

Population Growth of *Aphis gossypii* and *Myzus persicae* (Hemiptera: Aphididae) in the Presence of *Linepithema humile* and *Tapinoma sessile* (Hymenoptera: Formicidae)

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ABSTRACT Invasive ant species can have dramatic impacts on native ants, through direct predation and by usurping common resources. Most invasive ants and many native ants use honeydew, produced by phloem-sucking hemipterans. Because colonies of invasive ants can become very large after establishment, these ants may facilitate greater hemipteran trophobiont population growth compared with their sympatric native ant counterparts. We examined the population growth of an aphid mutualist, *Aphis gossypii*, and a nonmutualist, *Myzus persicae*, exposed to two Dolichoderine ants, *Linepithema humile*, a globally widespread invasive species, and *Tapinoma sessile*, a widespread co-occurring native ant, in North America in an enemy-free laboratory study. *L. humile* worker foraging activity was at least twice that of *T. sessile*, and populations of the myrmecophile, *A. gossypii*, were greater when exposed to *L. humile* than *T. sessile*, possibly caused, in part, by more frequent encounters with *L. humile*. *L. humile* ignored *M. persicae* when *A. gossypii* was absent, whereas *T. sessile* preyed on it. Both ant species preyed on *M. persicae* when *A. gossypii* was also present. This suggested that both ants may assess nutritional gains from aphid species (i.e., honeydew versus body tissue), eliminating less productive aphids competing for host plant space. Through their impact on populations of hemipteran mutualists, we suggest that colonies of *L. humile* and perhaps other invasive ants may acquire more honeydew than native ants, thereby fueling colony growth that leads to numerical dominance and widespread success in introduced environments.

KEY WORDS Argentine ant, odorous house ant, ant–aphid interaction, cotton aphid, green peach aphid

Invasive species are one of the most influential factors in reshaping natural ecological systems (Elton 1958, Mack et al. 2000). The impact invasive species have on ecosystems includes biodiversity reductions from direct competition and differential resource utilization relative to native species (Dantonio and Vitousek 1992, Liebhold et al. 1995, Franklin et al. 1999). Invasive species may also disrupt ecosystems by exploiting mutualisms (e.g., pollinator displacement, usurping valuable nectar, and pollen resources), although they may not completely replace their native counterparts (Traveset and Richardson 2006). Invasive ants are among the most influential groups that alter mutualisms (Holway et al. 2002, Lach 2003, Ness and Bronstein 2004, Styrsky and Eubanks 2007).

The Argentine ant, *Linepithema humile*, a globally widespread invasive ant, frequently eliminates epigeic ant species (Human and Gordon 1996, Holway 1998), including seed-dispersing native ants, thus negatively impacting plant diversity (Bond and Slingsby 1984, Christian 2001). Recently established facultative mutualisms between exotic scale insects and the invasive

yellow crazy ant, *Anoplolepis gracilipes*, have produced large increases in both ant and hemipteran populations, with consequent cascading trophic effects, including reduced terrestrial arthropod abundance and altered forest structure (O'Dowd et al. 2003). Subsequent removal of *A. gracilipes* resulted in the collapse of the hemipteran populations (Abbott and Green 2007).

Ants can alter hemipteran communities and populations, especially aphids, by providing or withdrawing protection from natural enemies (Whittaker 1991). The degree of ant attendance can be negatively correlated to aphid mobility, alarm pheromone production, and comparatively lower honeydew quality and quantity than other aphid species in the area (Way 1963, Nault and Montgomery 1976, Buckley 1987, Stadler and Dixon 2005). Differential tending by ants can directly affect the fate of individual hemipterans (Sakata 1994, Sakata and Hashimoto 2000). *Lasius niger* systematically marks some individuals of the aphids *Lachnus tropicalis* and *Myzocallis kuircola* for honeydew acquisition and leaves unmarked aphids for consumption (Sakata 1995). Thus, ants may remove unsuitable or nonmutualist aphid species or genotypes

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from their host plant and thereby foster individuals/species that may provide sustained benefits to the ants (Sakata 1994). Given the range of ant behaviors as potential aphid mutualists, ant species most likely use different decision-making processes (Sakata and Hashimoto 2000).

