

COMPETITIVE MECHANISMS UNDERLYING THE DISPLACEMENT OF NATIVE ANTS BY THE INVASIVE ARGENTINE ANT

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Abstract. The Argentine ant (*Linepithema humile*) is a widespread invasive species that competitively displaces native ants throughout its introduced range. Although this pattern of displacement is well known, its underlying mechanisms remain little studied. To gain a more detailed understanding of this widespread competitive displacement, I compared the exploitative and interference abilities of the Argentine ant with those of seven species of native ants it displaces in riparian woodlands in northern California. I performed four different manipulative field experiments; each measured different aspects of the competitive ability of the eight species of ants in this study. The main goals of this study were to identify the mechanisms responsible for the Argentine ant's strong competitive ability, to determine if native ants are subject to species-specific trade-offs in exploitative and interference ability typically present among coexisting ants, and if so, to assess whether Argentine ants are subject to this trade-off as well.

Argentine ants located and recruited to baits as quickly or more quickly than did native ants—both in areas where Argentine ants and native ants occurred together (i.e., at the edge of invasion fronts) and where they occurred separately (i.e., away from invasion fronts). Along the edge of invasion fronts, Argentine ants also controlled a greater proportion of baits than did native ants. In one-on-one interactions, individual Argentine ant workers experienced mixed success in overcoming individual workers of the seven native ant species. When fighting against native ants, Argentine ants used both physical aggression and chemical defensive compounds, although the latter mechanism was more often successful in deterring opponents. Chemical defensive compounds produced by Argentine ants were repellent but appeared no more so than those of native ants. Although Argentine ant workers were not able to overcome native ant workers consistently, Argentine ant colonies succeeded in displacing most native ant colonies from baits. The discrepancy between worker-level and colony-level interference ability suggests that numerical advantages are key to the Argentine ant's proficiency at interference competition.

Like ants in other communities, the native ants in this study were subject to a competitive trade-off in which interference ability and exploitative ability were negatively correlated. In contrast, Argentine ants were proficient at both exploitative and interference competition relative to the native ants they displaced and are thus removed from this trade-off. These findings imply that Argentine ants secure a majority of available food resources where this species comes into contact with native ants. Argentine ants may be able to break the competitive trade-off constraining native ants because of their unique colony structure and because they have escaped their natural enemies. The observation that Argentine ants are uncoupled from the competitive trade-off constraining native ants may provide a general explanation for patterns of dominance within ant communities and for the success of other introduced species.

Key words: ants; Argentine ants; biological invasion; California; competition; competitive asymmetry; competitive displacement; competitive trade-offs; exotic species; exploitative competition; field experiment; interference competition.

INTRODUCTION

For the past several decades, research in invasion biology has focused on predicting the outcome of biological invasions. To this end, ecologists have tried

to identify attributes common to highly invasive species, determine factors that govern establishment and subsequent rates of spread, and anticipate the number and magnitude of direct and indirect effects of successful invasions (Mooney and Drake 1986, Drake et al. 1989, Hengeveld 1989, Kareiva 1996). Despite progress in some of these areas, predicting the outcome of particular invasions remains a daunting task (Brown 1989, Ehrlich 1989, Pimm 1991, Lodge 1993). In an attempt to tackle this important challenge, ecologists have recently begun to scrutinize more closely the

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proximate causes of the success of invading species—a change in focus paralleling more reductionist approaches in community ecology (Schoener 1986). For example, recent studies have employed manipulative field experiments to test hypotheses concerning the factors controlling invasion success (Bergelson et al. 1993, D'Antonio 1993) and the competitive mechanisms responsible for invader superiority (Petren et al. 1993, Petren and Case 1996, Thebaud et al. 1996, Juliano 1998). Such manipulative experiments have great potential to improve the predictive power of invasion biology (Simberloff 1985, Simberloff 1991, Lodge 1993, Kareiva 1996).

It is perhaps less widely appreciated that invasions also offer unique opportunities for assessing the role of competition and other biotic interactions in the structure of communities (Diamond and Case 1986). For example, invasions allow the potential magnitude and form of interspecific competition to be gauged and characterized before species are lost through competitive exclusion or before the importance of competition is reduced over evolutionary time through niche partitioning and character displacement (Petren and Case 1996). Studies of invasions may thus serve to clarify the mechanistic bases of competitive asymmetries.

Although the importance of interspecific competition relative to other kinds of biotic interactions is debated (Connell 1983, Schoener 1983, Gurevitch et al. 1992), its central role in the structure of ant communities is widely recognized (reviewed in Hölldobler and Wilson [1990]). Because ant colonies are long-lived and often relatively immune from predators, ants commonly saturate the environment, reducing food or nest sites to levels at which competition occurs (Hölldobler and Wilson 1990). Both interference and exploitative competition occur among ants, although the former is more frequently documented (Hölldobler and Wilson 1990). Competitive asymmetries are common among species of ants and often give rise to linear dominance hierarchies (Vepsäläinen and Pisarski 1982, Fellers 1987, Savolainen and Vepsäläinen 1988, Morrison 1996). A species's position in a competitive hierarchy depends both on worker-level and colony-level attributes. For example, the outcome of an interference interaction between two workers often depends on disparities in worker size and agility (Fellers 1987) or whether repellent chemical defensive compounds are used (Adams and Traniello 1981), whereas the outcome of an interference interaction between two colonies often depends on numerical advantages stemming from asymmetries in recruitment ability or colony size (Hölldobler and Lumsden 1980, Adams 1990). Similarly, a colony's proficiency at exploitative competition hinges both on the ability of individual scouts to locate food and on the ability of groups of recruits to retrieve it subsequent to discovery (Johnson et al. 1987).

Ant species within a community are often subject to a trade-off between exploitative and interference ability

that permits species with different foraging strategies to coexist. For example, Wilson (1971) described three common foraging strategies: "opportunists" typically arrive first at baits but are timid and withdraw in the face of interspecific competition; "extirpators" often take longer to locate baits but recruit in large numbers and aggressively displace other species; lastly, "insinuators" depend on their small size and inconspicuous behavior to collect food while in the presence of other ants. In a similar vein, Fellers (1987) found a negative correlation between discovery time and dominance for eight species of sympatric ants. In her study, subordinate species used their ability to locate food quickly to acquire resources before the arrival of more aggressive species (Fellers 1987). Other examples of this trade-off in ants are described in Levins et al. (1973), Lynch et al. (1980), Perfecto (1995), and Morrison (1996); Nagamitsu and Inoue (1997) describe an example for social Meliponine bees. Although the best examples of exploitation–interference trade-offs may come from the social insects, this trade-off is probably more general. For example, Case and Gilpin (1974) argue that because the ability of a species to excel at interference competition often requires specialized physiological, morphological, and behavioral characteristics that reduce its ability to compete via exploitation, a species will often trade off interference ability with exploitative ability (and vice versa).

