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ORIGINAL PAPER

Interspecific competition between the red imported fire ant, *Solenopsis invicta* Buren and ghost ant, *Tapinoma melanocephalum* Fabricius for honeydew resources produced by an invasive mealybug, *Phenacoccus solenopsis* Tinsiley

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Abstract In natural as in agricultural ecosystems, interactions between ants and honeydew-producing hemipterans are commonly observed. Mutualisms between invasive ants and hemipterans have been extensively studied in recent years. However, native ant species can equally exploit the honeydew excreted by hemipterans, and establish close relationships with them. Up till present, little is known about the competition between exotic ants (such as *Solenopsis invicta*) and its co-occurring species (e.g., *Tapinoma melanocephalum*) for this food resource. In this study, we compared the competitive ability of the invasive ant *S. invicta* and its co-occurring species *T. melanocephalum* in the laboratory. We also determined whether the two ant species could coexist and share honeydew resource. Our results indicate that the foraging activity of *T. melanocephalum* was restrained by *S. invicta*. Mortality of *S. invicta* and *T. melanocephalum* was significantly higher in *T. melanocephalum* colony case than that in other cases. The invasive ability between the two ant species was significantly different. These results suggest that *S. invicta* suppresses exploitation of honeydew-producing hemipterans by native ants and occupies most of honeydew resource. *S. invicta* could not completely drive *T. melanocephalum* out of honeydew competition, with small numbers of *T. melanocephalum* workers coexisting and sharing the honeydew with *S. invicta*. This finding permits a better understanding of the invasion success of *S. invicta*, and its ability to occupy new habitats.

Keywords *Solenopsis invicta* · *Tapinoma melanocephalum* · Interspecific competition · Honeydew

Introduction

Mutual interactions between ants and hemipterans occur commonly in ecosystems (Holway et al. 2002). Ants protect hemipterans against their predators and parasitoids. In return, the ants receive large amounts of honeydew, which is essential to their colony growth and survival because it contains sugars mixed with various amino acids (Yao and Akimoto 2001; Fischer and Shingleton 2001; Helms and Vinson 2002, 2003; Brightwell and Silverman 2010). Previous studies have shown that the mutualism between *Solenopsis invicta* and *Phenacoccus solenopsis* facilitates population increase and fitness of each other (Zhou et al. 2012a). The invasive ants *S. invicta* are able to protect the exotic honeydew-producing mealybug *P. solenopsis* with their ability to deter natural enemies (Zhou et al. 2013). Honeydew produced by *P. solenopsis* significantly enhanced the colony growth and worker survival of *S. invicta* (Zhou et al. 2012b). Similar results indicated that carbohydrates could increase worker survival and colony growth rates of fire ants (Wilder et al. 2011a, b). Adult workers can not digest solid food sources directly because they have a sieve-like structure in their throats that prevents them from swallowing solids. Honeydew from mutualist hemipterans is considered as an important liquid source of energy for adults *S. invicta* workers (Vinson 1983; Tschinkel 2006).

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Besides invasive ants, some co-occurring ant species can also utilize the honeydew excreted by *P. solenopsis*. Honeydew is a critical resource for both introduced and native ants (Wilder et al. 2013). Colony growth of native ants decreased if they lost mutualist-provided resources even when other sources of energy and nutrients were available (Wilder et al. 2013). The ghost ant, *Tapinoma melanocephalum,* is a worldwide invader, whose native range is unknown but is believed to come from Africa or Asia (Wheeler 1910). It has been a well established species in southern China. *T. melanocephalum* is a highly competitive sugar-feeding species. They can also establish a close relationship with hemipterans. We found that the density of mealybugs had a significantly linear correlation with the number of foraging *T. melanocephalum* workers on a given plant (unpublished data, Zhou et al.). They compete with *S. invicta* frequently for honeydew resources produced by *P. solenopsis* on plants. Previous study has demonstrated that tending by both *S. invicta* and *T. melanocephalum* has positive impacts on the fitness of individuals of *P. solenopsis*. However, compared with *T. melanocephalum*, *S. invicta* acquired more honeydew and protected *P. solenopsis* more effectively, which may facilitate the invasion of these two alien species in south China (Zhou et al. 2012a).

