

9 The Ecological Consequences of a Fragmentation Mediated Invasion: The Argentine Ant, *Linepithema humile*, in Southern California

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9.1 Introduction

Habitat fragmentation can facilitate species loss through a number of processes. The remaining habitat may only sample a subset of the existing fauna (Preston 1962). Alternatively, species may become locally extinct within the remaining habitat after fragmentation (Bolger et al 1991). Small populations associated with the reduction in total area may become sensitive to stochastic processes, both demographic (Shaffer 1981; Gilpin and Soulé 1986; Goodman 1987) and environmental (Shaffer 1981). Fragmentation may reduce colonization, or immigration into the habitat remnants, especially by less mobile species (Turner and Corlett 1996). Deterministic processes associated with detrimental edge effects (Wilcove 1985; Yahner 1988; Robinson et al. 1995) and the loss of landscape level processes, such as fire regimes (Leach and Givnish 1996), also cause local extinctions post fragmentation. Fragmentation may also facilitate the immigration or invasion of exotic species that may directly compete with, prey upon, parasitize or otherwise indirectly affect native species (Diamond and Case 1986). Some of these processes are correlated. For example, an increase in edge around a habitat fragment will facilitate the penetration of exotic species that may be prominent along those edges. This is particularly a problem in urban landscapes because many successful exotic species are associated with human-mediated disturbance (Elton 1958; Fox and Fox 1986; Orians 1986; Petren and Case 1996).

Exotic ants have been inadvertently introduced worldwide (Williams 1994). Many species, such as the big headed ant (*Pheidole megacephala*), the little fire ant (*Wasmannia auropunctata*), the imported fire ant (*Solenopsis invicta*) and the Argentine ant (*Linepithema humile*, formerly *Iridomyrmex humilis*) have wreaked ecological havoc where they have become established (Williams 1994). Most of the impact of these species has been measured in loss of native ant diversity, which is greatly reduced or completely eliminated

in areas where they have invaded. Ants are important components of many ecosystems and changes in the native ant community may have repercussions on other taxa and trophic levels. Ants compete with rodents for seeds in desert and montane systems (Brown et al. 1975) and may help shape the plant community. In South African fynbos shrublands, native ant displacement by the Argentine ant has reduced the establishment of a native shrub whose seeds are ant-dispersed (Bond and Slingsby 1984). Some islands, like Hawaii, have no native ant species, and there is evidence that the introduction of the Argentine ant has negatively impacted the native arthropod fauna (Cole et al. 1992). There is also evidence that exotic ants detrimentally impact vertebrates (Mount et al. 1981; Allen et al. 1995).

The San Diego coastal horned lizard (*Phrynosoma coronatum blainvillei*) is listed by the California Department of Fish and Game as an animal of special concern, and is also a candidate for listing by the US Fish and Wildlife Service (Jennings and Hayes 1994). Like most horned lizards, this species specializes on ants (Pianka and Parker 1975; Montanucci 1989), particularly harvester ants of the genera *Messor* and *Pogonomyrmex* (Rissing 1981; Munger 1984; Suarez et al. 2000). The upland scrub habitats where they live have been subject to massive fragmentation as a result of urbanization over the past 100 years (Westman 1981; Alberts et al. 1993). In addition to habitat loss, the native ants which horned lizards eat are being displaced by an exotic invader, the Argentine ant, which has been invading the remaining suitable habitat in southern California (Suarez et al. 1998).

The Argentine ant was inadvertently introduced to the United States around 1891 in New Orleans (Titus 1905; Newell 1908). It was first detected in California in 1905 and spread rapidly throughout much of the state (Woodworth 1908; Smith 1936; Mallis 1941). Argentine ants have general and opportunistic nesting and dietary requirements (Newell and Barber 1913; Mallis 1942; Flanders 1943; Markin 1970a). Colonies have multiple queens which are inseminated within the nest prior to dispersal and do not undergo nuptial flights (Markin 1970b). The Argentine ant has been shown to displace native ant species throughout California (Erickson 1971; Tremper 1976; Ward 1987; Holway 1995, 1998a; Human and Gordon 1996; Suarez et al. 1998) through a combination of exploitative and interference competition (Human and Gordon 1996; Holway 1999).

In this study we provide evidence for the facilitation of spread of an exotic species, the Argentine ant (*Linepithema humile*), into natural areas through increased urban edges associated with habitat fragmentation. We demonstrate the negative impact of Argentine ants on native ground-foraging ants, and also provide evidence that these changes in ant communities may affect a specialist ant predator, the coastal horned lizard (*Phrynosoma coronatum*).

9.2 Methods

9.2.1 Ant Communities of Coastal Scrub Fragments in Southern California

Habitat fragments of native scrubland were isolated from the surrounding continuous vegetation throughout the last 100 years as a result of urban and suburban development (Soulé et al. 1988). Suarez et al. (1998) sampled the ant communities in 40 habitat fragments throughout coastal San Diego County, and one area of continuous scrub habitat, to determine how fragmentation promotes species loss. The habitat fragments vary in size (ranging in size from 0.4 to 101.6 ha), the number of years since isolated from the surrounding vegetation (age ranging from 3 to 95 years), the remaining percentage of native vegetation, the degree of isolation from areas of continuous vegetation, and the relative amount of urban edge surrounding the fragment. Detailed methods of how these parameters were obtained can be found in Suarez et al. (1998). Ant communities within the habitat fragments were compared to communities in plots of similar size, vegetation and topography within a continuous habitat in the University of California's Elliot Chaparral Reserve and the Miramar Naval Air Station (Fig. 9.1). These plots were at least 500 m from the nearest developed edge and represented areas of 1, 4, 10, 20, 30, and 50 ha. Additional point sampling throughout the 88-ha Elliot reserve was used to estimate the ant fauna for the entire reserve.

