

Effects of Interspecific Competition Between Two Urban Ant Species, *Linepithema humile* and *Monomorium minimum*, on Toxic Bait Performance

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J. Econ. Entomol. 98(2): 493-501 (2005)

ABSTRACT We evaluated the effects of interspecific competition on ant bait performance with two urban pest ants, the Argentine ant, *Linepithema humile* (Mayr), and the little black ant, *Monomorium minimum* (Buckley). In a laboratory study, the impact of a solid sulfluramid bait on *M. minimum* was diminished when *L. humile* were present, whereas the presence of *M. minimum* reduced the performance of a liquid fipronil bait against *L. humile*. Argentine ants were not adversely affected by sulfluramid bait at any time, whereas *M. minimum* was unaffected by fipronil bait until 14 d of exposure. In field studies measuring diel foraging activity, *M. minimum* seemed to delay *L. humile* foraging to food stations by ≈ 30 min during summer 2001. However, *L. humile* subsequently recruited to food stations in very high numbers, thereby displacing *M. minimum*. *L. humile* visited food stations over an entire 24-h period, whereas *M. minimum* was only observed visiting food stations during daylight hours. Adjusting the timing of bait placement in the field may minimize any negative effects of interspecific competition between these two species on toxic bait performance.

KEY WORDS *Linepithema humile*, *Monomorium minimum*, competition, bait, foraging

THE ARGENTINE ANT, *Linepithema humile* (Mayr), and the little black ant, *Monomorium minimum* (Buckley), are urban pest ants that co-occur through parts of their range (Newell and Barber 1913, Smith 1965). The Argentine ant is a serious urban, agricultural, and ecological pest (Markin 1970a, Knight and Rust 1990, Holway 1998 Vega and Rust 2000), whereas the little black ant is an occasional invader of human dwellings (Smith 1965). Both species use a mass-recruitment foraging strategy (Baroni-Urbani and Kanno 1974, Adams and Traniello 1981, Jones and Phillips 1990) and therefore can dominate clumped food resources (Adams and Traniello 1981, Human and Gordon 1996, Holway 1999). In addition, their foraging activity patterns and food preferences overlap to some degree, e.g., both are active during daylight hours and consume immobilized arthropods as well as sternorhynchan honeydew (Newell and Barber 1913, Smith 1965, Markin 1970b, Claborn and Phillips 1986, Stein and Thorvilson 1989). Thus, we predict that these species will compete for resources where their niches overlap.

Toxic baits are commonly used in urban pest ant management programs. We predict that the same factors important in diet partitioning during interspecific encounters also may reduce the level of toxicant received by a target ant species, thereby compromising bait performance. Therefore, we conducted labora-

tory experiments to evaluate the effect of interspecific competition on the performance of two ant bait formulations. The species we selected may serve as a model system for other ant species' interactions at baits.

The structure of ant communities can be affected, in part, by diel and/or seasonal foraging activity patterns (Baroni-Urbani and Kanno 1974, Lynch et al. 1980, Sanders and Gordon 2000). Furthermore, competitive trade-offs may permit species coexistence (Lynch et al. 1980, Fellers 1987, Perfecto 1994, Morrison 1996). For example, ant species that find baits quickly and feed before other ants discover the bait (exploitative competitors) may coexist with interference competitors, who take longer to discover resources but dominate them after discovery. *M. minimum* excels at interference competition (Baroni-Urbani and Kanno 1974, Adams and Traniello 1981), thereby dominating food resources. Argentine ants, however, seem to be removed from the exploitative-interference trade-off, both finding food quickly and dominating it once discovered (Holway 1999). We examined the diel activity of *L. humile* and *M. minimum* in the field, both in areas where the species' boundaries overlapped and were separated, in an effort to identify mutually exclusive foraging periods. This information may be used to adjust the timing of bait placement, thereby ensuring that the target ant receives an effective toxicant load.

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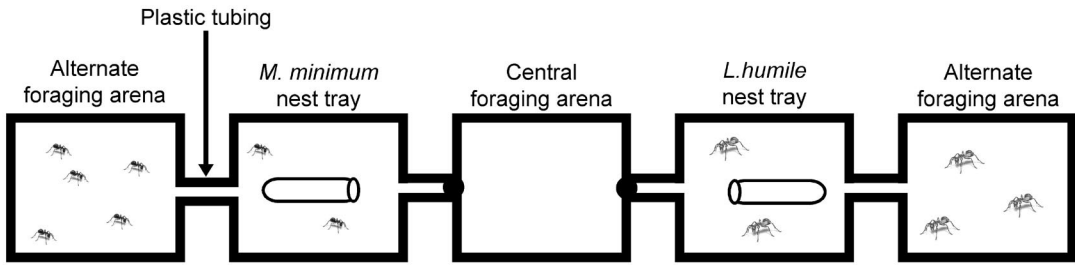


Fig. 1. Schematic design of experimental setup to measure the effect of interspecific competition on bait performance.

