Aggressive Interactions Between *Solenopsis invicta* and *Linepithema humile* (Hymenoptera: Formicidae) Under Laboratory Conditions

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ABSTRACT The Argentine ant, *Linepithema humile* (Mayr), and the red imported fire ant, *Solenopsis invicta* Buren, are natural agonists in their country of origin. Since the first report of *L. humile* in California in 1907 its range expanded statewide, displacing native ant species wherever it spread. Since the discovery of established populations of *S. invicta* in southern California in 1998, it has been restricted to discrete areas of southern California. However, as these discrete populations expand, they are encountering large populations of *L. humile*, which are effective competitors for available resources and are particularly aggressive in their encounters with other ant species such as *S. invicta*. Most Dolichoderine ants such as *L. humile* do not prefer to forage on baits made with defatted corn grit and soybean oil typically used in red imported fire ant control programs. Applications of these baits in areas where distributions of these species overlap might selectively affect populations of *S. invicta* and give *L. humile* a competitive advantage. Three laboratory experiments were conducted to determine the competitive outcomes between *S. invicta* pitted against *L. humile*: 1) agonistic behavior of workers in small arenas, 2) colony interactions with different population ratios, and 3) the effects of pyriproxyfen on the competitiveness of *S. invicta* against *L. humile*. Populations of *S. invicta* consisting of major workers killed more *L. humile* than did minors or a mixture of majors and minors. When paired against *L. humile* colonies consisting of 1,100 workers, colonies consisting of 38 *S. invicta* workers were easily defeated by *L. humile*. Colonies consisting of 450 *S. invicta* workers plugged their nest entrances, but they were ultimately defeated by *L. humile* after 13 d. The *S. invicta* colonies consisting of 1,100 workers took control of the bridge connecting the colonies, invaded the *L. humile* colony, killed the Argentine ant queens, and removed their brood. Pyriproxyfen-treated fire ant workers took significantly longer to chase the Argentine ants from a connecting bridge than did untreated fire ants. Thus, fire ant baits may have long-term effects on intercolonial aggression between *S. invicta* and *L. humile*, especially when Argentine ant populations are high in the summer.

KEY WORDS *Linepithema humile*, *Solenopsis invicta*, interspecific aggression, competition

The Argentine ant, *Linepithema humile* (Mayr), was introduced into the continental United States through New Orleans around 1891 and has since been recorded in 335 counties in 21 states (Suarez et al. 2001). Since the first report of *L. humile* in California in 1907 (Newell and Barber 1913), its range expanded statewide, displacing native ant species wherever it spread (Knight and Rust 1990, Suarez et al. 2001). The red imported fire ant, *Solenopsis invicta* Buren, became established in urban areas of southern California in 1998 (CDFA 1998). *S. invicta* is currently restricted to discrete areas of southern California. However, like *L. humile, S. invicta* has the potential to spread throughout much of California, displacing native ant species, and to become a major pest species in agricultural and urban settings. As these discrete populations expand, they are encountering large populations of *L. humile.*

Several factors have contributed to the success of both species: the absence of native predators, competitors, and parasites; human mediated dispersal via commerce (Suarez et al. 2001); and colony dynamics. For example, polydomous (multiple nests per colony) and polygynous (multiple queens per colony) colonies of both species can attain tremendous numbers that overwhelm and displace other ant species (Hölldobler and Lumsden 1980, Holway and Suarez 1999, Davidson 1997, Porter and Savignano 1990). Before intensive eradication efforts, *S. invicta* had become the dominant ant species in the infested areas, although *L. humile* and native ant species could still be found in urban areas within the quarantine area (J.N.K., personal observation).

