Detrimental Effects of Highly Efficient Interference Competition: Invasive Argentine Ants Outcompete Native Ants at Toxic Baits

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ABSTRACT The Argentine ant (*Linepithema humile*) is an invasive species that disrupts the balance of natural ecosystems by displacing indigenous ant species throughout its introduced range. Previous studies that examined the mechanisms by which Argentine ants attain ecological dominance showed that superior interference and exploitation competition are key to the successful displacement of native ant species. The objective of this research was to test the hypothesis that effective interference competition by Argentine ants may also be detrimental to the survival of Argentine ant colonies where Argentine ants and native ants compete at toxic baits used to slow the spread of Argentine ants. To study this hypothesis, we examined the competitive interactions between Argentine ants and native odorous house ants, *Tapinoma sessile*, in the presence and absence of toxic baits. Results showed that Argentine ants aggressively outcompete *T. sessile* from toxic baits through efficient interference competition and monopolize bait resources. This has severe negative consequences for the survival of Argentine ants as colonies succumb to the toxic effects of the bait. In turn, *T. sessile* avoid areas occupied by Argentine ants, give up baits, and consequently suffer minimal mortality. Our results provide experimental evidence that highly efficient interference competition may have negative consequences for Argentine ants in areas where toxic baits are used and may provide a basis for designing innovative management programs for Argentine ants. Such programs would have the double benefit of selectively eliminating the invasive species while simultaneously protecting native ants from the toxic effects of baits.

KEY WORDS Argentine ant, competition, *Linepithema humile*, odorous house ant, *Tapinoma sessile*

Biotic invasions by a wide range of plant and animal taxa are altering the fundamental ecological properties of natural ecosystems worldwide and are considered a leading threat to biodiversity, agricultural productivity, human health, and economics (Vitousek et al. 1996, Mack et al. 2000, Pimentel et al. 2000). Exotic ants are among the most adverse biological invaders and can cause radical population- and ecosystem-level changes in the environments they invade (McGlynn 1999, Holway et al. 2002). The Argentine ant, *Linepithema humile* (Mayr), is a widespread, abundant, and ecologically damaging invasive ant species. Native to Argentina (Tsutsui et al. 2001), the Argentine ant has spread worldwide (Ward 1987, Holway 1995, Human and Gordon 1996, Giraud et al. 2002, Buczkowski et al. 2004) and is present on all continents except Antarctica and numerous oceanic islands. Within introduced populations, *L. humile* is unicolonial and forms extensive supercolonies that lack intraspecific aggression (Suarez et al. 1999, Tsutsui et al. 2000, Giraud et al. 2002). In invaded areas, the Argentine ant alters the native biota and causes profound changes in the abundance of native ant species and other arthropods (Cole et al. 1992, Holway 1998, 1999, Human and Gordon 1999, Touyama et al. 2003). The interactions between the Argentine ant and native ants have been examined in numerous laboratory and field studies (Human and Gordon 1996, Holway 1998, 1999, Thomas and Holway 2005, Zee and Holway 2006, Rowles and O'Dowd 2007) that indicate the competitive ability of Argentine ants stems from numerical dominance (Holway and Suarez 2004), aggressiveness (Human and Gordon 1999), superior interference and exploitation competition (Human and Gordon 1996, Holway 1999), and ability to quickly recruit to food (Holway 1999).

To limit the spread and impact of invasive ant species, chemical management practices are often used. Toxic baits are a popular method to control invasive ant species including the red imported fire ant, *Solenopsis invicta* (Lofgren 1986, Rust and Knight 1990), the Argentine ant, *Linepithema humile* (Krushelnycky and Reimer 1998), and the little fire ant, *Wasmannia auropunctata* (Causton et al. 2005). However, caution must be exercised when performing areawide treatments with toxic baits because the baits are nonselective and may also kill nontarget organisms, including native ants and possibly other arthropods, which