Materials and Methods

Effects of Competition on Bait Performance. We conducted a laboratory study to determine the effects of competition on toxic bait performance. *L. humile* were collected from a residential neighborhood in Chapel Hill, NC, whereas *M. minimum* were collected from the J.C. Raulston Arboretum at North Carolina State University, Raleigh, NC. Ants were separated from field debris, placed in plastic trays (53 by 39 by 13 cm) lined with Fluon (Northern Products Inc., Woonsocket, RI) to prevent ant escape, and provided a nest. Nests consisted of glass tubes (10 by 75 mm for *M. minimum* and 25 by 150 mm for *L. humile*) filled to approximately one-fourth with water and plugged with cotton. Glass tubes were covered with aluminum foil to keep nest interiors dark. Ants were fed 25% sucrose water, freshly killed *Blattella germanica* (L.), and artificial diet (Bhatkar and Whitcomb 1970) ad libitum, and maintained at $27 \pm 2^\circ\text{C}$, $50 \pm 10\%$ RH, and a photoperiod of 12:12 (L:D) h.

Experimental Colonies. Colony fragments consisting of 500 workers, 50 brood, and one queen each of *L. humile* and *M. minimum* were paired and given access to a central arena (CA) (Fig. 1). Each colony was placed in a plastic tray (24 by 17 by 11 cm) and provided a nest (specifications described previously). *M. minimum* were housed in 10 by 75-mm glass tubes, whereas *L. humile* were housed in 25 by 150-mm glass tubes. The glass tubes were covered with aluminum foil so the interior remained dark. During the acclimation period, and throughout the entire experiment, each colony was provided 25% sugar water, artificial diet (Bhatkar and Whitcomb 1970) and freshly killed *B. germanica* in an alternate foraging arena (AFA). Each colony had access to the CA and AFA through a clear plastic tubing connection (17 cm in length by 0.8 cm in diameter). All trays (24 by 17 by 11 cm) were lined with Fluon to prevent ant escape. Ants were allowed to acclimate for 5–7 d during which time access to the CA was blocked, thereby preventing species interaction.

After the acclimation period, the tubing leading to the CA was unblocked and a glass vial (6 × 50 mm) containing 25% sucrose water was placed in this arena. The small opening in the food vial facilitated interactions between the two ant species during feeding. The sucrose remained in the central arena for 3 d during

which time the ants could interact as well as establish territories and develop foraging strategies. After this 3-d period, the sucrose water was replaced with toxic bait, either $5 \times 10^{-4}\%$ fipronil (Clorox Co., Oakland, CA) in 25% sucrose water or Raid Double Control ant bait (0.5% *N*-ethyl perfluorooctanesulfonamide, SC Johnson, Racine, WI), a solid matrix. Based on the diet breadth of *L. humile* and *M. minimum*, we expected that both baits would be accepted by each species. Baits were placed in a small (6 × 50-mm) glass vial to facilitate contact between the species when feeding. The ants had access to the toxic bait for 2 wk. Dead ants were counted and removed from all trays daily. Dead ants inside the tubing connecting arenas also were counted daily but were not removed until the end of the experiment to minimize disturbance.

Treated controls (no competition in the presence of toxic bait) consisted of 500 workers, 50 brood, and one queen of each species placed in an arena with a nest, connected to arenas on either side of the nest arena. One arena contained food (sucrose water and cockroaches), and the other contained bait. Untreated controls for each species, in the presence or absence of competition, were prepared as described above; however, ants were not exposed to toxic bait. Each treatment, treated control, and untreated control was replicated five times.