Ant communities were sampled with a combination of pitfall trapping and visual surveys. Pitfall sampling consisted of placing an array of five pitfall traps every 100 m along a transect through the longest axis of the habitat fragment or plot within the continuous area. Each trap consisted of a 60-mm-wide, 250-ml glass jar and was filled halfway with a mixture of water and non-toxic Sierra brand antifreeze. The jars were collected after 5 days. This method provides an estimate of ant activity for each array by counting the number of workers falling into the jars in each 5-day sample period. Pitfall trapping was repeated three times seasonally, with sample periods in the fall, winter, and spring/summer. At each array, we measured the distance to the nearest urban edge and relative amount of exotic vegetation (Suarez et al. 1998). Extensive visual surveys, consisting of walking throughout the area and overturning objects, were conducted in each fragment and control plot to compliment the pitfall trapping. Each fragment was visited and inspected visually for ants six times. Only ground-foraging ants were included in analyses (Suarez et al. 1998).

To examine within-fragment differences in ant species distributions, the average number of Argentine ant workers per jar and native ant species per array were calculated for each five-jar pitfall array. This average is compared to the percentage of exotic vegetation and the distance to the nearest devel-



Fig. 9.1. Map of southwestern San Diego County, California, USA. Extensive urbanization (the light gray “background” color indicates developed areas and the white intersecting lines indicate highways) has eliminated most native vegetation, leaving behind a system of habitat fragments (black). Some of the larger fragments used to measure the distance to potential source populations include the UC Elliot Reserve, the southeastern corner of the Miramar Naval Air Station, the Cabrillo National Monument, Proctor Valley, and Otay Valley. In addition, 38 of 40 fragments surveyed in Suarez et al. (1998) are indicated with numbers in order of size

oped edge. All arrays, regardless of the fragment they occurred in, were grouped together for these analyses.

To examine between-fragment distributions of native ant species, an average number of Argentine ants per jar (later referred to as Argentine ant activity) was determined for each fragment by pooling the information from each pitfall array in the fragment and all sampling dates. Linear and stepwise regressions were used to test for correlations between various fragment descriptors (age, area, vegetation, amount of edge and degree of isolation), the relative abundance of the Argentine ant, and the number of native ant species (Suarez et al. 1998).

Native ant species may vary in their sensitivity to habitat fragmentation and the subsequent invasion of the Argentine ant. Logistic regressions were used to construct incidence functions for the more common ant species and genera in relation to fragment size: *Solenopsis molesta*, *Leptothorax andrei*, *Prenolepis imparis*, *Dorymyrmex insanus*, *Solenopsis xyloni* and *Crematogaster californica*. Genera were used rather than species for some uncommon groups in order to increase the power of the tests. These include the genera *Camponotus*, *Pheidole*, and *Neivamyrmex*. The genera *Messor* and *Pogonomyrmex* are both commonly referred to as harvester ants because of their diets and behaviors (Davidson 1977; Holldobler and Wilson 1990). For this reason, and their importance as food for ant predators such as the coastal horned lizard (Pianka and Parker 1975; Rissing 1981; Munger 1984), they were also combined into one group.

9.2.2 The Effects of Argentine Ants on Coastal Horned Lizard Diet

Coastal horned lizard diet information was obtained through the examination of fecal pellets in three reserves in southern California, USA. Lizards were collected from the University of California's Elliot Chaparral Reserve (Elliot), Torrey Pines State Park (Torrey Pines), and the Southwestern Riverside County Multispecies Reserve (Riverside). Lizards were brought into the lab until they deposited a fecal pellet and then returned to the field. These areas were also visually searched for horned lizards fecal pellets, which are very distinctive (Rissing 1981, pers. observ.). Fecal pellets were dissected and ants were identified to species when possible using a reference collection and a key to the head capsules of ants from fecal pellets (Snelling and George 1979). Other insects were identified to order. While Argentine ants are absent from our study sites in Riverside, they are invading Elliot and Torrey Pines (Suarez et al. 2000).

To compliment data collected on horned lizard diet in the wild, we performed laboratory experiments consisting of paired presentations of ants to lizards (Suarez et al. 2000). Lizards were collected from Elliot and Riverside and brought into the lab. Each lizard was marked and placed into its own 25 ×

50-cm terrarium. Each terrarium contained sand, a water dish and some sparse vegetation. A heat lamp was placed over the terrarium on a timer set from 6 a.m. to 6 p.m. The temperature was maintained at 92–96 °F during mid-day. The lizards were kept in the lab only for the duration of the trials and then were returned to the field at the site of capture.

The lizards were starved for 2 days before the start of their feeding experiments. The experiments consisted of a prey preference trial repeated every other day. Trials took place in a different 25 × 50-cm terrarium which was coated with limousine grade tinting, allowing an observer to peer into the tank and watch the lizard's behavior without being seen. The lizard was allowed to become accustomed to the tank for 5 min before the trial began. Five individuals each of two species of ants were then placed into the tank with lizard. Ants were replaced as they were eaten by the lizard so there were five individuals of each species of ant at all times during the trial. The trial lasted for 45 min or until the lizard buried itself in the sand. The following information was recorded during the trial: each time the lizard fixed on an ant, whether the ant was eaten, and how many steps the lizard took to reach the ant.