The present study applies the concept of exploitation–interference trade-offs to Argentine ant (*Linepithema humile*) invasions in an effort to identify the underlying causes of the ecological success of this widespread invader. Native to South America, Argentine ants are now common and widespread in temperate and subtropical latitudes throughout the world (Newell and Barber 1913, Crowell 1968, Erickson 1971, Bond and Slingsby 1984, Ward 1987, Majer 1994, Cammell et al. 1996). This species was first recorded in California around 1907 (Newell and Barber 1913) and is now widespread, firmly established, and spreading in that state (Tremper 1976, Ward 1987, Holway 1995, Human and Gordon 1996, Suarez et al. 1998). The Argentine ant competitively displaces indigenous ants throughout its introduced range (Hölldobler and Wilson 1990, Major 1994), but surprisingly little is known about these interactions. Anecdotal accounts suggest that a large and aggressive worker force may be key to the Argentine ant's competitive ability (Newell and Barber 1913, Michener 1942, Lieberburg et al. 1975, DeCock 1990). Both Tremper (1976) and Human and Gordon (1996) provide more detailed descriptions of different aspects of the competitive ability of the Argentine ant, but specific tests of mechanistic hypotheses for the competitive asymmetry between Argentine ants and native ants have not been conducted. This shortage of information reflects the inadequate state of knowledge concerning the causes of invasion success in general (D'Antonio 1993, Petren et al. 1993), which is

somewhat surprising given the many serious problems caused by invasive species (Vitousek et al. 1996).

Building off of previous work on Argentine ant invasions (Human and Gordon 1996, Tremper 1976), this study is the first attempt to test an explicit hypothesis regarding the competitive asymmetry between Argentine ants and native ants. I predict that, compared to native ants, Argentine ants are removed from the exploitation–interference trade-off and are proficient at both forms of competition as a consequence. To address this hypothesis, I conducted a variety of manipulative field experiments aimed at documenting the relative exploitative and interference abilities of the Argentine ant and seven species of native ants in order to answer the following questions: (1) What mechanisms determine the competitive ability of the Argentine ant? (2) Are native ants governed by a trade-off between exploitative ability and interference ability? and (3) If so, are Argentine ants subject to this trade-off in their introduced range? This study provides a wealth of new information on the competitive mechanisms employed by Argentine ants against native ants, tests a specific hypothesis concerning the basis of this competitive asymmetry in terms of an understudied competitive trade-off, and, in doing so, presents a novel and potentially general approach towards understanding the success of invasive species.

METHODS

Study area and system

This study was conducted in 1994–1996 in riparian woodland along Putah and Cache Creeks in the lower Sacramento River Valley of northern California (38°30' N, 122°00' W). This part of California experiences a Mediterranean climate with a cool wet season (November–April) and a hot dry season (May–October). In this region, Argentine ants thrive in riparian, urban, and some agricultural habitats (e.g., citrus orchards) but are absent from drier areas (e.g., chaparral and oak woodland) (Ward 1987). Argentine ants occur patchily in riparian woodlands in the lower Sacramento River Valley (Ward 1987) but are well established and actively spreading in this habitat (Holway 1995), displacing epigeic native ants as they advance (Holway, 1998a, b, b).

I compared the competitive ability of the Argentine ant relative to those of seven native ants: *Aphaenogaster occidentalis*, *Dorymyrmex insanus*, *Formica aerata*, *F. moki*, *Liometopum occidentale*, *Monomorium ergatogyna*, and *Tapinoma sessile*. These natives are among the most common ants in the study areas (Ward 1987, Holway, 1998a), are all actively displaced by Argentine ants (Holway, 1998a) and, like that species, are omnivores, foraging mostly on dead arthropods, vertebrate carrion, and homopteran exudates (Creighton 1950, P. S. Ward, *personal communication*, D. A. Holway, *personal observation*). The native ants

in this study defend valuable resources but do not appear to defend absolute territories (*sensu* Hölldobler and Lumsden 1980), at least against other species.

General baiting methods

This study used baits to assay competitive ability. Baits are a convenient and commonly used method to study exploitative and interference competition in ants (Hölldobler and Wilson 1990). Unless otherwise noted, each bait consisted of ~2.5-g canned tuna in oil together with ~2.5-g apple jelly representing sources of proteins, lipids, and carbohydrates (Lynch et al. 1980, Fellers 1987). “Recruitment” was defined as 10 workers of one species present at a bait simultaneously. For most species, the presence of 10 workers was indicative of the early stages of recruitment; for the weakly recruiting *Formica* spp., however, 5 workers present simultaneously at a bait was considered sufficient. Except for a few cases (noted below), all experiments were conducted over intervals of temperature (18°–25°C) and season (May to mid-July) for which both Argentine ants and native ants were most active.

Short-term removal experiment

Removal experiments of ants at baits may be used to examine the nature of competitive asymmetries (Lynch et al. 1980, Morrison 1996). The short-term removal experiments in this study took place at the leading edges of invasion fronts—the only locations in the study areas where native ants and Argentine ants co-occurred. At each of five independent invasion fronts I conducted a removal experiment over the course of several days to measure the competitive ability of Argentine ants and native ants in the presence and absence of one another. The first day of each experiment served as a control; I placed 16 baits (in 5-cm-diameter plastic petri dishes) on the ground in areas where native ants and Argentine ants foraged within 10 cm of one another. At each invasion front, I placed baits at least 4 m apart in an irregular transect. I recorded the identity and number of ants at each bait at 30-min intervals for 3 h, and then removed baits and marked their exact location with colored toothpicks. On the second day, I placed baits at the same locations, removed (by aspiration) either native ants or Argentine ants from within 0.25 m of each bait, and recorded the time it took the remaining group to locate and to recruit to the bait. On the third day, I performed the complement removal at each bait. On each day of each removal experiment, I removed native ants from half of the baits and Argentine ants from half of the baits. At each site, I conducted removals at the same time (0700–1000) and on consecutive days during mid-May to mid-June 1994.

The results of the short-term removal experiment were analyzed in three different ways. First, for the control transects, I used a *G* test to compare the proportion of baits recruited to by Argentine ants after 3

h with the number recruited to by native ants after 3 h; baits were pooled across the five fronts in this analysis. Second, for Argentine ants and native ants separately, I computed the difference between the number of baits recruited to in the control (putative competitor present) and the number of baits recruited in the removal (putative competitor absent). I tested if these mean differences were greater than zero using a one-sample *t* test. Lastly, for each front, I computed the mean times for Argentine ants to discover and to recruit to removal baits in the absence of native ants and for native ants to discover and to recruit to removal baits in the absence of Argentine ants. Using the means from each of the five fronts as data points, I compared Argentine ant and native ant discovery and recruitment times using a paired *t* test. These and all other analyses in this study were conducted in SYSTAT for Windows, Version 5 (Wilkinson et al. 1992) except where noted.

