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WIDESPREAD ASSOCIATION OF THE INVASIVE ANT *SOLENOPSIS INVICTA* WITH AN INVASIVE MEALYBUG

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Abstract. Factors such as aggressiveness and adaptation to disturbed environments have been suggested as important characteristics of invasive ant species, but diet has rarely been considered. However, because invasive ants reach extraordinary densities at introduced locations, increased feeding efficiency or increased exploitation of new foods should be important in their success.

Earlier studies suggest that honeydew produced by Homoptera (e.g., aphids, mealybugs, scale insects) may be important in the diet of the invasive ant species *Solenopsis invicta*. To determine if this is the case, we studied associations of *S. invicta* and Homoptera in east Texas and conducted a regional survey for such associations throughout the species' range in the southeast United States. In east Texas, we found that *S. invicta* tended Homoptera extensively and actively constructed shelters around them. The shelters housed a variety of Homoptera whose frequency differed according to either site location or season, presumably because of differences in host plant availability and temperature. Overall, we estimate that the honeydew produced in Homoptera shelters at study sites in east Texas could supply nearly one-half of the daily energetic requirements of an *S. invicta* colony. Of that, 70% may come from a single species of invasive Homoptera, the mealybug *Antonina graminis*. Homoptera shelters were also common at regional survey sites and *A. graminis* occurred in shelters at nine of 11 survey sites. A comparison of shelter densities at survey sites and in east Texas suggests that our results from east Texas could apply throughout the range of *S. invicta* in the southeast United States. *Antonina graminis* may be an exceptionally important nutritional resource for *S. invicta* in the southeast United States. While it remains largely unstudied, the tending of introduced or invasive Homoptera also appears important to other, and perhaps all, invasive ant species. Exploitative or mutually beneficial associations that occur between these insects may be an important, previously unrecognized factor promoting their success.

Key words: Antonina graminis; Antoninoides; *ants; biological invasion; energy budget; Homoptera; honeydew; invasive species; mealybugs; mutualism; Pseudococcidae;* Solenopsis invicta.

INTRODUCTION

Species are considered invasive if they are transported outside their native range and become established, spread, and adversely impact the environment (Mack et al. 2000). Invasive species are now recognized as one of the most important current threats to ecosystems (e.g., U.S. Congress 1993, Vermeij 1996, Vitousek et al. 1996). Considerable effort has been devoted to determining characteristics invasive species share in common in order to evaluate the risk of invasion by ''new'' species and to identify approaches to management of those already established (e.g., Reichard and Hamilton 1997, Mack et al. 2000). While these attempts are largely unsuccessful when comparing the characteristics of taxonomically diverse species, they can be more successful at identifying shared characteristics among invasive species of closer taxonomic affinity (e.g., Crawley 1987, Mack et al. 2000). Invasive ant species appear to be one case where shared characteristics do occur (Passera 1994, McGlynn 1999).

Of the ~9000 known ant species, only ~150 are known to be established outside their native ranges, and only nine are generally considered invasive: *Anopolepis custodiens* (F. Smith), *Linepithema humile* (Mayr), *Paratrechina fulva* (Mayr), *Paratrechina longicornis* (Latreille), *Pheidole megacephala* (Fabricius), *Solenopsis geminata* (Fabricius), *Solenopsis invicta* (Buren) (=*S. wagneri* (Santschi)), *Solenopsis richteri* Forel, and *Wasmannia auropunctata* (Roger) (Hölldobler and Wilson 1990, McGlynn 1999). Of these, the impacts of *L. humile*, *P. megacephala*, *S. invicta*, and *W. auropunctata*, are considered particularly severe (Hölldobler and Wilson 1990, Williams 1994). Shared characteristics that appear important in the success of invasive ants are aggressiveness toward other ant species, and generalist ecologies adapted to disturbed environments (e.g., Passera 1994, McGlynn 1999). In addition, invasive ants are commonly associated with honeydew-producing Homoptera (e.g., aphids, mealy-

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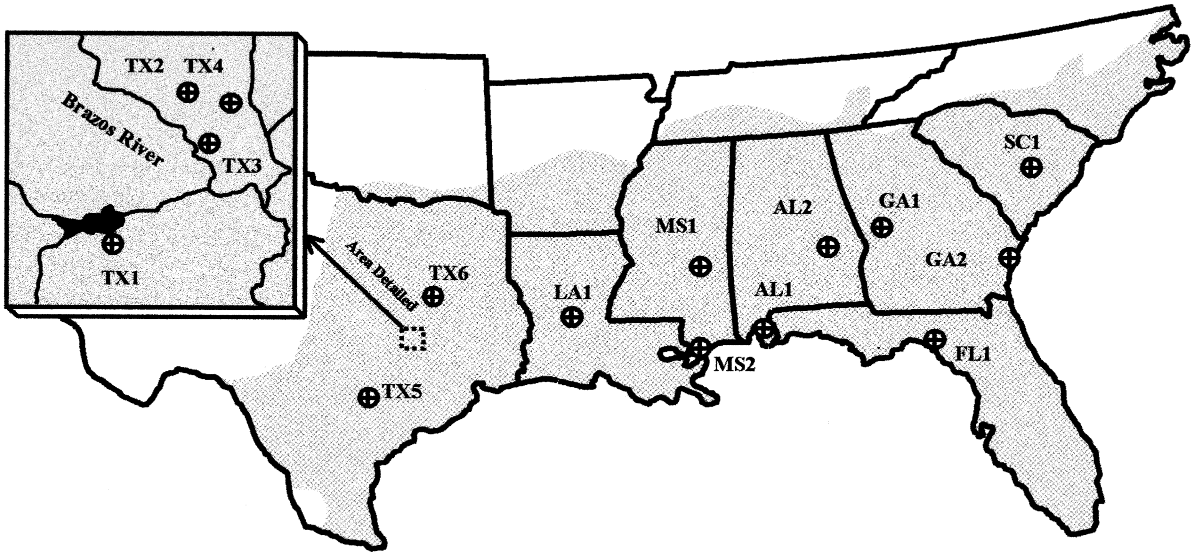

FIG. 1. Study sites located throughout the range of *Solenopsis invicta* in the southeast United States. The shaded area approximates the range of *S. invicta* in the region and is adapted from a quarantine map for imported fire ants (dated May 2000) produced by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (available online).[2] Information on the sites is given in Appendix A.

bugs, scale insects; e.g., Edwards 1936, Steyn 1955, Markin 1970, Clark et al. 1982, Lubin 1984, Wojcik 1986, Rohrbach et al. 1988, Bach 1991, Delabie et al. 1994, Wetterer et al. 1999). Such associations could be important in the invasion process (Simberloff and Von Holle 1999), but the theory that Homoptera promote the success of invasive ants (Davidson 1998) has remained untested.

The red imported fire ant, *S. invicta*, is native to South America, and is now an exceptionally important invasive species in the United States. It reaches tremendous densities and causes local if not regional extinctions of some native ants and reduced frequencies of others (Porter and Savignano 1990, Gotelli and Arnett 2000). It also adversely affects other invertebrate and vertebrate species, and is an important pest in natural or seminatural, agricultural, and urban ecosystems (Porter and Savignano 1990, Vinson 1997, Taber 2000). *Solenopsis invicta* and other invasive ant species can exhibit tremendous increases in biomass at introduced locations (e.g., Porter and Savignano 1990, Zenner-Polania 1994), suggesting that either increased feeding efficiency or increased exploitation of new foods is associated with invasion success (Moller 1996). The role of *S. invicta* as a predator and scavenger of arthropods has been addressed extensively (reviewed by Taber 2000), while tending Homoptera for honeydew has been addressed less frequently (e.g., Burns 1964, Smith and Denmark 1984, Wojcik 1986). However, a study of *S. invicta*, found that nearly 80% of successful foragers returning to their nests return with only liquid food (Tennant and Porter 1991). The nutritional composition of these liquids included sugars in concentrations consistent with honeydew, but may also have come from extrafloral nectaries or otherwise directly from plants (Tennant and Porter 1991). Tennant and Porter (1991) were unable to determine which might be the case. In our study, we determine the importance of Homoptera to *S. invicta*, and determine which Homoptera are most important. Our results show that an apparently important association occurs between *S. invicta* and an invasive mealybug, and that such associations may be an important shared characteristic of invasive ant species.