The percentage of total ants eaten was calculated for each prey species after every trial (Suarez et al. 2000). By using the percentage of total ants eaten during the trial instead of the absolute number of ants eaten, we can reduce the effects of hunger or other random variation that may result in more or less total numbers of ants being eaten in any trial. These values summarize the prey preference of the lizards including any effect the behavior of the ants may have had. Each time a lizard turned its head and noticed an ant we recorded a fix. The ratio of fixed to eaten ants then gives us an approximation of how many ants were eaten after detection by the lizard. Finally, by measuring the number of steps taken by the lizard to reach the prey item we are quantifying effort or cost (in terms of energy expenditure or increased predation risk) the lizard is willing to take for that particular prey type.

The following native ants were paired with the exotic Argentine ant: *Pogonomyrmex rugosus*, *Pogonomyrmex californicus*, *Messor andrei*, and *Crematogaster californica*. The order the ant pairs were presented to the lizards was chosen at random. The three harvester ants vary in size, *P. rugosus* (6.5–7.5 mm) is the largest, then *P. californicus* (5.5–6.8 mm), and *Messor andrei* (4.5–6.0 mm) is the smallest, although there is considerable overlap in size between *P. californicus* and *M. andrei*. *Crematogaster californica* (3–4 mm) and the Argentine ant (2.5–3.0 mm) are considerably smaller than the harvester ants (Wheeler and Wheeler 1973). The native ant species were chosen because they are common prey items for coastal horned lizards in southern California (Suarez et al. 2000).

9.3 Results

9.3.1 Ant Communities of Coastal Scrub Fragments in Southern California

Within fragments, the number of native ant species detected at any sample array decreased in the presence of the Argentine ant from an average of almost seven to two (Fig. 9.2). The average number of Argentine ants per jar was negatively correlated with the distance to the nearest urban edge (Fig. 9.3a). Only at points greater than 100 m from the nearest urban edge were Argentine ants found at densities of less than five workers per jar. Subsequently, the number of native ant species at any point was positively correlated with the distance from the nearest urban edge (Fig. 9.3b). The amount of exotic vegetation also decreased with distance from an urban edge (Fig. 9.3c).

The direct role of urbanization on the success of Argentine ants (and the subsequent loss of native ant species) within remaining habitat patches is illustrated in one of the fragments, Rice Canyon. Rice Canyon was isolated approximately 3 years before sampling from a larger area of continuous scrub habitat. Urbanization began at the east and south end of the canyon and has continued until the present, slowly working westward. This has resulted in a gradient of disturbance from the east to west end of the fragment. While native ants are abundant in the west end of the fragment, the east end is dom-

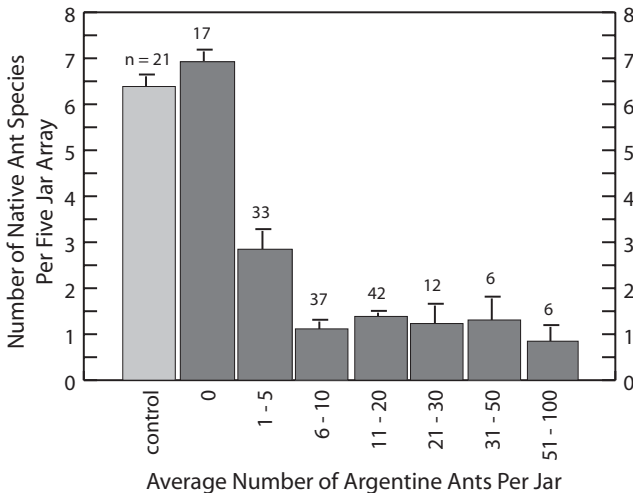


Fig. 9.2. The number of native ant species detected at an array vs. the average number of Argentine ants per trap at that array. All arrays placed within fragments are shown, but not those within the plots at the Elliot Reserve. Numbers of Argentine ants were averaged across the three sample seasons for each array

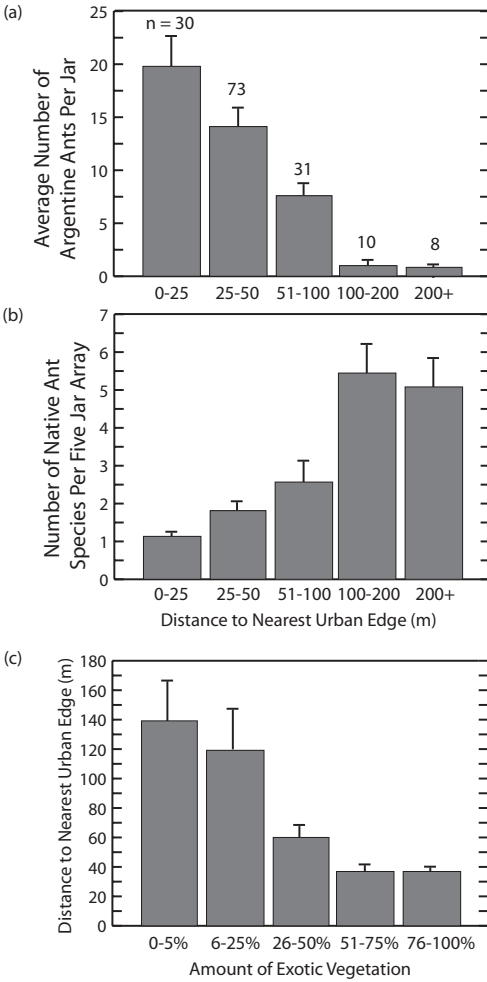


Fig. 9.3. Associations between the distance of an array to the nearest urban edge and the average number of Argentine ants per jar at that array (a), the number of native ant species detected at the array (b), and the approximate cover of exotic vegetation surrounding the array (c). Error bars indicate one standard error. These graphs include all points sampled within the 40 habitat fragments

inated by Argentine ants. The transition between the decline in native ant species and the penetration of Argentine ants corresponds spatially with the onset of development (Fig. 9.4).