Seasonal and Diel Activity. Knowledge of the foraging activities and interactions of coexisting ant species can influence toxic bait placement (timing and location) decisions. Therefore, we monitored the daily foraging activity of co-occurring and isolated field colonies of *L. humile* and *M. minimum* during different seasons. From June through September 2001, we placed ≈ 1.5 g of apple jelly and ≈ 1 g of cooked canned tuna within each of 10 plastic petri dish bases (8.5 cm in diameter). We distributed the dishes 30 cm apart in a 2 by 5 array at each of three sites: 1) site containing both *L. humile* and *M. minimum*, 2) site containing *L. humile* only, and 3) site containing *M. minimum* only. All sites were chosen based on preliminary mapping of ants using jelly and tuna baits. The site containing both *L. humile* and *M. minimum* as well as the *L. humile*-only site were located in a residential neighborhood in Chapel Hill. The *L. humile*-only site was located in a resident's front yard on a section of grass adjacent to the road, whereas the site

containing both species was located on a section of grass ≈ 1 m wide that separated the sidewalk from the road. The two sites were ≈ 4.5 m apart and separated by a paved road. The *M. minimum*-only site was located at the J.C. Raulston Arboretum at North Carolina State University. This site within the arboretum contained cone flowers (*Echinacea* spp.), and the ground was covered with hardwood mulch. Ants were counted on each food during three time periods: 0600–0800, 1400–1700, and 2200–2400 hours. Counts at each time period (morning, afternoon, and evening) were replicated five times (days) at all sites. On each of the 5 d, we made ant counts on each of 10 baits every 30 min for a total of four counts per bait for each time period.

Field counts at baits also were examined at all three sites during fall 2001 (October–November) as well as in the spring (May) and summer (July–September) 2002 from 1400 to 1700 hours (five separate days [replicates] per season). We did not examine morning and evening periods during these remaining seasons, in both years, because little black ant activity was not evident at the sites containing both *L. humile* and *M. minimum* during these cooler times of the day during summer 2001.

Initially, *M. minimum* fed on baits in the field and were not displaced until Argentine ants recruited to these same baits in large numbers. Therefore, we predicted that individual encounters between Argentine ants and *M. minimum* would favor the latter species. To determine the outcome of one-on-one interactions between *L. humile* and *M. minimum* in the laboratory, we placed single ants of each species in Fluon-coated 5-ml glass vials. We observed the confined ants every 30 min for 90 min and recorded which individuals, if any, were dead or mortally injured.

Data Analysis. For the laboratory experiments, the number of surviving ants of both species was recorded 1) after day 3, just before the placement of toxic bait; and 2) after bait placement on days 7, 10, and 17. Mortality due strictly to competition (day 3) was assessed and survivorship curves for the baited arenas with and without interacting species were derived with linear regression and the slopes compared with analysis of variance (ANOVA) (PROC GLM, SAS Institute 1990). The percentage of ants feeding on each food type (jelly or tuna) during each season was compared using ANOVA (PROC GLM) and protected least significant difference (LSD) means separation (SAS Institute 1990). A *t*-test was used to compare the number of ants present on occupied baits at each site containing only one species with the site containing both species (Minitab Statistical Software 2000). The outcome of direct one-on-one interactions between *L. humile* and *M. minimum* was analyzed with χ^2 contingency tables (Minitab Statistical Software 2000).

Results

Effects of Competition on Bait Performance. Some mortality (mean \pm SD, *L. humile*, $8.3 \pm 2.72\%$; *M.*

minimum, $9.0 \pm 1.80\%$) occurred during the acclimation period, before the central arena could be accessed.

Ants Exposed to Raid Double Control Ant Bait (Sulfluramid). Fighting was observed, and many workers of both species died in the 3 d before bait placement ($F = 189.9$, $df = 7$, $P < 0.0001$; Fig. 2a and b, day 3). There was no difference in the survival rate of *L. humile* exposed to sulfluramid bait, whether or not *M. minimum* was present ($F = 0.14$, $df = 1$, $P = 0.95$; Fig. 2a). In fact, there was a no bait effect on *L. humile* throughout the study ($F = 0.15$, $df = 1$, $P = 0.72$). Sulfluramid bait caused *M. minimum* mortality 7 d after bait placement ($F = 3.67$, $df = 1$, $P = 0.04$). *M. minimum* survivorship declined at a greater rate under conditions where *L. humile* was absent than where both species had equal access to the bait ($F = 4.22$, $df = 1$, $P = 0.05$; Fig. 2b) suggesting that *M. minimum*'s access to the toxic bait was somehow restricted by *L. humile*.

