniality is responsible for the strong competitive ability of Argentine ants against indigenous ants.

Argentine ants became established in Japan quite recently (Sugiyama 2000). Being first detected in 1993, they have invaded some coastal areas of western Japan (see Fig. 1 of Nishisue *et al.* 2006). In Port-Island, a part of Kobe Port, southern Kobe City, Hyogo Prefecture, Argentine ants were first detected in 1999 (Murakami 2002). In Maya Wharf, which is approximately 3 km away from Port-Island, Argentine ants were detected in 2002 (Ito *et al.* under revision). In our previous study, two antagonizing supercolonies were detected in Port-Island, suggesting that this island might harbor a contact zone of these supercolonies (Sunamura *et al.* in prep.).

In the present study, we investigated the situation of Argentine ant invasion in part of Kobe Port, including Port-Island. First, we conducted a visual survey to investigate the Argentine ant distribution there. Second, we performed aggression tests among Argentine ant colonies sampled within the invaded areas to reveal the presence and distribution of four supercolonies. Third, we compared the ant species richness between the invaded and uninvaded areas to evaluate the effects of the Argentine ant supercolonies on indigenous ants.

MATERIALS AND METHODS

Study Area

The investigation was carried out in Port-Island, Onohama, and Maya Wharf, Kobe City $(34^{\circ}\ 39.0\text{-}41.9\ \text{^{'}}\ \text{N}$ and $135^{\circ}\ 12.1\text{-}14.7\ \text{^{'}}\ \text{E}$, Fig. 1). These regions are

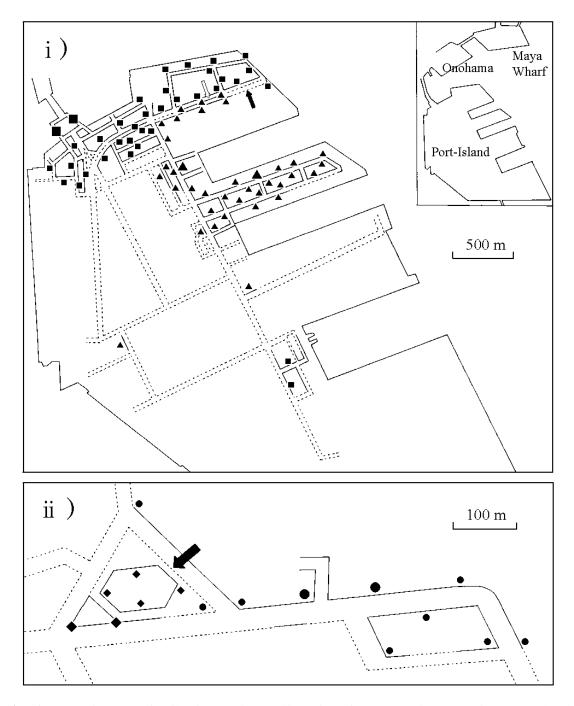


Fig. 1 Argentine ant distribution and sampling sites for aggression tests in Port-Island (i) and Maya Wharf (ii). The roads on which Argentine ants were (were not) detected are drawn with a solid (broken) line. In Onohama, Argentine ants were not detected. By the aggression tests, sampling sites were assigned to either the Kobe A (\blacksquare), Kobe B (\blacktriangle), Kobe C (\spadesuit) or Kobe D (\blacksquare) supercolony. Sites for the collection of reference colonies are shown with large symbols. The distance between the Kobe A and B supercolony was only 20 m across a pavement indicated by an open arrow in i). On the road indicated by a closed arrow on i), these supercolonies were separated by approximately 300 m of uninvaded area. The arrow in ii) shows the triangular block (see study sites and methods for further explanation).

part of Kobe Port, where many ships sail into. Port-Island and Onohama, Onohama and Maya Wharf are connected by bridges of which length are approximately 300 m and 200 m, respectively. Since their completion (Onohama: 1922, Maya Wharf: 1967, Port-Island: 1981), these regions have been redeveloped by reclamation several times. Trees are planted along the roads at steady intervals.

Distribution of Argentine ants

The distribution of Argentine ants was investigated along roads by visual survey. In Port-Island, we mainly investigated the major roads (Fig. 1- i). Narrower roads were investigated only when Argentine ants were detected on the major roads nearby. In Onohama and Maya Wharf, all roads that could be passed were investigated. In Maya Wharf, there was a triangular block (indicated by an arrow in Fig. 1- ii) that consisted of a triangular building and a hexagonal park. In this block, we conducted a visual survey not only along the road, but also around the park.