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the treatments are designed to protect. Ideally, the goal of a management program would be to eradicate the target species (i.e., the invader) without affecting the native fauna. However, because insecticide baits are attractive to a number of ant species, bait selectivity is virtually impossible to achieve directly. We hypothesized that when toxic baits are used to manage *L. humile* in natural ecosystems, bait selectivity may be achieved indirectly as a result of *L. humile*'s superior interference and exploitative competitive ability. Effective interference and exploitative competition normally allows Argentine ants to outcompete native ants and dominate food resources where they come into contact with native ants (Human and Gordon 1996, Holway 1999, Rowles and O'Dowd 2007). Here we propose that effective interference and exploitative competition may be highly detrimental to Argentine ants in areas where toxic baits are used for the selective eradication of Argentine ants. When Argentine ants dominate interactions at baits through effective interference and/or exploitative competition, they may become the primary target of toxic baits. This would have the double benefit of selectively eliminating the invasive species while simultaneously protecting native ants from the toxic effects of the baits. Previously, Alder and Silverman (2005) studied the effect of interspecific competition between *L. humile* and *Monomorium minimum* on bait performance in an urban setting where the bait was intended to target both species. The authors showed that interference competition at baits negatively affected bait performance by protecting the outcompeted species from the toxic effects of the bait.

To study the hypothesis that toxic baits may have a selective negative effect on Argentine ants in areas where Argentine ants actively compete against native ant species, we examined the competitive interactions between Argentine ants and native odorous house ants, *Tapinoma sessile* (Say), in the presence and absence of toxic bait. The odorous house ant is a native species widely distributed throughout North America and its range overlaps with that of the Argentine ant (Holway 1999, Human and Gordon 1999). Both *L. humile* and *T. sessile* are in the subfamily Dolichoderinae (Shattuck 1992) and are remarkably similar with respect to their ecological and behavioral attributes. Both species can form large polygynous and polydomous colonies with hundreds of thousands of workers (Markin 1970, Buczkowski and Bennett 2006). Both are associated with anthropogenically modified habitats (Passera 1994, Buczkowski and Bennett 2006) and are highly opportunistic, inhabiting a variety of nesting sites. Both species also share numerous similarities in their foraging ecology including mass recruitment foraging strategy along well defined trails, diel feeding periodicity, and similar dietary preferences with heavy reliance on homopteran excretions. Given the similarities that *L. humile* and *T. sessile* share, it is likely that the two species may aggressively compete for food resources where their geographic ranges overlap. Indeed, previous laboratory and field studies indicate that *L. humile* depress the foraging success of *T. sessile* and ultimately lead to their displacement (Human and Gordon 1996, 1999, Holway 1998, Buczkowski and Bennett 2007).

Materials and Methods

Collection and Maintenance of Laboratory Colonies. Argentine ants, *L. humile* (Mayr), were collected on the campus of Genentech in South San Francisco, CA. This colony represents Argentine ants that most likely belong to the large supercolony previously described from California (Suarez et al. 1999, Tsutsui et al. 2000). Odorous house ants, *T. sessile* (Say), were collected on the campus of Purdue University in West Lafayette, IN. This colony represents odorous house ants from a large polydomous supercolony (Buczkowski and Bennett 2006). Given the unicolonial nature of *L. humile* and *T. sessile*, we collected ants from numerous nests but raised them as a single colony. For each species, we established a single colony consisting of 5,000–10,000 workers, a few hundred queens, and numerous brood. Colonies of both species were maintained in soil-free, Fluon-coated trays containing moist plaster nests. Both species were provisioned with 20% sucrose solution and artificial diet (Bhatkar and Whitcomb 1970) ad libidum and hard-boiled egg once a week. All colonies were maintained and all assays performed at 24 ± 1°C, 50 ± 10% RH, and a 12:12 L:D cycle.

