



RESEARCH ARTICLE - ANTS

Food competition mechanism between *Solenopsis invicta* Buren and *Tapinoma melanocephalum* Fabricus

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Abstract

This study compared the amount of food resource depletion and interference competition at the individual and colony levels between *Solenopsis invicta* and *Tapinoma melanocephalum* in laboratory. The consumption of sausage, honey water, and mealworm by *S. invicta* colonies were of equal worker number was higher than that by *T. melanocephalum* colonies. However, the amounts of sausage, honey water, and mealworm depleted by *S. invicta* colonies were of equal worker biomass were lower than those by *T. melanocephalum* colonies. The consumption of sausage and mealworm by *S. invicta* colonies were of equal worker biomass were also significantly lower than that by *T. melanocephalum* colonies. Individual-level interference competition between *S. invicta* and *T. melanocephalum* colonies in small space was intense. Competition intensity and the mortality rate reached their maximum when the worker numbers of both colonies were equal. In any proportion, the mortality rate of *T. melanocephalum* reached over 80%, higher than that of *S. invicta*. *S. invicta* colonies were of equal worker biomass and number recruited more workers for colony-level interference competition and used more resources. But the death rates of *S. invicta* colonies were higher than those of *T. melanocephalum* colonies. The highly exploitative and interference-competitive of *S. invicta* in trails had restricted the foraging behavior and active region of *T. melanocephalum*.

Introduction

Solenopsis invicta Buren is a dangerous quarantine pest that significantly affects public safety, human health, husbandry, and the ecological environment in its invasion regions. *S. invicta* builds its nests in soil, workers may infiltrate and destroy infrastructure, especially underground wires, cables, and electrical equipment, at cost of millions of dollars; meanwhile, because of its aggressive, death of creatures also leads by fire ant (Vinson, 2013). *S. invicta* has spread to and propagated in China, and occasionally threaten the people's health (Wang et al., 2013). *S. invicta* directly feeds on crops, livestock, and poultry and have thus caused huge economic losses in husbandry (Lofgren et al., 1975; Stewart & Vinson, 1991; Jetter et al., 2002). *S. invicta* also attacks young birds, spawn, calves of sea turtles and other reptiles, and small rodents (Drees, 1994; Giuliano et al., 1996; Allen et al., 1997;

Parris et al., 2002; Pascoe, 2002; Allen et al., 2004).

Invasive ants significantly influence local ant populations, especially ant species with similar ecological characteristics (Holway et al., 2002). For instance, *S. invicta* has replaced *Solenopsis geminata* (F.) and *Solenopsis xyloni* McCook in the North American ecological system through competitive exclusion after invasion (Wilson and Brown Jr, 1958; Porter et al., 1988; Porter, 1992; Porter and Savignano, 1990). Such replacement decreased the abundance and diversity of local ant colonies (Porter & Savignano, 1990) and even changed the coexistence mode of surviving local ant colonies in the biogeographic balance (Gotelli & Arnett, 2000). In 2004, *S. invicta* was found in Wuchuan, Guangdong Province, indicating that the species had invaded the continental China (Wang et al., 2013).

The invasion of South China by *S. invicta* has significantly decreased the diversity of local ant communities



(Shen et al., 2007; Wu et al., 2008). However, few studies have investigated the influence of *S. invicta* invasion on the dominant local species in Guangdong, *Tapinoma melanocephalum* (Wu et al., 2008), as well as the coexistence and competition mechanisms between these species. This study examined the food resource depletion and interference competition at the individual and colony levels between *S. invicta* and *T. melanocephalum* laboratory populations to explore the competition and coexistence mechanisms of *T. melanocephalum* in response to *S. invicta* invasion in Guangdong.

Materials and methods

Ant samples

S. invicta and *T. melanocephalum* colonies were collected from polygyne colonies at wild grass ground or litchi orchard in Southern China and maintained at the South China Agricultural University and Red Imported Fire Ant Research Center, Guangdong province. Colonies of *S. invicta* and *T. melanocephalum* contained queens, workers and included immature at all developmental stages. These colonies were separated from the soil and placed in an open plastic box (23.5 cm length × 15.5 cm width × 9.0 cm high) with small plastic boxes (8.5 cm length × 6.0 cm width × 5.0 cm high) with wet plaster to serve as nest chambers, and then placed in floors at 28 °C, on a diet of 20% honey water (a test tube half full of honey water and plugged with cotton) and fresh mealworms (Coleoptera: Tenebrionidae) until needed for experiments. The inside walls of the bigger boxes were coated with the fluoropolymer resin, Fluon (polytetrafluoroethylene, ICI Fluoropolymers, Exon, PA) to prevent them from escaping.