Among fragments, bivariate regressions reveal that log area ($R^2=0.441$, $P<0.0001$) and percent native vegetation ($R^2=0.349$, $P<0.0001$) were positively correlated, while log age ($R^2=0.152$, $P<0.02$) and log Argentine ant activity ($R^2=0.483$, $P<0.0001$) were negatively correlated with the remaining number of native ants species within a fragment (Fig. 9.5). The amount of edge and degree of isolation were not correlated with the number of native ant species. In a stepwise multiple regression with the number of native ant species as the dependent variable, however, only log area ($P<0.0001$), log age ($P<0.0005$), and log Argentine ant activity ($P<0.0002$) significantly explained any variance in the number of native ant species among the fragments (total model:

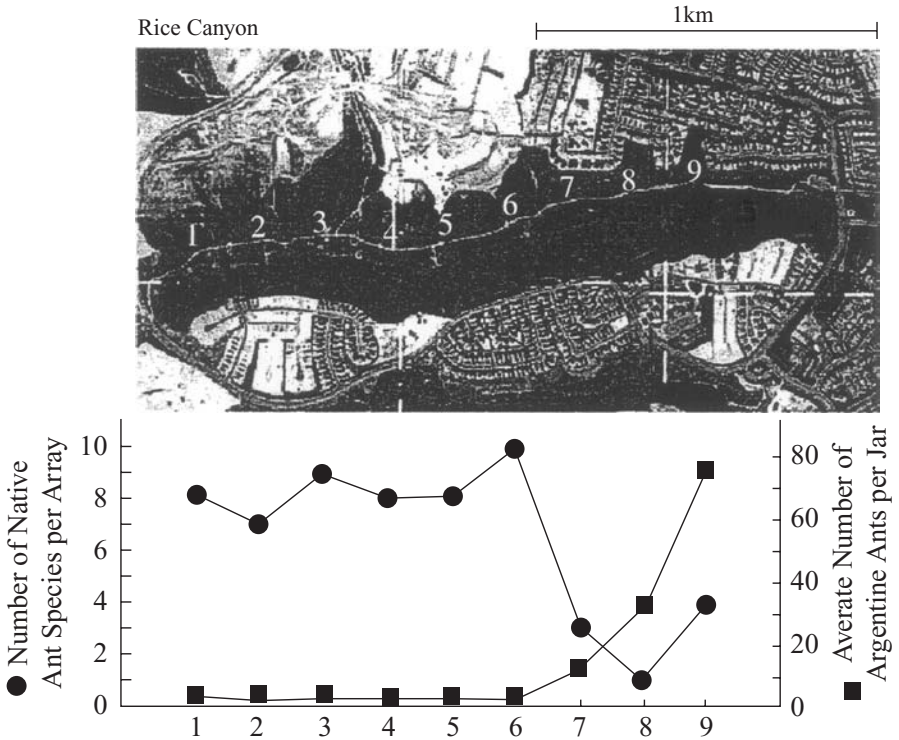


Fig. 9.4. A photograph of Rice Canyon (San Diego County, California, USA) and a transect of sampling points which runs the length of the canyon. The developed area at the northern end of the canyon begins at *point 7* and continues east through *point 9*. The number of native ant species detected at each sample array along with the average number of Argentine ants per jar at each array are plotted below the photograph

d.f.=36, $R^2=0.747$, $P<0.001$). A stepwise multiple regression with Argentine ant activity as the dependent variable, revealed log area as the only significant predictor of log Argentine ant activity (total model: d.f.=38, $R^2=0.195$, $P<0.005$; Suarez et al. 1998).

Sample plots within continuous vegetation averaged more native ant species, 16.4 ± 4.6 (mean \pm SD), than the isolated fragments that only averaged 5.9 ± 4.9 species. In addition, the regression slope of log native ant species on log area was significantly lower in plots within continuous vegetation than in isolated canyons ($t=2.52$; $v=40$; $P<0.01$; Fig. 9.6).

Native ant species/genera varied in their probability of going locally extinct due to habitat fragmentation and the subsequent invasion of Argentine ants. Incidence functions of presence/absence data versus fragment size found *Prenolepis imparis* and *Dorymyrmex insanus* were the least sensitive species, and the genera *Neivamyrmex*, the army ants, and *Pogonomyrmex* and *Messor*, the harvester ants, were the most sensitive (Fig. 9.7). *Solenopsis molesta* and