METHODS

Study sites and plants

Our study was conducted from September 1999 through July 2000. Four sites in east Texas (sites TX1–TX4) were studied extensively, while a regional survey was conducted at 11 other sites located in seven states throughout the range of *S. invicta* in the southeast United States (Fig. 1). Although the sites varied in specific habitat type (Appendix A), all were located outside of agricultural systems. We did not determine whether the *S. invicta* colonies at our study sites were monogyne (single queen) or polygyne (multiple queen); however, it is very likely that both forms occurred (e.g., Porter 1993). Our study focused on Homoptera occurring in Homoptera shelters (e.g., Way 1963), of which two types occurred: shelters on plants above ground level (aboveground shelters), and those at ground level (ground shelters). In our study, aboveground shelters occurred on a single species of broadleaf forb, *Helenium amarum*, while ground shelters occurred on grasses

[2] URL: ⟨http://www.aphis.usda.gov/ppq/maps⟩

in the genera *Andropogon*, *Aristida*, *Bouteloua*, *Chasmanthium*, *Cynodon*, *Dactyloctenium*, *Dicanthelium*, *Eragrostis*, *Leptoloma*, *Panicum*, *Paspalum*, and *Tridens*, and on broadleaf forbs in *Ambrosia*, *Helenium*, and a number of unidentified genera. A partial list of the individual plant species is provided by Helms and Vinson (2000). Plant identifications follow the taxonomy of Gould (1975) and Hatch and Pluhar (1999).

Association of shelters, Homoptera, and Solenopsis invicta

Since ground shelters housing Homoptera have never been reported associated with *S. invicta*, we first conducted a quantitative test for their association with this species. To do so, we unearthed plants where ground shelters occurred and plants where they did not occur and determined whether Homoptera or *S. invicta* were present on plants under shelters. To control for potential host plant species or location preferences of Homoptera and *S. invicta*, we assessed plants without ground shelters only if they were a species on which ground shelters occurred and only when both occurred together (i.e., plants with and without shelters were intermixed). Plants were sampled as encountered, so that frequencies of plant species in samples would approximate the frequencies at which they occurred at the sites. Samples were from six species of grasses and three species of broadleaf forbs. The areas in which these samples were unearthed ranged in size from 150 m^2 at TX2 to 550 m^2 at TX3. A total of 863 plants were sampled, 224 plants at TX1 (127 with shelters, 97 without shelters), 184 plants at TX2 (119 with shelters, 65 without shelters), 196 plants at TX3 (101 with shelters, 95 without shelters), and 259 plants at TX4 (181 with shelters, 78 without shelters). This study was conducted from late September through mid-October 1999, at sites TX1–TX4.

In mid-May 1999, we also tested for association between *S. invicta* and aboveground shelters occurring in a 0.6-ha meadow, ~1 km from site TX3. The location is described by Helms and Vinson (2001). As with ground shelters, we determined whether or not Homoptera and *S. invicta* were present on intermixed plants with and without shelters.

Characteristics and construction of Homoptera shelters

To provide a description of Homoptera ground shelters, we measured a sample of those occurring on four plant species where ground shelters occurred commonly. We also measured the upper and lower location of Homoptera relative to surrounding ground level to determine whether Homoptera would be exposed above ground level in the absence of ground shelters. Observations on Homoptera ground shelter construction and repair were made ad libitum (Altmann 1974) during 28 d (>200 h) in the field during the 10-mo study. We also observed ground-shelter construction by experimentally destroying shelters on 30 individuals of four grass species in September 1999. We observed those shelters for 1 h following shelter destruction, then returned the following day to determine shelter conditions.

Because aboveground shelters occurred for only a short time during our study, we were unable to observe construction or repair of those shelters. Those shelters always housed aphid colonies; however, aphid colonies were common on plants without shelters as well as on plants with shelters. Therefore, we tested whether *S. invicta* was associated with shelter occurrence by measuring the distance between plants with aphid colonies housed in shelters to the nearest *S. invicta* mound and measuring the distance between plants with aphid colonies but without shelters to the nearest *S. invicta* mound. All aphid colonies we were able to locate ($N = 48$) were measured. We predicted that if *S. invicta* constructed the shelters that aphid colonies in shelters would be closer to *S. invicta* nests than would aphid colonies without shelters.

Homoptera identification, numbers, and biomass

Samples of Homoptera occurring in shelters were preserved, mounted on microscope slides, and identified under a compound microscope as described by Helms and Vinson (2000). Based on these identifications, we classified Homoptera into five groups that could be distinguished unambiguously in the field or under low (64-power) magnification: (1) *Antoninoides* spp. (legless mealybugs), (2) *Antonina graminis* (legless mealybug), (3) legged mealybugs, (4) soft scales (Coccidae), and (5) aphids (Aphididae). Of these groups that occurred at our study sites, only *Antoninoides* spp. and *A. graminis* are similar morphologically, but can be distinguished without mounting because of marked differences in integument color as well as by sclerotization at the posterior end of the body (McDaniel 1972, Hendricks and Kosztarab 1999).

To estimate the number of Homoptera in ground shelters, we collected plants where shelters occurred, then counted them under low magnification. Legged mealybugs were collected at site TX1 in mid-October 1999, from 18 shelters on four species of broadleaf forbs. *Antoninoides* were collected at sites TX1, TX3, and TX4, in mid-July 2000, from 33 shelters on four grass species. *Antonina graminis* were collected on the same dates, at the same sites, as the *Antoninoides* samples, but from 73 shelters on seven grass species. We also estimated the numbers of aphids in aboveground shelters occurring near site TX3 in mid-May 1999. There, we selected three plants, one with a large shelter, one with a medium-sized shelter, and one with a small shelter, and counted the number of aphids present under low magnification.

To estimate the mass of Homoptera occurring in ground shelters, we collected host plants with shelters, took them to the laboratory, and separated Homoptera from plants. Individuals from each Homoptera group were weighed in aggregate while alive. The wax felt that covers *Antoninoides* spp. and *A. graminis* (Chada and Wood 1960, Hendricks and Kosztarab 1999) was removed before weighing. Average mass of legged mealybugs was estimated from 50 individuals of two typical species collected in mid-May 2000. One species occurred in shelters on a grass at TX3 (19 individuals), and the other occurred in shelters on a broadleaf forb at TX4 (31 individuals). Average mass of *Antoninoides* species was estimated from 69 individuals occurring on four grass species, and average mass of *A. graminis* was estimated from 149 individuals occurring on seven grass species. The *Antoninoides* and *A. graminis* were collected in July 2000 at sites TX1 (16 *Antoninoides*, 39 *A. graminis*), TX3 (43 *Antoninoides*, 82 *A. graminis*), and TX4 (10 *Antoninoides*, 28 *A. graminis*). Immature as well as adult individuals occurred in samples of *A. graminis*, *Antoninoides* spp., and legged mealybugs in all seasons, and we observed no obvious differences between seasons in body size distributions.