Resource competition by *S. invicta* has been considered as one of the key factors shaping the reduction of native ant diversity (Epperson and Allen 2010). Recent studies indicate that introduced ants compete for honeydew produced by hemipterans with native ants, and exclude native ant species from this critical resource (Wilder et al. 2013). A lot of literature shows that invasive ants control the food resources based on their forceful competitiveness, and inhibit native species (Holway et al. 2002; Zhou et al. 2012a; Wilder et al. 2013). Previous studies also indicate that native ant species could coexist and neighbor each other (Calixto et al. 2007a, b). However, few efforts have focused on the competitive mechanisms between exotic ants *S. invicta* and its co-occurrence with *T. melanocephalum*.

Here, we investigated possible behavioral mechanisms underlying the coexistence of *S. invicta* and *T. melanocephalum* using short geographical range competition experiments in the laboratory to compare their competitive ability for honeydew resource.

Materials

Plants

Hibiscus rosa-sinensis, a Chinese native species cultivated worldwide, was purchased from a commercial horticultural farm. Each plant was approximately 25–30 cm in height and had 25–30 true leaves. All plants were cultivated in plastic flowerpots (the diameters of the upper and lower edges were 18 and 14 cm, respectively, with a height of 17 cm) in greenhouses.

Insects

Colonies of *P. solenopsis* were collected from the campus of South China Agricultural University and fed on *H. rosa-sinensis*. First instar mealybug nymphs were inoculated on each plant and raised for several generations. *H. rosa-sinensis* plants with established mealybug colonies were used for subsequent experiments. All colonies were reared in the laboratory with the temperature maintained at 27 ± 2 °C and a relative humidity of 60–70 %. Colonies of *S. invicta* and *T. melanocephalum* were collected from a suburb of Guangzhou and reared in plastic boxes (116 L 72 cm × 56 cm × 29 cm). Ant colonies were separated from the soil by dripping water into plastic boxes until the colonies floated (Jouvenaz et al. 1977). Each colony was divided into sub-colonies (approximately 1.0 g) using a microbalance (Sartorius, BS, 224S). Each sub-colony included one queen and adult workers, pupae, larvae, and eggs. The ants were placed in a 9-cm plastic Petri dish, which served as an artificial nest. All ant colonies were reared in plastic cases (26 cm × 18 cm × 8 cm) at 28 °C. *Solenopsis invicta* colonies were given fresh live *Tenebrio molitor* larvae, frozen crickets, and a 10 % solution of honey mixed with water (50 ml) weekly. *T. melanocephalum* sub-colonies were maintained with tubes filled with distilled water plus 10 % honey solution.

Experimental procedure

Before the beginning of the experiments, all experimental colonies were starved for 48 h to produce a uniform state of hunger. Each experimental colony consisted of workers (0.8 g), brood (0.2 g), and a single queen. A microbalance (Sartorius, BS, 224S) was used to weigh workers and brood. Five adjacent boxes (26 cm × 18 cm × 8 cm) were arranged in a row and connected by tubes. The cases containing the ant colonies on each end are considered as colony cases; the empty cases adjacent to each colony case are considered as adjacent cases; and the connecting case in the middle is considered as the center case (Morrison 2000). The whole equipment included *S. invicta* colony case (SCC), *S. invicta* adjacent case (SAC), center case (CC), *T. melanocephalum* adjacent case (TAC), and *T. melanocephalum* colony case (TCC) (Fig. 1). At the beginning of the experiments, 0.4 g honeydew produced by *P. solenopsis* was placed in CC, 0.2 g in SAC and TAC, respectively. Each plastic case was connected to (1 cm

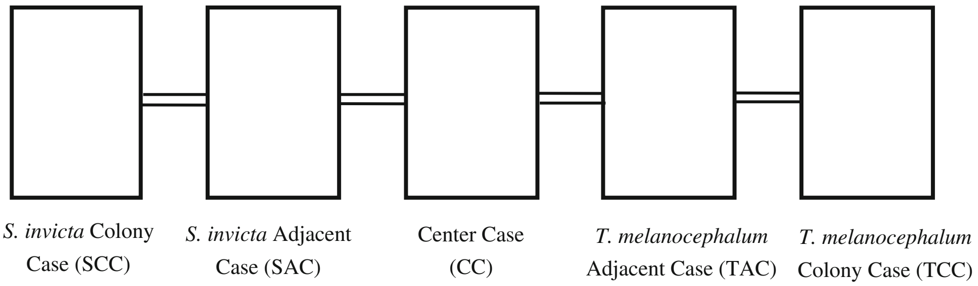

Fig. 1 Design of the short-distance, colony-level interference competition experiments between *S. invicta* and *T. melanocephalum* (Morrison 2000)

inside diameter) to an adjacent case via a 12-cm long silicone tube (Fig. 1). The number of foraging workers of the two ant species in SAC, CC, and TAC after 0.5 h, 24 h, 48 h, and 72 h was counted, respectively. The mortality of each ant species in SCC, SAC, CC, TAC, and TCC was recorded after 72 h. We also recorded the number of *S. invicta* and *T. melanocephalum* colonies, which intruded the opposite colony case after 72 h. All treatments were replicated 10 times.