There is some evidence that hemipteran populations respond differently to the tending of native and invasive ants. For example, Haines and Haines (1978) showed that *Ceroplastus rubens* and *Coccus viridis* were ≈ 5 - to 160-fold more abundant on citrus trees in areas where *Anoplolepis gracilipes* tended them than in areas tended by the native ants. The tending mechanisms by which invasive ants differ from native ants are unknown but most likely are caused by behavioral differences (Holway et al. 2002).

Perhaps native and invasive ants respond differently to aphids, thereby causing shifts in aphid-community composition? Studies investigating differences between native and invasive ants have mostly been surveys comparing areas pre/postinvasion (Bond and Slingsby 1984, Christian 2001), presence/absence of invasive ants (O'Dowd et al. 2003, Abbott and Green 2007), or tending effects of ants without knowing the field population sizes of the ants involved in the mutualism (Haines and Haines 1978).

Herein we compare, in laboratory experiments, the impact of identical numbers of two dolichoderine ants, *Tapinoma sessile*, native to North America, and the widespread invasive *L. humile*, on populations of mutualist and nonmutualist honeydew-producing aphid species, both individually and in combination. We expected mutualist aphid populations to grow larger when tended by invasive *L. humile* and elicit larger numbers of ant foragers. We also expected nonmutualist aphids to be preyed on by both ant species and have fewer ants associated with them. If more than one hemipteran species is encountered, ants may prey on poorer honeydew producers to improve habitat for the more productive honeydew producers, so a mixed aphid species treatment was performed (Sakata and Hashimoto 2000). Understanding how a native and an invasive ant may differentially exploit hemipteran mutualisms can help identify factors underlying invasion success.

Materials and Methods

Organisms. *Linepithema humile* is a widespread invasive ant noted for its ability to disrupt mutualisms, aggressive nature, local abundance, and successful global spread (Holway et al. 2002, Rowles and O'Dowd 2007). Among the most ecologically and behaviorally similar native dolichoderine ant counterparts to *L. humile* occurring sympatrically in parts of North America is the odorous house ant, *Tapinoma sessile*. *L. humile* and *T. sessile* both form large polygynous and polydomous colonies, have impermanent nests, and sequester hemipteran honeydew (Buczowski and Bennett 2006, 2008). *Aphis gossypii* is widespread, polyphagous, and enters into facultative mutualisms with ants (Vinson and Scarborough 1989, Diaz et al. 2004, Kaplan and Eubanks

2005, Blüthgen et al. 2006) and is tended by both *L. humile* and *T. sessile* (Mondor et al. 2008, B.E.P., personal observations). *Myzus persicae* is a widespread, polyphagous aphid that excretes honeydew (Fisher et al. 1984, Hogervorst et al. 2007) but has never been reported to engage in mutualisms with ants.

Both ants and aphids were maintained in an insect growth chamber at 27°C and 70% RH. Ants were held in large Fluon-lined plastic containers (23.7 liters) supplied with nests of 75-mm petri dishes filled with grooved moist plaster. Ants were fed 25% sucrose solution, artificial diet (Bhatkar and Whitcomb 1970), and several freshly killed adult female cockroaches (*Blattella germanica*) weekly. Both *A. gossypii* and *M. persicae* were obtained from BASF (Research Triangle Park, NC) and were established on cotton (*Gossypium hirsutum*) and pepper (*Capsicum annuum*), respectively. Aphids were transferred every 10 d to fresh plant material. *Gossypium hirsutum* had two to four extra floral nectaries (EFN) throughout the course of the experiment (maximum on two cotyledons at the beginning of each experiment to a maximum of four at the end of the experiment). Although non-EFN (nectariless) cotton varieties are commercially available, modified plant physiology may influence the plant's palatability and thus adversely affect aphid honeydew production and quality (Scott et al. 1988, Hardee and Bryan 1997). Engel et al. (2001) showed that an individual EFN may produce up to twice the honeydew of a single aphid. We therefore set the starting aphid populations for our experiments at ≥ 100 individuals, giving a 25-fold advantage of honeydew production versus EFN production. Even though EFN can have a significant effect on certain ant-aphid interactions (Sakata and Hashimoto 2000), the trend is not universal (Del Claro and Oliveira 1993).