Temporal and spatial aspects of Homoptera ground-shelter density

To estimate the density of Homoptera shelters associated with *S. invicta* colonies, we counted the numbers of shelters within a circular area with a radius of 3 m from the center of active *S. invicta* mounds (area size = 28.26 m^2). Size of the area was selected because a distance of 3 m from a mound should generally be inside the territory of a colony occurring in a mound, while maintaining a distance of $>$3 m from the territory of a neighbor colony (Tschinkel et al. 1995; K. R. Helms, *unpublished observations*). In some cases (10/77), complete counts of all shelters within the 3 m radius were made; however, high shelter and/or plant density often made complete counts prohibitively time-consuming. When that occurred, the area sampled was a half circle with a radius of 3 m (24/77 cases), or a quarter circle with a radius of 3 m (43/77 cases). Which segment of the circular area was sampled was selected at random. Overall, 2147 shelters occurring around 86 *S. invicta* mounds were sampled in this part of the study. The shelters occurred on at least 20 different plant species. *Solenopsis invicta* mounds were common at all sites and selected for study as they were encountered. Although sites were studied in different seasons (see below), each mound was sampled only once.

To determine whether the density of ground shelters occurring around *S. invicta* colonies differed over time, we sampled shelters around 30 *S. invicta* mounds (10 at TX1, TX3, TX4) during the spring (24 April–8 May 2000), from around 12 mounds (four at TX1, TX3, TX4) during the summer (11–14 July 2000), and from around 44 mounds (11 at TX1, 9 at TX2, 10 at TX3, 14 at TX4) during the fall (23 September–11 October 1999). Site TX2 could only be sampled in the fall; however, data from the site was similar to fall data from the other sites (and not statistically different in any comparison), so data from the site were used in comparisons among seasons, but excluded from comparisons where data from different seasons were pooled within sites.

For each season, we estimated the frequency of different Homoptera groups in shelters by recording the numbers of shelters for each plant species and then collecting samples of those plants. Samples were collected for each plant species present around each *S. invicta* mound at each site. These samples were taken to the laboratory and the Homoptera present were determined. Homoptera present on samples were inferred present in shelters of individuals of those same plant species remaining in the field. If one to five individuals of a plant species were found with a ground shelter, at least one individual was collected; if six to 10 individuals were found with a ground shelter, at least two individuals were collected; if 11 or more individuals were found with a shelter, at least five individuals were collected. Overall, we collected 200 of 2147 plants with ground shelters for Homoptera determination. Occasionally, more than one Homoptera group occurred on the same plant species; in these cases, we assigned each Homoptera group as occurring in shelters on that plant species proportional to their occurrence in the collected samples.

Contribution of Homoptera honeydew to the energy budget of Solenopsis invicta

In order to estimate the contribution of Homoptera in shelters to the energy requirements of colonies of *S. invicta*, we first measured the dimensions of 31 *S. invicta* mounds where ground-shelter density was estimated at sites TX1–TX4. Twenty-one mounds were measured in the spring and 10 mounds were measured in the fall. These mounds were selected haphazardly, and appeared typical of mounds in our study. Mound dimensions were used to estimate a mean mound volume (Tschinkel 1993), which was used to estimate mean territory size (Tschinkel et al. 1995). We then estimated mean mass of Homoptera in shelters associated with an *S. invicta* colony for each Homoptera group i (M_i) by

$$M_i = T \times S \times N \times M$$

where T is mean *S. invicta* territory size in square meters, S is the number of shelters per square meter, N is the mean number of Homoptera per shelter, and M is the mass of an individual Homoptera. We then estimated the amount of honeydew these Homoptera produce by multiplying M_i by an estimate of the mass of honeydew produced per unit Homoptera body mass. Because there are no estimates for the rate of honeydew production by Homoptera in our study or, apparently, for any mealybug, we used an estimate of mass-specific honeydew production by the ant-tended aphid, *Tuberolachnus salignus* (Mittler 1958). Since Mittler

(1958) presented honeydew production rates for four instars and the adult, we have used the mean production rate across life stages for our estimate, i.e., mass of honeydew produced per hour = 70.2% of aphid body mass. Because there is no estimate of how closely the rate of honeydew production by the Homoptera in our study matches that of *T. salignus*, we also provide a range of estimates by assuming that honeydew production may vary by +50% of the *T. salignus* rate, i.e., that the rate of honeydew production may vary from 35.1% to 105.3% of Homoptera body mass per hour.

For our estimate of the energetic content of honeydew, we assumed that honeydew consists of 10% dry matter, of which 85% is carbohydrate and 15% protein (Auclair 1963, Degen et al. 1986). We also assumed that carbohydrate energy density is 16.74 kJ per gram dry mass and protein is 23.85 kJ per gram dry mass (Southwood 1966). Because soft scale and aphids, which occurred in ground shelters, were rare and occurred only in the spring, we were unable to estimate their biomass and did not include them in our estimate of the importance of honeydew to the energy budget of *S. invicta*. Aphid colonies in aboveground shelters were short-lived, did not occur at sites TX1–TX4, and were also excluded from energy budget estimates. We discuss the possible importance of Homoptera in aboveground shelters in a later section of the paper. In order to estimate the energetic requirements of an *S. invicta* colony in our study, we used our estimate of mound volume to estimate colony biomass (Tschinkel 1993), which allowed us to estimate energetic requirements from the mass specific energetic consumption found for *S. invicta* by Macom and Porter (1995) of 14.48 kJ/g ant dry mass/wk. This was compared to our estimate of energy available from Homoptera honeydew in ground shelters to provide a first estimate of the importance of honeydew to the energy budget of *S. invicta*.

Regional survey of Homoptera shelters

To determine whether Homoptera shelters are normally associated with *S. invicta* in the United States, we conducted a survey of 11 sites in addition to TX1–TX4. These sites were distributed across the range of *S. invicta* in the southeast United States (Fig. 1). Nine sites in six states other than Texas were sampled during 5–9 June 2000, with the remaining Texas sites (TX5, TX6) sampled on 28 and 30 June 2000 (Fig. 1). Two criteria were used in the selection of all sites: (1) sites were far enough apart such that they were fairly evenly distributed across the range of *S. invicta* in the southeast United States, and (2) the habitat was relatively open, such that *S. invicta* could be expected to occur (e.g., Tschinkel 1988). We had never visited the sites prior to this study and had no information on the occurrence of Homoptera shelters prior to sampling. At each site, we selected the first five active *S. invicta* mounds we encountered and determined Homoptera shelter density using the same procedures outlined for sites TX1–TX4. A secondary goal of the regional survey was to determine the frequency of occurrence of *A. graminis* in shelters, and therefore we identified the Homoptera found as either *A. graminis* or ‘‘other Homoptera.’’ Our estimates of the density of Homoptera shelters housing *A. graminis* at survey sites were used in estimating the importance of *A. graminis* to the energy budget of *S. invicta*, also using the same procedures outlined for sites TX1–TX4. We did not determine the numbers and biomass of *A. graminis* or the size of *S. invicta* mounds at survey sites, so we use the values for colony size and *A. graminis* biomass per shelter from TX1–TX4 to make our estimate.

Statistical procedures

Distributions of our data were significantly non-normal and/or exhibited significantly unequal variance. Transformations failed to correct these problems, so nonparametric tests were conducted. Post hoc, pairwise comparisons were conducted with the Student-Newman-Keuls method when sample sizes were equal among groups, or with Dunn's method when sample sizes differed among groups. Analyses were performed using SigmaStat version 2.03 software (SPSS, Chicago, Illinois). Tests for difference in the frequency of Homoptera and *S. invicta* on plants with shelters vs. plants without shelters were conducted with the G test of independence (Sokal and Rohlf 1995). All measures of statistical variance addressed are standard errors of the mean.