Fixed-distance baiting experiment

The short-term removal experiment may have provided biased estimates of competitive ability because it did not control for colony density and because native ants at invasion fronts were probably succumbing to Argentine ants. To remedy this problem, I estimated the intrinsic ability of each species to locate and to recruit to baits by measuring how long it took 30 colonies of each species (including *Linepithema humile*) to locate and to recruit to baits placed on index cards 1 m away (in a randomly determined compass direction) from nest entrances. For species with multiple nest entrances, I placed baits 1 m away from one of several nest entrances. All native ant colonies were located >100 m from Argentine ant invasion fronts. During the course of each experiment, all heterospecifics present within 0.25 m of a bait were removed by aspiration. After recruitment, I determined whether recruiting ants were from the focal colony; the few cases where another conspecific colony had recruited to the bait were excluded from the analysis. For each species, I sampled evenly across a 4-wk interval (mid-June to mid-July 1994). The discovery times and recruitment times of the eight species of ants were compared using one-way analysis of variance (ANOVA). All data were log-transformed prior to analysis. Following log-transformation, variances within each ANOVA did not differ from one another (Cochran's test for homogeneity of variances; $P > 0.05$). Subsequent to ANOVA, Dunnett's tests were used to compare the discovery times and recruitment times of the Argentine ant (used as a "control" in the Dunnett's tests) with each of the seven native ants.

Short-term introduction experiment

This experiment examined the mechanisms by which Argentine ants displaced native ants from baits. Because Argentine ants only co-occur with native ants along the edges of invasion fronts, replicated experi-

ments on interference competition are difficult to perform. To circumvent this problem, I transported laboratory colonies of Argentine ants into the field and staged interactions between laboratory colonies and colonies of native ants in a manner similar to Roubik (1978), Schaffer et al. (1983), and Human and Gordon (1996). Each laboratory colony contained 10–20 queens and 500–1400 workers collected from colonies along Putah Creek in May 1995. Each laboratory colony occupied a plastic container (30 cm long \times 16 cm wide \times 10 cm high) equipped with three test tubes half full of water and plugged with cotton to serve as nest chambers. Each container had a small exit hole at one end that remained plugged until colonies were used in the field. I fed colonies fresh insects, honey water, and a standard laboratory diet (Keller et al. 1989). Because Argentine ant workers are sterile, these experiments involved little risk of accidental introduction. I immediately stopped experiments on the rare occasions when queens or workers carrying brood were observed in the exit tube of the nest container.

Interactions between Argentine ants and native ants were staged as follows. I placed a bait on an index card within 20–30 cm of the nest entrance of each native ant colony. I let the native ant colony recruit to the bait until at least 30 workers were present (20 workers for the poorly recruiting *Formica* spp.) and recorded the number of native ants once recruitment stabilized. I then placed an Argentine ant laboratory colony 20–30 cm away from the bait, removed the exit hole plug, and replaced it with a 10-cm plastic tube. The tube allowed Argentine ant workers to leave their container and explore the vicinity of the bait. I let Argentine ants interact with native ants for 15–20 min, depending on the resistance offered by the native ant colony. At the end of 15–20 min, I counted the remaining native ants at the bait, aspirated all of the Argentine ant workers, and returned them to their nest container. Once all Argentine ants were removed, I waited 30 min and counted how many native ants recruited back to the bait.

I matched each of the 15 laboratory colonies with each of the seven native ants in this study no more than once. Thus, I conducted 15 replicate experiments for each species of native ant (except for the *Formica* spp., for which I conducted 12 replicates). For each species, I conducted experiments evenly spread throughout the duration of the experimental period (late May–early July 1995). All native ant colonies were used only once and were at least 100 m from invasion fronts. To analyze the trends in native-ant worker abundance before, during, and after Argentine ant introduction, I used repeated-measures multivariate analysis of variance (MANOVA) and single degree-of-freedom polynomial (linear and quadratic) contrasts as recommended by Gurevitch and Chester (1986). I ran a separate MANOVA for each species of native ant. The linear contrasts tested the null hypothesis that the number of native ants before Argentine ant introduction was not different

from the number of native ants present 30 min after Argentine ants were removed. The quadratic contrasts were more relevant; these contrasts tested the null hypothesis that the average number of native ants before and after Argentine ant removal was not different from the number of native ants in the presence of Argentine ants. I also used simple linear regressions to test if the ability of Argentine ants to displace native ants depended on the number of Argentine ant workers and queens in each laboratory colony. The dependent variable in this latter analysis was the percentage reduction in native ants (averaged across species) after introduction of each of the 15 laboratory colonies; arcsine transformations were used here because the dependent variables were proportions.

For each short-term introduction experiment, I also collected data on one-on-one interactions between Argentine ant workers and native ant workers. During each experiment I recorded no more than five one-on-one behavioral interactions, each separated by at least 3 min. For each interaction I recorded the initiator, the mechanisms employed by both species (i.e., physical aggression or chemical defensive compounds), the outcome (i.e., win or lose), the number of each species present, and the temperature. For data analysis these observations were pooled across replicates for each species of native ant. I analyzed the data on one-on-one interactions in several ways. First, I used pairwise G tests to determine if the proportion of one-on-one interactions won by Argentine ant workers differed from the proportion of one-on-one interactions won by workers of each species of native ant. Second, I used simple linear regressions to test if the proportion of one-on-one interactions won by native ants depended on native ant body size. Body mass was estimated using mean dry mass of a sample of 10 workers of each species (20 for *M. ergatogyna*) oven-dried at 60°C for 48 h (Tschinkel 1993). Lastly, I used logistic regression to test if the outcome of one-on-one interactions (native ant worker won or lost) depended on temperature, initiator, number of native ants present, and number of Argentine ants present. The logistic regressions were performed using LOGIT 2.0 (SYSTAT 1990).

Defensive-compound repellency experiment

Although Argentine ants employ chemical defensive compounds when fighting (Brown 1973, Lieberburg et al. 1975, Tremper 1976), no information exists on whether these compounds are more or less repellent than those produced by other ants. Using an approach similar to that used by Adams and Traniello (1981) and Anderson et al. (1991), I compared the repellency of the Argentine ant's defensive compounds with those produced by native ants. One colony fragment (i.e., workers and brood) of each of the eight species was collected near Davis, California, in early June 1996, transported to Salt Lake City, Utah, housed in the laboratory, and fed fresh insects, apple jelly, and a stan-

dard laboratory diet (Bhatkar and Whitcomb 1970) ad libitum. Defensive compounds of each species were isolated as follows. For the four species in the subfamily Dolichoderinae (*D. insanus*, *T. sessile*, *L. occidentale*, and *L. humile*), which store defensive compounds in pygidial glands in the gaster (Hölldobler and Wilson 1990), I dissected out pygidial glands from freshly freeze-killed workers and crushed each gland in 0.2 mL of a 95%-ethanol solution. For the four species in the subfamilies Formicinae (*F. aerata* and *F. moki*) and Myrmicinae (*A. occidentalis* and *M. ergatogyna*), which store defensive compounds in poison glands in the gaster (Hölldobler and Wilson 1990), dissection of the glands proved difficult. For the Formicines I collected defensive compounds of freshly freeze-killed workers by milking the posterior tip of the gaster against the lip of a glass vial and rinsing the gaster tip and vial lip with 0.2 mL of 95% ethanol. For the Myrmicines, I removed the gasters of freshly freeze-killed workers and crushed each gaster in 0.2 mL of 95% ethanol. Following preparation, all treatment solutions were stored at -25°C and used within a few hours of preparation.