Ants Exposed to Fipronil Bait. During the 3 d before the introduction of liquid fipronil bait, both species suffered significant daily mortality when barriers between colonies were removed ($F = 42.5$, $df = 7$, $P < 0.0001$; Fig. 3a and b, day 3). Liquid fipronil bait caused *L. humile* mortality within 4 d after bait placement ($F = 21.19$, $df = 1$, $P < 0.0001$); however, effects of this bait on *M. minimum* were not evident until 14 d post-treatment ($F = 3.16$, $df = 1$, $P = 0.04$). *L. humile* survivorship declined at a greater rate under conditions where *M. minimum* was absent than where both species had equal access to the bait ($F = 17.9$, $df = 1$, $P = 0.0002$; Fig. 3a) suggesting that *L. humile*'s access to the toxic bait was somehow restricted by *M. minimum*. There was no difference in the survival rate of *M. minimum* exposed to fipronil bait whether or not *L. humile* was present ($F = 0.22$, $df = 1$, $P = 0.87$; Fig. 3b).

Seasonal and Diel Activity. *L. humile* and *M. minimum* counts were lower in the fall than in spring and summer (Table 1). Counts of *L. humile* were similar throughout the day, whereas *M. minimum* were generally absent during the morning and evening (Table 1). In summer 2001, beginning at 1400 hours, *M. minimum* seemed to delay *L. humile* foraging by ≈ 30 min (Fig. 4). Within 1 h after bait placement, fewer Argentine ants were present on food baits at the site where the two species occurred together ($t = 7.92$, $df = 53$, $P < 0.05$) (Fig. 4). However, *M. minimum* workers were ultimately displaced by Argentine ants during the afternoon (Fig. 4). During a typical encounter with Argentine ants, most *M. minimum* would remain at the food and raise their gasters. Many Argentine ants would subsequently leave the food and/or vigorously rub their antennae and heads, presumably responding to a defensive compound released by *M. minimum*. However, after ≈ 1 h, Argentine ants began recruiting to the food in very large numbers, and 90 min after bait placement (beginning at 1530 hours) and throughout the remainder of the afternoon, Argentine ants significantly reduced *M. minimum* counts on baits ($t = 4.86$, $df = 32$, $P < 0.05$).

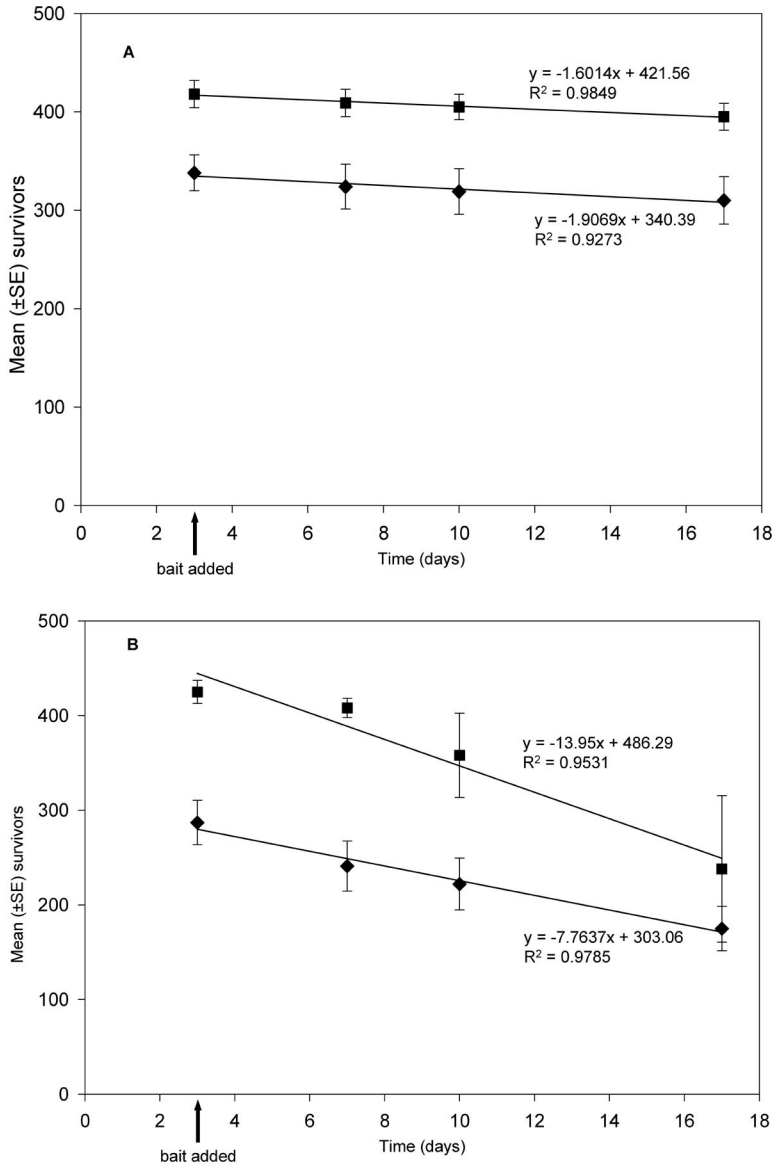


Fig. 2. Average (\pm SEM) surviving (A) *L. humile* exposed to sulfluramid bait. Diamonds, *M. minimum* present; squares, *M. minimum* absent. (B) *M. minimum* exposed to sulfluramid bait. Diamonds, *L. humile* present; squares, *L. humile* absent.