RESULTS

Homoptera ground shelters are roughly conical or ellipsoidal, with the apex occurring at or near the center of the plant (Fig. 2A). They are often inconspicuous and usually small, although size varies according to the species of plant on which they occur. The mean dimensions of shelters on two grasses (diameter × height) were 12.9 + 1.0 mm × 6.1 ± 0.5 mm (N = 35 *Aristida oligantha* plants) and 21.1 ± 1.2 mm × 10.8 ± 0.8 mm (N = 36 *Dicanthelium* spp. plants). The mean dimensions of shelters on two broadleaf plants were 71.8 ± 8.2 mm × 12.5 ± 3.45 mm (N = 11 *Helenium amarum* plants) and 44.2 ± 5.5 mm × 6.7 ± 0.6 mm (N = 20 plants of unidentified species). In general, larger plant species exhibit larger shelters (K. R. Helms, *unpublished observations*). Under shelters on the basal portion of plants, Homoptera nearly always occurred; more often than not, *S. invicta* also occurred. However, on plants of the same species but lacking shelters, Homoptera and *S. invicta* were largely absent. The association of Homoptera and *S. invicta* was strong and highly significant (Table 1).

Aboveground shelters were roughly shaped oblong structures, conforming to the general shape of the stem of the plants (Fig. 2B). They appear to have been constructed primarily of mud. Aphid colonies occurred

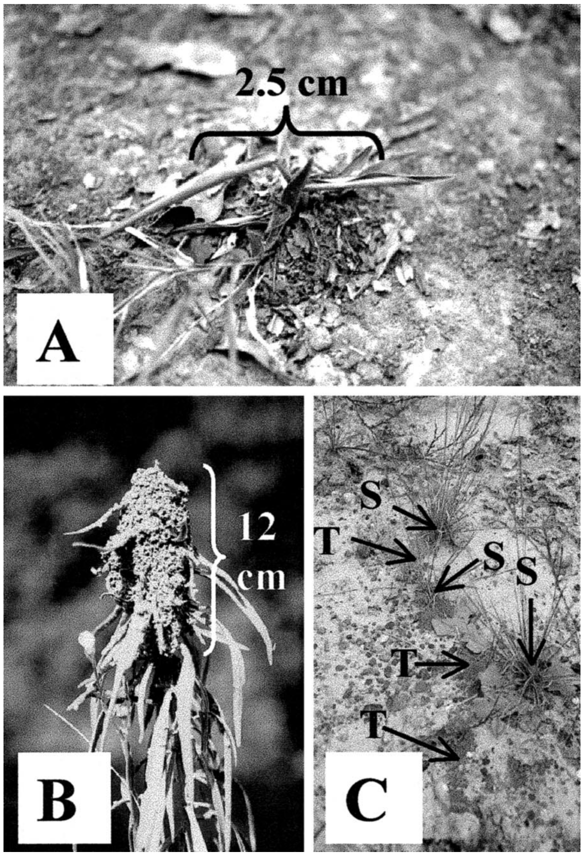

FIG. 2. Homoptera shelters constructed by *Solenopsis invicta*. (A) Ground shelter occurring on the grass *Dicanthelium* sp. housing the mealybug *Antonina graminis*. Debris surrounding the shelter has been brushed aside in order to make the shelter clearly visible. (B) Aboveground shelter occurring on the broadleaf forb *Helenium amarum* housing aphid colonies. (C) Soil deposited on the surface during repair of underground tunnel systems shows that ground shelters are linked via the underground tunnel system. The letter ''S'' indicates the location of shelters on the grass *Aristida oligantha*, and the letter ''T'' indicates deposited soil outlining tunnel locations.

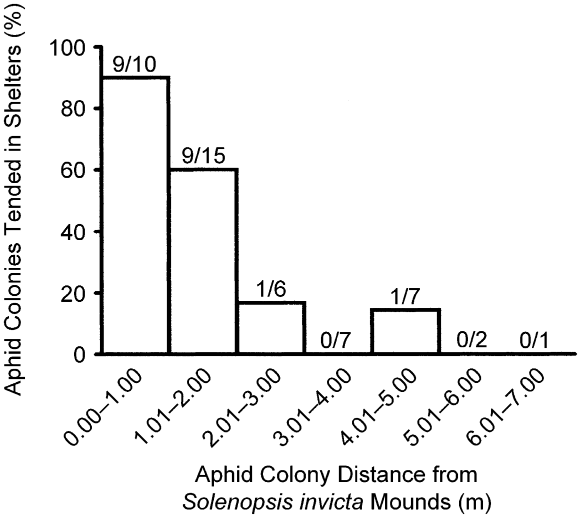

FIG. 3. The percentage of tended aphid colonies in aboveground shelters decreased with increasing distance from *Solenopsis invicta* mounds. All aphid colonies were being tended by *S. invicta*. Numbers above bars are numbers of aphid colonies with shelters/total numbers of aphid colonies at the particular distance range. Aphid colonies tended in shelters were significantly closer to *S. invicta* mounds than were aphid colonies tended without shelters ($T = 264.00$, $P < 0.001$, Mann-Whitney rank sum test).

within all 20 aboveground shelters found; aphid colonies were also found on 28 plants without shelters. Workers of *S. invicta* were tending aphids on all 48 plants. However, aphid colonies housed in shelters were significantly closer to *S. invicta* mounds than were aphid colonies without shelters, consistent with *S. invicta* construction of the shelters (Fig. 3). The average number of aphids in three aboveground shelters censused was 1421 ± 494 aphids.

Direct observation showed that Homoptera ground shelters are constructed by *S. invicta*. For example, rain on 24 and 25 September 1999, damaged shelters at sites TX2 and TX3. Afterward, we observed *S. invicta* workers repairing and reconstructing >50 shelters within 150-m^2 areas at both sites. Less frequently, we observed *S. invicta* workers placing debris on existing, apparently undisturbed shelter exteriors. When we ex-

TABLE 1. Homoptera and *Solenopsis invicta* are associated with Homoptera shelters.

		Homoptera				*Solenopsis invicta*			
Site	Shelters	Present	Absent	*G*†	*P*	Present	Absent	*G*†	*P*
TX1	present	114	13	186.4	<0.0001	70	57	98.9	<0.0001
	absent	5	92			0	97		
TX2	present	112	7	173.4	<0.0001	106	13	163.3	<0.0001
	absent	2	63			0	65		
TX3	present	92	9	166.3	<0.0001	29	64	42.5	<0.0001
	absent	6	89			0	95		
TX4	present	173	8	177.4	<0.0001	104	77	97.5	<0.0001
	absent	12	66			0	78		

† Test statistic from the *G* test of independence (Sokal and Rohlf 1995).

TABLE 2. A variety of honeydew-producing Homoptera are found in Homoptera shelters.

Homoptera	Host plants	Sites
Pseudococcidae (mealybugs)		
Legless		
Antonina graminis	grasses†	TX1, TX2, TX3, TX4, TX5, TX6, LA1, MS2, AL1,2, GA1,2, SC1
Antoninoides boutelouae	grasses†	TX3
Antoninoides nortoni	grasses†	TX2, TX3
Antoninoides parrotti	grasses†	TX1, TX2, TX3, TX4
Legged		
Chorizococcus sp.	grasses	TX1, TX2
Phenacoccus sp.‡	forbs	TX1, TX4
Trionymus sp.	grasses	TX3
Unidentified	grasses, forbs	TX1, TX2, TX3, TX4, TX5, TX6, LA1, MS1, MS2, AL1, AL2, GA1, GA2, SC1, FL1
Aclerdidae (grass scales)	grasses	LA1, MS1, GA1
Aphididae (aphids)	forbs	TX3, MS1, GA1
Coccidae (soft scales)	forbs	TX1

Note: Species taxonomy follows that of ScaleNet (Y. Ben-Dov, D. R. Miller, and G. A. D. Gibson [dated 2000]; available online).[3]

† See Helms and Vinson (2000) for list of host species found.