Statistical analysis

We used three-way ANOVA to test the number of foraging workers versus the effects of the box (SCC, SAC, CC, TAC, and TCC), the time interval and the species. One-way ANOVA using type III sum of squares was performed to compare the means among different resource cases. If ANOVA results were significant, multiple comparisons of means were performed using Tukey HSD post hoc analysis. Paired *t* test was used to analyze the foraging activity of the two ant species in same resource case. We used chi-square test to compare the invasiveness of *S. invicta* and *T. melanocephalum*. All statistical analyses were conducted using SPSS version 14.0 (SPSS Inc., Chicago, IL, USA).

Results

Foraging activity of *S. invicta* and *T. melanocephalum*

Foraging intensity showed significant difference between the two ant species in SAC ($F = 63.076$, $P < 0.001$). Number of foraging *S. invicta* was significantly more than that of *T. melanocephalum* in SAC (Table 1, Ants; Fig. 2a). In CC, number of foraging workers was not significantly different between the two ant species (Table 1, Ants; Fig. 2b). Foraging intensity was significantly different between the two ant species in TAC (Table 1, Ants; Fig. 2c). However, this difference declined with our investigative time sequence (Table 1, Ants*Time: $P = 0.043$).

Mortality of *S. invicta* and *T. melanocephalum*

Our results show that in both ant species mortality differed between cases (*S. invicta*: $F_{4,45} = 18.271$, $P < 0.0001$; *T. melanocephalum*: $F_{4,45} = 23.134$, $P < 0.0001$; Table 2). Mortality of *S. invicta* between SCC, SAC, and CC was no significantly different after 72 h ($P = 0.960$). It was obviously different between TAC and TCC ($P = 0.009$). Mortality of *T. melanocephalum* between SCC, SAC, and CC was also not significantly different after 72 h ($P = 0.257$). Mortality of *T. melanocephalum* in TCC was markedly greater than that in other case.

Mortality of *S. invicta* was observably more than *T. melanocephalum* in SCC ($t = 3.334$, $df = 12.200$, $P = 0.006$; Table 2). There was no significant difference in mortality between the two ants species in SAC, CC, TAC, and TCC, respectively ($t = 0.798$, $df = 18$, $P = 0.435$; $t = 0.796$, $df = 18$, $P = 0.436$; $t = 1.259$, $df = 18$, $P = 0.224$; $t = 1.290$, $df = 18$, $P = 0.213$; Table 2).

Invasiveness of *S. invicta* and *T. melanocephalum*

Our results indicated that the number of colonies in home-side case between *S. invicta* and *T. melanocephalum* was significantly different after 72 h ($\chi^2 = 5.333, df = 1$, $P = 0.021$). There were 8 colonies of *S. invicta* which had intruded into TCC. However, no colony of *T. melanocephalum* had intruded into SCC (Table 3).

Discussion

Interaction between ants and hemipterans facilitates colony growth and fitness of each other (Kaplan and Eubanks 2002; Flatt and Weisser 2000; Kaplan and Eubanks 2005; Daane et al. 2007). Honeydew produced by hemipterans is a critical resource for multiple species of ants. They can not be substituted by nutrients in insect prey (Wilder et al. 2013). Many studies show that honeydew is important as a fuel for activity and aggression of workers. Colony growth and reproduction of brood are facilitated by the mutualist-provided carbohydrates (Kay et al. 2010; Wilder et al.