Experiment 1: Honeydew Consumption. We measured worker weight change of *L. humile* and *T. sessile* as an indirect measure of *A. gossypii* and *M. persicae* honeydew consumption. Twenty workers were haphazardly collected from the plant stem as they traveled toward the aphids, and 20 more were collected as they returned from the aphids. Workers were collected from three host plants for each aphid species. *L. humile* and *T. sessile* were confined to separate plants, with six (3×2 plants) per aphid species, for a total of 12 (3 plants/aphid-species \times 2 aphid species \times 2 ant species) plants. Ants were collected on 3 consecutive d from different plants; e.g., for each day, one plant with *M. persicae* + *T. sessile*, one plant with *M. persicae* + *L. humile*, one plant with *A. gossypii* + *T. sessile*, and one plant with *A. gossypii* + *L. humile*. Individual ants were placed in preweighed gelatin capsules and weighed on an electrobalance (Cahn 27 Electrobalance; Thermo Scientific, Beverly, MA). We noted if aphids were being removed during the ant weight assessment. Changes in ant weight were analyzed using a mixed linear model, with the plant as a random effect nested within ant species and aphid species combination, and ant species, aphid species, and action (up, down) taken as fixed effects. A separate residual variance was modeled for each ant spe-

cies. Covariance parameters estimated as zero were dropped from model, and Satterthwaite's correction was applied in the calculation of denominator degrees of freedom for *F*-tests of fixed effects, and SE of the least squares means to account for missing observations and covariance structure (Little et al. 2006). Counts were square root transformed before analysis. One degree of freedom contrasts were used for comparison between ant species. Analyses were conducted using SAS 9.1.3 (PROC MIXED, SAS Institute 2002).

Experiment 2: Single Hemipteran Species Response to Ant Attendance. We studied the response of populations of each aphid species to either ant across time. One hundred *A. gossypii* were transferred to cotton cotyledons, revealing the first true leaf or 100 *M. persicae* were introduced to pepper plants revealing the first two true leaves. Host plants (≈ 150 mm tall) were rooted in 355-ml plastic pots (Solo Cup, Highland Park, IL) with commercial potting soil and placed in Fluon-coated plastic containers (3.75 liters). After the aphids were transferred to the plants (24 h), 100 workers and 1 queen of each ant species were placed into a 3.75-liter plastic container with a petri dish nest filled with moistened, grooved plaster, one ant species per container. Ants were provided water (25 ml), artificial diet (100 μ l), and two freshly killed adult female *B. germanica* weekly. Both *L. humile* and *T. sessile* quickly vacated the plaster nest and entered the soil-filled pots within 24 h. We established a full set of treatments, with each ant species exposed to plants that had either one of the aphid species or were control aphid-free plants; and, as additional control treatments, each aphid species was present in host control plants with no ants. Thus, there were two different controls: (1) each ant species foraging on aphid-free plants to account for nonspecific ant activity on plants or ant activity not necessarily associated with aphid attendance and (2) aphids on host plants with no ants present. All experimental and control treatments were replicated 10 times. We measured ant activity by counting all ants present on each plant at a single point in time (≈ 1030) daily. We recorded the number of aphids on each plant every 1–3 d for 3–4 wk. Experiments were terminated once the host plant began losing its leaves. We recorded ant mortality after drying the soil in which the ants were nesting and counted ants that moved into an adjacent petri dish nest filled with moistened, grooved plaster. Changes in ant foraging activity and aphid populations through time were analyzed using SAS 9.1.3 with plant as a random effect nested within treatment (which are defined depending on whether ant counts or aphid counts were studied, and represent each ant species present or no ant species, but either aphid species present; and for aphid counts, no aphids but either ant species present), and treatment, day, and their interaction taken as fixed effects. A separate residual variance with day as a repeated measure factor following a covariance structure that accounts for higher covariance between two time points close in time, and covariance

decreasing as time points increase their distance in time, was modeled for each response. Covariance parameters estimated as zero were dropped from model, and Satterthwaite's correction was applied in the calculation of denominator degrees of freedom for *F*-tests of fixed effects and of SE for least squares means (PROC MIXED, Little et al. 2006). Analyses were run for ant counts and aphid counts separately for each aphid species. Counts were square root transformed before analysis. One degree of freedom contrasts were used for comparison between treatments. Analyses were conducted in SAS 9.1.3 (PROC MIXED, SAS Institute 2002). Ant mortality was analyzed using an analysis of variance (ANOVA) model in SAS 9.1.3 (PROC GLM, SAS Institute 2002).