Aggression Tests

i) Collection of Reference Colonies

Argentine ants were detected in Port-Island and Maya Wharf by visual survey. In each of the two regions, two antagonizing supercolonies were detected in our preliminary aggression tests. We tentatively named the two supercolonies in Port-Island "Kobe A" and "Kobe B", and the other two in Maya Wharf "Kobe C" and "Kobe D". A reference colony from each of these four supercolonies was collected. In addition, a colony was collected in Iwakuni City, Yamaguchi Prefecture, which is approximately 300 km away from Kobe City. This colony represents the Japanese main supercolony, the most widespread supercolony in Japan that had been detected in Yamaguchi, Hiroshima and Aichi Prefectures in our previous study (Sunamura et al. in prep.).

ii) Five-on-five Aggression Test

Among and within these five reference colonies, we conducted five-on-five aggression tests largely following the method of Roulston $et\ al.$ (2003). Five workers from each of two colonies were introduced into a 5.2 cm diameter plastic dish, the side of which was coated with talcum powder. The interactions among these ten workers were observed for 10 min and scored as follows: 0 = ignore, 1 = ignore,

touch (prolonged antennation), 2 = avoid, 3 = aggression (lunging, pulling or biting), 4 = fight (prolonged aggression). Observations of 3 or 4 were considered aggressive. We performed six replicates of aggression tests for all inter- and intracolony pairs. An observer recorded data from six dishes simultaneously, recording the highest score observed during a 5-10 sec scan each minute. The highest score for each trial observed during 10 min was averaged across trials within each colony pair, and this average was used as the aggression index for the colony pair. The set of collections and aggression tests was conducted twice, once in October and once in December 2006. Between these two sets, sites for the collection of reference colonies were not the same (Fig. 1).

iii) Distribution of Supercolonies

To investigate the distribution of Argentine ant supercolonies in our study area, we collected colonies along the roads on which Argentine ants had been detected by the visual survey, and conducted aggression tests. In Port-Island, workers were collected at 71 sites (Fig. 1- i). When workers were collected at more than one site on a road not separated by pavements, the distance between neighboring sites was approximately 200 m.

In Maya Wharf, workers were collected at 15 sites (Fig. 1- ii). By the results of preliminary aggression tests, we predicted that the invaded area within the triangular block indicated by an arrow in Fig. 1- ii was inhabited by the Kobe C supercolony, and the other invaded area was inhabited by the Kobe D supercolony. Within the putative Kobe C boundary, which appeared to be very small, workers were collected at seven sites, each of them approximately 50 m apart from the neighboring sites. The remaining eight sites were within the putative Kobe D boundary, and when workers were collected at more than one site on a road not separated by pavements, the distance between neighboring sites was approximately 100 m.

We tested each of the 71 colonies collected in Port-Island against the reference Kobe A and B colonies, and each of the 15 colonies collected in Maya Wharf against the reference Kobe C and D colonies. For the colonies in which sufficient number of workers were available, five-on-five aggression tests were performed. For the other colonies, one-on-one aggression tests were performed. The method of the one-on-one aggression test was the same as that of the five-on-five aggression test except that it used one worker from each of two colonies in one trial. One-on-one aggression tests provide relatively low consistency compared to

five-on-five aggression tests, but with sufficient replication, their results are highly correlated with each other (Roulston *et al.* 2003). Aggression tests using colonies from Port-Island were conducted in October 2006, and aggression tests using colonies from Maya Wharf were conducted in December 2006. All of the tests were conducted in the laboratory within seven days after the field collection.

Ant Species Richness

Ants were collected along roads inside and outside of the areas invaded by Argentine ants (sampling sites not shown). A researcher collected as many species of foraging ants as possible on the ground, grasses and trees, during a 5 min survey. As the collection was conducted during the daytime, we collected only epigeic and diurnal ant species (see results).

In Port-Island, collection was conducted at 15 sites within the invaded area and 20 sites within the uninvaded area. All of the sampling sites within the invaded area were also used for the aggression tests. When ants were collected at more than one site on a road not separated by pavements, the distance between neighboring sites was approximately 400 m.