‡ *Phenacoccus solenopsis* and/or *Phenacoccus solani*.

perimentally destroyed shelters at TX2 and TX3, we observed *S. invicta* workers repairing 17 (11 of 15 at TX2, six of 15 at TX3) within one hour of shelter removal. Twenty-seven of 30 were completely reconstructed when we revisited them the following day. Our observations showed that ground shelters are constructed of pebbles and plant debris collected from the surface around plant perimeters as well as from soil and other debris brought to the surface from around the base of the plants. That material for shelter construction is gathered actively shows that ground shelters are not simply a side effect of excavation around plants with Homoptera. Our observations also showed that ground shelters are integrated into the underground tunnel system characteristic of *S. invicta* colonies (e.g., Markin et al. 1975). Tunnels as well as shelters were damaged by rainfall during our study; when this occurred we also observed repairs of the tunnel system. During tunnel construction, soil is deposited on the surface above tunnels, resulting in partial outlines of the tunnel system, including tunnel directions and branching patterns (Markin et al. 1975; K. R. Helms, *unpublished observations*). During tunnel repair, we commonly observed soil outlining tunnels leading to and interconnecting ground shelters (Fig. 2C). Tunnels leading into shelters were also observed when plants with shelters were unearthed. It appears to us that most, if not all, ground shelters are integrated into the underground tunnel system.

While only aphids occurred in aboveground shelters, at least 12 species of Homoptera in four families occurred in ground shelters (Table 2). Some Homoptera in ground shelters usually occurred just under the surface of the shelter while others occurred on the plant to varying depths, depending upon the plant species. The mean upper and lower position of Homoptera in shelters (relative to ground level) was -0.6 ± 0.2 mm to -6.9 ± 0.7 mm for the grass *A. oligantha* ($N = 35$ plants), 0.8 ± 0.3 mm to -4.5 ± 0.6 mm for the grasses *Dicanthelium* spp. ($N = 36$ plants), 7.5 ± 1.0 mm to 2.8 ± 0.8 mm for the broadleaf plant *H. amarum* ($N = 8$ plants), and 3.5 ± 3.8 mm to -27.6 ± 4.5 mm for an unidentified broadleaf plant ($N = 4$ plants). The number of these shelters where any Homoptera present would have been exposed above ground in the absence of their shelter was 15 of 35 shelters on *A. oligantha*, 31 of 36 shelters on *Dicanthelium* spp., three of eight shelters on *H. amarum*, and all four shelters on the unidentified broadleaf plant. All of the Homoptera we found in shelters excrete honeydew. On plants with shelters, Homoptera, and *S. invicta*, collected and brought into the laboratory, we frequently observed *S. invicta* soliciting honeydew by rapid antennation (e.g., Way 1963), followed by Homoptera secretion of honeydew droplet and ingestion by the ants.

At sites TX1–TX4, Homoptera shelters occurred around *S. invicta* nests during each of the three sample seasons (Fig. 4). The frequency of shelters did not differ significantly among these sites, but did differ significantly among seasons (Fig. 4). Overall, the mean number of shelters per *S. invicta* mound sample area was 2.29 ± 0.83 shelters/m^2 (mean per mound across sites and seasons). Most Homoptera shelters housed mealybugs (Pseudococcidae; Table 2, Fig. 5). Legged mealybugs usually occurred on broadleaf forbs; the frequency of their shelters differed among sites, but not among seasons (Fig. 5, Appendix B). Legless mealybugs always occurred on grasses, and the frequency of their shelters differed among seasons, but not among sites (Fig. 5, Appendix B). Legless mealybug shelters were significantly less frequent in the spring than in

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[3] URL: ⟨http://www.sel.barc.usda.gov/scalenet/scalenet.htm⟩

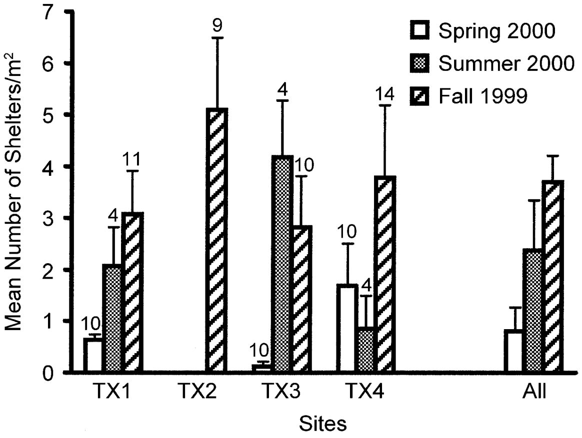

FIG. 4. Density of Homoptera shelters per square meter within a 3-m radius of *Solenopsis invicta* mounds according to site and season at sites TX1 through TX4. Data are means + 1 SE per mound. Shelter density did not differ between sites ($H = 1.577$, $P = 0.459$, df = 2, Kruskal-Wallis ANOVA on ranks), but shelter density did differ between seasons ($H = 24.777$, $P < 0.001$, df = 2, Kruskal-Wallis ANOVA on ranks [post hoc multiple comparisons using Dunn's method]: Fall and Summer differ from Spring [Fall vs. Spring, $Q = 4.925$, $P < 0.05$; Summer vs. Spring, $Q = 2.621$, $P < 0.05$], but Fall did not differ from Summer [($Q = 0.832$, $P > 0.05$)]. Site TX2 was excluded from statistical tests of difference between sites because only one season was sampled (explained in *Methods*). All = mean of site means.

the summer and fall (Fig. 5, Appendix B). Overall, Homoptera shelters were significantly greater in the summer and fall, when shelters housing *A. graminis* were significantly greater than shelters housing all other Homoptera (Fig. 5, Appendix B). Overall, 50.1% of shelters per *S. invicta* mound sampled per site housed *A. graminis* (mean across seasons; Fig. 5).

Individuals of *A. graminis* were larger than individuals of other Homoptera found in shelters. An individual *A. graminis* weighed 1.56 mg, an individual *Antoninoides* weighed 1.21 mg, and an individual legged mealybug weighed 0.40 mg. An average of 10.48 ± 1.63 *A. graminis*, 6.88 ± 1.85 *Antoninoides*, and 27.06 ± 5.76 legged mealybugs occurred per shelter. Combining the data on Homoptera mass, numbers per shelter, and shelter density for *A. graminis*, *Antoninoides* spp., and legged mealybugs, estimated live mass of Homoptera in ground shelters around *S. invicta* nests at Sites TX1–TX4 ranged from 9.37 mg/m^2 in the spring to 48.28 mg/m^2 in the fall (Fig. 5). Weighting each season equally, there was an average across sites of 30.59 mg live mass Homoptera/m^2 around an average *S. invicta* mound; 21.83 mg (71.35%) of this mass was *A. graminis* (Fig. 5).