Both *S. invicta* and *L. humile* have become established in arid environments of southern California because of their ability to colonize and adapt to disturbed areas, irrigated landscapes, and managed urban

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habitats. However, *L. humile* and *S. invicta* are natural antagonists in their country of origin. In direct confrontations, one *S. invicta* worker is able to kill several Argentine ants (Wilson and Eads 1949, Taber 2000). Numerous confrontation interaction studies at the individual and colony level between *S. invicta* and other ant species [*Lasius neoniger* Emery, *Pheidole dentata* Mayr, *Forelius foetidus* (Buckley), *Monomorium minimum* Buren, *Paratrechina longicornis* (Latreille), *Tetramorium bicarinatum* (Nylander), and *Solenopsis molesta* (Say)] in the areas it has invaded have been conducted at both the individual and colony level (Bhatkar et al. 1972, Bhatkar 1988, Obin and Vander Meer 1985, Rao 2002, Tsutsui et al. 2003). However, none of these studies included *L. humile,* which is an effective competitor for available resources and is particularly aggressive in their encounters with other ant species (Holway and Case 2001; Human and Gordon 1996, 1999).

Eradication treatment protocols for *S. invicta* in California call for applications of pyriproxyfen and hydramethylnon baits either simultaneously or separately, with the latter being applied 1 to 2 wk after the former. Hydramethylnon is an aminohydrazone insecticide that acts as a slow-acting toxicant that inhibits mitochondrial electron transport, causes a decrease in physical activity and decreases respiration, eventually resulting in death (Lovell 1979). Pyriproxyfen is an insect growth regulator (IGR) (juvenile hormone analog) that disrupts the hormonal system of *S. invicta,* affecting egg production, brood care, and other social interactions (Glancey et al. 1990, Sullivan 2000). Although pyriproxyfen inhibits colony growth, it does not kill adult workers.

Most Dolichoderine ants such as *L. humile* do not prefer to forage on baits made with defatted corn, *Zea mays* L., grit and soybean, *Glycine max* (L.) Merr., oil (Wagner 1983) typically used to control *S. invicta.* Red imported fire ants also prefer larger particles of solid bait (>3,000 μm) that are found in the soybean oil baits than do Argentine ants (Hooper-Búi et al. 2002). Particle size preference is directly related to forager head width. Consequently, applications of these baits in areas where both species overlap selectively affect *S. invicta.* The populations of *L. humile* seem to increase when fire ants have been treated and these ants have been seen raiding *S. invicta* colonies (J.N.K., personal observation). In other parts of North America, native ant species have effectively exploited and overcome small colonies of *S. invicta* (Nichols and Sites 1991; Rao and Vinson 2002, 2004). The objective of the study presented here was to directly test the hypotheses that 1) reduction in *S. invicta* colony size increases their susceptibility to aggression by *L. humile,* and 2) applications of pyriproxyfen to *S. invicta* colonies provide *L. humile* a competitive advantage.

Materials and Methods

Insect Maintenance. *S. invicta* used for interaction studies were collected from polygyne colonies in southern California and maintained at the University of California South Coast Research and Extension Center, Irvine, CA. Colonies of *S. invicta* contained >25,000 individuals and included immatures at all developmental stages. Colonies were provided with nest chambers maintained in plastic petri dishes (14.5 cm in diameter, Fisher Scientific, Houston, TX) with Castone (Dentsply International Inc., York, PA) floors at ≈26.7°C, on a diet of water, sucrose water (25%, wt:vol), crickets (Orthoptera: Gryllidae), and mealworms (Coleoptera: Tenenbrionidae) until needed for experiments. Castone dental plaster holds moisture that provides a humid environment in the brood chamber and is resistant to tunneling and damage. These brood chambers were placed in polycarbonate boxes (38 by 59 by 14 cm) (Banks et al. 1981). The inside walls of the boxes were coated with the fluoropolymer resin, Fluon (Headwin Corporation, Baltimore, MD), to prevent ants from escaping.