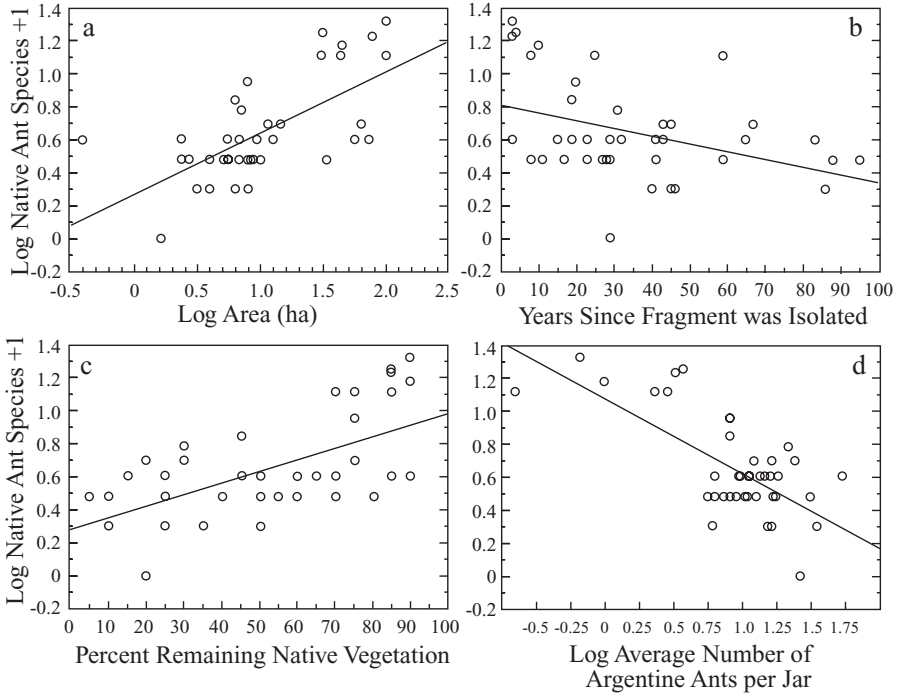


Fig. 9.5a–d. Linear regressions of various fragment descriptors on log native ant species detected within the 40 isolated habitat fragments surveyed. Only independent variables that were significantly correlated with log native ant species number are presented including: **a** log area of habitat fragment ($Y=0.271+0.372 \times X$, $R^2=0.441$, $P<0.0001$); **b** age, in years, since isolation ($Y=0.814-0.005 \times X$; $R^2=0.152$, $P<0.02$); **c** percent cover of native vegetation remaining within the fragment ($Y=0.283+0.007 \times X$, $R^2=0.349$, $P<0.0001$); and **d** log Argentine ant activity, measured in average number of workers per jar, within the fragment ($Y=1.076-0.451 \times X$, $R^2=0.483$, $P<0.0001$). Fragment descriptors that did not significantly correlate with the number of native ant species within the fragments include the distance to the nearest area of continuous vegetation and the relative amount of urban edge

Leptothorax andrei occurred in nearly every habitat fragment sampled, 34 and 32 of 40 fragments respectively, and were not significantly associated with fragment area or the presence of the Argentine ant. Species lists for the fragments and plots within continuous habitat can be found in Suarez et al. (1998).

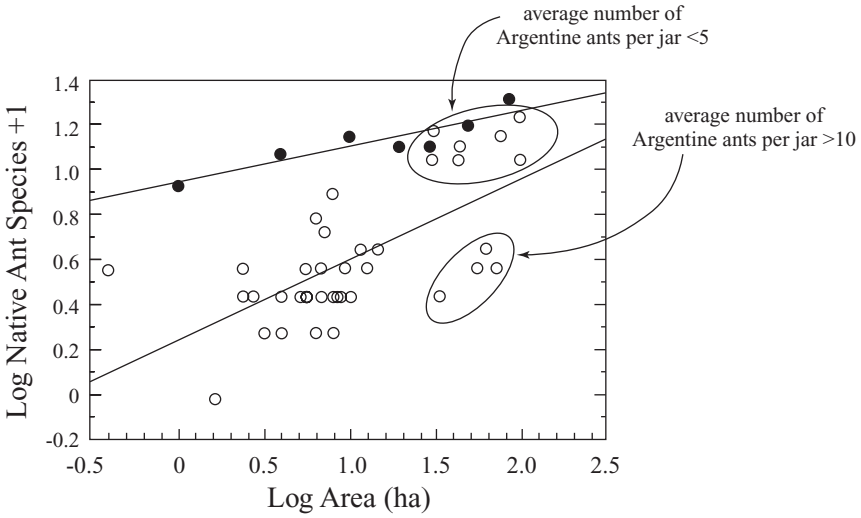


Fig. 9.6. Regression of the log number of native ant species +1 detected within isolated fragments (*open circles*, $Y=0.271+0.372 \times X$; $R^2=0.441$) and similarly sized plots within continuous habitat at the UC Elliot reserve (*closed circles*, $Y=1.013+0.164 \times X$; $R^2=0.806$) vs. their area in hectares

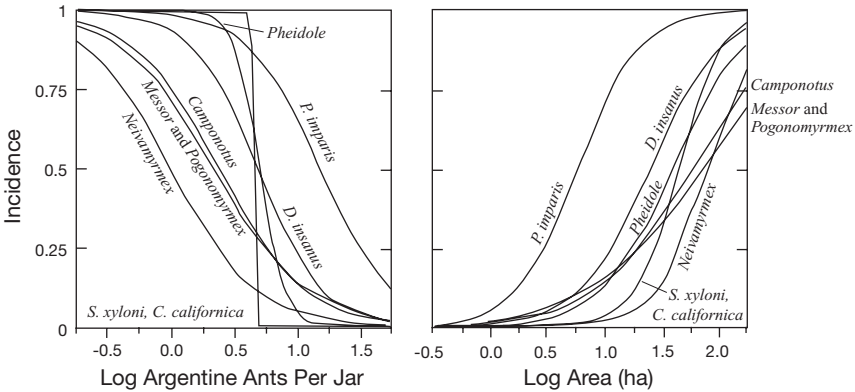


Fig. 9.7. Incidence functions of various ant species and genera as determined by logistic regressions of presence/absence data within a fragment vs. log fragment area. Only species with significant association ($P<0.05$) are shown. Species tested for which the logistic regression showed no significant correlation ($P>0.05$) include *Solenopsis molesta*, and *Leptothorax andrei*