I estimated the repellency of each compound using the recruitment behavior of the pavement ant (*Tetramorium caespitum*) in the field as a bioassay. I presented each *T. caespitum* colony with a pair of baits (each bait ~1-g tuna) placed at opposite ends of a microscope slide, and then I waited until at least 20 workers recruited. Using a 1.0-mL syringe, I surrounded the treatment bait with 0.2 mL of a 95% ethanolic solution containing one worker equivalent of the defensive compounds of one of the eight ant species and surrounded the control bait with 0.2 mL of 95% ethanol. I waited until at least 20 workers had returned (usually within 15 min) and counted the number of workers at each bait. I tested each *T. caespitum* colony ($n = 13$) with each of the eight defensive compounds on one occasion and on separate days during the last two weeks of June 1996. All experiments were conducted over narrow intervals of time (1800–2000) and temperature (22°–26°C). For each experiment, I calculated the recruitment differential (i.e., number of workers recruiting to the treatment bait – number of workers recruiting to the control bait); these differentials are a measure of the absolute repellency of worker-equivalent extracts. Using paired t tests, I compared the recruitment differentials from the Argentine ant treatment to the recruitment differentials from each of the seven native-ant treatments, correcting for seven comparisons using the Bonferroni method suggested by Rice (1989). The pavement ant was used in this bioassay because it exhibits strong recruitment behavior and shares no evolutionary history with any of the eight species of ants used in this study (thus reducing the chance that it has developed a tolerance towards any of the defensive compounds). Because *T. caespitum* might nonetheless exhibit idiosyncratic aversions to certain defensive

compounds, I also tested the repellencies of the eight compounds using colony fragments of *L. humile*, *L. occidentale*, and *M. ergatogyna* in the laboratory. Methods used were similar to those above except that each colony fragment was provided with each of seven defensive compounds (no conspecific comparisons) on one occasion only.

RESULTS

Short-term removal experiment

Argentine ants recruited to >3 times more baits in the control transect than did native ants (46/80 vs. 14/80; *G* test, *df* = 1, *P* = 0.002). Both Argentine ants and native ants recruited to more baits in the absence of one another than they did when together, although this trend was only marginally significant for Argentine ants. The mean of the difference between the number of baits recruited to in the treatment (putative competitor absent) vs. the control (putative competitor present) was greater than zero for both native ants (4.4 ± 0.7 baits [mean \pm 1 SE]; one-sample *t* test: $t_4 = -6.50$, *P* = 0.003) and Argentine ants (1.8 ± 0.7 baits; one-sample *t* test: $t_4 = -2.71$, *P* = 0.053). In addition, with native ants removed the Argentine ants discovered and recruited to baits in less than half the time it took native ants with Argentine ants removed (60.6 ± 13.6 vs. 125.1 ± 18.6 min; paired *t* test: $t_4 = -4.79$, *P* = 0.009).

Fixed-distance baiting experiment

Discovery times differed among the eight ant species (one-way ANOVA: $F_{7,207} = 23.30$, *P* < 0.001). Argentine ants discovered baits in an average of 4 min—more quickly than every species of native ant (Fig. 1A). Recruitment times (i.e., subsequent to discovery) also differed among the eight species (one-way ANOVA: $F_{7,168} = 11.66$, *P* < 0.001). Argentine ants recruited to baits in an average of 10 min—also more quickly than every species of native ant (Fig. 1B). Discovery and recruitment times were independent of temperature (linear regressions: *P* > 0.05) for all species except for *Dorymyrmex insanus*, which discovered and recruited to baits more quickly with increasing temperature (linear regressions: *P* < 0.05). The qualitative patterns of significance shown in Fig. 1, however, were unaffected when *D. insanus* was excluded from the analysis.

Short-term introduction experiment

One-on-one interactions.—At baits, the Argentine ants typically fought with native ants, but differed in their ability to overcome different species. Against *D. insanus* workers, for example, Argentine ants usually won, but, against *Monomorium ergatogyna* workers, Argentine ants always lost (Fig. 2A). Outcomes between Argentine ant workers and workers of the five remaining species were intermediate between these two extremes (Fig. 2A). The proportion of one-on-one in-

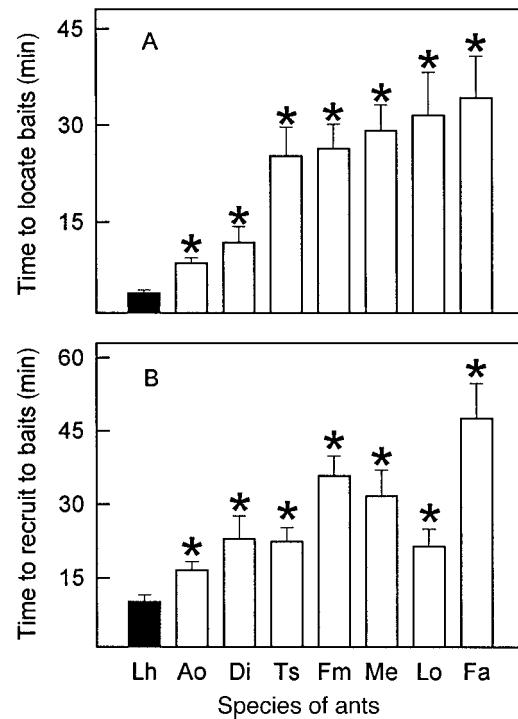


FIG. 1. Results of the fixed-distance ant-baiting experiment. Histogram bars show the length of time (mean \pm 1 SE) to (A) locate and (B) recruit to baits placed 1 m away (in a random compass direction) from nest entrances. Asterisks indicate statistically significant pairwise comparisons (Argentine ants vs. each species of native ant) using Dunnett's test. Lh = *Linepithema humile* (Argentine ant), Ao = *Aphaenogaster occidentalis*, Di = *Dorymyrmex insanus*, Ts = *Tapinoma sessile*, Fm = *Formica moki*, Me = *Monomorium ergatogyna*, Lo = *Liometopum occidentale*, and Fa = *Formica aerata*. Sample sizes for each species, in (A) and (B), respectively, are the following: Lh (30, 30), Ao (30, 30), Di (28, 26), Ts (27, 25), Fm (25, 14), Me (26, 18), Lo (21, 18), and Fa (28, 15).

teractions in which Argentine ants overcame native ants was independent of the average worker mass of the species of the opponent (linear regression: $F_{1,5} = 0.059$, *P* = 0.817, $r^2 = 0.012$).