Experiment 3: Mixed Hemipteran Species Response to Ant Attendance. We studied foraging ant activity and aphid population changes when each ant species was given access to both aphid species simultaneously. Paired cotton plants with 100 *A. gossypii* and pepper plants with 100 *M. persicae* were held in containers with ants as described in experiment 2. We included control plants with aphids but no ants. All experimental and control treatments were replicated 10 times. This experiment was terminated at a point when *C. annuum* was largely unsuitable to *M. persicae* so that ant effect on both aphids could be directly compared. We recorded and analyzed ant activity and aphid numbers as a repeated-measures model. For the ant-count response, the mixed model has treatment (ant-aphid combination) day and the treatment by day interaction as fixed effects; plant nested within each treatment as random effect, with day considered as repeated measures. For the aphid-count response, the mixed model includes ant-treatment (ant species + plus control), day, and treatment by day interaction considered fixed effects and plant nested within each treatment as random effect, with day considered as repeated measures. Residual covariance structure was modeled following a pattern that accounts for higher covariance between pair of time points close in time and covariance between any pair of points farther apart in time decreasing as a function of the time interval between the points (PROC MIXED, Little et al. 2006). For *A. gossypii*, covariance parameters were estimated separately for each treatment group, whereas for *M. persicae*, covariance parameters were estimated over all treatment groups. Covariance parameters estimated as zero were dropped from the model. Satterthwaite's correction was used to calculate degrees of freedom and SE of least square means. Analyses were conducted separately for ant counts and each aphid species count. *A. gossypii* counts were log-transformed before analysis. *M. persicae* counts were square-root transformed before analysis. Ant counts were not subjected to any transformation before analysis. Analyses were conducted in SAS 9.1.3 (PROC MIXED, SAS Institute 2002).

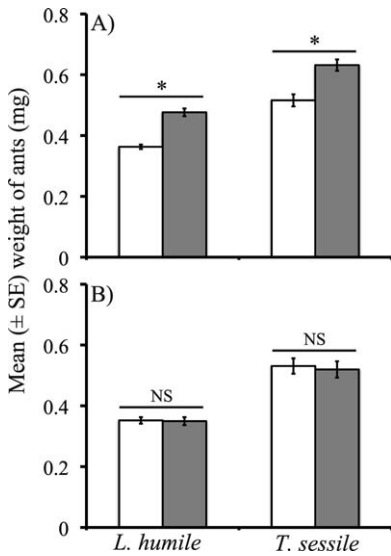


Fig. 1. Mean (\pm SE) weight of ants traveling up (\square) and down (\blacksquare) (A) *G. hirsutum* and (B) *C. annuum* infested with *A. gossypii* and *M. persicae*, respectively (* $P < 0.05$).

Results

Experiment 1: Honeydew Consumption. Differences in ant worker weight were recorded between aphid species, ant species, and direction of ant movement (ascend v descend) ($P < 0.0001$). There was also an aphid species by direction interaction ($P < 0.0001$). Analysis of 1-df contrasts for simple effects show that descending workers were heavier than ascending workers on plants with *A. gossypii* for both ant species

(*L. humile*: $F_{1,116} = 50.94$, $P < 0.0001$, *T. sessile*: $F_{1,116} = 12.71$, $P = 0.0005$; Fig. 1). In contrast, weights of descending worker ants on plants infested with *M. persicae* were not different from ascending workers for either *L. humile* or *T. sessile*, (*L. humile*: $F_{1,116} = 0.02$, $P = 0.88$, *T. sessile*: $F_{1,116} = 0.12$, $P = 0.73$; Fig. 1). Therefore, both ants were likely obtaining honeydew from *A. gossypii* but not *M. persicae*. *T. sessile* workers were observed carrying *M. persicae* in their mandibles from the plants during ant weight assessment. Covariance parameter estimate for plant effect was estimated as zero and dropped from the model.