Comparison between amounts of food resource depletion of *S. invicta* and *T. melanocephalum*

Test food

The following were the food used in the tests: honey - a high carbohydrate food resource (Guangzhou Baoshengyuan Corporation); sausage - a protein- and lipid- rich artificial food resource (Guangdong Shuanghui Food Corporation); and mealworm (Coleoptera: Tenebrionidae) - a high protein natural food resource (purchased from market).

Test method

Experimental colonies of *S. invicta* and *T. melanocephalum* were set up on both an equal worker biomass and equal worker number basis for average worker size varied among their forms (Morrison et al., 2000). Each experimental equal worker biomass colony contained 0.5 g of workers, 0.25 g of brood (included eggs, larvae and pupae) and two queens.

Each experimental equal worker number colony contained 1000 workers, 0.25g of brood and two queens.

Because counting live worker ants was not practical and the workers of *T. melanocephalum* were activity quickly, the method of workers added to colonies was operated like Morrison (2000). But both ants were anaesthetized with ethyl ether before weigh with an electronic balance. We found that ethyl ether had no effect on ants in preliminary trials.

Each experimental colony occupied a plastic box (25 cm length × 18 cm width × 7 cm high), equipped with a small plaster plastic box (8.5 cm length × 6 cm width × 5 cm high) to serve as nest chambers, the sides of which were coated with Fluon to prevent escapes. The mother colonies from which the experimental colonies were kept in the laboratory at 28°C for at least two weeks before experimental colony formation, on a diet of 20% honey water (a test tube half full of honey water and plugged with cotton) and fresh mealworms every day. The experimental colonies were placed in the laboratory at 28°C and 60% 75% RH, starved for 24 h before the beginning of the trials to produce a uniform state of hunger. Each box containing an experimental colony was connected via a test tubing (1 cm inside diameter) to an adjacent (empty) box of the same dimensions. Holes were drilled in the side of the box near the bottom to allow insertion of the tubing. 2.0g of sausage, mealworm, or 20% honey water (drop on the cotton) was placed in the test tube, the ants were allowed to forage for 24h, and then weighed the remaining food with an electronic balance. We conducted ten replicate trails for each food item, for each equivalent colony. Test was stopped when the workers carried larvae and spawn to food, but this situation was rarely observed.

Portions of 2.0g of sausage, mealworm, and honey water were placed in a clean plastic tube, kept at the same conditions, but protected from the ants as evaporation loss control.

Individual level interference competition

Testing method

Healthy and similar size workers of *S. invicta* and *T. melanocephalum* were selected to carry out the interference competitive abilities at the individual level, and the agonistic interactions between *S. invicta* and *T. melanocephalum* were staged in small arenas. Arenas consisted of a dry plastic Petri dish (12 cm inside diameter) which was sterilized with 75% alcohol, washed with distilled water, with inner sides coated with Fluon. Ants were counted by allowing them to climb onto a small paint brush and then placing them into separate plastic boxes (23.5 cm length × 15.5 cm width × 9.0 cm high) with inside walls coated with Fluon. *T. melanocephalum* workers were placed into the plastic Petri dish first, *S. invicta* workers were placed into the arena later. We chose five encounter ratios of *S. invicta* to *T. melanocephalum*, 1) 50 *S. invicta*

workers to 10 *T. melanocephalum* workers (5:1); 2) 45 *S. invicta* workers to 15 *T. melanocephalum* workers (3:1); 3) 30 *S. invicta* workers to 30 *T. melanocephalum* workers (1:1); 4) 15 *S. invicta* workers to 45 *T. melanocephalum* workers (1:3); and 5) 10 *S. invicta* workers to 50 *T. melanocephalum* workers (1:5). The number of major *S. invicta* workers used in areas interaction in each encounter ratio accounted for 10%. We chose the *T. melanocephalum* workers in agonistic interactions were at the uniform size. The ants were observed for 3 h at 26°C and 65% RH. Interaction behavior was recorded, and the number of dead or mortally wounded workers was noted at the end of the trials. We conducted ten replicate trials for each encounter ratio. Healthy individual ants (40 workers) of *S. invicta* and *T. melanocephalum* were independently placed in a clean and dry plastic petri dish; the number of dead workers was recorded to adjust the control death rate. This trail was conducted in ten replicates.