Argentine ant workers used both physical aggression and chemical defensive compounds against native ants but in different combinations depending on the species of native ant involved (Fig. 2B; *G* = 14.28, *P* = 0.027). Physical aggression most commonly involved an Argentine ant lunging at and seizing an opponent's antenna or limb. Argentine ant workers occasionally climbed on top of native ants (especially larger species such as *Formica* or *Liometopum*) to grab antennae from above. Instances of physical aggression usually resulted either in the native-ant worker retreating or in the conflict escalating into a bout of wrestling, in which case Argentine ants were commonly killed. The employment of chemical defensive compounds by Argentine ants followed a stereotyped set of behaviors: a worker would quickly rotate the long axis of its body

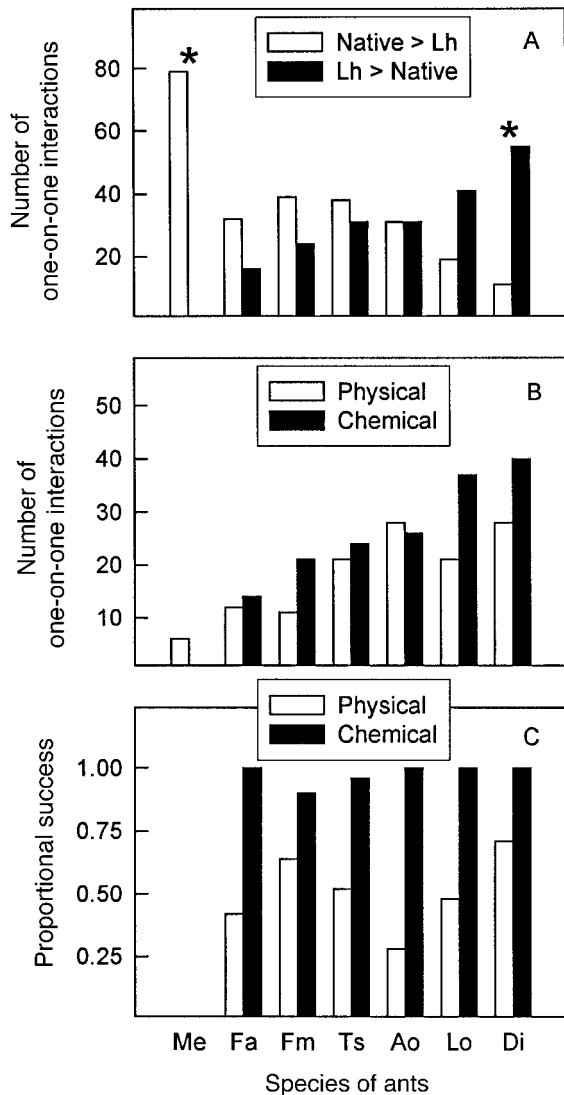


FIG. 2. Results of the short-term introduction experiment: one-on-one interactions. (A) The outcomes of one-on-one interactions between Argentine ants (*Linepithema humile*, "Lh") and seven species of native ants. Asterisks indicate combinations of wins and losses significantly different from equality ($P < 0.05$ from G tests). P values were Bonferroni adjusted (for seven comparisons) to maintain an experiment-wide error rate of $\alpha = 0.05$ (Rice 1989). (B) The number of times Argentine ant workers used physical aggression and chemical defensive compounds against workers of each of the seven species of native ants. (C) Proportions of one-on-one interactions in which Argentine ants, using either physical aggression or chemical defensive compounds, overcame each species of native ant. Proportional success is relative to the number of times each interference mechanism was used against each species. Species abbreviations are as in Fig. 1.

between 90° and 180° , lift its gaster $\sim 30^\circ$ above horizontal (pointing the posterior tip of its gaster toward the adversary), and exude chemical defensive compounds from the gaster. If the native-ant worker made contact with these compounds, it would retreat quickly,

wiping its mandibles and antennae vigorously on the ground.

The outcome of one-on-one interactions depended strongly on whether Argentine ant workers used chemical defensive compounds or physical aggression. Fig. 2C illustrates the relative success at overcoming different species of native ants for Argentine ant workers that employed either physical aggression or chemical defensive compounds. The median proportional success for chemical defensive compounds was greater than the median proportional success for physical aggression (Wilcoxon paired-sample test; $P < 0.05$). Temperature, initiator, number of native ants present, and number of Argentine ants present did not affect the outcome of one-on-one interactions (logistic regressions for each species of native ant; all parameter coefficients not different from zero). *M. ergatogyna* was excluded from this latter set of analyses since workers of this species won 100% (79/79) of one-on-one interactions with Argentine ant workers.

Colony-level results.—Argentine ant colonies reduced the number of workers present at baits for six of the seven native ant species (Fig. 3). With the exception of *M. ergatogyna*, all native ants recruited to baits in the absence of Argentine ants, largely abandoned baits in their presence, and then recruited back to baits subsequent to removal of Argentine ants. The results of the single degree of freedom quadratic contrasts (Table 1:B) confirm the patterns shown in Fig. 3. For all species except *M. ergatogyna*, the number of native-ant workers present during the introduction was different from the number present before and after the introduction (i.e., the quadratic contrast was significant). The linear contrasts were mostly not significant (Table 1:B), demonstrating that the number of native-ant workers present before the introduction was not different from the number present after the introduction. *Liometopum occidentale* was the only exception to this general pattern; workers of this species were slightly more common before the introduction than after the introduction (Fig. 3; Table 1). The average percentage reduction of native ants at baits was inversely related to the ability of native-ant workers to overcome Argentine ant workers in one-on-one contests (linear regression: $r^2 = 0.69$, $F_{1,5} = 11.28$, $P = 0.02$). For example, *M. ergatogyna* always deterred Argentine ants in one-on-one interactions (Fig. 2A); probably as a consequence, its colonies consistently resisted displacement (Fig. 3). Conversely, *D. insanus* lost a majority of its one-on-one interactions with Argentine ants (Fig. 2A) and mostly abandoned baits in their presence (Fig. 3).

The colony-level performance of the 15 Argentine ant laboratory colonies was independent of variation in colony size and queen number. The size of the worker population did not influence either the average number of workers leaving the nest container (linear regression: $r^2 = 0.02$, $F_{1,13} = 0.26$, $P = 0.623$) or the average