Table 1 Analysis of foraging intensity of the two ant species based on two-way analysis of variance

Source	SAC			CC			TAC		
	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Time	24,973.138	5.132	0.003	76,796.538	21.315	0.000	24,614.838	3.935	0.012
Ants	102,316.513	63.076	0.000	1,336.613	1.113	0.295	93,502.813	44.848	0.000
Time*Ants	6,517.238	1.339	0.268	2,881.938	0.800	0.498	17,809.438	2.847	0.043
Error	116,793.100			86,471.900			150,110.900		

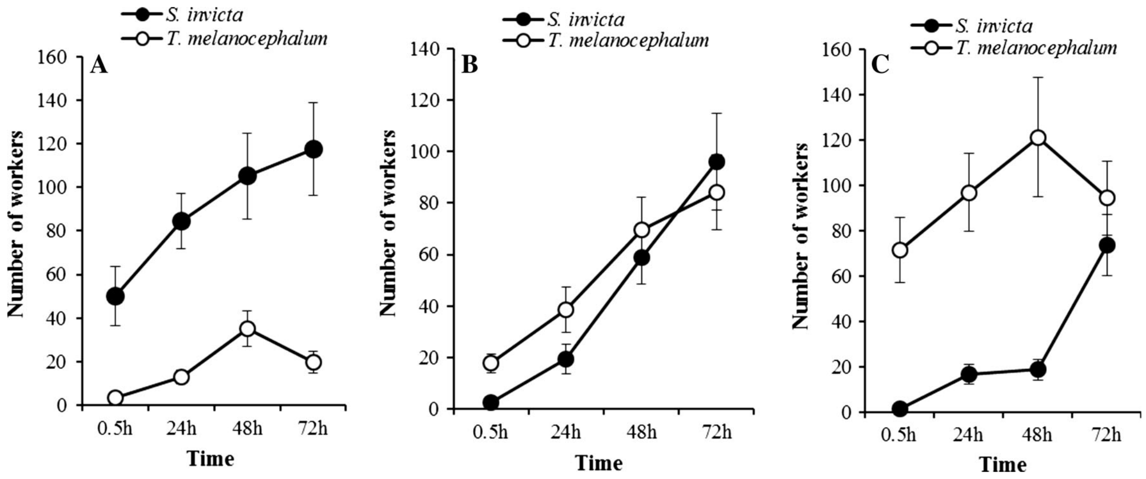

Fig. 2 Foraging intensity of *S. invicta* and *T. melanocephalum* (**a** in *S. invicta* adjacent case; **b** in central case; **c** in *T. melanocephalum* adjacent case)

Table 2 Mortality of *S. invicta* and *T. melanocephalum* in the cases after 72 h

Cases	Mortality of *S. invicta* (%)	Mortality of *T. melanocephalum* (%)
SCC	7.06 ± 1.45a	1.81 ± 0.62a*
SAC	5.46 ± 1.27a	4.26 ± 0.82a (ns)
CC	7.15 ± 1.12a	5.95 ± 1.01ab (ns)
TAC	14.65 ± 1.96b	11.30 ± 1.79b (ns)
TCC	23.36 ± 2.58c	19.00 ± 2.20c (ns)

Data with the same letter in column indicates no significant differences in mortality of workers between the treatments, $P > 0.05$ (Tukey-HSD test); data with "*" indicates significant differences in mortality of workers between *S. invicta* and *T. melanocephalum* at level of 0.05, and "ns" indicates no significant differences (paired *t* test)

Table 3 Comparison of invasiveness of two ant species after 72 h

Ant species	Colonies	
	Home-side case	Opposite side case
S. invicta	2	8
T. melanocephalum	10	0

2011a, b; Grover et al. 2007). Exotic ant species such as *S. invicta* compete with native species extensively for mutualist-provided carbohydrates and suppress the exploitation of mutualist carbohydrates by native ants. To honeydew-dependent native ant species, the effects of honeydew monopoly by *S. invicta* could negatively affect colony growth (Wilder et al. 2013).

Strength in numbers of foraging ants is key factor in interspecific competition for food resource (Holway et al. 2002). Our study determined the short-distance competitiveness of *S. invicta* and *T. melanocephalum* at colony level. The results demonstrate that the competitive ability of *S. invicta* is stronger than that of *T. melanocephalum*. Forager numbers of *S. invicta* was continually increased in determined resource case. On the contrary, foraging intensity of *T. melanocephalum* was restrained by interference from *S. invicta* (Fig. 1; Table 1). *T. melanocephalum* found the honeydew resource much earlier and arrived at honeydew more quickly than *S. invicta* (Zhou et al. 2012a). However, we found that most of honeydew was occupied by *S. invicta* after 72 h. The advantage of greater foraging intensity of *T. melanocephalum* gradually disappeared (Fig. 1; Table 1). Due to forceful aggressiveness by *S. invicta*, most of food resource was dominated by this ant. Previous study also indicated that domination of food resources by *S. invicta* depended on their forceful competitiveness and inhibition of native species. *S. invicta* occupied more of the foraging arenas against both native ants when colonies were equivalent by worker biomass (Morrison 2000).