General Assay Procedures. For each species, colony fragments consisting of 500 workers, 5 queens, and ≈50 brood were placed into plastic, Fluon-coated nesting boxes (32 by 26 by 10 cm high), provided with a moist plaster nest (9 cm diameter), and allowed to acclimate for 2 d. Each colony was provided with 20% sucrose solution and artificial diet (Bhatkar and Whitcomb 1970) ad libidum during the acclimation period. The nesting boxes were connected to a central foraging arena (70 by 70 by 5 cm high) by 3.1 m of coiled plastic tubing (10 mm diameter). After the acclimation period, all food was removed from the nesting boxes, tubing leading to the foraging arena was unblocked, and food (20% sucrose solution) and/or a small dish containing 0.5 g of insecticide bait (Advance Granular Ant Bait, 0.011% Abamectin B1; Whitmire-Micro-Gen Research Laboratories, St. Louis, MO; labeled for the control of numerous ant species including *L. humile* and *T. sessile*) was placed in the center of the foraging arena. We performed six assays designed to estimate the individual and combined effects of competitive interactions and toxic baits on the survival of *T. sessile* and *L. humile.* There was a control assay for each species (no competing species and no bait present), toxic bait assay for each species (bait present, competing species absent), a competition assay in the absence of toxic baits, and a competition assay in the presence of toxic baits. Each treatment was replicated five times using new nesting boxes and tubing, and assays were run for 7 d. In each assay, for each species, we recorded (1) daily worker foraging activity in the central arena, (2) daily worker mortality, and (3) daily queen mortality. Worker foraging

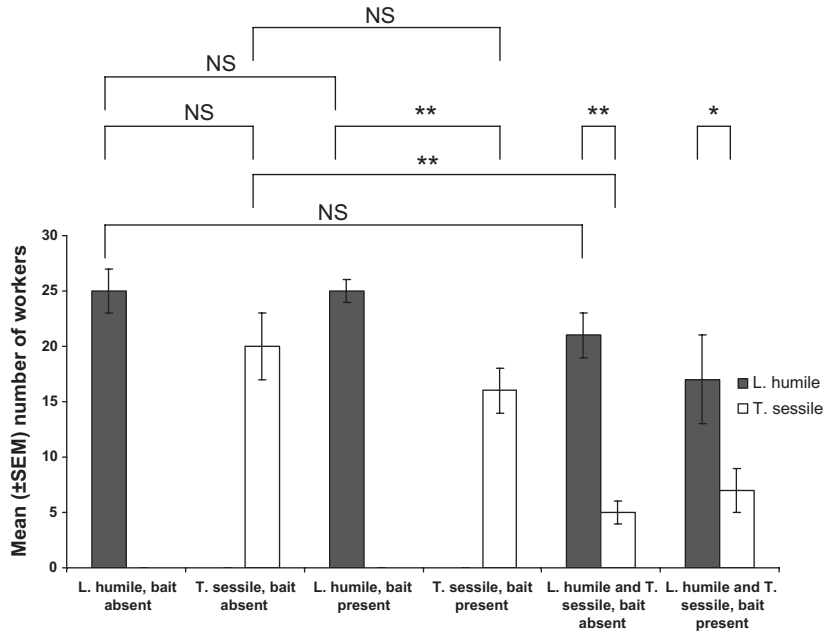

Fig. 1. Mean (±SEM) number of *L. humile* and *T. sessile* workers present in the central foraging arena over a period of 7 d. Means obtained by averaging over days (7) and then replicates ($n = 5$). NS, not significant. $^*P < 0.01$, $^{**}P < 0.001$. The terminals of each bracket indicate values being compared.

activity was recorded once daily for both species at ~1000 hours. Both species have similar foraging patterns, and both are active foraging 24 h a day. All data analyses were performed using SAS 8.1 statistical software (SAS Institute 2002) on means derived by averaging over days within a replicate. Differences in levels of foraging activity and worker and queen mortality were compared using the PROC NPAR1WAY procedure (Wilcoxon-Mann-Whitney test).