During summer 2002, *M. minimum* discovered and recruited to baits at the *M. minimum*-only site; however, only Argentine ants were found at the site where the two species had occurred together during summer and fall 2001 (Table 1).

L. humile preferred jelly over tuna within each season with the exception of spring 2002, where most Argentine ants (56%) fed on tuna (Table 2). Greater than 80% of *M. minimum* were present on the jelly during all seasons (Table 2).

In competitive interactions between individual *L. humile* and *M. minimum* workers, Argentine ants were killed in 70% of the one-on-one bouts, whereas little

black ants were either killed or injured in only 20% of the interactions ($\chi^2 = 55.5$, $df = 2$, $P < 0.0001$).

Discussion

We recognize that Argentine ants generally dominate native ant species in invaded habitats and therefore strategies targeting *L. humile* will usually not be undermined by the activities of one or more co-occurring species. Nevertheless, *M. minimum* does co-exist with *L. humile* in some urban locations and the potential for competition interfering with control measures exists. More importantly, when the entire

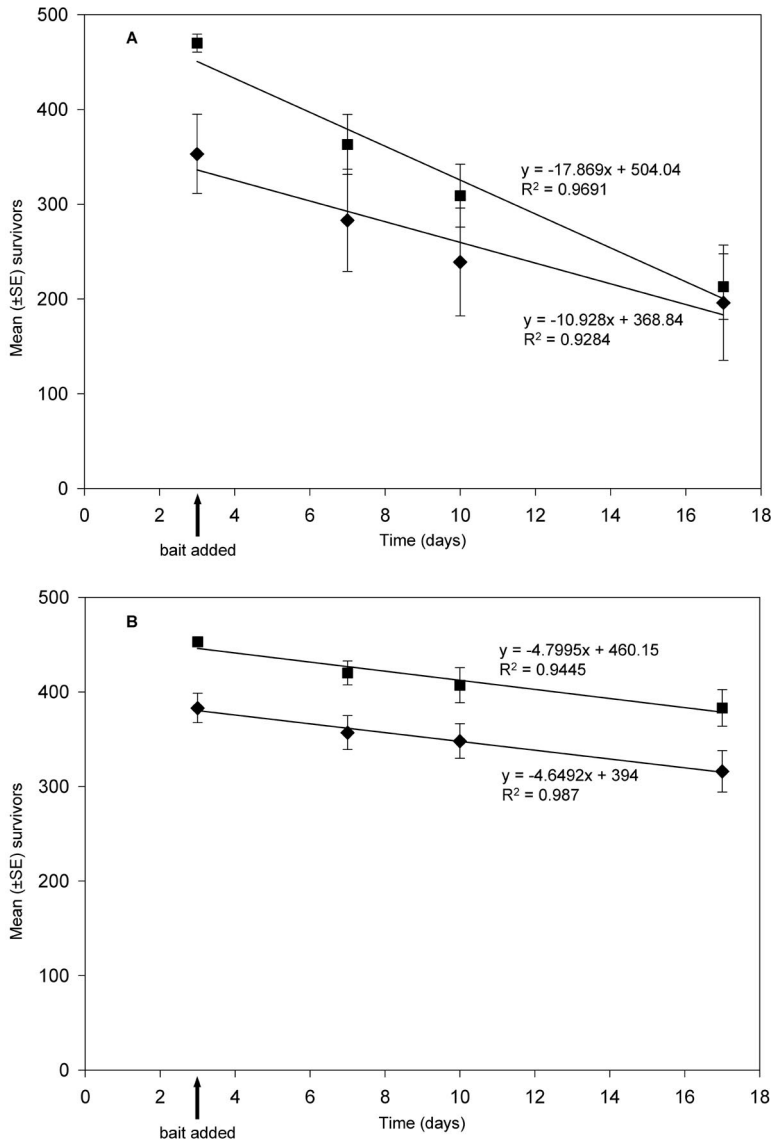


Fig. 3. Average (\pm SEM) surviving (A) *L. humile* exposed to fipronil bait. Diamonds, *M. minimum* present; squares, *M. minimum* absent. (B) *M. minimum* exposed to fipronil bait. Diamonds, *L. humile* present; squares, *L. humile* absent.