Calculation formula of adjusted death rate

$$\text{Adjusted death rate (\%)} = (\text{control survival rate \%} - \text{treatment survival rate \%}) / \text{control survival rate \%} \times 100$$

Colony level interference competition

Testing method

The experimental colonies of both ants which deal with like 1.2.2 were evaluated in two pairwise comparisons. An equal worker biomass or an equal worker number colony of *S. invicta* was connected to an equal 'size' colony of *T. melanocephalum* via three intervening (empty) boxes by 10 cm length of Tygon tubing (Fig. 1). In the experimental set-up, the boxes containing the ant colonies on each end are

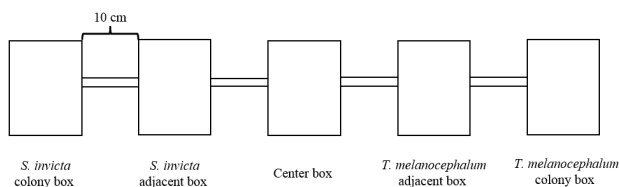


Fig. 1. Design of colony level interference competition experiments.

referred to as 'colony' boxes; the empty boxes adjacent to each colony boxes are referred to as 'adjacent' boxes; and the connecting box in the middle is referred to as the 'center' box (Morrison et al., 2000).

1.0 g of fresh mealworm and 0.5 g of sausage were placed in the center box and two adjacent boxes before the experiment, and then recorded the number of active and dead workers in the three empty boxes (center and both adjacent) when the ants foraging foods at 0.5 h, 24 h, 48 h, and 72 h, the number of dead workers and colonies, which invaded by another ants, in colony boxes when the ants foraging foods at 72 h were also noted. To statistically compare the survival rate of *S. invicta* and *T. melanocephalum* workers in the three empty boxes after 0.5 h min, 24 h, 48 h, and 72 h, the mortality of both ants in five boxes after 0.5 h, 24 h, 48 h, and 72 h, the number of invaded colonies at the end of trail. The interference competition between *S. invicta* and *T. melanocephalum* in each equal 'size' colony was conducted ten replicate trails.

Data processing

The mean amount of resource acquired by each equal *S. invicta* and *T. melanocephalum* colonies was compared by T-test, the mean amount of resource acquired by *S. invicta* or *T. melanocephalum* was compared by one-way ANOVA, for each type of resource. All pairwise comparisons of means were made by Tukey method of multiple comparisons. The data were processed by SPSS 18.0.

Results

Comparison amounts of food resource depletion between *S. invicta* and *T. melanocephalum*

Resource consumption of the different food types varied in *S. invicta* and *T. melanocephalum* (Table 1). When colonies were of equal worker number, *S. invicta* consumed significantly more sausage and honey water than did *T. melanocephalum* ($p < 0.05$). When colonies were of equal worker biomass, *S. invicta* consumed significantly less sausage and mealworm than did *T. melanocephalum* ($p < 0.01$).

Table 1. Amount of food resource depletion of *S. invicta* and *T. melanocephalum* after 24 h

Food resource	Colonies were of equal worker number		Colonies were of equal worker biomass	
	<i>T. melanocephalum</i>	<i>S. invicta</i>	<i>T. melanocephalum</i>	<i>S. invicta</i>
Sausage	0.020±0.001	0.027±0.003*	0.045±0.005	0.016±0.002**
Honey water	0.044±0.002	0.127±0.028*	0.065±0.004	0.054±0.007 ^{ns}
Mealworm	0.018±0.001	0.019±0.002 ^{ns}	0.033±0.003	0.015±0.001**

Note: "^{ns}" indicates lack of significance. "*" and "**" represent significance between the quantities of food transferred by *T. melanocephalum* and *S. invicta* with equal worker number or biomass at the 0.05 and 0.01 probability levels, respectively (independent T-test).