Results

The results clearly showed that efficient interference competition by *L. humile* at toxic baits has a negative effect on *T. sessile* foraging and consequently a positive effect on *T. sessile* survival. First, aggressive behaviors by *L. humile* observed in this study significantly reduced the foraging activity by *T. sessile* (Fig. 1). On average, 20 ± 3 *T. sessile* workers were observed in the central foraging arena when both the competitor and the bait were absent. In contrast, only 5 ± 1 *T. sessile* workers foraged when the competitor was present and the bait was absent ($Z = -2.51$, df = 1, $P = 0.01$), and 7 ± 2 workers foraged when both the competitor and the bait were present ($Z = -2.50$, df = 1, $P = 0.01$). When *L. humile* and *T. sessile* competed for food (in the absence of bait) *L. humile* were first to discover the food, rapidly recruited additional nestmates, and aggressively displaced *T. sessile* from the food. Over the course of seven day 21 ± 2 SE *L. humile* workers and 5 ± 1 SE *T. sessile* workers were found in the central arena ($Z = 2.52$, df = 1, $P = 0.01$). Similarly, when *L. humile* and *T. sessile* competed in the presence of food and bait, *L. humile* clearly dominated the central foraging arena, and 17 ± 4 SE *L. humile* workers and 7 ± 2 SE *T. sessile* workers were found in the central arena ($Z = 1.88$, df = 1, $P = 0.03$). In contrast to *T. sessile*, which were aggressively displaced from feeding on the food and/or bait and avoided visiting the foraging arena altogether, *L. humile* were unaffected by the presence of *T. sessile.* On average, 25 ± 2 *L. humile* workers foraged when *T. sessile* and the bait were absent, and 21 ± 2 *L. humile* foraged when *T. sessile* was present and the bait absent ($Z = -1.67$, df = 1, $P = 0.13$). The presence of the bait (in the absence of competition) did not have an effect on the intensity of foraging by either species (*L. humile:* $Z = -0.10$, df = 1, $P = 0.92$; *T. sessile:* $Z = 1.04$, df = 1, $P = 0.30$), indicating that the bait is no more attractive that sugar water. Furthermore, no difference in the intensity of foraging in the control experiments was detected (*L. humile:* 25 ± 2 workers present, *T. sessile:* 21 ± 3 workers present; $Z = 1.25$, df = 1, $P = 0.21$), indicating that both species use a similar number of foragers when their feeding is undisturbed by the presence of a competing species. This is not surprising given that we used colony fragments of equal size (500 workers), and both species have similar dietary preferences with heavy reliance on carbohydrate-rich liquids. However, a significant species-specific difference in the intensity of foraging at the toxic bait was detected (*L. humile:* 25 ± 1 workers present, *T. sessile:* 16 ± 2 workers present; $Z = 2.51$, df = 1, $P = 0.01$), indicating that the bait may be less attractive (or perhaps more repellent) to *T. sessile.*