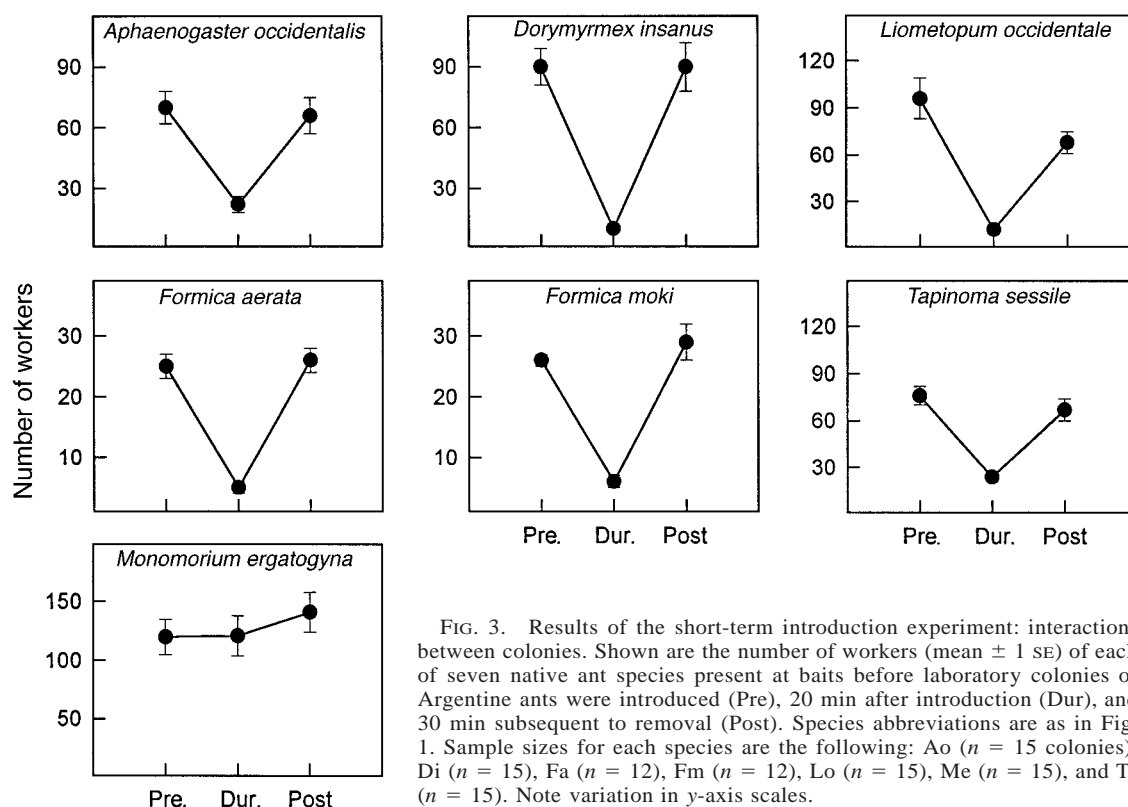


FIG. 3. Results of the short-term introduction experiment: interactions between colonies. Shown are the number of workers (mean \pm 1 SE) of each of seven native ant species present at baits before laboratory colonies of Argentine ants were introduced (Pre), 20 min after introduction (Dur), and 30 min subsequent to removal (Post). Species abbreviations are as in Fig. 1. Sample sizes for each species are the following: Ao ($n = 15$ colonies), Di ($n = 15$), Fa ($n = 12$), Fm ($n = 12$), Lo ($n = 15$), Me ($n = 15$), and Ts ($n = 15$). Note variation in y-axis scales.

percentage reduction of native ants (linear regression: $r^2 = 0.03$, $F_{1,13} = 0.41$, $P = 0.541$). Likewise, queen number did not influence the average number of workers leaving the nest container (linear regression: $r^2 = 0.02$, $F_{1,13} = 0.24$, $P = 0.638$) or the average percentage reduction of native ants (linear regression: $r^2 = 0.09$, $F_{1,13} = 1.23$, $P = 0.292$).

Defensive-compound repellency experiment

Not surprisingly, extracts of all eight chemical defensive compounds repelled pavement ant (*Tetramorium caespitum*) workers. The means of all eight recruitment differentials were negative (Fig. 4; Sign test: $P = 0.004$). Moreover, all extracts also repelled workers of *L. humile*, *L. occidentale*, and *M. ergatogyna*. For single colony fragments of each of these three species, more workers recruited to control baits than to treatment baits in seven out of seven tests (Sign tests: $P < 0.05$, Bonferroni adjusted for three comparisons). Although repellent, the Argentine ant's chemical defensive compounds were no more repellent to pavement ant workers than those of the seven native ant species (Fig. 4).

DISCUSSION

Because the native ants in this study do not defend absolute territories (at least against heterospecifics), the relative importance of exploitative vs. interference

competition probably depends largely on the size distribution of resources (Maurer 1984, Fellers 1987, Johnson et al. 1987). For example, small food items (e.g., small, dead insects) may be retrieved by individual workers without recruitment of nestmates; as a consequence, competition for such items is probably in large part exploitative. In contrast, retrieval of large (e.g., vertebrate carrion) or stationary (e.g., aggregations of Homoptera) items may require recruitment. To procure such a resource, a colony will often need to defend it against other ants or drive off those already present. For these reasons, the acquisition of large or stationary resources will commonly entail interference competition.

Exploitative competition

Although the existence of exploitative competition is difficult to demonstrate in ants, the findings of this study strongly imply that Argentine ants excel at exploitative competition, especially compared to the native ants they displace. The best evidence is that Argentine ants discovered and recruited to baits much more quickly than did native ants, both in areas where they occurred together and where they occurred separately. Rapid discovery and recruitment times are generally believed to be important correlates of exploitative ability in omnivorous ants (Wilson 1971, Levins et al. 1973, Feller 1987) but are also determinants of

TABLE 1. Analytical results from the short-term ant-colony-introduction experiments. Repeated-measures MANOVA was performed for each of the seven native-ant species to analyze the trends in native-ant worker abundance before, during, and after Argentine-ant introduction; single-degree-of-freedom polynomial contrasts were run to test null hypotheses. *P* values that are in bold are significant ($P < 0.05$) after correction for seven comparisons using the Bonferroni procedure (Rice 1989).

Species	A) MANOVA results				B) Polynomial contrasts									
	Wilks' Λ	<i>F</i>	df	<i>P</i>	Linear†					Quadratic‡				
					Source	ss	df	<i>F</i>	<i>P</i>	Source	ss	df	<i>F</i>	<i>P</i>
<i>Aphaenogaster occidentalis</i>	0.14	39.05	2,13	<0.001	Time	0.09	1	1.45	0.25	Time	18.15	1	83.97	<0.001
					Error	0.87	14			Error	3.03	14		
<i>Dorymyrmex insanus</i>	0.09	68.34	2,13	<0.001	Time	0.02	1	0.80	0.39	Time	54.95	1	147.18	<0.001
					Error	0.42	14			Error	5.23	14		
<i>Formica aerata</i>	0.07	62.79	2,10	<0.001	Time	0.01	1	0.20	0.66	Time	28.02	1	116.24	<0.001
					Error	0.38	11			Error	2.65	11		
<i>Formica moki</i>	0.10	44.25	2,10	<0.001	Time	0.001	1	0.02	0.90	Time	22.53	1	97.27	<0.001
					Error	0.68	11			Error	2.54	11		
<i>Liometopum occidentale</i>	0.05	117.53	2,13	<0.001	Time	0.78	1	13.96	0.002	Time	41.93	1	247.60	<0.001
					Error	0.79	14			Error	2.37	14		
<i>Monomorium ergatogyna</i>	0.70	2.83	2,13	0.10	Time	0.16	1	3.60	0.08	Time	0.03	1	0.91	0.36
					Error	0.63	14			Error	0.52	14		
<i>Tapinoma sessile</i>	0.10	57.96	2,13	<0.001	Time	0.21	1	6.34	0.03	Time	13.30	1	123.01	<0.001
					Error	0.46	14			Error	1.51	14		

† Tests the hypothesis that the first sampling time (i.e., before Argentine ant introduction) is different from the third sampling time (i.e., after Argentine ant removal).

‡ Tests the hypothesis that the second sampling time (i.e., Argentine ants present) is different than the average of the first and third sampling times.

interference ability (see below). Additional evidence for the strong exploitative ability of the Argentine ant comes from Human and Gordon (1996), who showed that this species foraged for longer periods throughout the day than did most native ants.