Table 2. Mortality rates of *S. invicta* and *T. melanocephalum* workers in individual level interference competition after 3 h.

Ant species	Confrontation ratio (<i>S. invicta</i> : <i>T. melanocephalum</i>)				
	1:5	1:3	1:1	3:1	5:1
<i>S. invicta</i>	0.15	0.22	0.57	0	0
<i>T. melanocephalum</i>	80.72	87.14	100	99.33	100

Individual level interference competition

In individual level competition, four interference conditions were observed: 1) *T. melanocephalum* workers voluntarily evading *S. invicta* to avoid fighting are referred to as 'ignore'; 2) When both ants encounter, they touch each other by antennae then avoiding rapidly are referred to as 'contact', we can see this condition frequent when *T. melanocephalum* workers less than *S. invicta*; 3) two or more native ants touch a invader ant by antennae, turn-back to eject defensive compounds from pygidial glands and avoiding quickly are referred to as 'chemical defense'; 4) Ants engaging in "fights" often in prolonged grappling with frequent biting and flexing their gaster in the direction of opponents are referred to as 'physical aggression', fighting usually occurred "group" attack (2 or more workers) by *T. melanocephalum* ants on single *S. invicta* ant, although this condition rarely saw in trails. There was no incidence of multiple invaders fighting lone native opponent.

The individual-level interference competition between *S. invicta* and *T. melanocephalum* after 3 h were shown in Table 2. The mortality rates of both ant workers were the lowest when the ratio of *S. invicta* to *T. melanocephalum* was 1:5. The mortality rates of both ant workers increased when the number of *T. melanocephalum* workers equal to *S. invicta*. When both ant workers were 30 (*S. invicta* to *T.*

melanocephalum=1:1), the death rate of *T. melanocephalum* was 100%, and the mortality of *S. invicta* was more than 50%. The mortality rates of *T. melanocephalum* were over 99% in the ratio of 3:1 and 5:1 (*S. invicta* to *T. melanocephalum*), but no dead workers of *S. invicta* were observed.

Colony level interference competition

Proportion of active *S. invicta* workers in two adjacent boxes and center box

To count the survival workers of *S. invicta* in each kind of food foraging in adjacent and center boxes, the number of survival workers appearing in each box accounts for the total workers (including dead and alive ants) which foraging in adjacent and center boxes as proportion of active *S. invicta* workers (Table 3). When colonies were of equal worker biomass, sausage was used as the food resource, the active *S. invicta* workers in *S. invicta* colony adjacent box accounted for the maximum proportion (14.97%) at 0.5 h, and no workers were found in the center box and *T. melanocephalum* colony adjacent box. At 24 and 48 h, active *S. invicta* workers in the *S. invicta* colony adjacent box reached their maximum proportions (12.24% and 11.11%, respectively), which were significantly higher than those in *T. melanocephalum* colony adjacent box. At 72 h, active *S. invicta* workers in center box

Table 3. Proportion of active *S. invicta* workers in the two adjacent boxes and center box.

		Colonies were of equal worker biomass		Colonies were of equal worker number	
		Sausage	Mealworm	Sausage	Mealworm
0.5 h	<i>S. invicta</i> colony adjacent box	14.97±13.56 a	16.54±8.87 a	14.98±11.94 a	16.22±9.65 a
	Center box	0.00±0.00 b	0.85±2.68 b	0.00±0.00 b	0.00±0.00 b
	<i>T. melanocephalum</i> colony adjacent box	0.00±0.00 b	0.00±0.00 b	0.00±0.00 b	0.00±0.00 b
24 h	<i>S. invicta</i> colony adjacent box	12.24±4.08 a	13.37±4.28 a	13.61±6.02 a	10.15±4.24 a
	Center box	7.63±3.21 b	9.18±4.32 b	4.74±5.68 b	10.91±2.91 a
	<i>T. melanocephalum</i> colony adjacent box	4.75±5.66 b	4.05±5.06 c	5.72±6.34 b	7.89±5.35 a
48 h	<i>S. invicta</i> colony adjacent box	11.11±3.84 a	12.39±5.35 a	13.66±2.47 a	11.46±5.56 a
	Center box	10.83±5.23 a	9.81±3.39 a	7.00±2.73 b	9.68±4.99 a
	<i>T. melanocephalum</i> colony adjacent box	6.07±4.63 b	5.25±4.97 b	7.86±5.20 b	7.04±3.28 a
72 h	<i>S. invicta</i> colony adjacent box	11.49±3.18 a	12.25±7.36 a	12.74±4.73 a	12.93±3.32 a
	Center box	11.89±2.84 a	5.32±5.95 b	7.62±6.26 ab	9.76±4.19 a
	<i>T. melanocephalum</i> colony adjacent box	4.65±5.01 b	7.31±5.28 b	5.45±5.79 b	5.19±4.60 b