Mortalities of *S. invicta* and *T. melanocephalum* in TCC were greater than that in other cases. Food competition was more intense in TCC than in other cases. Because of higher aggressiveness, *S. invicta* often intruded into colony of *T. melanocephalum*. However, *T. melanocephalum* barely intruded into colonies of *S. invicta*.

Although most of honeydew resource was forcibly occupied by *S. invicta*, our results indicate that there were still small numbers of *T. melanocephalum* workers in resource cases. *S. invicta* could not completely drive *T. melanocephalum* out of honeydew competition. *T. melanocephalum* could coexist and share the honeydew with *S. invicta*. Activity of native ants can play a certain restraining role to invasive ants (Vogt et al. 2005). Previous studies also show that some native ant species such as *Dorymyrmex* spp. and *Forelius* spp. are usually located adjacent to *S. invicta* colonies, and they are rarely attacked by *S. invicta*. Native ant species could regulate their abundance to suit the density of fire ants (Calixto et al. 2007a, b). *T. melanocephalum* can scare off attackers through their chemical defense. We found that secretions from pygidial gland could be sprayed over the *S. invicta* workers by *T. melanocephalum* when they encounter each other. Workers of *S. invicta* usually act slowly after they are sprayed by the secretions of *T. melanocephalum*. Similar results also indicate that pygidial gland secretions of *T. melanocephalum* play an important role in fighting against each other between *S. invicta* and *T. melanocephalum* (Tomalski et al. 1987).

Compared with co-occurring ant species, such as *T. melanocephalum* and *Pheidole fervida*, *S. invicta* not only have significant advantage of individual body size, but also can attack native species using their well developed mandibles and venom (Gao et al. 2011). Our results suggest that although *S. invicta* are more aggressive than *T. melanocephalum*, mutual tussle was not intense at individual level between the two ant species. Chemical defense of *T. melanocephalum* may restrain the aggressiveness of *S. invicta*. The aggressiveness of *S. invicta* is stronger than that of the two ants *T. melanocephalum* and *P. fervida*. Aggressiveness between *S. invicta* and *P. fervida* was stronger than that between *S. invicta* and *T. melanocephalum* (Gao et al. 2011). This result also indicates that chemical defensive ability was important for *T. melanocephalum* against fire ants.

Conclusion

This study determined the competitive ability for food resource of the fire ant and the ghost ant at short range in colony level. We found that *S. invicta* suppressed the exploitation of honeydew-producing mealybug by ghost ants, and occupied most of honeydew resource due to forceful aggressiveness. However, ghost ants have not been completely driven out of honeydew competition by fire ants, because chemical defense of ghost ants may restrain the aggressiveness of fire ants. The exact competitive mechanisms between invasive and native ants in a recently invaded area may vary among species, because ants are a very diverse group. Effects of invasive ants on subdominant and subordinate ant species in the recipient biota may be mediated through a diversity of competitive mechanisms (Morrison 2000). Therefore, the study which elucidate the underlying mechanisms of species replacement and interspecific competition are important to the understanding of why invasions fail or succeed.

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References

Brightwell RJ, Silverman J (2010) Invasive Argentine ants reduce fitness of red maple via a mutualism with an endemic coccid. Biol Invasions 12(7):2051–2057

Calixto AA, Harris MK, Barr C (2007a) Resurgence and persistence of *Dorymyrmex flavus* after reduction of *Solenopsis invicta* buren with a broadcast bait. Environ Entomol 36(3):549–554

Calixto AA, Harris MK, Knutson A, Barr CL (2007b) Native ant responses to *Solenopsis invicta* Buren reduction using broadcast baits. Environ Entomol 36(5):1112–1123

Daane KM, Sime KR, Fallon J, Cooper ML (2007) Impacts of Argentine ants on mealybugs and their natural enemies in California's coastal vineyards. Ecol Entomol 32(6):583–596

Epperson D, Allen C (2010) Red imported fire ant impacts on upland arthropods in Southern Mississippi. Am Midl Nat 163(1):54–63

Fischer M, Shingleton A (2001) Host plant and ants influence the honeydew sugar composition of aphids. Funct Ecol 15(4):544–550