In Maya Wharf, collection was conducted at 14 sites within the invaded area and 10 sites within the uninvaded area. Sampling sites within the invaded area included 12 sites that were also used for the aggression tests. The remaining two sites were not used for the aggression tests, but as each of these sites was connected by an Argentine ant foraging trail to another site that was used for the aggression tests, we could determine which supercolonies these two sites belonged to. Within the putative Kobe C boundary, we collected ants at eight sites, each of them approximately 50 m apart from the neighboring sites. Within the putative Kobe D boundary or the uninvaded area, the distance between neighboring sampling sites was approximately 100 m when collection was conducted at more than one site on a road not separated by pavements.

Except for the sites within the putative Kobe C boundary, all of the sampling sites in the study area were more than 100 m away from the invasion fronts.

RESULTS

Distribution of Argentine ants

By the visual survey, Argentine ants were detected within four apparent areas

in Port-Island and one area in Maya Wharf (Fig. 1). Within the triangular block (indicated by an arrow in Fig. 1- ii) in Maya Wharf, Argentine ants were detected around the triangular building, along the fence of the hexagonal park, and on a part of the road. In Onohama, Argentine ants were not detected.

Aggression Tests

Intercolony aggression tests using the reference Kobe A-D colonies always detected aggressive behaviors (Table 1). In contrast, no aggressive behaviors were observed in the intracolony aggression tests. Also, the reference colonies of the Kobe D and Japanese main supercolony were not aggressive toward each other. Results in October and December 2006 were consistent.

Colonies collected in Port-Island that were aggressive toward the reference Kobe A / B colony were not aggressive toward the reference Kobe B / A colony (Fig. 2), indicating that each colony was clearly assigned to either the Kobe A or B supercolony. Results of these aggression tests are mapped onto Fig. 1- i . The one apparent large invaded area in the northern Port-Island harbored both the Kobe A and B supercolony. In this area, the maximum distance between the colonies sampled was approximately 2000 m for the Kobe A and 1600 m for the Kobe B supercolony. There was a contact zone of these supercolonies. For example, the distance between the two supercolonies was only 20 m across a pavement (indicated by an open arrow in Fig. 1- i). On the road shown by a closed arrow on Fig. 1- i , two supercolonies were separated by approximately 300 m of uninvaded area. Note that in this paper we use the term 'contact zone' to refer to an area where antagonistic Argentine ant supercolonies are in close proximity so that they might come into direct contact currently or will do so in the near future.

Table 1 Results of the five-on-five aggression tests within and among the reference colonies. Interactions of workers were scored 0 (ignore), 1 (touch), 2 (avoid), 3 (aggression) or 4 (fight). Mean \pm SD aggression indices of the results in October and November 2006 are shown.

| | Kobe A | Kobe B | Kobe C | Kobe D | Japanese main |
|-------------|--------|--------|----------------|----------------|----------------|
| Kobe A | 0 | 4 | 4 | 4 | 4 |
| Kobe B | | 0 | 3.8 ± 0.23 | 3.4 ± 0.12 | 3.7 ± 0.23 |
| Kobe C | | | 0 | 4 | 4 |
| Japanese ma | in | | | 0 | 0 |

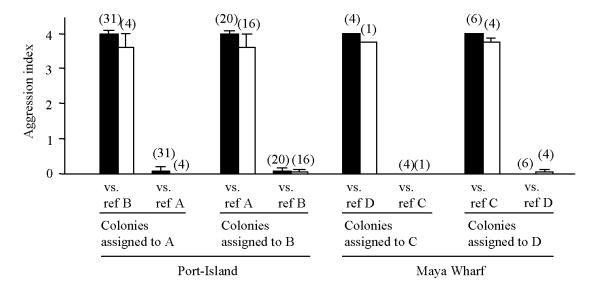


Fig. 2 Results of the aggression tests for 86 colonies collected in Port-Island and Maya Wharf. Colonies from Port-Island were tested against the reference Kobe A and B colonies, and colonies from Maya Wharf against the reference Kobe C and D colonies. Closed / open columns show aggression indices (mean \pm SD) for the five-on-five / one-on-one aggression tests. Interactions of workers were scored by the same measures shown in Table 1. Symbols A-D denote the Kobe A-D supercolonies, and ref A-D denote the reference Kobe A-D colonies. Numbers in parentheses denote numbers of colonies tested.