Note: Same-column means followed by the same letter are not significantly different at the 0.05 and 0.01 levels, respectively, as in Table 4.

Table 4. Proportion of active *T. melanocephalum* workers in two adjacent boxes and center box.

		Colonies were of equal worker biomass		Colonies were of equal worker number	
		Sausage	Mealworm	Sausage	Mealworm
0.5h	<i>S. invicta</i> colony adjacent box	0.00±0.00 b	0.00±0.00 b	0.00±0.00 b	0.00±0.00 b
	Center box	0.00±0.00 b	0.00±0.00 b	0.00±0.00 b	0.00±0.00 b
	<i>T. melanocephalum</i> colony adjacent box	16.98±7.91 a	17.17±7.34 a	15.10±11.67 a	15.29±11.33 a
24h	<i>S. invicta</i> colony adjacent box	3.08±4.50 b	2.87±5.30 b	2.91±5.04 b	0.60±1.88 b
	Center box	6.40±5.03 b	5.09±6.01 b	6.48±7.04 b	10.03±4.88 a
	<i>T. melanocephalum</i> colony adjacent box	14.05±7.62 a	14.13±7.54 a	13.91±5.38 a	13.23±6.47 a
48h	<i>S. invicta</i> colony adjacent box	3.31±3.71 b	5.28±7.51 a	4.24±5.74 b	1.07±3.38 b
	Center box	9.14±6.82 a	7.85±7.29 a	3.63±4.79 b	8.55±6.37 a
	<i>T. melanocephalum</i> colony adjacent box	11.33±8.23 a	8.92±8.88 a	14.23±8.03 a	12.87±7.65 a
72h	<i>S. invicta</i> colony adjacent box	3.38±4.62 b	7.21±11.66 a	3.11±5.12 b	2.05±4.41 b
	Center box	7.29±6.62 ab	4.86±8.28 a	4.80±7.04 b	8.27±6.08 a
	<i>T. melanocephalum</i> colony adjacent box	12.06±8.89 a	4.86±8.28 a	14.61±5.19 a	12.48±8.19 a

reached their maximum proportion (11.89%), which was significantly higher than that in *T. melanocephalum* colony adjacent box. When mealworm was used as the food resource, active *S. invicta* workers in *S. invicta* colony adjacent box reached their maximum proportions and significantly higher than those in *T. melanocephalum* colony adjacent box at 0.5, 24, and 48 h. At 72 h, active *S. invicta* in workers in center box reached their maximum proportion (12.25%) and significantly higher than those in center box and *T. melanocephalum* colony adjacent box.

When colonies were of equal worker number, sausage as the food resource, active *S. invicta* workers in *S. invicta* colony adjacent box had their maximum proportion at 0.5 h, and no workers were found in center box and *T. melanocephalum* colony adjacent box. At 24 and 48 h, active *S. invicta* workers in *S. invicta* colony adjacent box reached their maximum proportions (13.61% and 13.66%, respectively), significantly higher than those in center box and *T. melanocephalum* colony adjacent box. At 72 h, active *S. invicta* workers in *S. invicta* colony adjacent box reached their maximum proportion (12.74%), significantly higher than that in *T. melanocephalum* colony adjacent box. When mealworm was the food resource, active *S. invicta* workers in *S. invicta* colony adjacent box reached their maximum proportion (16.22 %) at 0.5 h, and no workers were found in the center box and *T. melanocephalum* colony adjacent box. At 24 h, active *S. invicta* workers in center box reached their maximum proportion (10.91%), indistinctively with those in center box and *T. melanocephalum* colony adjacent box. At 48 and 72 h, active *S. invicta* workers in *S. invicta* colony adjacent box reached their maximum proportions (11.46% and 12.93%, respectively), significantly higher than that in *T. melanocephalum* colony adjacent box.