complex of urban ants is considered, we have demonstrated that bait performance against a target ant can be diminished by interspecific competition and we infer that the timing of bait placement can reduce the impact of competition. Over the course of 14 d, *M. minimum* had a measurable effect on the performance of liquid fipronil bait against *L. humile*, whereas *L. humile* reduced sulfluramid bait performance against *M. minimum*. Although we did not observe competitive interactions and feeding each day, bait was made available for 14 d. Therefore, it is unlikely that one species could simply remove all bait before the other had the opportunity to feed. Instead, decreased bait performance seems to be the result of competing ants generally avoiding the central foraging arena where

the toxic bait was located, and as a result less toxicant was ingested.

Bait performance depends, in part, on bait base acceptance. Low *M. minimum* mortality after exposure to liquid fipronil bait may have resulted from low bait acceptance. This was surprising because *M. minimum* workers visit floral and extrafloral nectaries of plants and tend some honeydew-producing insects (Smith 1965). Therefore, we would have expected better acceptance of our sugar-based liquid bait. Perhaps the presence of alternate food resulted in low bait intake. Alternatively, the active ingredient may have been somewhat repellent to *M. minimum* workers. Compared with the liquid fipronil bait, the solid sulfluramid bait produced significant *M. minimum* worker mortal-

Table 1. Seasonal diel activity of *L. humile* and *M. minimum* at jelly and tuna baits (total for both baits) at single species and co-occurring sites

Species/site	Time of day ^{a,b}					
	Summer 2001	Fall 2001	Spring 2002	Summer 2002	0600–0800	Summer 2001
<i>L. humile</i>	30.0 ± 3.01 (30.7°C)	7.6 ± 1.33 (22.5°C)	30.8 ± 2.55 (23.6°C)	33.7 ± 3.47 (30.0°C)	38.6 ± 3.49 (22.3°C)	25.1 ± 3.11 (19.3°C)
<i>M. minimum</i>	43.4 ± 5.71 (25.2°C)	7.6 ± 1.86 (21.5°C)	26.6 ± 2.84 (29.6°C)	28.9 ± 4.63 (33.1°C)	9.0 ± 3.96 (21.3°C)	0.0 (21.1°C)
<i>L. humile</i> / <i>M. minimum</i>	29.8 ± 9.05/10.6 ± 3.23 (29.8°C)	20.3 ± 5.81/7.6 ± 6.82 (22.1°C)	37.9 ± 2.54/0.0 (23.1°C)	22.3 ± 3.29/0.0 (29.6°C)	35.4 ± 4.26/0.0 (22.2°C)	35.1 ± 4.01/0.0 (19.3°C)

^a Average ± SD ant counts on baits.

^b Average ground surface temperature.

ity, a possible consequence of high bait acceptance. *M. minimum* readily consumes nontoxic baits relatively high in protein, including peanut butter (Baroni-Urbani and Kanno 1974, Glancey et al. 1976, Jones and Phillips 1990). Perhaps the sulfuramid bait contained levels of protein that stimulated feeding. The sulfuramid bait performed poorly against *L. humile*, possibly due to low bait consumption. In laboratory trials, Knight and Rust (1991) recorded lower Argentine ant mortality from sulfuramid than most other toxicants tested. The authors did not mention whether reduced mortality resulted from low bait consumption or from the delayed action of the active ingredient. Of the toxicants available for urban pest ant control, sulfuramid generally requires longer exposure to reduce ant populations (Reid and Klotz 1992, Forschler and Evans 1994). In our study, fipronil in sucrose solution reduced *L. humile* worker numbers by >50%, which may reflect high bait consumption. This is not surprising considering that Argentine ants prefer liquids with high sugar content (Markin 1970b, Baker et al. 1985). Hooper-Bui and Rust (2000) also reported significant mortality in Argentine ants exposed to sucrose solution containing fipronil, the most efficacious compound of those tested.

Our findings in the field were similar to those of Markin (1970b) and Baker et al. (1985) in that Argentine ants had an overall preference for jelly over tuna, a high-protein food. Even though Argentine ants preferred jelly overall, a higher percentage of Argentine ants fed on tuna in the spring, which could reflect seasonal changes in the colony's nutritional requirements. Krushelnycky and Reimer (1998) reported an increase in the intake of a protein-based bait in the spring and summer and stated that the increased intake of protein may be important at this time when egg production and larval growth increase. Rust et al. (2000) also reported an increase in the amount of protein consumed by Argentine ants in the spring and summer. *M. minimum* had an overall preference for jelly across all seasons. Seasonal food preferences by ants may be an important consideration in toxic bait acceptance.