Colonies collected in Maya Wharf that were aggressive toward the reference Kobe C / D colony were not aggressive toward the reference Kobe D / C colony (Fig. 2), indicating that each colony was clearly assigned to either the Kobe C or D supercolony. Results of these aggression tests are mapped onto Fig. 1- ii. One of the seven colonies sampled within the putative Kobe C boundary actually belonged to the Kobe D supercolony. Data from this site were not included in the following analyses of ant species richness. The maximum distance between colonies sampled was < 200 m for the Kobe C, and approximately 600 m for the Kobe D supercolony.

Ant Species Richness

In total, 15 ant species other than the Argentine ants were collected (Table 2). Of these, *Paratrechina amia* is an exotic species. Hereafter we refer to the 15 species, including *P. amia*, as indigenous. Because the number of sampling sites differed among the invaded and uninvaded areas, we could not compare the total numbers of indigenous ant species among areas. Instead, the number of

indigenous ant species per sampling site was compared among areas. In Port-Island, the number of indigenous ant species per site within the Kobe A boundary did not differ significantly from that within the Kobe B boundary, but both of them were significantly lower than the number of indigenous ant species per site within the uninvaded area [average number of ant species ± SD within the invaded area (Kobe A) = 0.43 ± 0.79 , (Kobe B) = 0.75 ± 0.70 , uninvaded area in Port-Island (PI) = 3.0 ± 1.5, Steel-Dwass test, (Kobe A - Kobe B) : P = 0.56, (Kobe A - PI uninvaded): P < 0.01, (Kobe B - PI uninvaded): P < 0.01]. In Maya Wharf, the number of indigenous ant species per site within the Kobe D boundary was significantly lower than that within the uninvaded area, but the number of indigenous ant species per site within the Kobe C boundary did not differ significantly from those within the Kobe D boundary and the uninvaded area [average number of ant species \pm SD within the invaded area (Kobe C) = 1.4 ± 1.6 , (Kobe D) = 0.67 ± 0.52 , uninvaded area in Maya Wharf (MW) = 2.5 \pm 1.3, Steel-Dwass test, (Kobe C - Kobe D) : P = 0.82, (Kobe C - MW uninvaded): P = 0.29, (Kobe D - MW uninvaded): P < 0.05]. These results come from the peculiar distribution of indigenous ants within the Kobe C boundary (Fig. 1- ii): indigenous ants were detected at four sites along the fence of the hexagonal

Table 2 Frequencies of indigenous ant species within the uninvaded areas and the Kobe A-D boundaries. U: uninvaded area, A-D: the Kobe A-D boundaries. The number of sampling sites within each area is given in parentheses. The number of sites where each indigenous ant species were detected are shown.

| | Port Island | | | Maya Wharf | | |
|--------------------------|-------------|-------|-------|------------|-------|-------|
| | U (20) | A (7) | B (8) | U (10) | C (7) | D (6) |
| Monomorium chinense | 4 | 2 | 4 | 0 | 1 | 3 |
| Paratrechina sakurae | 4 | 0 | 2 | 1 | 1 | 0 |
| Camponotus vitiosus | 1 | 0 | 0 | 0 | 0 | 1 |
| Temunothorax congruous | 0 | 1 | 0 | 0 | 0 | 0 |
| Tetramorium tsushimae | 15 | 0 | 0 | 8 | 1 | 0 |
| Pachycondyla chinensis | 6 | 0 | 0 | 0 | 1 | 0 |
| Pheidole noda | 5 | 0 | 0 | 4 | 0 | 0 |
| Paratrechina amia | 5 | 0 | 0 | 3 | 1 | 0 |
| Formica japonica | 4 | 0 | 0 | 4 | 2 | 0 |
| Ochetellus glaber | 4 | 0 | 0 | 3 | 0 | 0 |
| Temunothorax spinosior | 4 | 0 | 0 | 1 | 1 | 0 |
| Pristomyrmex punctatus | 3 | 0 | 0 | 0 | 1 | 0 |
| Crematogaster matsumurai | 3 | 0 | 0 | 0 | 0 | 0 |
| Lasius japonicus | 1 | 0 | 0 | 0 | 0 | 0 |
| Camponotus japonicus | 0 | 0 | 0 | 1 | 1 | 0 |

park, but were not detected at three sites around the triangular building (sampling sites not shown).