Proportion of active T. melanocephalum workers in two adjacent boxes and center box

The proportion of the active *T. melanocephalum* workers in which colonies were equivalent by worker biomass or number was counted and shown in table 4. When colonies were of equal worker biomass, sausage was used as the food resource, active *T. melanocephalum* workers were found only foraging in *T. melanocephalum* colony adjacent box at 0.5 h. Active *T. melanocephalum* workers in *T. melanocephalum* colony adjacent box reached their maximum proportions (14.05%, 11.33%, and 12.06%, respectively) at 24, 48, and 72 h, therefore the minimum proportion of native ants foraging in *S. invicta* colony adjacent box was observed at the same time. At 24 and 48 h, the proportions of active *T. melanocephalum* workers in *T. melanocephalum* colony adjacent box were significantly higher than those in *S. invicta* colony adjacent box; at 72 h, the proportion of active *T. melanocephalum* workers in *T. melanocephalum* adjacent box was significantly higher than that in *S. invicta* colony adjacent box. When mealworm was used as the food resource, active *T. melanocephalum* workers were found only in *T. melanocephalum* colony adjacent box at 0.5 h. At 24 and 48 h, active *T. melanocephalum* workers in *T. melanocephalum* colony adjacent box reached their maximum proportions (14.13% and 8.92%, respectively), and the proportions of active *T. melanocephalum* workers in *T. melanocephalum* adjacent box were significantly higher than those in *S. invicta* colony adjacent box at 24 h. At 72 h, the proportions of active *T. melanocephalum* workers foraging in two adjacent and center boxes was non-significant.

When colonies were of equal worker number, sausage was used as food resource, active *T. melanocephalum* workers

Table 5. Comparison of workers mortality rate in five boxes after 72 h

Test box	Colonies were of equal worker biomass				Colonies were of equal worker number			
	Sausage		Mealworm		Sausage		Mealworm	
	Si	Tm	Si	Tm	Si	Tm	Si	Tm
<i>S. invicta</i> colony box	31.29	0	21.55	0	27.88	0.96	28.64	0
<i>S. invicta</i> colony adjacent box	12.93	0	11.21	0	7.69	2.40	8.04	0
Center box	2.72	2.04	5.60	0	3.85	1.44	4.02	2.01
<i>T. melanocephalum</i> colony adjacent box	5.44	2.72	3.88	9.05	1.92	3.37	2.01	4.52
<i>T. melanocephalum</i> colony box	21.09	21.77	28.88	19.83	22.12	28.37	24.12	26.63

Note: Si = *S. invicta* and Tm = *T. melanocephalum*.

were found only in *T. melanocephalum* colony adjacent box at 0.5 h. At 24, 48, and 72 h, active *T. melanocephalum* workers in *T. melanocephalum* colony adjacent box reached their maximum proportions (13.91%, 14.23%, and 14.6%, respectively), significantly higher than that in center box and *S. invicta* colony adjacent box. When mealworm was used as food resource, active *T. melanocephalum* workers were found only in the *T. melanocephalum* colony adjacent box at 0.5 h. At 24, 48, and 72 h, active *T. melanocephalum* workers in *T. melanocephalum* colony adjacent box and center box reached their maximum proportions (13.23%, 12.87%, and 12.48%, respectively), significantly higher than that in *S. invicta* colony adjacent box.

Comparison of workers mortality rate in five boxes after 72 h

Although the case of invaders presenting to each other nest chamber can be saw in trails, intense fighting between *S. invicta* and *T. melanocephalum* was rarely observed, and ants usually establish their territories after 72 h (Morrison et al., 2000). Therefore, we recorded the workers mortality rate foraging in two colony boxes, two adjacent boxes, and center box after 72 h (Table 5). When colonies were of equal worker biomass, in the case of sausage depletion by two ants, the mortality rates of both ants in *T. melanocephalum* colony box were the highest (>21%), followed by those in *T. melanocephalum* colony adjacent box and center box. The death rates of *T. melanocephalum* in *S. invicta* colony box and adjacent boxes were zero. In the case of mealworm depletion, the death rates of both ants in *T. melanocephalum* colony box were the highest, followed by those in *T. melanocephalum* colony adjacent box. The death rates of *T. melanocephalum* in center box, *S. invicta* colony adjacent box, and *S. invicta* colony box were zero.