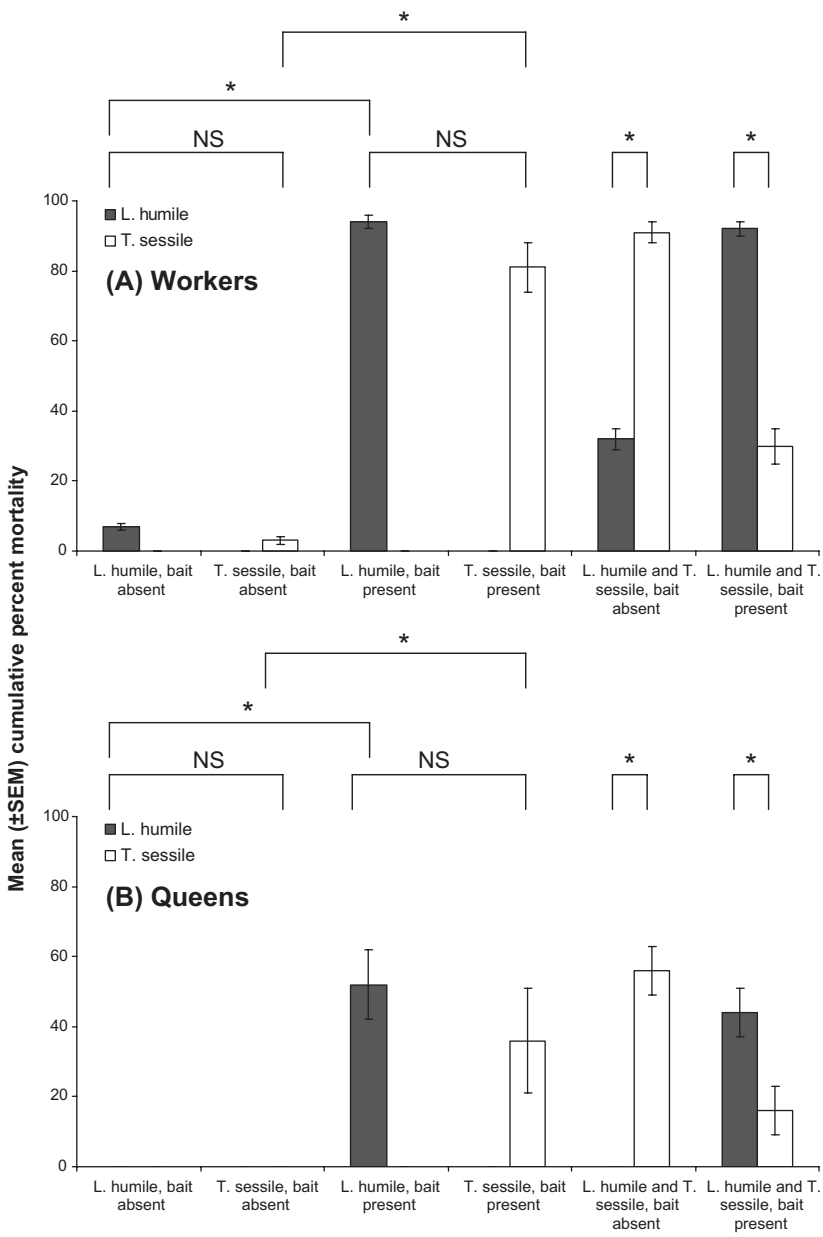

Fig. 2. Mean cumulative (day 7) percent mortality (±SEM) in *L. humile* and *T. sessile* (A) workers and (B) queens. Means obtained by averaging over replicates ($n = 5$). NS, not significant. *$P < 0.01$, **$P < 0.001$. The terminals of each bracket indicate values being compared.

The highly detrimental effects of efficient interference competition by *L. humile* are apparent in a comparison of worker and queen mortality when the two species interacted in the presence or absence of bait (Fig. 2). When *L. humile* and *T. sessile* interacted in the absence of bait, *L. humile* had a substantial negative effect on the survival of *T. sessile.* The average cumulative (day 7) mortality was 32 ± 3% for *L. humile* workers and 91 ± 3% for *T. sessile* workers ($Z = -2.51$, $df = 1$, $P = 0.01$). No *L. humile* and 56 ± 7% SE *T. sessile* queens died in interactions without toxic bait ($Z = -2.70$, $df = 1$, $P = 0.007$). This shows that, in the absence of bait, *L. humile* outcompetes *T. sessile* through highly aggressive fighting. *T. sessile* workers sustained the highest mortality during the first 3 d, when *L. humile* first explored the central arena and invaded *T. sessile* nesting space (Fig. 3B). The fighting subsided past day 3, and few ants fought by day 7. In contrast to aggressive interactions in the absence of bait, *T. sessile* suffered significantly lower mortality when the two species interacted in the presence of bait. The average cumulative mortality for *L. humile*