The ability of Argentine ants to discover and to recruit to food resources quickly must stem in large part from their high population densities. Evidence for high population densities comes from Holway (1998a, b). Because these studies were conducted at the same time and location as the present study, their results are directly relevant. Holway (1998a) found that Argentine

ants, on average, were 4–10 times more abundant (depending on the season) in unbaited pitfall traps in five invaded areas than were native ants in traps in five (otherwise similar) uninvaded areas. In addition to their higher numerical abundance, Argentine ants were recovered from between 92% and 100% (depending on the season) of all pitfall traps in invaded areas—significantly higher percentages than for the three most common native ants (*Tapinoma sessile*, *Formica* spp., and *Liometopum* spp.) in uninvaded areas (Holway 1998a). These findings demonstrate that where Argentine ants displace native ants, their colonies attain higher population levels and saturate the available habitat to a greater extent. Consistent with these findings, Argentine ants typically recruit to food in higher numbers than do native ants. Holway (1998b) estimated ant abundance at over 2000 baits from 20 sites over a four-year period and found that Argentine ants, on average, recruited to more baits and in higher numbers than did native ants. Working in grassland habitats with a mostly different set of native ants, Human and Gordon (1996) also found that Argentine ants recruited to baits in higher numbers than did a majority of native ant species. The Argentine ant's high population densities are probably largely a result of its unusual colony structure. At least in their introduced range, Argentine ants are unicolonial, forming extensive supercolonies in which numerous queens and abundant workers mix freely among spatially separated nests between which territorial boundaries are weak to non-existent (Newell and Barber 1913, Markin 1970, Hölldobler and Wilson 1990). Worker population sizes are large in unicolonial species

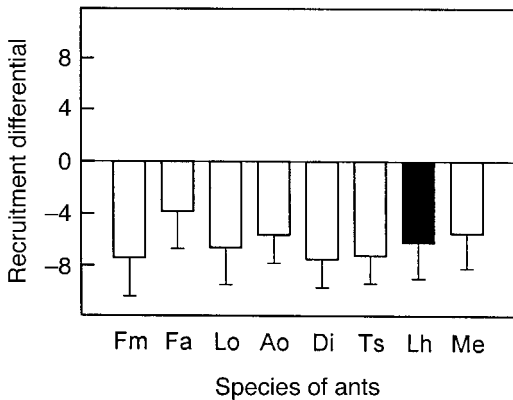


FIG. 4. Results of the chemical defensive-compound repellency experiment. Shown are recruitment differentials (mean - 1 SE) for the repellencies of extracts of the chemical defensive compounds of the eight species of ants in this study. Species abbreviations are as in Fig. 1 (filled bar = Argentine ant).

mainly due to reduced levels of intraspecific aggression (Hölldobler and Wilson 1990).

Interference competition

In one-on-one interactions, Argentine ants experienced mixed success in overcoming native-ant workers. This variation, however, was unrelated to the body size of native ants. Because ants commonly use chemical defensive compounds, their dominance hierarchies are not always strictly a function of worker body size (Fellers 1987). In this study, for example, *Monomorium ergatogyna*, the smallest species, won 100% of its interactions with Argentine ants (Fig. 2A) by using highly repellent chemical defensive compounds—an ability *M. ergatogyna* shares with its congeners (Adams and Traniello 1981, Anderson et al. 1991). In contrast, the two largest species, *Formica aerata* and *F. moki*, were also fairly successful in fighting with Argentine ants (Fig. 2A) but depended primarily on their large size and dexterity to repel Argentine ants.

Perhaps due to their small size (only *M. ergatogyna* workers are smaller), Argentine ants relied heavily on chemical defensive compounds, using them often (Fig. 2B) and with great success (Fig. 2C). The behavior of Argentine ant workers employing defensive compounds closely resembled that of the related *Forelius pruinosus* (formerly *Iridomyrmex pruinosus*) described by Hölldobler (1982). Although repellent, the Argentine ant's defensive compounds did not appear to differ in repellency from those of native ants (Fig. 4). Moreover, when *Tapinoma sessile* and *Dorymyrmex insanus* workers used their chemical defensive compounds against Argentine ant workers, they won 95% (38/40) and 100% (4/4) of these interactions, respectively. Together, these results suggest that the repellency of the Argentine ant's defensive compounds does not solely determine the strong interference ability of this species, as suggested for other ants (Adams and Traniello 1981, Hölldobler 1982, Anderson et al. 1991). An unexplored possibility, however, is that Argentine ants produce defensive compounds cheaply and, as a consequence, are able to use them more often than do other ants (Davidson 1997). Support for this hypothesis comes from the observation that Argentine ants often tend honeydew-excreting Homoptera (Newell and Barber 1913, Way 1963) that supply them with an abundant source of carbohydrates with which to produce defensive compounds. The main component of these compounds is iridomyrmecin, a molecule composed solely of carbon, oxygen, and hydrogen (Attygalle and Morgan 1984).

In contrast to individual workers, Argentine ant colonies excelled at controlling baits in the presence of native ants. In the short-term introduction experiments, for example, Argentine ant colonies consistently overcame colonies of six out of seven native ant species (Fig. 3). Although their methods differed from those used here, Human and Gordon (1996) reported quali-

tatively similar results for three different species of native ants. The strong interference ability of Argentine ant colonies is underscored by the finding that, in the present study, laboratory colonies were small relative to Argentine ant nests in the field (*personal observation*), yet were still able to drive off native ants despite strong initial asymmetries in worker abundance (Fig. 3). Furthermore, in the short-term removal experiment, Argentine ants recruited to more baits in the control transect than did native ants, and native ants were much less likely to recruit to baits in the presence of Argentine ants than in their absence.

From the results discussed above, a clear disparity exists between the worker-level and colony-level interference abilities of the Argentine ant. Individual Argentine ant workers often lost when fighting against native-ant workers, and the repellency and effectiveness of their chemical defensive compounds appeared similar to those used by native ants. At the level of the colony, however, Argentine ants were highly effective at interference competition, displacing a majority of native ant colonies from baits. This discrepancy is best explained by numerical advantages resulting from large colony size. Tremper (1976) arrived at a similar conclusion using laboratory confrontation experiments that involved differing ratios of Argentine ants and native ants confined in small containers. As discussed above, Argentine ants maintain much higher worker population sizes than do the native ants they displace. Such numerical advantages are of general importance in determining the outcome of interference interactions between ant colonies (Hölldobler and Lumsden 1980, Lynch et al. 1980, Fellers 1987, Adams 1990).