When colonies were of equal worker number, in the case of sausage depletion, the death rates of both ants in *T. melanocephalum* colony box were the highest (>22%). The death rate of *T. melanocephalum* workers in *S. invicta* colony box and *S. invicta* workers in *T. melanocephalum* colony adjacent box were the lowest. In the case of mealworm depletion, the death rates of both ants in *T. melanocephalum* colony box were the highest (>24%), followed by those in

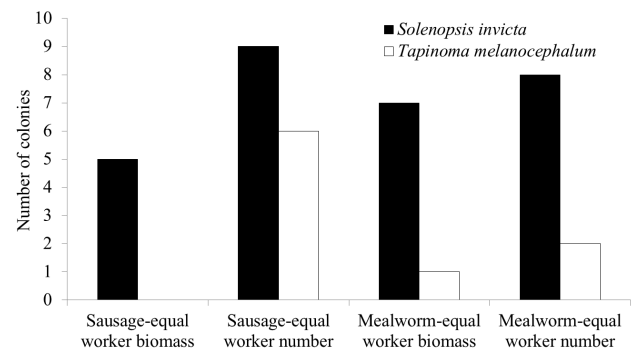


Fig. 2. Colonies of *S. invicta* and *T. melanocephalum* invading to each other nest chamber after 72 h.

T. melanocephalum colony adjacent box and center box. The death rates of *T. melanocephalum* in *S. invicta* colony and adjacent boxes were zero.

Colonies of *S. invicta* and *T. melanocephalum* invading to each other nest chamber after 72 h

We recorded and counted the colony number of *S. invicta* and *T. melanocephalum* workers invaded to opponent colony boxes after 72 h (Fig. 2). When sausage was used as food resource, five *S. invicta* colonies (50% of all colonies in trails) which colonies were of equal worker biomass invaded to *T. melanocephalum* colony box, and no-one *T. melanocephalum* colony invaded to *S. invicta* colony box. Nine *S. invicta* colonies (90% of all colonies in trails) which colonies were of equal worker number invaded to *T. melanocephalum* colony box, and six *T. melanocephalum* colonies (60% of all colonies in trails) invaded to *S. invicta* colony box. When mealworm was used as food resource, seven *S. invicta* colonies (70% of all colonies in trails) which colonies were of equal worker biomass, invaded *T. melanocephalum* colony box, while only one *T. melanocephalum* colony invaded *S. invicta* colony box. Eight *S. invicta* colonies (80% of all colonies in trails) which colonies were of equal worker number, invaded *T. melanocephalum* colony box, while only two *T. melanocephalum* colonies invaded *S. invicta* colony box. These results indicate that *S. invicta* was more aggressive.

Discussion

Interspecific competition refers to the mutual interference or inhibition between two or more species. The essence of interspecific competition lies in the efficiency reduction of the reproduction, survival, growth, and other aspects of individuals of one species because of the exploitation or interference of common resources by individuals of another species. Interspecific competition primarily refers to resource competition, namely, the mutually unfavorable effects of commonly exploiting scarce resources on biological individuals. Resource competition can be classified into exploitation and interference competition. In exploitation competition, individuals of one species obtain more common resources than those of another species; in interference competition, individuals of one species limit or prevent individuals of another species from using the resources (Reitz and Trumble, 2002). Interspecific competition is considered key in structuring local ant communities, and it has been described as the “hallmark of ant ecology” (Cerdeira et al., 2013).

Local ants have been replaced by *S. invicta* because this species is highly exploitative and interference-competitive (Porter and Savignano, 1990; Bhatkar et al., 1972; Obin and Vander Meer, 1985; Jones and Phillips Jr, 1987; Hook and Porter, 1990; Jones and Phillips Jr, 1990; Morrison, 2000, 1999, 2002). In this study, we found that food consumption of *T. melanocephalum* colonies which colonies were of equal worker number, was less than did *S. invicta*, *T. melanocephalum* workers (monomorphic, one-sized) are extremely small, 1.3 to 1.5 mm long (Scheurer et al., 1998), only *S. invicta* worker (involving major and minor ants) was 3.24 times the average weight of *T. melanocephalum* may be responsible for the results. Higher amount of food resource depleted by equal worker biomass *T. melanocephalum* colonies may be due to the number of *T. melanocephalum* workers more than *S. invicta*. In other words, one *T. melanocephalum* worker need less food than *S. invicta* to maintain its daily activities.