The mean dimensions of the 31 *S. invicta* mounds measured at TX1–TX4 were 33.09 ± 2.24 cm (width) × 10.06 ± 1.16 cm (height). From these dimensions, we estimate the mean volume of mounds was 16.9 ± 2.3 L (Tschinkel 1993) and mean territory size was 58.74 m^2 (Tschinkel et al. 1995). Based on mean ter-

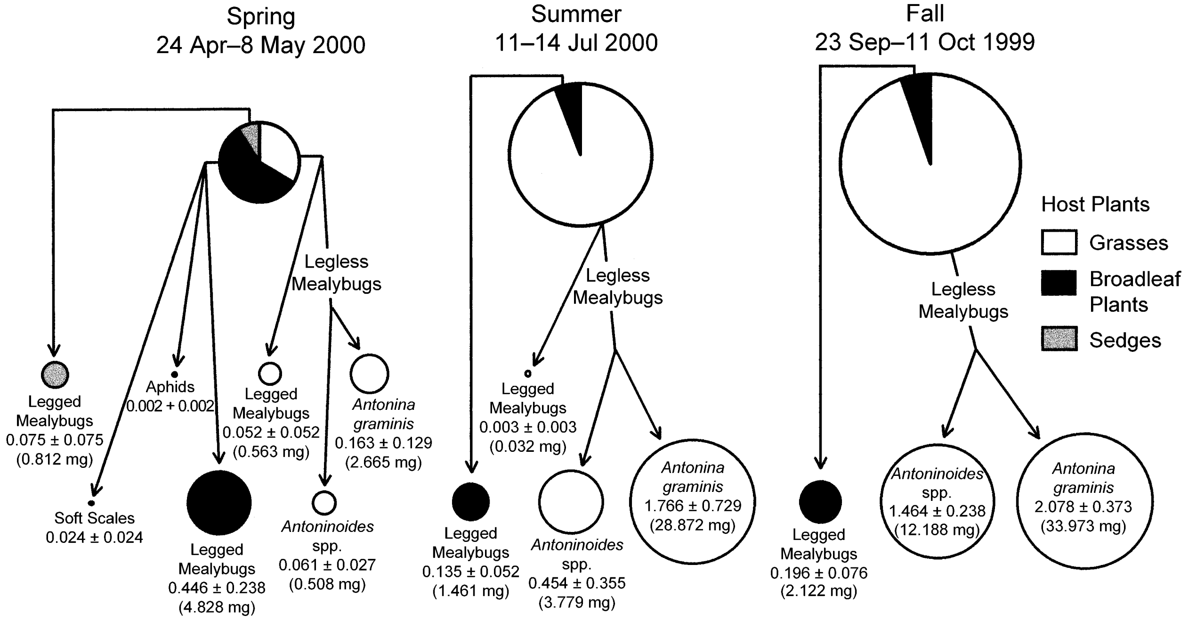

FIG. 5. Density of Homoptera shelters per square meter within a 3-m radius of *Solenopsis invicta* mounds according to plant group and Homoptera taxa in shelters at sites TX1–TX4. The size of the circles is proportional to the mean shelter density per *Solenopsis invicta* mound sampled per season; those means along with standard errors are given below the names of the taxonomic groups. The estimated live mass of Homoptera groups per square meter is in parentheses. Site data are pooled within seasons. Statistical comparisons among seasons and sites for these data are given in Appendix B.

ritory size and the frequency and biomass of Homoptera in shelters, we estimate that an average *S. invicta* colony at TX1–TX4 tends 1569.3 Homoptera in shelters; 822.2 Homoptera are estimated to be *A. graminis* (mean across sites and seasons). We estimate the combined live mass of Homoptera tended by an *S. invicta* colony to be 1.79 g, with 1.28 g being *A. graminis*, 71.51% of the total Homoptera mass in shelters (mean per colony across sites and seasons).

We estimate that the Homoptera around an *S. invicta* colony at TX1–TX4 would produce 30.2 g of honeydew per day, consisting of 3.02 g of dry matter (2.57 g of carbohydrate and 0.45 g of nitrogenous compounds), of which 21.6 g would be available from *A. graminis* (mean per *S. invicta* colony across sites and seasons). Based on mound volumes, we estimate the dry mass of an average *S. invicta* colony in our study is 57.88 g (Tschinkel 1993), which would require 119.70 kJ of energy per day (Macom and Porter 1995). Using a caloric content of 16.74 kJ per gram dry mass for carbohydrates and 23.85 kJ per gram dry mass for proteins (Southwood 1966), we estimate that 30.2 g of honeydew would supply 53.68 kJ, or ~45% of the daily energy requirements of an *S. invicta* colony in our study; 32% of the daily energy requirement would be available from *A. graminis* honeydew (mean per colony across sites and seasons). If the Homoptera in our study produce honeydew at ±50% the rate of the aphid *T. salignus* (Mittler 1958), the percentage of the energetic requirements of *S. invicta* colonies supplied by Homoptera in ground shelters would range from 22.4% to 67.5%, with 16.1% to 48.2% available from *A. graminis* (mean per colony across sites and seasons).

Because the density of Homoptera shelters around *S. invicta* colonies differed among seasons, the importance of Homoptera honeydew to the energy budget of *S. invicta* differed among seasons as well. At Sites TX1–TX4, the percentage of *S. invicta* energetic requirements estimated available from Homoptera honeydew ranged from 13.2% in the spring (3.0% from *A. graminis*), to 50.3% in the summer (42.5% from *A. graminis*), to 71.1% in the fall (50.0% from *A. graminis*). If the Homoptera in our study produced honeydew at ±50% the rate of our standard, *T. salignus*, the range of possible values is 6.6–19.8% in the spring, 25.1–75.4% in the summer, and 35.5–107.3% in the fall.

Homoptera shelters occurred at each of the 11 survey sites across the southeast United States (Fig. 6). All were ground shelters. The mean density of ground shelters per *S. invicta* mound sampled per site was 1.40 ± 0.17 shelters/m^2. Ground-shelter density differed significantly between survey sites, as did the frequency of shelters housing *A. graminis* (Fig. 6). In addition, ground-shelter density at survey sites differed significantly from those at TX1–TX4 ($H = 30.733$, df = 3, $P < 0.001$, Kruskal-Wallis ANOVA on ranks). Density at regional survey sites was less than the density at sites TX1–TX4 in the fall ($Q = 2.989$, $P < 0.05$, Dunn's method), greater than in the spring ($Q = 3.007$, $P < 0.05$, Dunn's method), but not significantly different than in the summer ($Q = 1.048$, Dunn's method).

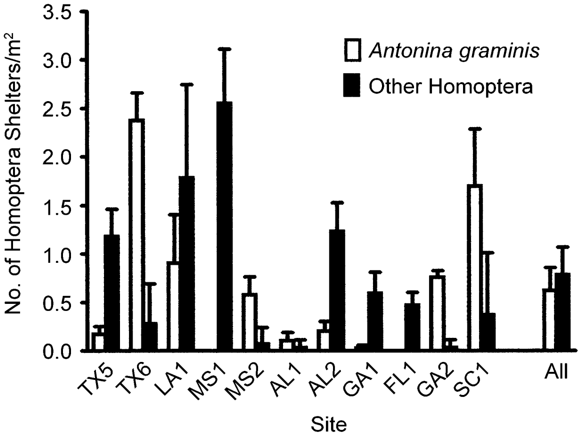

FIG. 6. Density of shelters housing *Antonina graminis* and other Homoptera within a 3-m radius of *Solenopsis invicta* mounds at 11 survey sites across the range of *Solenopsis invicta* in the southeast United States. Data are means + 1 SE per mound. Total shelter density differed between sites ($H = 34.175$, df = 10, $P < 0.001$, Kruskal-Wallis ANOVA on ranks) as did the density of shelters housing *A. graminis* ($H = 37.184$, df = 10, $P < 0.001$, Kruskal-Wallis ANOVA on ranks). All = mean of site means.

Antonina graminis were found in ground shelters at nine (81.8%) of the 11 survey sites; the mean density of ground shelters housing *A. graminis* per *S. invicta* mound sampled per site was 0.62 ± 0.24/m^2, 44% of the total mean density of shelters per site (Fig. 6). The density of ground shelters housing *A. graminis* differed significantly from density at sites TX1–TX4 ($H = 39.303$, df = 3, $P < 0.001$, Kruskal-Wallis ANOVA on ranks). Density at survey sites was less than at TX1–TX4 in the fall ($Q = 3.987$, $P < 0.05$, Dunn's method) and summer ($Q = 2.744$, $P < 0.05$, Dunn's method), but not significantly different than in the spring ($Q = 2.197$, Dunn's method).