L. humile were collected from Riverside County, CA, and maintained in (26- by 32- by 10-cm) plastic boxes (Spectrum Containers Inc., Evansville, IN) with inner sides coated with Fluon. Each box was provisioned with two 7-cm polystyrene weighing boats, one boat filled with water and the other boat filled with 25% sucrose water, and an "ant condo." Ant condos were constructed by placing a shoe lace (24-cm length) in the bottom of a plastic petri dish (9 cm in diameter) so that the lace lined the inside perimeter of the petri dish bottom and one end protruded through a hole to the outside of the dish. Plaster of Paris was poured into the petri dish to completely conceal the lace within the dish and allowed to harden for 1 d. Four holes were drilled into the side on opposite ends of the petri dish just above the plaster to give the ants easy access. The petri dish top was added to complete the condo. The Plaster of Paris provided an absorbent material to retain moisture for the ant colony, and the lace conducted ≈5 ml of water into the plaster from a 7-cm polystyrene weighing boat reservoir into which the free end was placed every other day (Soeprono and Rust 2004).

Fire ant workers are weakly allometric (Wilson 1978). As worker size increases, the head width above the eyes increases, making the major worker's head proportionately larger than that of the minor worker. We chose minor workers for experiments by selecting the smallest workers from a nest and major workers by their larger body and head size.

Small Arena Interactions. Agonistic interactions between *S. invicta* and *L. humile* workers were staged in small arenas. Arenas consisted of a 13.5-cm plastic petri dish with inner sides coated with Fluon. Ants were counted by allowing them to climb onto a small paint brush and then placing them into separate 60-ml plastic containers with inside walls coated with Fluon. Argentine ants were then placed into arenas by inverting the cup and gently tapping until the ants fell into the plastic petri dish. Fire ants were placed into the arena ≈10 min later. We also did reciprocal trials where the *S. invicta* workers were placed into the arenas first. Preliminary trials indicated that a major *S. invicta* worker was able to kill 10 or more *L. humile* workers. We therefore chose encounter ratios of 100 *L. humile* workers to 10 *S. invicta* workers to determine whether the size of the fire ants was correlated with the percentage of dead Argentine ants. The Argentine ants were paired up with three size distributions of fire ant workers: 1) 10 minors ($n = 18$), 2) 10 of mixed size (five minors and five majors, $n = 15$), and 3) 10 majors ($n = 9$). After 1 h, the ants were collected from the arenas, and the number of dead and moribund of each species was counted. We measured percent mortality of the workers and also calculated the mortality ratio (the average ratio of the number of dead *L. humile* to dead *S. invicta*). The former data were transformed by an arcsine square-root transformation, and the latter data were log transformed, before performing analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) test for means separation (Systat Software Inc. 2002). Three control dishes for each species were set up to see the natural mortality during the 1-h experiment.

Colony Interactions at Different Population Ratios. To determine the effect of the number of *S. invicta* workers on confrontations with *L. humile,* colonies of both species were tested against each other. Colonies with two *S. invicta* queens and 38, 450, or 1,100 workers, and colonies of 1,100 Argentine ants with two queens, were maintained in 5-cm-diameter plastic petri dish cells (Fisher Scientific) with Castone floors. These dishes were placed in Fluon-coated plastic 22.5- by 15- by 5-cm Rubbermaid containers (Rubbermaid, Fairlawn, OH) that served as foraging arenas.

The numbers of fire ants chosen for encounters with Argentine ants were based upon the mortality data from our small arena trials and a study by Rao (2002) involving other ant species. Of the three different types of fire ant colonies paired with Argentine ants, those with 38 workers gave an overwhelming advantage to the Argentine ants, those with 1,100 workers gave the advantage to the fire ants, and those with 450 workers had an unpredictable outcome.

Confrontations between *S. invicta* and *L. humile* were initiated by placing the colony containers next to each other and providing access between containers with a 2.54- by 25.4-cm paper bridge. The following events and when they first occurred were recorded: bridge crossing by *L. humile;* death of *L. humile* queens; nest entrance plugging by *S. invicta;* nest departure by *S. invicta* queens; removal of *S. invicta* brood from their nest by *L. humile;* control of the bridge by *S. invicta;* invasion of the *L. humile* nest by *S. invicta;* percent mortality of both species; and duration of each trial.

