# Interspecific Competition Between Solenopsis invicta and Two Native Ant Species, Pheidole fervens and Monomorium chinense

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# Interspecific Competition Between *Solenopsis invicta* and Two Native Ant Species, *Pheidole fervens* and *Monomorium chinense*

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**ABSTRACT** This study was designed to understand the effects of the interspecific competition between red imported fire ant, *Solenopsis invicta* Buren and two native ant species, *Pheidole fervens* Smith and *Monomorium chinense* Santschi, by conducting colony interference and individual confrontation tests under laboratory conditions. The colony interference test showed that both native ant species, owing to their numerical advantage, killed the *Solenopsis invicta* virus-1 (SINV-1)–infected or healthy queens of *S. invicta*. Significantly less time was required for *M. chinense* to kill all SINV-1–infected *S. invicta* compared with the time required to kill the healthy *S. invicta*. Compared with healthy *S. invicta*, SINV-1–infected *S. invicta* spent a longer time eliminating the *P. fervens* colonies. In confrontation tests, *M. chinense* killed a significantly higher number of infected *S. invicta* minors than they did healthy minors, but the number of *S. invicta* majors (either infected or healthy) killed was substantially less. This study found that the viral infection weakened the competitive ability of *S. invicta* and made them prone to be eliminated by *M. chinense* but not by *P. fervens*.

**KEY WORDS** *Solenopsis invicta*, *Solenopsis invicta* virus-1, interspecific competition, *Monomorium chinense*, *Pheidole fervens*

After their accidental introduction to Taiwan in 2003, the red imported fire ant, *Solenopsis invicta* Buren, has become an important economic pest, as well as a problem for native biodiversity and public health in both rural and urban areas (Kafle et al. 2010). Yang et al. (2008) indicated that the distribution of polygyne colonies in Taiwan is small and concentrated in the center of Taoyuan County and that the distribution of monogyne colonies is larger and random, especially in the outlying areas of Taoyuan. In Taiwan, 80% of the fire ant control is due to the control of ants in the core polygyne area. The polygyne colony has been reported to be more susceptible to bait treatments because of frequent intercolony food exchanges and a higher nest density (Drees et al. 1992). Consequently, the monogyne colonies present a potential problem and future control programs should consider adding alternative control strategies to the bait control of *S. invicta.*

*S. invicta* can be suppressed by a wide range of natural enemies, especially parasitoids, pathogens and native competitors (Porter et al. 1997, Keck et al. 2005). It has been reported that the main predators of *S. invicta* are other ant species (Wilson 1971). Due to predation by other species, the mortality rate of a newly mating queen of *S. invicta* has been reported to be ≈99% (Whitcomb et al. 1973). This interspecific competition among ants also restrains the ability of *S. invicta* to spread (Hung and Vinson 1978). Hence, using native ant species might be an alternative concept for the biological control of fire ants.

Viruses are being evaluated as biological control agents against fire ants after the discovery of the picorna-like virus *Solenopsis invicta* virus (SINV)-1 and SINV-2 (Valles et al. 2004, 2007). Both viruses infect all stages and castes of fire ants (eggs, larvae, pupae, workers, and queens) and induce significant mortality of the brood. In Taiwan, only SINV-1– (46%) and SINV-2 (16.7%)–infected *S. invicta* populations have been observed so far (Yang et al. 2010).

Tsai et al. (2009) reported that *Monomorium chinense* Santschi was the most abundant ant species and that *Pheidole fervens* Smith was one of the subdominant species in Taiwan. We also found the same two species were most common in the study area. Therefore, we hypothesize that there might be some interaction between native ants and *S. invicta* either infected with virus or not.

Although SINV-1 has been evaluated in United States against *S. invicta,* there is no study that explains the interspecific competition between SINV-1–infected *S. invicta* and *M. chinense* and *P. fervens.* Therefore, this study was designed to evaluate the interspecific competition between healthy and SINV-1–infected *S. invicta* and those two native ant species.

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## Materials and Methods

**Collecting and Rearing of Ants.** All S. *invicta* colonies were collected from Taoyuan and Taipei counties, Taiwan by excavating mounds. Ants were separated from soil by exposing the excavated mounds under heat lamps. Separated ants were transferred to plastic boxes (26 cm long by 22 cm wide by 6 cm high) containing an artificial nest (Kafle et al. 2008). The native ant species *P. fervens* and *M. chinense* were collected from Changhua County, Taiwan and from the study area, Shan-Shia, Taipei, respectively. *P. fervens* and *M. chinense* were transferred to a plastic box, as was done for *S. invicta.* All plastic boxes were coated with Fluon to prevent the ants from escaping. All colonies were held at 30 ± 1°C, 65 ± 10% RH, and a photoperiod of 12:12 (L:D) h under laboratory conditions. Each ant colony was fed with sugar water and crickets. In total, 14 *S. invicta* colonies (seven healthy colonies and seven SINV-1–infected colonies), 10 *P. fervens* colonies, and seven *M. chinense* colonies were reared for this study.