At our survey sites, we estimate that *A. graminis* honeydew could supply 14.9 ± 5.7% of the energetic requirements of colonies (mean per colony across sites). However, the importance of *A. graminis* honeydew may vary considerably among sites, with the estimated percentage of energy available from their honeydew ranging from zero (two sites) to 57.2%. If *A. graminis* produces honeydew at ±50% the rate of the aphid *T. salignus* (Mittler 1958), the mean percentage of energy available to *S. invicta* colonies from *A. graminis* honeydew across sites would range from 7.5 ± 2.8% to 22.4 ± 8.5%, and the percentage within sites would range from zero to 28.6% (lower range) or zero to 85.8% (upper range). Because our survey only noted whether Homoptera in shelters were *A. graminis* or were other Homoptera, we are unable to estimate the percentage of energetic requirements that might be available from all Homoptera found in shelters at those sites.

DISCUSSION

We found that Homoptera shelters are constructed by *S. invicta* throughout their range in the southeast United States. These shelters were common, they housed significant numbers and biomass of Homoptera, and they often occurred at great density. Our estimates suggest that Homoptera within shelters could, on average, produce enough honeydew to provide *S. invicta* colonies with ~45% of their daily energetic requirements, with the percentage ranging from 22% to 68% if we assume honeydew production at ±50% the rate of the aphid *T. salignus* (Mittler 1958). Honeydew produced by Homoptera may provide the major source for liquids found to be the food most frequently collected by foraging workers (Tennant and Porter 1991). Other studies of *S. invicta* have noted Homoptera tending in shelters on trees (Clarke and DeBarr 1989, Tedders et al. 1990) and *S. invicta* moving Homoptera between plants (Vinson and Scarborough 1991, Michaud and Browning 1999). Our study shows that these observations are not exceptional. Homoptera tending and construction of Homoptera shelters appears characteristic of *S. invicta* in the southeast United States.

The construction of Homoptera shelters appears frequent only in ant species where Homoptera are fundamental to their ecology, e.g., in *Acropyga*, *Formica*, *Lasius*, and *Oecophylla* (Wheeler 1910, Way 1963, Hölldobler and Wilson 1990). The frequency of their construction by *S. invicta* is consistent with the importance of Homoptera to the ecology of this species. However, the precise nature of the benefits of *S. invicta*'s Homoptera shelters remains unstudied. In general, ant-constructed Homoptera shelters may protect Homoptera and/or foraging ants, either from natural enemies or abiotic factors; shelters may also enable ants to monopolize the Homoptera present (e.g., Way 1963, Hölldobler and Wilson 1990). In our study, Homoptera would often have been exposed above ground in the absence of shelters, suggesting that they offer protection from weather and/or Homoptera predators and parasites. If so, *S. invicta* may interfere with the parasitic wasp *Neodusmetia sangwani*, introduced into the United States for control of *A. graminis* (e.g., Dean et al. 1979). It is also possible that shelters provide additional protected space on plants for colonization, enabling *S. invicta* to ‘‘cultivate’’ larger Homoptera populations than would normally occur. Shelters may also offer protection for tending *S. invicta* workers. This is particularly relevant because shelters are connected to the underground tunnel system; honeydew can be collected and returned to the nest without emerging on the surface. Foraging workers of *S. invicta* are most active at moderate surface temperatures (~30°C; Cokendolpher and Francke 1985, Porter and Tschinkel 1987), temperatures much lower than commonly occur during warm seasons in the southeast United States. Homoptera shelters may allow *S. invicta* to tend Homoptera during times when surface temperatures would otherwise prohibit foraging. In addition, parasitic flies in the Family Phoridae are important parasites of *S. invicta* in their native range in South America (Orr et al. 1995). These flies require that *S. invicta* workers be exposed on the surface in order to attack (Porter et al. 1995). Underground tunnels connected to Homoptera shelters allow for subterranean foraging, clearly advantageous in thwarting attack by parasitic flies (Porter et al. 1995). However, whether *S. invicta* constructs Homoptera shelters in their native range remains to be determined, although they are known to tend Homoptera there (Wojcik 1986). It is worth noting that *S. invicta*, and at least some other species in the *Solenopsis geminata* group (Trager 1991), construct shelter-like covers over long-lived food sources other than honeydew-producing Homoptera, e.g., baits placed in the field by researchers (Bhatkar 1987; K. R. Helms, *unpublished observations*). An interesting question is whether *S. invicta*'s Homoptera shelters are indicative of an adaptation specific to Homoptera tending or whether they are a general adaptation for exploiting any long-lived food source.

Our study of aboveground Homoptera shelters shows that *S. invicta* do not always construct shelters for the Homoptera they tend. In fact, whether a shelter is constructed may be related to the proximity of Homoptera to *S. invicta* colonies (Fig. 3). It may be costly to construct shelters when Homoptera are far from the nest and are not economically defendable. Other reasons related to the economics of shelter construction might also be important.

Differences in Homoptera shelter density at sites TX1–TX4 show that the importance of Homoptera to *S. invicta* (both overall and of particular groups) can differ both temporally and spatially. Shelters housing legged mealybugs and soft scale differed among sites (Appendix B), which could be due to differences among sites in the availability of different host plants. Site characteristics may determine plant and Homoptera assemblages (e.g., Dixon 1973). However, the frequency of shelters housing legless mealybugs (*A. graminis*, *Antoninoides* spp.) differed among seasons, but not among sites (Fig. 5, Appendix B). Insight into why *A. graminis* did not exhibit site-specific differences in abundance may come from its tremendous host range, consisting of over 100 grass species in over 50 genera (Chada and Wood 1960); see also Ben Dov et al. [available online, see footnote 3]). Although sites may differ in plant communities, suitable hosts for *A. graminis* may be present most places where grasses occur. In addition, seasonal differences in the abundance of *A. graminis* are consistent with an earlier study showing that the species exhibits a temperature dependent annual cycle, where populations are low throughout the winter, increase from spring until midsummer, decrease temporarily, then increase again in the fall (Chada and Wood 1960). Species of *Antoninoides* exhibited a seasonal pattern of abundance similar to *A. graminis* (Fig. 5). Although little is known of the ecology of species of *Antoninoides*, both they and *A. graminis* occur almost exclusively on grasses, inhabit the same locations on plants, and are morphologically convergent (McDaniel 1972, Hendricks and Kosztarab 1999) see also Ben Dov et al. [available online, see footnote 3]). *Antoninoides* spp. may undergo seasonal patterns of abundance similar to those of *A. graminis*.

At our regional survey sites, overall Homoptera shelter density and the density of shelters housing *A. graminis* were intermediate to densities during spring and summer at TX1–TX4 (Figs. 5 and 6). Because the regional survey was conducted between our spring and summer sampling periods at TX1–TX4, our estimates of the importance of *A. graminis* and other Homoptera to *S. invicta* could, on average, apply throughout the range of *S. invicta* in the southeast United States. However, it is also important to note that there were significant differences among regional survey sites, in both the density of shelters overall and the density of shelters housing *A. graminis*, even though those sites were all sampled over a short time period. It appears that the importance of *A. graminis* and other Homoptera to *S. invicta* can differ according to regional as well as seasonal conditions. It is also likely that differences in weather patterns affecting Homoptera and their host plants may result in site-specific as well as regional differences among years.

Contribution of Homoptera to the energy budget of Solenopsis invicta

Our estimate that, on average, ~45% of the daily energy requirements of an *S. invicta* colony can be produced in Homoptera shelters is consistent with our other evidence suggesting that Homoptera tending is important to this species. This estimate is, however, a first approximation. Our estimates depend greatly on the rate of honeydew production by the aphid *T. salignus* (Mittler 1958), and it is unclear how closely this matches the honeydew production rate of the Homoptera in our study. In addition, estimated territory size of colonies in our study was greater than the area used in estimating the frequency of Homoptera shelters. If shelter density decreases with increasing distance from *S. invicta* mounds, our estimate of Homoptera shelter density would be greater than actual density. There are, of course, other possible sources of error in our estimates, as well. In our study of aboveground shelters, hundreds of aphids occurred in colonies, but they persisted for only about three weeks (K. R. Helms, *unpublished data*). Because aphids and other Homoptera may often be ephemeral (e.g., Dixon 1973), large amounts of honeydew may sometimes be collected over a short time period, and missed easily by researchers conducting periodic observations.