Colony interactions were video recorded (Sony TRV 20 digital video camera, Sony Corporation, Tokyo, Japan) for the first 20 min and then for other behaviors noted above. Confrontations were observed closely for the first 8 h, then every 24 h, and randomly throughout the day. Dead ants were collected and counted from all boxes after each major aggressive encounter. Once aggressive behavior ceased, the trial was ended. We performed $\log_{10}$ transformations on the ratios of ants killed and on time of event duration, and arcsine square-root transformations on the percent mortality data, before conducting ANOVAs (Systat Software Inc. 2002). Means were separated by Tukey's HSD test. The time for *S. invicta* queens to abandon nests and for removal of *S. invicta* brood by *L. humile* were analyzed using the Kruskal–Wallis one-way ANOVA (Systat Software Inc. 2002).

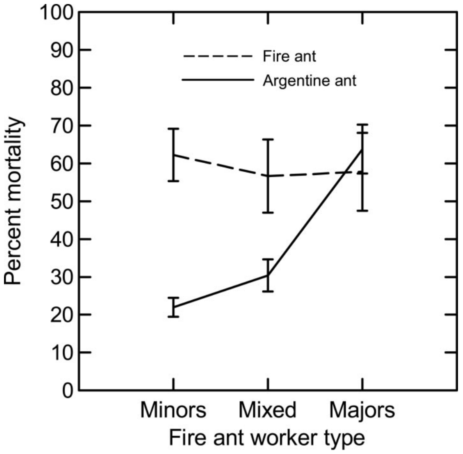

Fig. 1. Percent mortality (means ± SE) of *L. humile* and *S. invicta* as a function of the *S. invicta* worker size in small arena trials. In all cases, 10 *S. invicta* were paired with 100 *L. humile.*

Effects of the IGR Pyriproxyfen on *S. invicta* Interactions with *L. humile*

In all the experiments, the size of the *L. humile* and *S. invicta* ant populations were kept constant (1,100 workers and two queens) and set up as described previously for the colony interaction studies. Pyriproxyfen was introduced into five *S. invicta* containers when brood production was observed (indicating viable queens) by placing 1.5 g of Esteem Ant Bait (0.5% pyriproxyfen, Valent U.S.A. Corp., Walnut Creek, CA) in a plastic weighing boat and allowing the colonies to feed ad libitum for 24 h. After 5 wk, IGR-treated colonies stopped producing normal brood and the confrontation trials were started.

Confrontations between *S. invicta* and *L. humile* were done with paper bridges, as described above. The same events were recorded and videotaping procedures followed as described in the previous experiments on colony interaction at different populations ratios. The data were not normally distributed; therefore the Kruskal–Wallis one-way ANOVA was used on all trials (Systat Software Inc. 2002).

Results

Small Arena Interactions. Fig. 1 shows the results of the small arena trials. The percent mortality of *L. humile* workers ($F = 26.4$; df = 2, 39; $P < 0.001$) but not *S. invicta* workers ($F = 0.1$; df = 2, 39; $P > 0.05$) varied significantly with the size of fire ant workers used. Major *S. invicta* workers killed more *L. humile*

Table 1. Colony interactions at different population ratios

Confrontation ratio (*S. invicta*:*L. humile*)	*n*	% mortality		Mortality ratio *L. humile* to *S. invicta*	Trial duration (h)
		S. invicta	*L. humile*		
38:1,100	5	99 ± 1.1a	15 ± 2.5a	4.4 ± 0.76a	10.4 ± 4.34
450:1,100	5	90 ± 5.9a	66 ± 1.8b	1.8 ± 0.13b	313.8 ± 50.68
1,100:1,100	5	45 ± 6.3b	99 ± 2.3c	2.4 ± 0.37b	10.6 ± 3.37

Mortality ratio is the ratio of the number of dead *L. humile* to dead *S. invicta* workers. Log_{10} transformation of data was done on the mortality ratio and trial duration data, and an arcsine transformation was done on the percentage of mortality data. Means ± SE were then compared using Tukey's HSD method. Means followed by the same letter are not significantly different ($P < 0.05$).