9.3.2 The Effects of Argentine Ants on Coastal Horned Lizard Diet

At the three reserves where diet information was gathered, native ants made up over 98 % of the prey items identified from all fecal pellets combined in areas never occupied by the exotic Argentine ant. In contrast, ants averaged only 11 % of total prey items in fecal pellets collected from lizards in areas that were occupied by Argentine ants at Elliot. Harvester ants (genera *Messor* and *Pogonomyrmex*) were the most common prey item in all three reserves. The proportion of total diet consisting of harvester ants ranged from 49 % (by prey item) at the Riverside Multispecies Reserve to 69 % at the Elliot Reserve. In areas occupied by Argentine ants, however, harvester ants only made up from 0 to 6 % of their diet (Table 9.1). At Torrey Pines, the native ant *Dorymyrmex insanus* persisted in areas that were invaded by Argentine ants resulting in a diet shift from harvester ants to *D. insanus* in those areas. Argen-

Table 9.1. Summary of diet composition for coastal horned lizards (*Phrynosoma coronatum*) obtained from fecal pellets at three reserves. The data from the UC Elliot Reserve and Torrey Pines State Park have been separated into areas with and without Argentine ants (*Linepithema humile*). The numbers represent the percentage of total diet for all fecal pellets combined. The numbers in parentheses next to present and absent represent the number of fecal pellets examined

	Elliot <i>L. humile</i>		Torrey pines <i>L. humile</i>		Riverside <i>L. humile</i>
	Absent (67)	Present (10)	Absent (4)	Present (3)	Absent (98)
Hymenoptera: Formicidae					
<i>Messor andrei</i>	69.19	6.19	a	a	2.21
<i>Pogonomyrmex subnitidus</i>	a	a	62.83	0	a
<i>Pogonomyrmex rugosus</i>	a	a	a	a	28.73
<i>Pogonomyrmex californicus</i>	a	a	a	a	18.52
<i>Crematogaster californica</i>	23.46	3.26	0	0	7.95
<i>Dorymyrmex insanus</i>	0.31	0.98	36.43	77.78	0.16
<i>Pheidole vistana</i>	2.25	0	0	2.22	0.04
<i>Formica</i> spp.	0.06	0	0	0	14.74
<i>Myrmecocystus</i> spp.	0.06	0	0	0	14.45
<i>Camponotus</i> spp.	1.86	0.65	0.74	6.67	11.86
<i>Forelius</i> spp.	1.31	0	a	a	0
<i>Solenopsis xyloni</i>	0.03	0	0	0	0
<i>Neivamyrmex californicus</i>	0.05	0	0	0	0
Other ant	0.09	0	0	0	0.02
Total harvester ants	69.19	6.19	62.83	0	49.46
Total ants	98.62	11.07	100	86.67	98.69
Total non-ants	1.38	88.93	0	13.33	1.3

^a Ant species does not occur in the reserve.