The frequency of each indigenous ant species was compared among the invaded and uninvaded areas. *Tetramorium tsushimae*, the most common species within the uninvaded areas [Table 2, frequency within the uninvaded areas (PI) = 75%, (MW) = 80%], was never detected within the Kobe A, B and D boundaries [Steel-Dwass test, (PI uninvaded - Kobe A): P < 0.01, (PI uninvaded - Kobe B): P < 0.01, (MW uninvaded - Kobe D): P < 0.01]. Within the Kobe C boundary also, *T. tsushimae* was detected less frequently than within the uninvaded area [Steel-Dwass test, (MW uninvaded - Kobe C): P = 0.026]. *Monomorium chinense* occurred more frequently within the Kobe D boundary than within the uninvaded area [Steel-Dwass test, (MW uninvaded - Kobe C): P = 0.46, (MW uninvaded - Kobe D): P < 0.05, (Kobe C - Kobe D): P = 0.37]. For the other ant species, their frequencies did not differ significantly among areas (Steel-Dwass test, P > 0.05).

Indigenous ants were detected in the contact zones of Argentine ant supercolonies. At one sampling site on the road indicated by a closed arrow in Fig. 1- i (the Kobe A - B contact zone), *M. chinense*, *Paratrechina sakurae*, *Camponotus vitiosus*, *T. tsushimae*, *Formica japonica*, *Temunothorax spinosior*, and *Crematogaster matsumurai* were collected. Around the hexagonal park (the Kobe C - D contact zone, Fig. 1-ii) in Maya Wharf, indigenous ants were commonly observed (Table 2).

DISCUSSION

We detected four Argentine ant supercolonies in the study area (Table 1, Fig. 2). Each of Port-Island and Maya Wharf harbored two supercolonies and their contact zone (Fig. 1). In Port-Island, the Kobe A and B supercolony were separated by approximately 300 m of uninvaded area on the road indicated by a closed arrow in Fig. 1- i . Considering that the spread of Argentine ants by local colony budding occurs at a rate of 0-275 m per year (Suarez *et al.* 2001), these supercolonies might collide in a few years. The minimum distance between these two supercolonies was 20 m (Fig. 1- i), but the physical barrier (i. e., pavement) might limit opportunities for them to interact. In Maya Wharf, we found a site where the distance between the Kobe C and D supercolonies was at most 50 m (Fig. 1- ii). Further detailed study might detect interactions between these two

supercolonies.

To study the competition between Argentine ants and indigenous ants in the contact zone of Argentine ant supercolonies, it is important to evaluate the competitive ability of each supercolony used in the study against indigenous ants within the areas apart from the contact zone. In this study, we indicated that the Kobe A, B and D supercolonies had already caused serious reduction of ant species richness within their boundaries, just like Argentine ants in other invaded areas worldwide (Holway et al. 2002). Within the Kobe A, B and D boundaries, four species of indigenous ants were collected (Table 2). Of these species, M. chinense, P. sakurae and C. vitiosus were previously reported to tolerate Argentine ant invasion (Touyama 2001, Miyake et al. 2002, Touyama et al. 2003, Terayama et al. 2006). Curiously, the frequency of M. chinense within the Kobe D boundary was significantly higher than that within the uninvaded area in Maya Wharf. The reason is unclear. The remaining one species is Temunothorax congruous. Although occasionally found within invaded areas in Japan, previous studies suggested that this species is adversely affected by Argentine ant invasion because of its reduced frequency within the invaded area (Miyake et al. 2002, Terayama et al. 2006). The 11 species that did not occur within the Kobe A, B and D boundaries (Table 2) had been reported to be adversely affected by Argentine ant invasion (Miyake et al. 2002, Touyama et al. 2003, Terayama et al. 2006). In the present study also, T. tsushimae, which was the most abundant species in the uninvaded areas, was indicated to have been displaced by the three supercolonies. For the other species, however, significant difference in their frequencies between areas was not detected, probably because of their low frequencies within the uninvaded areas.

The indigenous ants that occurred in the contact zone of the Kobe A and B supercolony included four species that were previously reported to be adversely affected by Argentine ant invasion (*T. tsushimae*, *F. japonica*, *T. spinosior and C. matsumurai*) (Miyake *et al.* 2002, Touyama *et al.* 2003, Terayama *et al.* 2006).