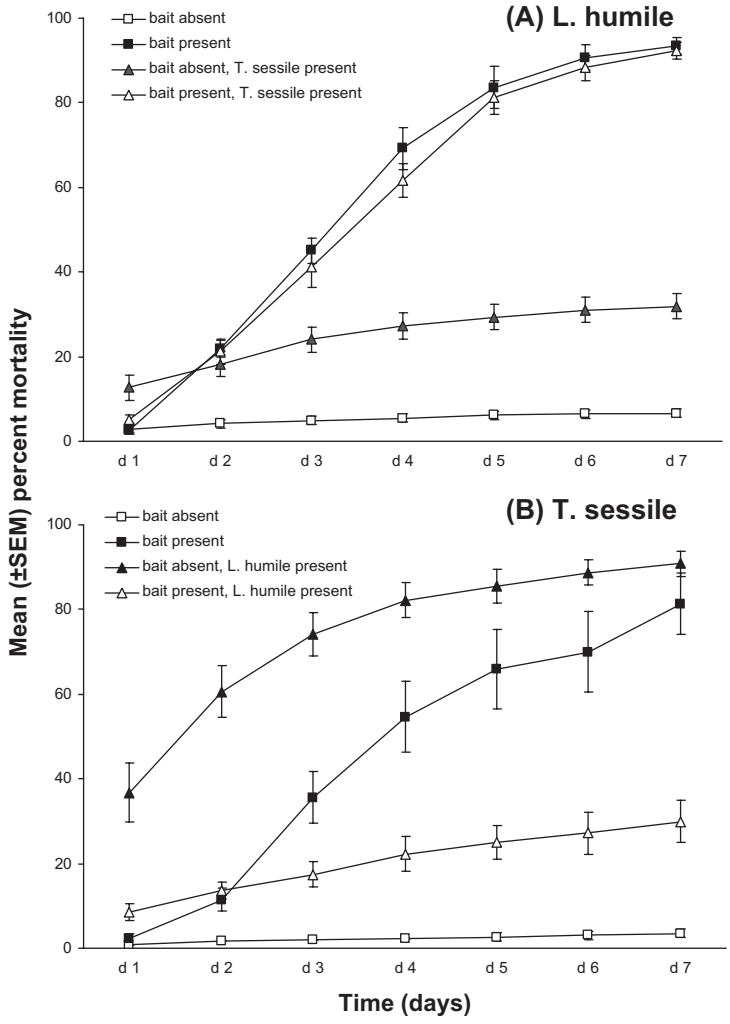

Fig. 3. Mean daily percent mortality (±SEM) in (A) *L. humile* workers exposed to *T. sessile* workers, toxic baits, or both and (B) *T. sessile* workers exposed to *L. humile* workers, toxic baits, or both.

workers was 92 ± 2 and 30 ± 5% for *T. sessile* workers ($Z = 2.50$, df = 1, $P = 0.01$). Queen mortality caused by bait was also similar, and 44 ± 7% *L. humile* and 16 ± 7% *T. sessile* queens died ($Z = 1.04$, df = 1, $P = 0.29$). Interestingly, approximately as many *T. sessile* workers died when the bait was absent as *L. humile* workers when the bait was present. Mortality in *L. humile* when the competitor and the bait were present reflects the combined mortality caused by fighting and bait consumption. Although we cannot partition the total mortality into these two components, our observations indicate that the majority of *L. humile* died as a result of bait consumption and not from fighting with *T. sessile.* A comparison of mortality in *T. sessile* caused by bait alone versus bait and competition showed that the presence of *L. humile* has a significant effect on the survival of *T. sessile.* On average, 81 ± 7% *T. sessile* workers died because of bait alone and 30 ± 5% *T. sessile* workers died when exposed to both *L. humile* and the bait ($Z = 2.51$, df = 1, $P = 0.01$). No significant difference in the efficacy of the bait against workers or queens was detected in either species. The average cumulative percent mortality was 94 ± 2% for *L. humile* workers and 81 ± 7% for *T. sessile* workers ($Z = 1.04$, df = 1, $P = 0.29$). This is despite the fact that fewer *T. sessile* workers foraged on the bait (Fig. 2). Furthermore, control mortality was similar for *L. humile* and *T. sessile* workers and queens (Fig. 2, A and B).