than did minors or the mixed worker sizes ($P < 0.001$). The numbers of Argentine ants killed by minor and mixed worker size fire ants were not significantly different ($P > 0.05$). Differences in the mortality ratio were significant among minor, mixed, and major workers ($F = 13.4$; df = 2, 38; $P < 0.001$), with respective ratios of 3.8, 8.5, and 14.7. Multiple comparisons among the three ratios were all significant ($P < 0.05$, Tukey's HSD test). Differences in the mortality ratios comparing which species was introduced first into the test arena were not significant ($F = 0.7$; df = 1, 30; $P > 0.40$). In the control dishes, Argentine ant mortality during 1 h was 2.7%. For the fire ants, it was 3.3%.

Colony Interactions at Different Population Ratios. Mortality as a ratio of dead *L. humile* to dead *S. invicta* workers was significantly higher when the colony size of *S. invicta* was the smallest ($F = 9.48$; df = 2, 12; $P = 0.003$ (Table 1). The percent mortality of *L. humile* significantly increased ($F = 195.8$; df = 2, 12; $P < 0.001$) (Table 1) as the size of the *S. invicta* colony increased. Similarly, the percent mortality of *S. invicta* workers significantly decreased ($F = 31.9$; df = 2, 12; $P < 0.001$) (Table 1) as size of the *S. invicta* colony increased. All trials were terminated when confrontation activity ceased. Trial duration of the 450 worker fire ant colonies was significantly longer than that of the other treatments ($F = 43.3$; df = 2, 12; $P < 0.001$) (Table 1) because workers in the intermediate sized fire ant colonies plugged their nest entrances after an average of 9.3 h (Table 2).

Only the colonies with 1,100 *S. invicta* workers took control of the bridge connecting the colony boxes (Table 2). The time for the first *S. invicta* queen to abandon its nest was significantly longer when there were 450 fire ants than for 38 fire ants ($U = 20$, $P = 0.014$, $n = 9$) (Table 2). In *S. invicta* colonies with 1,100 workers, queens did not abandon their nests, nor did workers plug the nest entrances, because *L. humile* were never able to successfully attack the *S. invicta* colony box or brood chamber. *S. invicta* brood in the 38 and 450 worker colonies were removed from their nest by *L. humile.* It took significantly longer for the Argentine ants to remove brood from the 450 fire ant worker populations than from the 38 fire ant worker colonies ($U = 20$, $P = 0.014$, $n = 9$) (Table 2) due, at least in part, to the blocking of the nest entrances by the fire ants. Colonies of 38 *S. invicta* workers were easily overwhelmed by *L. humile.*

L. humile were always the first to cross the bridge between the two species, regardless of the fire ant colony size. *L. humile* crossed the bridge into the *S. invicta* nest in significantly less time when both colonies contained 1,100 workers than when *L. humile* colonies had a numerical advantage ($F = 6.8$; df = 2, 12; $P = 0.011$) (Table 3). *S. invicta* workers were able to kill *L. humile* queens only when their colonies were the same size (Table 3).

Effects of Treatment with IGR Pyriproxyfen on *S. invicta*. When comparing encounters between IGR-treated and IGR-untreated ants (Table 4), there were no significant differences in the percent mortality of *S. invicta* ($U = 8$, $P = 0.3$, $n = 10$), *L. humile* ($U = 16$, $P = 0.5$, $n = 10$), or in the mortality ratio of the two species ($U = 21$, $P = 0.08$, $n = 10$). However, untreated *S. invicta* workers took control of the bridge between colonies of the two species sooner than did the IGR-treated fire ant workers ($U = 19$, $P = 0.027$, $n = 10$) (Table 4). Also, trial length differences were significant ($U = 25$, $P = 0.007$, $n = 10$) (Table 4) with antagonistic behavior between untreated fire ant colonies and *L. humile* colonies ending sooner than between IGR-treated fire ant and *L. humile* colonies (Table 4).