Results of one-on-one encounters between individual *L. humile* and *M. minimum* workers might suggest that *M. minimum* could dominate food resources; however, *L. humile* displaced *M. minimum* from food dishes in the field. Most likely, numerical advantages contributed to the dominance of the Argentine ant over *M. minimum* as reported for other native ants (Holway 1996, Human and Gordon 1999). Numerical advantages over native ants also may be important in the success of other economically important ant species, such as *Solenopsis invicta* Buren (Phillips et al. 1986, Morrison 2000).

Resource distribution should affect food or bait retrieval efficiency by competing ant species. For example, Adams and Traniello (1981) reported that individual *M. minimum* workers retrieved small food particles (<1 mg). However, as food items became too large for a single worker to carry, *M. minimum* experienced a much greater chance of interference by

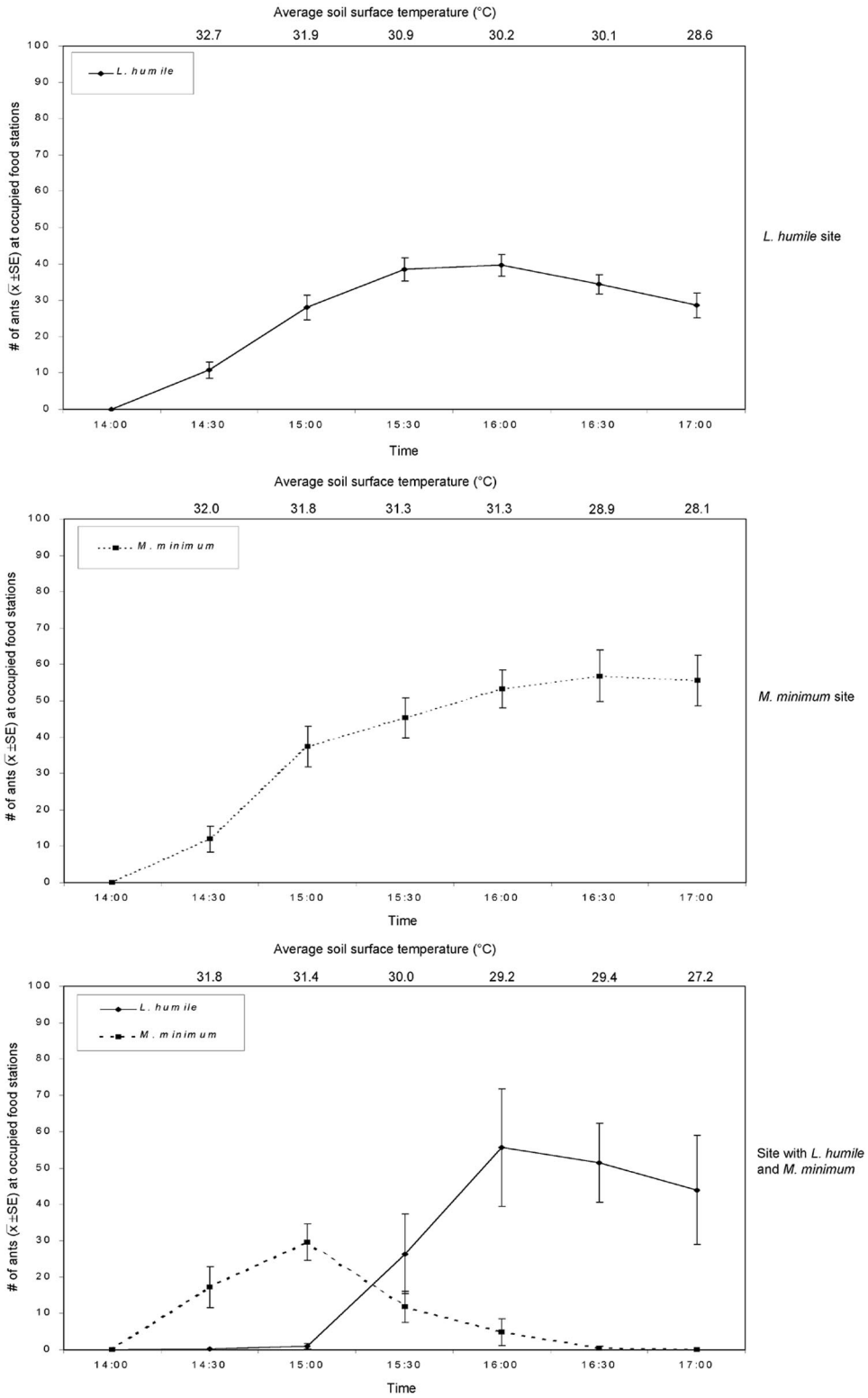


Fig. 4. *L. humile* and *M. minimum* visits to food stations from 1400 to 1700 hours, June–September 2001.