Exploitation-interference trade-off

The results of this study illustrate a plausible basis for the strong competitive asymmetry between Argentine ants and the native ants they displace. The native ants in this study exhibited a trade-off between exploitative and interference ability resembling that described by Fellers (1987). The time it took native ants to discover and to recruit to baits (times summed) was inversely correlated with their dominance in one-on-one interactions with Argentine ants (Fig. 5). Since interactions among native ants were not studied, the dominance ranking used here assumes that the ability to deter Argentine ant workers approximates how native ants interact among themselves—a realistic assumption given the frequency of linear dominance hierarchies in ants (Hölldobler and Wilson 1990). Due to their omnivory, the native ants in this study may have limited opportunities to partition food resources. As a consequence, these ants probably coexist in large part through differences in foraging strategies. As in Fellers (1987), for example, subordinate species in this study (e.g., *Dorymyrmex insanus*, *Aphaenogaster occidentalis*) probably rely on their ability to discover food quickly to procure resources before the arrival of

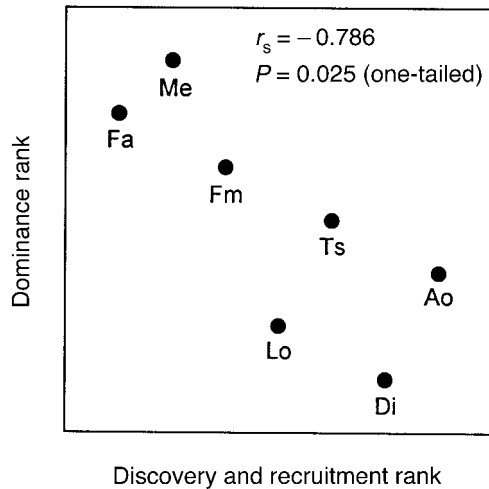


FIG. 5. Trade-off between exploitation ability and interference ability for the seven species of native ants examined in this study. The discovery and recruitment ranks come from the fixed-distance baiting experiment; species are ranked in decreasing order of their discovery and recruitment times (summed). Dominance ranks come from the short-term introduction experiment; species are ranked in order of increasing success at deterring Argentine ant workers in one-on-one interactions. Species abbreviations are as in Fig. 1.

dominant species (e.g., *Monomorium ergatogyna*, *Formica moki*), which take longer to locate food but are more effective at interference competition. In contrast to these native ants, Argentine ants appear removed from the exploitation–interference trade-off, excelling at both forms of competition relative to native ants. Their proficiency at both exploitative and interference competition implies that Argentine ants secure a majority of food resources whenever they meet native ants.

There are several reasons why Argentine ants, at least in their introduced range, might be relatively free from the exploitation–interference trade-off constraining native ants. First, as discussed above, unicoloniality probably underlies the Argentine ant's strong competitive ability because it allows supercolonies to achieve enormous population sizes. The importance of unicoloniality as a determinant of competitive ability is underscored by the fact that most highly invasive ants tend towards this form of colony structure (Passera 1994). Examples include *Solenopsis invicta* (polygyne form), *Wasmannia auropunctata*, *Pheidole megacephala*, and *Monomorium pharaonis*. Second, like many invading organisms in novel environments, Argentine ants may be released from the harmful effects of their coevolved natural enemies. For example, host-specific phorid fly parasitoids reduce the competitive ability of many species of dominant ants (Feener 1981, Orr et al. 1995, Feener and Brown 1997). Preliminary evidence suggests that phorids greatly restrict the foraging behavior of Argentine ants in their native range in South America as well (M. Orr, *personal communication*).

Because the phorids that beset Argentine ants are absent in California and because Argentine ants are not attacked by the phorids that parasitize native ants there, populations of Argentine ants in California may attain higher levels than they do in South America. Similar hypotheses have been advanced for other invasive species, such as *S. invicta* (Ross et al. 1996, Porter et al. 1997). Third, as mentioned above, the Argentine ant's proclivity for tending honeydew-excreting Homoptera could supply colonies with large quantities of carbohydrates that could be used to fuel workers at high tempo, subsidize the maintenance of absolute territories, and produce defensive compounds and trail pheromones cheaply and abundantly (Davidson 1997). These three factors—unicoloniality, release from natural enemies, and carbohydrate surplus—probably all interact with one another in the Argentine ant's introduced range, allowing the size, structure, and behavior of colonies to reach levels at which they become competitively invincible.

Why focus on competition for food?

The findings presented here do not directly demonstrate that competition for food underlies the displacement of native ants by Argentine ants. Competition for food was assumed because of its ubiquitous importance in ant communities (reviewed in Hölldobler and Wilson [1990]). Nonetheless, this study demonstrates that interspecific competition for food occurs and that it has molded the ecology and behavior of ants in this community. First, two results clearly demonstrate interference competition. In the short-term removal experiments, both Argentine ants and native ants recruited to more baits in the absence of their putative competitor than they did when together. Additional evidence of interference competition comes from the short-term introduction experiments, in which ants fought aggressively (and often to the death) over the acquisition of food resources. Second, like other, taxonomically similar guilds of temperate omnivorous ants (Lynch et al. 1980, Fellers 1987), the native ants in this study were subject to the exploitation–interference trade-off discussed above, suggesting that interspecific competition for food resources has influenced the foraging behavior of these species in such a way that numerous species are able to coexist at the same location.

Compared with competition for food, alternative hypotheses for the displacement of native ants by Argentine ants seem less plausible. Argentine ants and native ants are not known to share major predators, parasites, or pathogens, so apparent competition (Settle and Wilson 1990, Grosholz 1992) is probably of little relevance in this system. Argentine ants and native ants may compete to some extent for nest sites, but two lines of evidence suggest that such competition is of less significance than competition for food. First, Argentine ants have non-overlapping nesting require-

ments with some of the native ants they displace. For example, Argentine ants usually nest superficially in the soil or in rotting logs, whereas *Liometopum occidentale* nests in or at the base of trees, and *Dorymyrmex insanus* nests deep in the soil and in open, exposed locations. Second, to the extent that nest sites are limiting among native ants, Argentine ants would have to supplant natives from favored nest sites as they invaded. To do so would require large worker forces that could only be produced through efficient resource acquisition (i.e., a strong competitive ability). Argentine ants do usurp native ants from nests (Fluker and Beardsley 1970, DeCock 1990), but, at least at the sites studied here, do not typically occupy these sites once native ants are driven off or killed (*personal observation*).

Conclusions

The results of this study underscore the potential magnitude of interspecific competition in ant communities. Like other guilds of omnivorous ants, the native ants in this study may coexist, at least partly, by means of a species-specific trade-off in exploitative and interference abilities (Fig. 5). In contrast, Argentine ants, proficient at both forms of competition, appear to have broken this trade-off and, as a consequence, must secure a majority of food resources where they come into contact with native ants. Perhaps largely due to this asymmetry in competitive ability, Argentine ants are able to drive native ants locally extinct in these habitats (Ward 1987, Holway, 1998a, b). These results may pertain to ant communities in general. For example, Davidson (*in press*) argues that the ability of ants to break competitive trade-offs may explain the success of other invasive ants (Clark et al. 1982, Porter and Savignano 1990) as well as cases where intact ant communities are dominated by one or a few species (Savolainen et al. 1989, Davidson 1997).

The results of this study are also of interest with respect to biological invasions. Given the surprising lack of information concerning the proximate causes of invasion success, studies, such as this one, that address these causes in detail provide crucial information for the design of effective control strategies and might contribute to a more general understanding of the factors responsible for the success of invading species. Furthermore, the use of competitive trade-offs as a tool to study invasions represents a new and possibly general way to assess invasion success. For example, F. R. Adler (*unpublished manuscript*) explores this issue on theoretical grounds and concludes that invading species might commonly break competitive trade-offs in their introduced range, if, in their native range, specialized consumers regulate their populations and trade-off curves are higher.

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