Table 2. Time required (hours) for *S. invicta* queen to abandon its nest, for *S. invicta* to control the bridge between colonies, for *S. invicta* to plug its nest entrance, and for *L. humile* to remove *S. invicta* brood

Confrontation Ratio *S. invicta*:*L. humile*	*n*	*S. invicta* queen abandons nest (h)	*S. invicta* controls bridge (h)	*S. invicta* plugs nest entrance (h)	*S. invicta* brood removed by *L. humile* (h)
38 × 1,100	5	4 ± 2.8	—[b]	—[b]	5.7 ± 3.44
450 × 1,100	5	246 ± 14.7	—[c]	9.3 ± 3.88	313.0 ± 62.8
1,100 × 1,100	5	—[a]	3.7 ± 0.67	—[a]	—[a]

Kruskal–Wallis one-way analysis of variance was used for tests of significance (see text).

[a] L. *humile* suffered 99% mortality and did not threaten *S. invicta* queens or brood.

[b] Most of the *S. invicta* were outside of the nest and easily overwhelmed by *L. humile.*

[c] *S. invicta* plugged nest entrance after 9 h.

Table 3. Time required for *L. humile* workers to cross the bridge into the *S. invicta* colony and the time required for *S. invicta* to kill *L. humile* queens

Confrontation ratio *S. invicta:L. humile*	First *L. humile* crossed bridge (s)	*L. humile* queen killed by *S. invicta* (mean ± SE, h)	
		First queen	Second queen
38 × 1,100	59.0 ± 21.36a	—[a]	—[a]
450 × 1,100	50.2 ± 16.73a	—[b]	—[b]
1,100 × 1,100	8.2 ± 2.25b	3.4 ± 2.19	7.5 ± 1.12

Log$_{10}$ transformation of the bridge data is compared using Tukey's HSD method. Means followed by the same letter are not significantly different ($P < 0.05$).

[a] Most of the *S. invicta* were easily overwhelmed by *L. humile* and never posed a threat to *L. humile* queens.

[b] *S. invicta* plugged nest entrance after 9 h and eventually suffered 90% losses to *L. humile.*

Discussion

In small arena studies with isolated groups of *S. invicta* workers, the mortality ratios were higher than those observed in colony confrontations, especially for the major workers. This difference may be because in small arenas, workers cannot avoid contacting the other species. Also, due to the large size of fire ant majors compared with minors, they may be able to survive more injuries and encounters with Argentine ants, thereby increasing Argentine ant mortality. However, in colony trials, fighting was concentrated at the base of the bridge, entrance to the nest, and at the sucrose water and water tubes, but workers were not forced to contact the other species.

Extrapolating from this laboratory study to field situations can be risky because other variables may affect the competitive outcome between the two species, but we can at least begin a discussion based on our findings. A typical monogyne *S. invicta* colony has a standing population of ≈160,000 workers, with ≈35% being majors (Haight and Tschinkel 2003). Using the 160,000 worker and the 2.5 mortality ratio of dead *L. humile* to dead *S. invicta* (Table 4), based on our laboratory study it could take 396,800 *L. humile* workers to successfully overcome a typical monogyne *S. invicta* colony. A younger, smaller colony would have fewer majors as a percentage of the population, and fewer workers that could successfully defend against an *L. humile* attack. Similarly, a *S. invicta* colony reduced in size or vitality as a result of a successful baiting treatment could be susceptible to predation by *L. humile.* A large unicolonial, polygyne fire ant colony could have even more workers than a monogyne colony and would require even more Argentine ants to successfully attack it.