Experiment 2: Single Hemipteran Species Response to Ant Attendance. Aphid counts for both aphid species were significant ($P < 0.0001$) for treatment, day, and treatment by day interaction. Similarly, ant counts for both aphid species were significant ($P < 0.0001$) for treatment, day, and treatment by day interaction. One degree of freedom contrasts for aphid count differences between treatments on average over days show that *L. humile* and *T. sessile* both tended *A. gossypii*; however, *L. humile*-tended populations of *A. gossypii* were approximately twice as large as those tended by *T. sessile* ($F_{1,34} = 93.12$, $P < 0.0001$; Fig. 2A). We did not observe *L. humile* interacting with *M. persicae*, and numbers of *M. persicae* did not differ on tended plants from numbers on untended plants when *L. humile* was present ($F_{1,44.9} = 0.42$, $P = 0.5183$; Fig. 2C). *T. sessile* were observed preying on *M. persicae* and consequently all aphids were eliminated by day 4, showing an overall significant difference on average count over time with respect to the control ($F_{1,36.5} = 483.13$, $P < 0.0001$; Fig. 2C). Both ant species, on average over time, were more numerous on plants

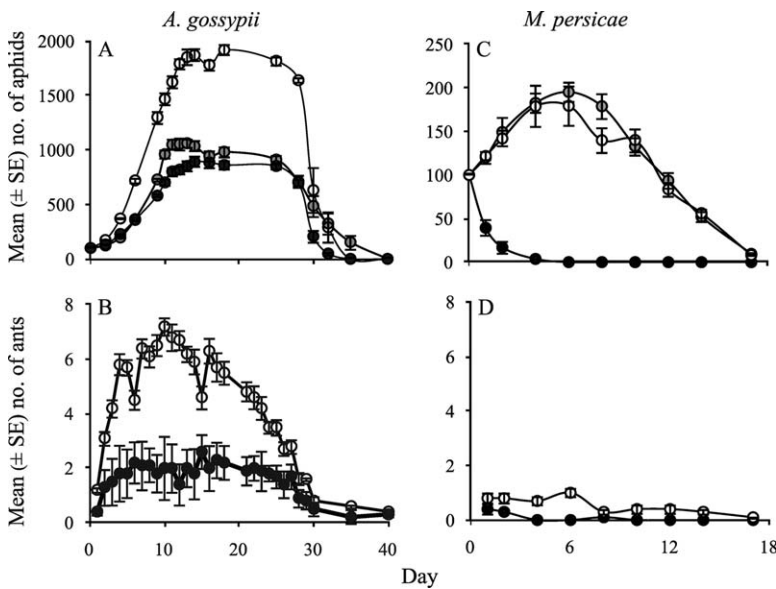


Fig. 2. Effect of ants on aphid populations and ant activity in single aphid species assays. (A) Mean (\pm SE) *A. gossypii* populations per plant over time. (B) Mean (\pm SE) number of ants on cotton plants over time. (C) Mean (\pm SE) *M. persicae* populations per plant over time. (D) Mean (\pm SE) number of ants on pepper plants over time. \circ = *L. humile* present; \bullet = *T. sessile* present, $\bullet\bullet$ = no ants present.