In contrast to the obvious damage that the other three supercolonies had caused, the effect of the Kobe C supercolony on indigenous ants was ambiguous. Although the number of indigenous ant species per site within the Kobe C boundary was lower than that within the uninvaded area, this difference was not significant. Indeed, the indigenous ants detected within the Kobe C boundary included several species (e. g. *T. tsushimae*) that had been suggested in previous

studies to be displaced by Argentine ants (Miyake et al. 2002, Touyama et al. 2003, Terayama et al. 2006). However, the frequency of T. tsushimae within the Kobe C boundary was significantly lower than that within the uninvaded area. Several hypotheses can be advanced to explain the peculiar pattern of species coexistence within the Kobe C boundary. First, the competitive ability of the Kobe C supercolony against indigenous ants might be inferior to those of the other supercolonies. In this hypothesis, the absence of indigenous ants at three sites within the Kobe C boundary would be considered natural. Second, sufficient time might not have passed for the Kobe C supercolony to occupy a large area within which almost all of the indigenous ants had been displaced since it established itself in Maya Wharf. In this hypothesis, the absence of indigenous ants at the three sites within the Kobe C boundary can be interpreted as the consequence of competition between the Kobe C supercolony and indigenous ants. Third, competition between the Kobe C and D supercolonies might have provided indigenous ants with a competitive edge and allowed them to coexist with Argentine ants. Although the Kobe C supercolony appeared more prevalent than the Kobe D supercolony around their contact zone (i. e. around the hexagonal park in Fig. 1-ii), it is possible that the Kobe D supercolony was as prevalent as the Kobe C supercolony and fighting vigorously with it.

Although the competitive ability of the Kobe C supercolony against indigenous ants must be further examined, long-term studies in the contact zones of Argentine ant supercolonies in Kobe Port would give insight into the competitive mechanism underlying the displacement of indigenous ants by Argentine ants. To date, evidence supporting the hypothesis that a lack of intraspecific aggression is responsible for the ecological dominance of Argentine ants in the invaded area has come from laboratory and manipulated field experiments (Holway *et al.* 1998, Holway 1999, Holway & Suarez 2004). The density of Argentine ants, the competitive ability of Argentine ants against indigenous ants, and long-term consequences of competition in the contact zones of Argentine ant supercolonies in the Kobe study area merit examination.

The contact zones detected in this study are the products of an unusual pattern of Argentine ant invasion. The situation of Argentine ant invasion in southern Kobe City seems unusual in two ways. First, detection of more than two supercolonies within such a restricted area has, to our knowledge, never been reported from the invaded areas. Second, the supercolonies in the study area are

several orders of magnitude smaller than those in other invaded areas worldwide (Suarez et al. 1999, Giraud et al. 2002). These unusual features are likely to derive from recent multiple introduction of Argentine ants into the study area. Further research is necessary to reveal the invasion history of each supercolony. The invasion history of the Kobe D supercolony is particularly of interest considering that this supercolony is regarded as a part of the Japanese main supercolony (Table 1), which had been detected in Yamaguchi, Hiroshima and Aichi Prefectures (Sunamura et al. in prep.). Although the supercolonies in the study area are currently as small as those in the native area (Heller 2004, Pedersen et al. 2006), they will probably get larger if not controlled. The dispersal of Argentine ants involves two processes: local colony budding and human-mediated jumping (Suarez et al. 2001, Ward et al. 2005). Comparing the current Argentine ant distribution in the northern Port-Island with the previous distribution reported by Murakami (2002), it is obvious that the Kobe A and B supercolonies expanded their distribution locally during these four years. In addition, we found three small areas invaded either by the Kobe A or B supercolony in the southern Port-Island, away from the northern invaded area (Fig. 1- ii). Also, the Japanese main (i. e. Kobe D) supercolony occurred in Maya Wharf, approximately 200 km away from the nearest neighboring distribution of this supercolony ever known (Tahara City, Aichi Prefecture) (Sunamura et al. unpublished). These findings demonstrate that the Argentine ant supercolonies in Kobe Port have expanded their distributions either by colony budding or jump dispersal, just like Argentine ants in invaded areas abroad (Suarez et al. 2001, Ward et al. 2005).

ACKNOWLEDGMENTS

We would like to thank Dr. F. Ito (Kagawa University) and Dr. O. Kitade (Ibaraki University) for valuable information about Argentine ants in Kobe Port, T. Honda for helping with our preliminary survey, and R. Nakano for thoughtful advice.