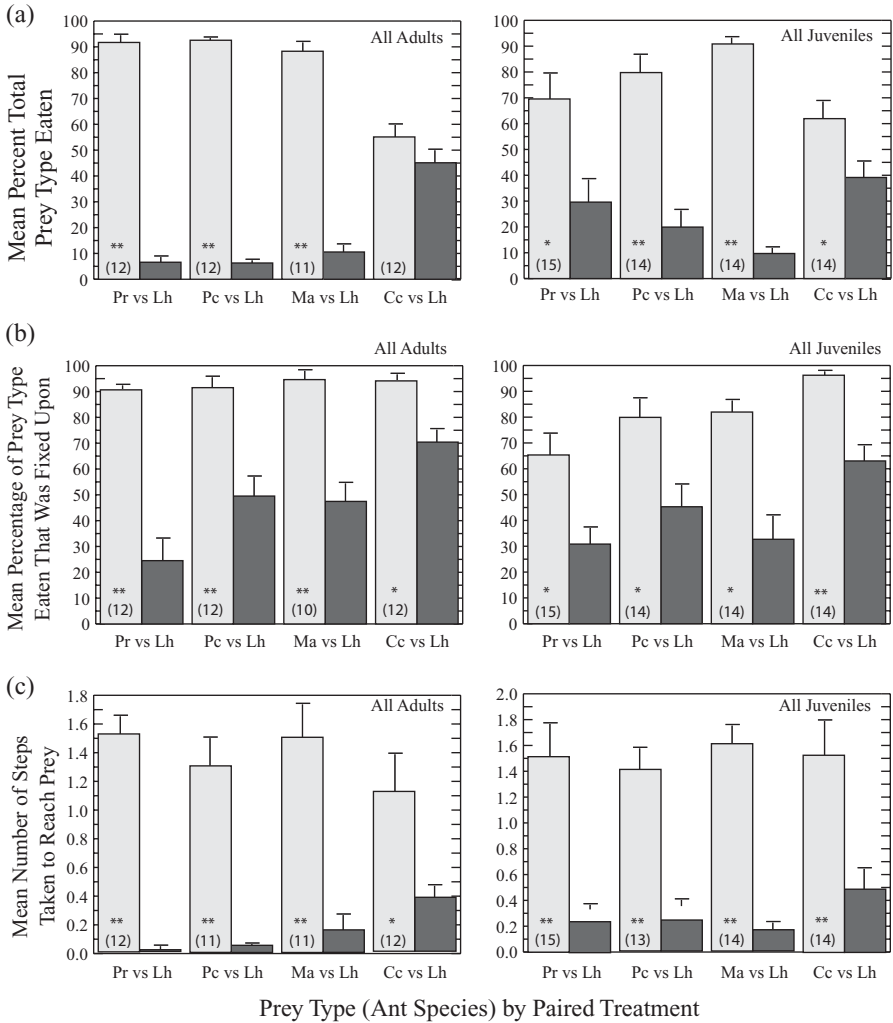


Fig. 9.8a-c. Summary of results of the laboratory prey preference experiments. Average percent of prey items eaten during prey preference trials (a), average percent of detected (fixed upon) prey items that were consumed during prey preference trials (b), and the mean number of steps taken to reach prey items (c) by horned lizards during paired prey preference trials of various native ant species vs. the exotic Argentine ant (*Linepithema humile*). Between 25 and 27 lizards were tested in each category. Error bars represent one standard error. The abbreviated ant species are Pr = *Pogonomyrmex rugosus*; Pc = *Pogonomyrmex californicus*; Ma = *Messor andrei*; Cc = *Crematogaster californica*; and Lh = *Linepithema humile*. Significant differences in values between the native ant species tested and the Argentine ant are represented by asterisks (* $P < 0.05$; ** $P < 0.001$; Mann-Whitney U-Test)

tine ants were never detected in their diet, even in areas where they had invaded and displaced native ant species.

In laboratory prey preference experiments, horned lizards always preferred native ant species to the Argentine ant in paired trials (Fig. 9.8). Lizards always ate more of the three harvester ants than the Argentine ant, averaging 87 % of prey items eaten. The preference for *C. californica* over the Argentine ant was not as strong, averaging about 60 % of prey eaten (Fig. 9.8a). For ants that were clearly fixed upon visually by the horned lizards, and then either eaten or not, lizards always significantly preferred the native ant species tested to the Argentine ant (Fig. 9.8b). Lizards ate between 78 % (*Pogonomyrmex rugosus*) and 95 % (*Crematogaster californica*) of the native ants they fixed upon, while only eating 45 %, on average, of the Argentine ants they fixed on. Horned lizards also took significantly more steps to reach the native ant species than the exotic Argentine ant (Fig. 9.8c). For all native ant species combined, lizards averaged 1.44 steps to reach prey, while only taking 0.21 steps to reach Argentine ants when they were eaten.

9.4 Discussion

9.4.1 Local Extinction of Native Ground-Foraging Ants

The native ground-foraging ant communities in the scrub habitats of coastal southern California are prone to local extinction due to fragmentation and the subsequent presence of the invasive Argentine ant (Suarez et al. 1998). Argentine ants penetrate into habitat fragments from surrounding urban edges where they are more abundant. This results in smaller fragments, which have a higher edge to interior ratio, to become saturated with Argentine ants. Native ant species, which may already be vulnerable to extinction in smaller fragments due to stochastic processes, are lost in these fragments due to interference and exploitative competition from the invading Argentine ants (Human and Gordon 1996; Holway 1999). In larger fragments, the effective size of the remaining habitat is reduced by the Argentine ant, which can displace native species up to 200 m in from a developed edge. In addition, internal edges may be as detrimental as external, boundary edges, and preventing the penetration of exotic species such as the Argentine ant into reserves may be difficult. In South African fynbos shrublands, Argentine ants were more common in human disturbed areas, and penetrated into the reserve along roads, particularly paved roads, regardless of the presence of exotic vegetation (De Kock and Giliomee 1989).

The role of urban development in facilitating the spread of Argentine ants is seen in Rice Canyon which is completely isolated from other vegetation, but has only been developed on the east side (Fig. 9.4). Argentine ants have spread

into the canyon from housing developments in place on the east end of the fragment and native species are only persisting in the west end where Argentine ant have not yet penetrated. Argentine ants appear to be limited by water availability (Smith 1936; Holway 1998b). It is likely that Argentine ants are benefiting from water runoff into the fragment from the landscaped areas above the canyon. Like Argentine ant density, the abundance of exotic vegetation is also correlated with distance to the nearest urban edge. However, in Rice Canyon (Fig. 9.4) the vegetation in the east end is predominately native, implying that the spread of Argentine ants into the habitat fragment and the subsequent loss of native species is not dependent on exotic vegetation. This is also supported at the University of California's Elliot Reserve and Torrey Pines State Park where Argentine ants have penetrated over 400 and 1000 m, respectively, into the reserves in areas dominated by native scrub vegetation (Suarez et al. 1998; J. King, unpubl.). This also highlights that the degree to which Argentine ants can penetrate into natural habitat varies depending upon the topography and abiotic conditions of the landscape. For example, in more xeric sites in Riverside County, California, Argentine ants appear only able to penetrate up to 50 m into native vegetation from neighboring urban developments (Suarez and Case, unpubl. data).

Within fragments, the number of native ants declines from an average of seven species per sample array to one or two species in areas occupied by the Argentine ant. The species that persist with Argentine ants include *Solenopsis molesta*, *Leptothorax andrei*, and *Prenolepis imparis* (Suarez et al. 1998). Both *S. molesta* and *L. andrei* are small species (1–2 mm) that are often categorized as hypogeic, or belowground foraging (Ward 1987). *Prenolepis imparis*, however, is an aboveground foraging ant similar in size and biology to the Argentine ant. The coexistence between *P. imparis* and Argentine ants is likely due to temporal niche partitioning between these species. While Argentine ants forage most abundantly during summer and spring months, *P. imparis* is exclusively active in the cold and wet winter months (Tschinkel 1987; Ward 1987; Suarez et al. 1998). The most vulnerable species to fragmentation and Argentine ant invasion, as detected by logistic regressions on presence/absence data, included *Neivamyrmex* (the army ants), and *Messor* and *Pogonomyrmex* (the harvester ants; Fig. 9.8) both of which are important to ecosystem level processes (Brown et al. 1975; Gotwald 1995). The loss of harvester ants, in particular, can have drastic effects on both plant species, which depend on them for seed dispersal (see Bond and Slingsby 1984), and on horned lizards, whose diets are composed primarily of harvester ants (Pianka and Parker 1975; Rissing 1981; Munger 1984; Suarez et al. 2000).