Flatt T, Weisser WW (2000) The effects of mutualistic ants on aphid life history traits. Ecology 81(12):3522–3529

Gao Y, He Y, Qi G, Zhang J (2011) Interference competition between the red imported fire ant (*Solenopsis invicta* Buren) and two native ant species (Hymenoptera: Formicidae). Acta Entomol Sin 54(5):602–608

Grover CD, Kay AD, Monson JA, Marsh TC, Holway DA (2007) Linking nutrition and behavioural dominance: carbohydrate scarcity limits aggression and activity in Argentine ants. Proc R Soc B Biol Sci 274(1628):2951–2957

Helms KR, Vinson SB (2002) Widespread association of the invasive ant *Solenopsis invicta* with an invasive mealybug. Ecology 83(9):2425–2438

Helms KR, Vinson SB (2003) Apparent facilitation of an invasive mealybug by an invasive ant. Insectes Soc 50(4):403–404

Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. Annu Rev Ecol Syst 33:181–233

Jouvenaz D, Allen G, Banks W, Wojcik DP (1977) A survey for pathogens of fire ants, *Solenopsis* spp., in the southeastern United States. Fla Entomol 60:275–279

Kaplan I, Eubanks MD (2002) Disruption of cotton aphid (Homoptera: Aphididae)—natural enemy dynamics by red imported fire ants (Hymenoptera: Formicidae). Environ Entomol 31(6):1175–1183. doi:10.1603/0046-225x-31.6.1175

Kaplan I, Eubanks MD (2005) Aphids alter the community-wide impact of fire ants. Ecology 86(6):1640–1649

Kay AD, Zumbusch T, Heinen JL, Marsh TC, Holway DA (2010) Nutrition and interference competition have interactive effects on the behavior and performance of Argentine ants. Ecology 91(1):57–64

Morrison LW (2000) Mechanisms of interspecific competition among an invasive and two native fire ants. Oikos 90(2):238–252

Tomalski M, Blum M, Jones T, Fales H, Howard D, Passera L (1987) Chemistry and functions of exocrine secretions of the ants *Tapinoma melanocephalum* and *T. erraticum*. J Chem Ecol 13(2):253–263

Tschinkel WR (2006) The fire ants. Belknap Press of Harvard University Press, Cambridge, MA

Vinson SB (1983) The physiology of the imported fire ant revisited. Fla Entomol 66(1):126–139

Vogt J, Reed J, Brown R (2005) Timing bait applications for control of imported fire ants (Hymenoptera: Formicidae) in Mississippi: efficacy and effects on non-target ants. Int J Pest Manag 51(2):121–130

Wheeler WM (1910) Ants: their structure, development, and behavior. Columbia University Press, New York

Wilder SM, Holway DA, Suarez AV, Eubanks MD (2011a) Macronutrient content of plant-based food affects growth of a carnivorous arthropod. Ecology 92(2):325–332

Wilder SM, Holway DA, Suarez AV, LeBrun EG, Eubanks MD (2011b) Intercontinental differences in resource use reveal the importance of mutualisms in fire ant invasions. Proc Natl Acad Sci 108(51):20639–20644

Wilder SM, Barnum TR, Holway DA, Suarez AV, Eubanks MD (2013) Introduced fire ants can exclude native ants from critical mutualist-provided resources. Oecologia 172(1):197–205

Yao I, Akimoto S (2001) Ant attendance changes the sugar composition of the honeydew of the drepanosiphid aphid *Tuberculatus quercicola*. Oecologia 128(1):36–43

Zhou AM, Lu YY, Zeng L, Xu YJ, Liang GW (2012a) Does mutualism drive the invasion of two alien species? The case of *Solenopsis invicta* and *Phenacoccus solenopsis*. PLoS One 7(7):e41856

Zhou AM, Lu YY, Zeng L, Xu YJ, Liang GW (2012b) Does mutualism drive the invasion of two alien species? The case of *Solenopsis invicta* and *Phenacoccus solenopsis*. PLoS One 7(7). doi:10.1371/journal.pone.0041856

Zhou AM, Lu YY, Zeng L, Xu YJ, Liang GW (2013) *Solenopsis invicta* (Hymenoptera: Formicidae), defend *Phenacoccus solenopsis* (Hemiptera: Pseudococcidae) against its natural enemies. Environ Entomol 42(2):247–252. doi:10.1603/en12168