REFERENCES

Giraud, T., J.S. Pedersen & L. Keller. 2002. Evolution of supercolonies: the

- Argentine ants of southern Europe. Proc. Natl. Acad. Sc. 99: 6075-6079.
- Heller, N.E. 2004. Colony structure in introduced and native populations of the invasive Argentine ant, *Linepithema humile*. Insect. Soc. 51: 378-386.
- Hölldobler, B. & E.O. Wilson. 1990. The ants. The Belknap Press of Harvard University Press, Cambridge, Mass., 732 pp.
- Holway, D.A., A.V. Suarez & T.J. Case. 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. Science 282: 949-952.
- Holway, D.A. 1999. Competitive mechanism underlying the displacement of native ants by the invasive Argentine ant. Ecology 80: 238-251.
- Holway, D.A., L. Lach, A.V. Suarez, N.D. Tsutsui & T.J. Case. 2002. Causes and consequences of ant invasions. Ann. Rev. Ecol. Syst. 33: 181-233.
- Holway, D.A. & A.V. Suarez. 2004. Colony-structure variation and interspecific competitive ability in the invasive Argentine ant. Oecologia 138: 216-222.
- Jaquiéry, J., V. Vogel & L. Keller. 2005. Multilevel genetic analyses of two supercolonies of the Argentine ant, *Linepithema humile*. Mol. Ecol. 14: 589-598.
- Miyake, K., T. Kameyama, T. Sugiyama & F. Ito. 2002. Effect of Argentine ant invasions on Japanese ant fauna in Hiroshima Prefecture, western Japan: a preliminary report (Hymenoptera: Formicidae). Sociobiology 39: 465-474.
- Murakami, K. 2002. Exotic ants in PortIsland, Kobe City. Ari (Journal of the Myrmecological Society of Japan) 26: 45-46. (in Japanese with English summary)
- Nishisue, K., Y. Tanaka, E. Sunamura, M. Terayama & S. Tatsuki. 2006. Distribution of the Argentine ant, *Linepithema humile*, in Kuroiso-machi and its surrounding area in Iwakuni City, Yamaguchi Prefecture. Ari (Journal of the Myrmecological Society of Japan) 28: 7-11. (in Japanese with English summary)
- Pedersen, J.S., M.J.B. Krieger, V. Vogel, T. Giraud & L. Keller. 2006. Native supercolonies of unrelated individuals in the invasive Argentine ant. Evolution 60: 782-791.
- Roulston, T.H., G. Buczkowski & J. Silverman. 2003. Nestmate discrimination in ants: effect of bioassay on aggressive behavior. Insect. Soc. 50: 151-159.
- Suarez, A.V., N.D. Tsutsui, D.A. Holway & T.J. Case. 1999. Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. Biol. Invasions 1: 43-53.

- Suarez, A.V., D.A. Holway & T.J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proc. Natl. Acad. Sc. 98: 1095-1100.
- Sugiyama, T. 2000. Invasion of Argentine ant, *Linepithema humile*, into Hiroshima Prefecture, Japan. Jpn. J. Appl. Entomol. Zool. 44: 127-129. (in Japanese with English summary)
- Terayama, M., Y. Tanaka & S. Tatsuki. 2006. Effects of the invasive ants *Linepithema humile* (Hymenoptera: Formicidae) on native ant and homopterous insect communities in Japan. Ari (Journal of the Myrmecological Society of Japan) 28: 13-27. (in Japanese with English summary)
- Thomas, M.L., C.M. Payne-Makrisâ, A.V. Suarez, N.D. Tsutsui & D.A. Holway. 2006. When supercolonies collide: territorial aggression in an invasive and unicolonial social insect. Mol. Ecol. 15: 4303-4315.
- Touyama, Y. 2001. Report of Argentine ant's invasion into Iwakuni City, Yamaguchi Prefecture. Ari (Journal of the Myrmecological Society of Japan) 25: 1-3. (in Japanese with English summary)
- Touyama, Y., K. Ogata & T. Sugiyama. 2003. The Argentine ant, *Linepithema humile*, in Japan: assessment of impact on species diversity of ant communities in urban environments. Entomol. Science 6: 57-62.
- Ward, D.F., R.J. Harris & M.C. Stanley. 2005. Human-mediated range expansion of Argentine ants *Linepithema humile* (Hymenoptera: Formicidae) in New Zealand. Sociobiology 45: 401-407.
- Wild, A.L. 2004. Taxonomy and distribution of the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 97: 1204-1215.