Table 2. Seasonal distribution of *L. humile* and *M. minimum* workers on jelly or tuna baits in the field

Ant species	% (\pm SD) workers on jelly at season ^a			
	Summer 2001	Fall 2001	Spring 2002	Summer 2002
<i>L. humile</i>	60.4 \pm 14.31b	75.5 \pm 11.41a	44.3 \pm 2.61c	59.2 \pm 12.34b
<i>M. minimum</i>	84.3 \pm 8.60a	87.2 \pm 7.55a	85.3 \pm 3.88a	85.9 \pm 3.75a

^a Rows with same letters indicate no significant difference between seasons ($P < 0.05$; LSD).

other ant species, although large food clumps were frequently dominated by *M. minimum*. Argentine ants are efficient exploitative and interference competitors, dominating both dispersed and clumped resources (Human and Gordon 1999). Unless foods (or bait) of equal palatability are placed in proximity to a *M. minimum* nest they will most likely be removed by *L. humile*.

Diel foraging patterns for both ant species were consistent with those reported previously, with *L. humile* active both day and night during summer 2001 (Markin 1970b, Human et al. 1998), and *M. minimum* active only during the day (Baroni-Urbani and Kannonowski 1974, Glancey et al. 1976, Claborn and Phillips 1986, Vogt et al. 2004). Knowledge of the activity pattern of a target ant(s) before toxic bait placement is necessary to ensure that the target species finds the bait.

During summer 2001, Argentine ants depressed *M. minimum* numbers at food stations. Although *M. minimum* recruited to several food stations during the afternoon in summer 2001, they were ultimately displaced by *L. humile*. Holway (1999) reported that Argentine ants both found baits more quickly and dominated those baits more consistently than native ant species, including a related *Monomorium* species, *Monomorium ergatogyna* Wheeler. In our study, *M. minimum* seemed to delay Argentine ant foraging by ≈ 30 min before they were ultimately displaced. Adams and Traniello (1981) reported that chemical interference by little black ants delays invasion of food resources by competitors and that *M. minimum* may be able to better withstand higher temperatures and direct sunlight than other ant species. The findings of Howard and Oliver (1979) reflected our field results in that *M. minimum* was able to repel individual *S. invicta* workers from baits for some time, presumably using chemical defenses, before eventually being displaced by the latter species. Baroni-Urbani and Kannonowski (1974) reported that *M. minimum* was almost always successful in competition with *S. invicta* if the interactions took place in direct sunlight. Other studies have reported the persistence of *M. minimum* in areas invaded by *S. invicta* (Stein and Thorvilson 1989, Porter and Savignano 1990). Perhaps chemical interference coupled with an ability to tolerate greater temperatures enabled *M. minimum* to feed at food baits for some time before ultimately being displaced by Argentine ants.

The absence in 2002 of *M. minimum* at the site shared with *L. humile* in 2001 suggests that *M. minimum* was displaced by *L. humile*; however, further surveys would be required to confirm this observation.

Ward (1987) reported that *M. minimum* occurred in five of 10 sites without Argentine ants, but only two of 10 sites with Argentine ants.

Using *L. humile* and *M. minimum*, we demonstrated that toxic bait performance can be compromised by interspecific competition. Adjusting the timing of bait placement or changing the bait base could minimize the negative effects of interspecific competition on toxic bait performance.

Depending on bait acceptance, foraging behavior, and the interactions of coexisting ants, interspecific competition between other ant species also may diminish the effects of toxic bait. By considering food preference, colony boundaries, and diel activity patterns, it may be possible to effectively manage a particular species without interference from nontarget ants.

Acknowledgment

We thank A. Carper for technical assistance and C. Brownie for statistical advice. E. Vargo and M. Waldvogel provided helpful comments on the manuscript. This work was supported by the Blanton J. Whitmire Endowment at North Carolina State University and the North Carolina Pest Control Association.

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Received 29 October 2004; accepted 20 December 2004.