Discussion

The effects of Argentine ants on native ant species are well described, and studies indicate that Argentine ants reduce the foraging success of native ant species and ultimately lead to their extinction, or in rare cases, emigration or coexistence with Argentine ants (Cole et al. 1992, Holway 1998, 1999, Human and Gordon 1999, Touyama et al. 2003). Superior interference and exploitation competition and the ability to break the

competitive trade-off between interference and exploitation competition have been shown to be critically important for the invasiveness of Argentine ants (Human and Gordon 1996, Holway 1999). We showed that the very mechanism that allows Argentine ants to outcompete native ant species can also be highly detrimental to Argentine ants, when Argentine ants and native ants compete at toxic baits. This in turn has a positive effect on a native ant species, which are outcompeted from the baits and thus spared the toxic effects of bait active ingredients. Argentine ants reduced the foraging efficiency of odorous house ants and dominated all aspects of interactions with odorous house ants including access to the central foraging arena and control over food sources. Argentine ants aggressively displaced odorous house ants and killed many odorous house ants that visited the foraging arena. The remaining live odorous house ants retreated into the safety of their nest and avoided interactions with Argentine ants. This corroborates the results of a previous laboratory study that showed that Argentine ants recruit rapidly, numerically dominate food and nesting sites, and aggressively displace odorous house ants from food sources (Buczkowski and Bennett 2007). Previous field studies also showed that relative to Argentine ants, odorous house ants spend less time at baits, recruit fewer workers, give up baits without fights, and are eventually displaced from 90% of all baits (Human and Gordon 1996, Human and Gordon 1999). Holway (1998) used pitfall traps to compare ant species diversity and abundance in areas with and without Argentine ants. Odorous house ants were one of the most dominant species in areas free of Argentine ants and were completely absent from areas invaded by Argentine ants.

Results showed that efficient interference competition by Argentine ants at toxic baits has severe negative consequences for the survival of Argentine ant colonies. As such, our results may provide a basis for planning and evaluating innovative management and/or eradication programs for Argentine ants. Previous studies that evaluated granular baits for areawide management of Argentine ants in natural ecosystems reported good short-term control and low potential for long-term areawide eradication (Krushelnycky and Reimer 1998, Krushelnycky et al. 2004). However, these studies did not indicate whether native ants were present in the treated areas or the potential impact of the baits on those species. We propose that Argentine ants may be selectively eliminated from invaded areas, especially where Argentine ants and native ant species interact (e.g., at invasion fronts or in areas where Argentine ants coexist with other ant species). However, the efficacy of this approach remains to be tested in the field and a number of factors need to be considered. First, factors such as the presence of other competing species or the presence of other competing food sources may affect the outcome of the baiting program. Second, bait dispersion pattern may affect bait efficacy, especially when native ant species are present. Computer simulation and mathematical models (Johnson et al. 1987, Jaffe and Deneubourg 1992) and previous laboratory experiments (Roulston and Silverman 2002) showed that food acquisition is influenced by food distribution and resource patch size. As a result, mass foraging strategy is most efficient when resources are clumped. Therefore, broadcast aerial baits treatments may not be the optimal method for applying toxic baits against Argentine ants. Finally, the fate of native ant species will also depend on their aggressiveness toward Argentine ants. Previous research showed that certain native ants are more likely to fight with Argentine ants, whereas other species emigrate immediately after aggressive encounters with Argentine ants. Relatively docile species that give up baits without fighting and emigrate into alternative nesting areas may indeed be spared. Other, more aggressive species may perish as a results of injuries sustained during aggressive fights and/or winning access to toxic baits.

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