9.4.2 Diet and Prey Preference in Coastal Horned Lizards

Horned lizards have been declining in California (Jennings 1988) and their decline in some areas has been correlated with the presence of Argentine ants (Fisher et al. 2002). We provide a potential mechanism behind the decline of horned lizards in these areas. The loss of native ground-foraging ants due to interactions with Argentine ants directly affects the preferred diet of coastal horned lizards. Native ground-foraging ants made up at least 98 % of the total diet based on prey items in all three reserves examined (Table 9.1). Harvester ants are the most common prey item found in horned lizard diets, making up between 50 and 70 % of their diet in undisturbed areas. These ants are very sensitive to habitat fragmentation and the subsequent presence of Argentine ants. Harvester ants were only found in the largest of the fragments surveyed and then only in areas where Argentine ants had not invaded (Suarez et al. 1998).

In areas where Argentine ants have invaded, the diet of coastal horned lizards changed from primarily ants to non-ant arthropods, and Argentine ants were never eaten. The small sample sizes of fecal pellets within areas occupied by Argentine ants is due to the fact that horned lizards were rarely seen in invaded areas and will actively avoid them (Suarez et al. 2000; Fisher et al. 2002). In addition, recent experiments suggest that hatchling horned lizards are unable to maintain positive growth rates on diets of Argentine ants or arthropods typical of an invaded community (Suarez and Case 2002).

Argentine ants were never preferred in paired prey preference tests with native ant species. In context of total percentage of ants eaten in any trial, native ants were always preferred over Argentine ants (Fig. 9.8). The lack of a strong preference for *C. californica* over Argentine ants in total ants eaten, is probably due to the behavior of *C. californica* which will frequently freeze, and remain motionless when a predator is nearby (pers. observ.). Therefore, *C. californica* may not have been detected as often during the trials. This is reflected in the percentage of ants that were eaten after being fixed upon. When *C. californica* was detected, lizards did eat them much more frequently than Argentine ants (Fig. 9.8b).

Horned lizards tend to pick a spot near a foraging trail or concentration of ants (i.e., the colony entrance) and consume ants as they approach the lizard (Munger 1984; J. Richmond and A. Suarez, pers. observ.). This “sit and wait” behavior may minimize detection of the lizard by potential predators as well as by the prey, preventing a colony response or attack. Lizards in both age classes took significantly fewer steps to predate Argentine ants than any native ant tested (Fig. 9.8 c). This suggests that when they do consume an Argentine ant they do so at a minimal “cost” compared to native ant species, which they are willing to pursue or even seek out (Shafir and Roughgarden 1998).

Argentine ants were never eaten by horned lizards in the wild, even though at Torrey Pines horned lizards ate the similarly sized *Dorymyrmex insanus*.

This may reflect an avoidance of Argentine ants due to their aggressive, swarming behavior (pers. observ., see Rissing 1981). It is also possible that Argentine ants differ chemically from the native ants typically eaten, and are either not recognized as potential prey by the lizards or are avoided outright (Suarez et al. 2000). Horned lizards ate Argentine ants in the lab, although rarely, but this reflects the fact that lizards were starved every other day and then limited in the choice and availability of prey. Statistical differences in prey choice, as seen under these conditions, probably reflects strong preferences against eating Argentine ants, as seen in the wild.

9.5 Conclusions and Implications for Reserve Management

Among other detrimental consequences of habitat fragmentation, the subdivision of natural areas facilitates the invasion of exotic species into the remaining habitat. We demonstrate that native ground-foraging ants are prone to local extinction due to habitat fragmentation through the subsequent invasion of Argentine ants from urban edges. Native ants vary in their vulnerability to these processes, the most sensitive include army ants and harvester ants, both of which are important to ecosystem level processes. Harvester ants, in particular, are important seed dispersers, seed predators, and food sources for certain native species such as horned lizards.

Coastal horned lizards have a diet dominated by ants, particularly harvester ants of the genera *Messor* and *Pogonomyrmex*. In areas where the Argentine ant has invaded and native ants are displaced, horned lizards are forced to change their diet to incorporate more non-ant arthropods. While habitat loss, in the form of fragmentation due to urbanization, is likely a major cause of the coastal horned lizard's decline, the invasion of Argentine ants into the remaining natural areas in southern California compounds the detrimental effects of habitat loss on horned lizards.

Changes in non-ant arthropod communities associated with Argentine ant invasion (e.g., Cole et al. 1991; Bolger et al. 2000) may have detrimental effects on many insectivorous vertebrates, and still needs to be quantified. To preserve viable populations of sensitive species, such as coastal horned lizards, we not only need to save an adequate amount of habitat, but also manage the remaining areas to prevent the penetration of exotic species. Some practical guidelines include minimizing the penetration of roads and landscaping into the reserve. If any type of replanting or landscaping is to be done, care must be taken to ensure that Argentine ants are not imported with the plants.

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