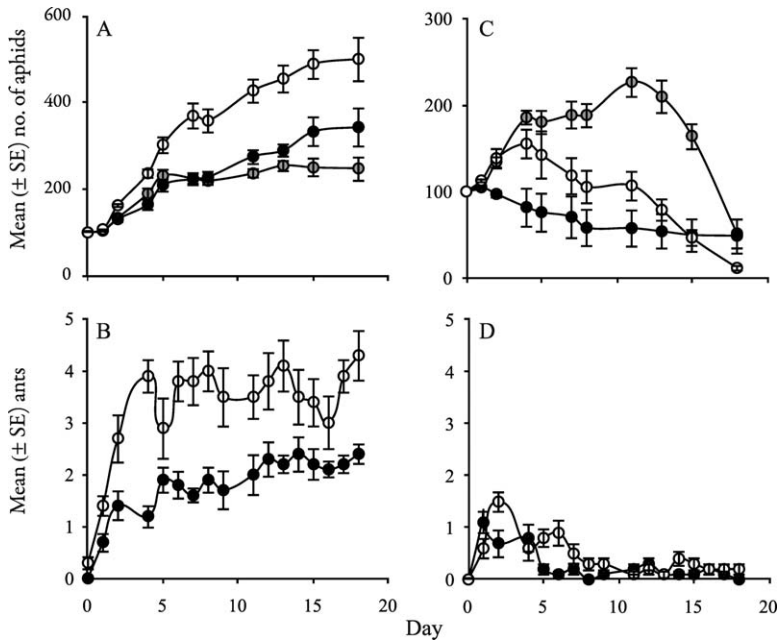


Fig. 3. Effect of ants on aphid populations and ant activity in mixed aphid species assays. (A) Mean (\pm SE) *A. gossypii* populations per plant over time. (B) Mean (\pm SE) number of ants on cotton plants over time. (C) Mean (\pm SE) *M. persicae* populations per plant over time. (D) Mean (\pm SE) number of ants on pepper plants over time. \circ = *L. humile* present; \bullet = *T. sessile* present; $\bullet\bullet$, no ants present.

with *A. gossypii* than on uninfested *G. hirsutum* (*L. humile*: $F_{1,36.5} = 108.43$, $P < 0.0001$, *T. sessile*: $F_{1,33.8} = 41.78$, $P < 0.0001$; Fig. 2B). Over time, the number of *L. humile* foraging on plants with *A. gossypii* was approximately three-fold greater than the number of foraging *T. sessile* ($F_{1,37.6} = 35.99$, $P < 0.0001$; Fig. 2B). Pepper plants with or without *M. persicae* showed almost no foraging activity by either ant (*L. humile*: $F_{1,39.9} = 2.74$, $P = 0.11$; *T. sessile*: $F_{1,19.9} = 0.00$, $P = 0.9652$; Fig. 2D). There was no difference in the mortality of worker ants between aphid-present treatments or controls among the *A. gossypii* ($F_{3,36} = 0.13$, $P = 0.94$) or *M. persicae* ($F_{3,36} = 1.16$, $P = 0.34$) trials. We noted ant brood and queens in all applicable replicates at the end of the experiments.

Experiment 3: Mixed Hemipteran Species Response to Ant Attendance. Aphid counts for both aphid species were significant ($P < 0.0001$) for treatment, day, and treatment by day interaction. Similarly, ant counts were significant ($P < 0.0001$) for treatment, day, and treatment by day interaction. One degree of freedom contrasts were used to analyze aphid count and ant count differences between treatments on average over days. When either ant species had access to both *A. gossypii* and *M. persicae*, *A. gossypii* numbers were significantly larger when tended by *L. humile* than *T. sessile* ($F_{1,29.6} = 11.89$, $P = 0.0017$; Fig. 3A) or when *A. gossypii* were left untended ($F_{1,29.6} = 16.06$, $P = 0.0004$; Fig. 3A). There was no difference in *A. gossypii* population size through time when untended by ants or tended by *T. sessile* ($F_{1,29.6} = 0.31$, $P =$

0.5801; Fig. 3A). In contrast to the neutral effect *L. humile* had on *M. persicae* in single aphid treatments (Fig. 2C), *M. persicae* numbers declined in the presence of either ant species in treatments when *A. gossypii* were also present (*L. humile*: $F_{1,21.5} = 10.74$, $P = 0.0035$, *T. sessile*: $F_{1,16.9} = 14.45$, $P = 0.0014$; Fig. 3B). *M. persicae* populations declined similarly in the presence of either ant species ($F_{1,17.3} = 3.18$, $P = 0.0922$; Fig. 3B). Similar to the single aphid species trials, analysis of ant counts show that when ants had access to both *A. gossypii* and *M. persicae*, *L. humile* activity was higher than *T. sessile* on cotton ($F_{1,54.2} = 52.95$, $P < 0.0001$; Fig. 3C) but not on pepper ($F_{1,6.81} = 1.65$, $P = 0.24$; Fig. 3D). Again, there was no difference in the mortality of worker ants ($F_{3,36} = 2.21$, $P = 0.15$), and brood and queens were present in all applicable replicates at the end of the experiments.