Because Homoptera shelter density differed between seasons, our estimates of the importance of Homoptera honeydew to *S. invicta* differed between seasons as well. Based on study at sites TX1–TX4, it appears that honeydew may supply relatively little of the energetic requirements of colonies in the spring, while supplying a substantial amount of that energy in the summer and fall. However, like other ants, *S. invicta*, stores food, either in the crop, or as fat (Hölldobler and Wilson 1990, Tschinkel 1993). In *S. invicta*, the fat content of workers peaks in July, then decreases through the winter to a low point the following June; colonies presumably utilize that fat during overwintering and spring production of reproductive brood (Tschinkel 1993). Because energy can be stored, our mean estimates across sites and seasons may be a better overall indicator of the importance of honeydew to *S. invicta* colonies than our estimates according to season.

Association of Antonina graminis *and* Solenopsis invicta

Based on our information (Table 2), *A. graminis* was the only nonnative Homoptera occurring in shelters during our study. It was also the most frequent and made up a clear majority of Homoptera biomass (~70%). Our study suggests that *A. graminis* may be an exceptionally important nutritional resource for *S. invicta* in the southern United States. Because both *S. invicta* and *A. graminis* are invasive species, this association is of special importance. Species invasions appear quite difficult (e.g., Elton 1958, Mack et al. 2000) and mutualism between species such as *S. invicta* and *A. graminis* could help explain their extraordinary success at introduced locations (Simberloff and Von Holle 1999).

Antonina graminis is thought to be of Asian origin and was first recorded from the United States in 1942 (Chada and Wood 1960). However, this species is exceptionally inconspicuous because of its location on host grasses, and by 1942, it was already an important pest of agriculturally important grasses in south Texas (Chada and Wood 1960). The species may have been present in the southern United States by the early 1900s, but the site of introduction and pattern of subsequent spread are unknown (Chada and Wood 1960). In contrast, the history of *S. invicta* in the United States is well documented. This species was first recorded in 1945 and was likely introduced near Mobile, Alabama, sometime between 1933 and 1945 (Buren et al. 1974). From there, its range expanded to the north, east, and west (Buren et al. 1974). Because information on *A. graminis* is so limited, we cannot test for correlation between its invasion and that of *S. invicta*. All that is clear is that they are currently associated, and their current ranges are remarkably similar (Figs. 1 and 6; see also Ben Dov et al. [available online, see footnote 3]). More information is clearly needed to assess whether *S. invicta* and *A. graminis* were associated in time and space during their invasion of the United States.

Whether *A. graminis* and *S. invicta* were associated

TABLE 3. Invasive ants are often associated with introduced and invasive Homoptera.

Invasive ant species	Introduced or invasive Homoptera tended	Source
Anopolepis custodiens	*Aphis gossypii, Coccus hesperidum, Planococcus citri*	Steyn (1955), Samways (1983)
Linepithema humile	*Coccus hesperidum, Dysmicoccus neobrevipes, Dysmicoccus brevipes, Icerya purchasi, Planococcus citri, Pseudococcus longispinus, Saissetia oleae*	González-Hernández et al. (1999), Markin (1970), Rohrbach et al. (1988), Reimer et al. (1990)
Paratrechina fulva	*Aleurothrixus flococcus, Antonina* sp.,† *Coccus viridis, Dysmicoccus brevipes, Saccharicoccus sacchari*	Zenner-Polania (1990)
Paratrechina longicornis	*Dysmicoccus neobrevipes, Pseudococcus longispinus*	Reimer et al. (1990)
Pheidole megacephala	*Coccus hesperidum, Coccus viridis, Dysmicoccus brevipes, Dysmicoccus neobrevipes, Planococcus citri, Pseudococcus longispinus, Saccharicoccus sacchari*	Steyn (1955), Rohrbach et al. (1988), Bach (1991), Reimer et al. (1990, 1993), Campbell (1994), González-Hernández et al. (1999)
Solenopsis geminata	*Coccus viridis, Dysmicoccus brevipes, Dysmicoccus neobrevipes, Planococcus citri, Pseudococcus longispinus*	González-Hernández et al. (1999), Wolcott (1933), Edwards (1936), Reimer et al. (1990), Rohrbach et al. (1988)
Solenopsis invicta	*Antonina graminis, Toxoptera citricida*	Michaud and Browning (1999), see *Results*
Solenopsis richteri	unknown‡	
Wasmannia auropunctata	*Aphis gossypii, Coccus viridis, Icerya purchasi, Planococcus citri, Saissetia hemisphaerica, Toxoptera aurantiae*	Spencer (1941), Flower et al. (1990), Lubin (1984), Delabie et al. (1994)

† Probably *Antonina graminis* (see *Discussion*).

‡ This species tends Homoptera and also constructs Homoptera shelters (Green 1952) but we were unable to find information concerning which Homoptera they tend.

early in their invasion, or whether their association is more recent, the success of *A. graminis* as an invader is not dependent upon *S. invicta*. *Antonina graminis* occurs in over 80 countries throughout the tropics and subtropics of Asia, Africa, Europe, North and South America, and many oceanic islands, mostly as an invasive species (Chada and Wood 1960); see also Ben Dov et al. [available online, see footnote 3]). In contrast, *S. invicta* is native to South America, and the range where it is firmly established is currently limited to the southern United States, the Virgin Islands, and Puerto Rico (McGlynn 1999). As a result, *A. graminis* appears to occur throughout the world range of *S. invicta*, but *S. invicta* does not occur throughout the world range of *A. graminis*. However, regions in the world where *A. graminis* is established but *S. invicta* is not are regions inhabited by other species of invasive ants (McGlynn 1999); see also Ben Dov et al. [available online, see footnote 3]). In Colombia, the invasive ant *P. fulva* was first recorded when it became abundant in association with a mealybug identified as *Antonina* sp. (Zenner-Polania 1990); the only *Antonina* known to occur in Colombia (and South America) is *A. graminis* (Ben Dov et al. [available online, see footnote 3]). However, whether *A. graminis* is associated with invasive ants throughout its range is currently unknown.

In studies addressing characteristics invasive ant species share in common, association with Homoptera has apparently not been considered. Nevertheless, studies suggest that Homoptera tending is integral to the ecology of most, if not all, invasive ants (e.g., Edwards 1936, Steyn 1955, Markin 1970, Clark et al. 1982, Lubin 1984, Rohrbach et al. 1988, Bach 1991, Delabie et al. 1994, Wetterer et al. 1999). In addition, invasive ants are often associated with invasive Homoptera, and in these associations, the ants and Homoptera commonly occur at great densities (Table 3 and references therein). However, while our study of *S. invicta* was conducted outside of agricultural systems (Appendix A), we note that most studies of associations of invasive ants and Homoptera have focused on agricultural systems (Table 3 and references therein). Whether associations between invasive ants and introduced or invasive Homoptera are common outside of those systems appears unknown. Even if such associations are uncommon, however, agricultural systems may be important as refuges and beachheads for the invasion of invasive ants and invasive Homoptera into adjacent ecological systems.

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APPENDIX A

A list of descriptions of study sites illustrated in Fig. 1 is available in ESA's Electronic Data Archive: *Ecological Archives* E083-048-A1.

APPENDIX B

Statistical comparisons among seasons and sites for Homoptera shelters at sites TX1–TX4 are available in ESA's Electronic Data Archive: *Ecological Archives* E083-048-A2.