Both *M. chinense* and *P. fervens* are native to tropical Asia, including Taiwan. *P. fervens* colony is polygynous (having more than one queen per colony) with more than a thousand workers per colony. *P. fervens* are dimorphic consisting of large-headed workers (majors or soldiers) and proportionately much narrower headed workers (minors). The total body length of the majors and the minors is ≈4.5 and ≈3 mm, respectively. The *P. fervens* is a numerically and behaviorally dominant species and can recruit a large numbers of workers to occupy food and aggressively attack their competitors. They are primarily scavengers, eating human foodstuffs and the remains of dead insects, but they are omnivores, killing insects as well as collecting seeds (Herris et al. 2005).

*M. chinense* has a monomorphic worker caste, their average body length being 1.3 mm. *M. chinense* is also polygynous with more than a thousand workers per colony. Some species of *Monomorium* are primary omnivores, relatively slow moving and less aggressive ants. They can recruit large numbers of workers and can seriously interfere by monopolizing food resources (Andersen et al. 1991, Jones et al. 2003).

**Detection of Social Form of S. *invicta*, SINV-1/SINV-2.** The social form of *S. invicta* was confirmed using a *Gp*-9 polymerase chain reaction (PCR) protocols as reported by Valles and Porter (2003). Similarly, to confirm whether *S. invicta* was infected by SINV-1/SINV-2, the protocol developed and used by several researchers was applied (Valles et al. 2007, Hashimoto and Valles 2008). The prevalence of intracolony SINV-1 infection of *S. invicta* (adults and brood) was not estimated. Therefore, throughout the whole study, the infected ants were the ants from the fire ant colony with SINV-1 infection.

**Individual Interference Competition.** Each pair competition was staged in small artificial arenas under the laboratory conditions. The healthy workers used during this test were from the fire ant colony without SINV-1/SINV-2 infection and the infected workers were from the fire ant colony with SINV-1 infection. The interference competition tests were quantified by placing 10 workers of each ant species into a 9-cm-diameter plastic petri dish that had the inside rim coated with Fluon. The mortality of each ant species workers was counted for 1 h. To calculate the percentage of competitive ability of *S. invicta,* the following equation was used:

$$(S/ST) \times 100,$$

where $S$ is the number of live *S. invicta* and $ST$ is the number of live *S. invicta* and live competing ants.

To understand the interaction between *S. invicta* and *P. fervens,* the following five combinations were tested: 1) SINV-1–infected/healthy *S. invicta* majors versus *P. fervens* soldiers, 2) SINV-1–infected/healthy *S. invicta* majors versus *P. fervens* workers, 3) SINV-1–infected/healthy *S. invicta* minors versus *P. fervens* soldiers, 4) SINV-1–infected/healthy *S. invicta* minors versus *P. fervens* workers, and 5) SINV-1–infected/healthy *S. invicta* mixed size (minors:majors; 1:1) versus *P. fervens* mixed size.

In addition, to understand the interaction between *S. invicta* and *M. chinense,* another set of tests was designed. Because *M. chinense* workers are *monomorphic, M. chinense* were paired and forced to compete with SINV-1–infected/healthy majors, minors and mixed size *S. invicta*. Because *M. chinense* workers are smaller than the *S. invicta* workers (1.3 versus 2–7 mm in length), 75 *M. chinense* workers were used to equalize the biomass between the species. As a control, 10 individuals of each ant species were placed without opposite species into a 9-cm-diameter plastic petri dish has explained in the previous section.

Each treatment was replicated 10 times. The mortality data were transformed by an arcsine square-root transformation and analyzed for normality using the Shapiro–Wilk test. Significant differences in mortality were determined by a Wilcoxon–Mann–Whitney *U* test (SAS Institute 2008).

**Colony Interference Competition.** This experiment was set up to understand the interspecific competition between *S. invicta* and native ants at the colony level. Both *P. fervens* and *M. chinense* colonies were tested against SINV-1–infected and healthy *S. invicta* colonies.