Intense fighting between *S. invicta* and *T. melanocephalum* was found in individual level interference competition in a small arena when worker number in both ants was equivalent or there were more workers of *S. invicta* than *T. melanocephalum*. *S. invicta* workers attacking *T. melanocephalum* usually by ‘physical aggression’, but *T. melanocephalum* worker would prefer to use ‘chemical defense’ to repel invader ants, which *T. melanocephalum* displayed alerting, alarm behavior, and the daubing of pygidial gland secretions (Tomalski et al., 1987). *T. melanocephalum* ants would initiative attacking *S. invicta* when its workers were more than invaders, and a single *S. invicta* worker kept far away from *T. melanocephalum* ants to avoid attacked for application of the pygidial gland secretion to the legs or antennae of a foreign ant often resulted in a hindrance of movement or in the limbs adhering together (Tomalski et al.,

1987). However, mortality rate of *T. melanocephalum* was more than 80% in all treatments, *S. invicta* workers were more aggressive and its size (involving major and minor ants) bigger than *T. melanocephalum* may be the main reasons. In colony level interference competition, both ant colonies of equal worker biomass or number foraging in colony boxes and each colony adjacent box were more, and then foraging in farther distance food resources. Intense fighting in both ants was usually saw in *T. melanocephalum* colony box for native ant nest chamber intruded by *S. invicta* workers, but *S. invicta* paying its stronger aggressiveness for the higher mortality rate in this interference competition.

In the indoor interference competition between *S. invicta* and *T. melanocephalum*, *S. invicta* recruited larger workers on food resources, intruded to *T. melanocephalum* colony box, indicated that *S. invicta* was highly exploitative and interference-competitive, which restricts the activity of *T. melanocephalum*. Chemical defense used by *T. melanocephalum* repelled the exotic ant was a major reason to explain the highly mortality rate in *S. invicta*, and implied that *T. melanocephalum* was the native ant against with *S. invicta* in invaded region.

The reasons can explain the phenomenon of coexistence between *T. melanocephalum* and *S. invicta* in invaded region in South China are as follow: 1) *T. melanocephalum* is opportunistic nester in places that sometimes remain habitable for only a few days or weeks (Hölldobler and Wilson, 1990), and highly adaptable in its nesting habits outdoors or indoors, the colonies occupy local sites include tufts of dead but temporarily moist grass, plant stems, and cavities beneath detritus in open, rapidly changing habitats (Oster and Wilson, 1978). Indoors, the ant colonies wall void or spaces between cabinetry and baseboards. It will also nest in potted plants (Smith and Whitman 1992) and the ant nest which abandon by *S. invicta* populations (we found in wild grass ground or litchi orchard in South China); 2) Multiple queens may be spread out in multiple subcolonies, new colonies are probably formed by budding and there does not appear to be any infighting between members of different colonies or nests (Smith and Whitman 1992); 3) *T. melanocephalum* workers are favor many food resources, they are fond of honeydew and tend honeydew-excreting insects, and foraging on honeydew more efficiently than *S. invicta* (Zheng and Zhang, 2010) and *T. melanocephalum* workers are extremely small, a little food can maintain its daily activities; 5) *T. melanocephalum* has the habit of running rapidly and erratically when disturbed (Li et al., 2008), using pygidial gland secretions to repel invaders; in addition, this native ant has higher tolerance to high temperature than *S. invicta* (Zheng et al., 2007).

S. invicta, the invaders, is foraging all year in Guangdong province, has great capacity for plundering food resources, more aggressive, and a larger population, therefore they exhibits intense competitiveness than *T. melanocephalum* in our research. Short-term invasions by *S. invicta* also

significantly affect *T. melanocephalum* in simple habitats (unpublished). If *S. invicta* invaded in a shortage resource and vegetation over simplified habitat, for example in lawn (*T. melanocephalum* workers only can be saw foraging in the border), may overcome *T. melanocephalum* and eventually replace it as the only dominant species would be further research.

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