The mortality ratio and behavioral differences during encounters between the two species may explain some field observations. For example, founding fire ant colonies may be susceptible to attack from *L. humile* because they have few and small workers typical of new colonies. In this experiment, 1,100 *L. humile* workers easily defeated fire ant colonies consisting of 38 workers. Colonies consisting of 450 fire ant workers were the only ones that plugged their nest entrances, a strategy also used by *S. geminata* as a defense against *S. invicta* (Bhatkar et al. 1972). *S. invicta* colonies with 450 workers succeeded in blocking their nest entrances after 9 h of battles with the Argentine ants, but they were finally overwhelmed at 313 h (Table 2). That Argentine ants crossed the bridge most quickly when they were connected to the 1,100 worker fire ant colony suggests that the Argentine ants may be reacting to the presence of the fire ants by launching an invasion of their nest.

Experiments by Rao (2002) revealed a sequence of major events in *S. invicta* colonies after the invasion by opposing predatory species. These events included 1) brood abandonment by all *S. invicta* workers due to the overwhelming presence of other species in their nest, 2) death of all *S. invicta* or attacking workers, and 3) death of *S. invicta* or opposing queens. In our fire ant colonies that were under attack by Argentine ants, we saw brood abandonment and death of workers. However, the fire ant queens escaped from nests that were under attack by the Argentine ants, and they were not killed during the experiments. Although Argentine ants were quick to attack fire ant colonies consisting of 1,100 workers, the fire ants did not abandon their brood or queens. On the contrary, they took control of the bridge connecting the colonies, invaded the *L. humile* colony, killed its queens, and removed its brood.

Argentine ants are proficient at both exploitative and interference competition with respect to native ant species (Holway 1999). As a measure of interference competition, individual Argentine ants had only mixed success in one-on-one interactions with native ant species. However, due to numerical advantage, the Argentine ants displaced most native species from baits. In our experiments pairing 100 Argentine ants with 10 red imported fire ants, the ratio of dead Argentine ants to dead *S. invicta* varied from 3.8 to 14.7. In our colony encounters, the ratio was 1.8–4.4 (Table 1). Both Argentine ants and polygyne *S. invicta* have large, unicolonial populations. Therefore, where these

Table 4. Mortality, mortality ratio, control of the connecting bridge, and trial length of IGR-treated and untreated confrontations

IGR condition	% mortality (mean ± SE)		Mortality ratio (mean ± SE)	*S. invicta* control bridge (mean ± SE, h)	Trial length (mean ± SE, h)
	S. invicta	*L. humile*	*L. humile* to *S. invicta*		
Untreated	35 ± 2.8	85 ± 5.9	2.5 ± 0.08	3.0 ± 0.70	7.2 ± 0.20
IGR treated	31 ± 2.4	92 ± 1.0	3.1 ± 0.22	36.6 ± 26.51	37.6 ± 6.28

Kruskal–Wallis one-way analysis of variance was used for tests of significance (see text).

two species meet the Argentine ants may not be able to overcome their individual competitive disadvantage with numerical superiority.

Debilitation of workers in *S. invicta* colonies can have a dramatic impact on their ability to defend the colony or forage for food. Keck et al. (2005) demonstrated that infection of workers with the microsporidian pathogen, *Thelohania solenopsae,* reduced the ability of the colony to prevent invasion by the native ant species *M. minimum.* Presence of parasitic phorid flies in the genus *Pseudacteon* significantly reduced the competitive ability of *S. geminata* (Morrison 1999). In our experiments there were no significant differences in percent mortality and the mortality ratio between pyriproxyfen-treated and untreated *S. invicta* and *L. humile.* However, the IGR-treated colony took significantly longer to control the bridge connecting the colonies and for aggressive activity to end. These results imply a reduction in the aggressiveness of the fire ants as a result of the treatments. Furthermore, because brood production ceases when a colony is treated with an IGR, in the long-term IGR treated queens and colonies will not be able to produce more ants. The remaining ants will have reduced venom stored for defense and prey capture (Haight and Tschinkel 2003), and workers will have less incentive to forage, which might accelerate reinvasion by *L. humile.* Thus, the Argentine ant may play a vital role in the elimination of remnant fire ants after they have been treated with pesticides, and a major role as a competing species that can slow the spread of *S. invicta* in heavily infested *L. humile* areas of California.

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