Discussion

Besides providing protection against natural enemies (Buckley 1987, Stadler and Dixon 2005), increased reproductive output may be one direct physiological benefit that aphids experience from ants (El-Ziady and Kennedy 1956, Flatt and Weisser 2000). However, ant attendance can lead to costs in life history parameters, including prolonged developmental time and delayed offspring production (Stadler and Dixon 1998, Stadler et al. 2002, Yao et al. 2000). We report *A. gossypii* population increases when tended by either *L. humile* or *T. sessile* in enemy-free space, although populations grew much larger when tended by *L. humile*, with

more foraging *L. humile* on *A. gossypii*-infested cotton plants. It is not clear why *L. humile*-tended *A. gossypii* populations were larger than those tended by *T. sessile*. Hemipteran honeydew is an important food resource for many ants (Tobin 1994, Davidson et al. 2004), and ants can manipulate hemipteran populations to optimize honeydew output (Sakata 1994, 1995). Therefore, sharp rises in *A. gossypii* numbers may be in response to specific interactions with *L. humile* and/or the frequency of these interactions. *L. humile* may not use a unique behavior(s) to stimulate increased aphid reproduction; instead, aphids may respond to a threshold level of individual tending interactions. Positive correlations between ant number and hemipteran population size have been documented between *Formica altipetens* and *Pubilia modesta* (Cushman and Whitman 1989). The relatively few *T. sessile* on cotton plants may have been insufficient to stimulate increased *A. gossypii* reproduction.

Linepithema humile workers largely ignored *M. persicae*, whereas *T. sessile* consumed *M. persicae* when *A. gossypii* was absent, suggesting that the nutritive assessment of *M. persicae* by these ants differed. Although *M. persicae* might use some type of chemical camouflage, it seems unlikely that such camouflage would be effective against only one of the ants in our system (Akino and Yamaoka 1998, Akino 2002). Interestingly, when *L. humile* had access to both *A. gossypii* and *M. persicae*, the latter was consumed, providing further evidence against chemical camouflage because *M. persicae* was discovered and removed. Aphids can compete for ant tending services both inter- and intraspecifically (Addicott 1978a, b) and under certain conditions ants will prey on both myrmecophilic and nonmyrmecophilic aphids (Sakata 1994, 1995, 1999; Sakata and Hashimoto 2000). It is possible that *L. humile* distinguished these aphids as productive or nonproductive, eliminating the presumably nonproductive *M. persicae*. This is somewhat puzzling because *M. persicae* produces honeydew with a composition similar to several other aphids, which is consumed by the parasitoid *Aphidius ervi* (Hogervorst et al. 2007).

We were unable to rear both *A. gossypii* and *M. persicae* on the same host plant, and thus, ant foraging may have been affected by the plant, directly through chemical and physical surface properties or indirectly through honeydew quality, rather than in response to the intrinsic characteristics of the aphids. However, we observed both *L. humile* and *T. sessile* foraging on aphid-free *G. hirsutum* and *C. annuum*. Ants, including *T. sessile* and *Linepithema* sp., occur where *C. annuum* is grown (Reddy 1985, Hernández-Ruiz and Castaño-Meneses 2006), and biological control of aphids on *C. annuum* was impaired by ants foraging on plant surfaces (Tulisalo et al. 1977), indicating that ants were not deterred by the surface of *C. annuum*.

Although showing an apparent benefit to *A. gossypii* from interactions with *L. humile* compared with *T. sessile*, we cannot conclude that this benefit is linked to one or more traits characteristic of invasive Argentine ant populations. Similar comparisons between other native and invasive ant species are needed to

better understand the role of mutualisms in invasion success (Ness and Bronstein 2004, Lach 2008). After their introduction, Argentine ants displace most epigeic native ants and many other arthropods (Holway et al. 2002), and they likely shift their diet to honeydew-producing Hemiptera (Tillberg et al. 2007). Thus, the expansive colonies of Argentine ants and other invasive ants may be, in large part, fueled by hemipteran honeydew (Helms and Vinson 2002, Holway et al. 2002, Abbott and Green 2007). Also, understanding the relative impact on hemipteran mutualist natural enemies by *L. humile* and other invasive ants compared with native ants is necessary to understand ant invasions within a broader ecological framework.

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