For *S. invicta* colonies, 20 minor workers, 10 brood, and one queen from polygyne colonies were used. This combination is the normal initial colony size of *S. invicta* that is colony initiated by a newly matted *S. invicta* queen (Booth and Dhami 2008). Colonies with 200, 100, and 20 worker:soldier combinations (soldier: workers; 1:4) with one queen were prepared for *P. fervens.* Similarly, colonies of 150 and 750 workers with one queen were prepared for *M. chinense.*

The pairing of 150 *M. chinense* and 20 S. *invicta* was replicated three times, and the other pair combinations were replicated five times. In each test, each experimental colony container (18 by 4 by 10 cm, length by height by width) was connected via 50-cm-long plastic tubes to a foraging arena (15 cm in diameter by 4 cm in height). A detail layout of the colony-

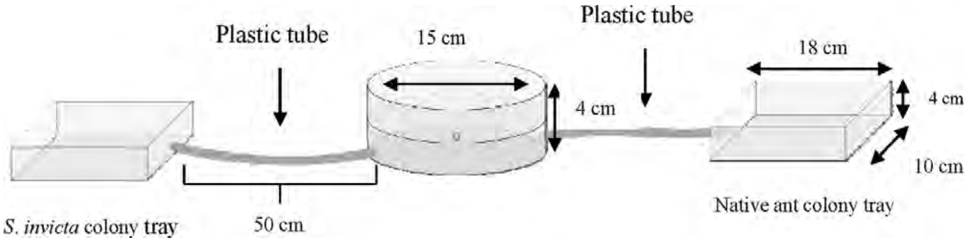

**Fig. 1.** Design of the colony-level interference experimental setup.

level interference experimental setup is mentioned in Fig. 1. One cricket was placed in the center of the foraging arena. In the controls, single ant colonies without opposing competitive ant species were prepared for each colony size category.

During the experiment, the following data were recorded: 1) the number of dead ants of each species and 2) the time required by either ant species to kill the other's queen. The number of ants and the species invading the opposite colony were recorded at every 15 min for first 2 h, every hour for next 12 h, and once at every 12 h until one colony was invaded by the opposite colony. The mortality data were transformed and analyzed using the Shapiro–Wilk test. The means were compared by a Wilcoxon–Mann–Whitney *U* test (SAS Institute 2008).

## Results

**Detection of *S. invicta* Social Form, SNV1 and SNV2.** In total, 123 *S. invicta* colonies were collected from Taoyuan and Taipei counties. From those colonies, 24 and 99 were monogyne and polygyne, respectively. Among the collected *S. invicta* colonies, the SINV-1 and SINV-2 infection rates were 46.3 and 12.1%, respectively. This study did not reveal any mixed infection by SINV-1 and SINV-2 in the same *S. invicta* colonies. Only ants from the SINV-1–infected colonies were used for the interference studies. The prevalence of intra-colony SINV-1–infected *S. invicta* (adults and brood) was not estimated.

**Individual Interference Experiment.** The mortality of P. *fervens* increased as the size of *S. invicta* workers increased. When *S. invicta* majors combated with *P. fervens*, *S. invicta* inflicted a higher level of mortality on *P. fervens.* In all cases, the mortality of *P. fervens* workers was >94%. Similarly, when virus infected or healthy *S. invicta* minors combated with *P. fervens* soldiers, the mortality of *P. fervens* soldiers was only 10% or less. A comparison of the mortality of *P. fervens* caused by either SINV-1–infected or healthy *S. invicta* showed no significant difference (Table 1).

The results from the individual confrontations between virus infected or healthy *S. invicta* and *M. chinense* showed that the mortality of *M. chinense* was higher when paired with *S. invicta* major workers than when paired with minor workers or workers of mixed size. The percentage of *M. chinense* killed by the healthy or SINV-1–infected *S. invicta* minor workers were ≈70% to 76% lesser than by the healthy or SINV-1–infected *S. invicta* major workers (Table 2).

Only SINV-1–infected *S. invicta* mixed sizes and minors suffered higher mortality. All *S. invicta* majors were alive after the individual confrontation. The *M. chinense* caused a significantly higher mortality among SINV-1–infected *S. invicta* minors than among healthy ones. No mortality of *S. invicta* majors was caused by the *M. chinense* during the study. The healthy or SINV-1–infected *S. invicta* minor workers killed by *M. chinense* were from ≈32 to 81% higher than the healthy or SINV-1–infected *S. invicta* major workers (Table 3).

When healthy *S. invicta* majors were paired with *P. fervens* workers, mixed sizes and soldiers, the competitive ability of *S. invicta* majors against *P. fervens* workers was significantly higher than the *P. fervens* soldiers; however, the competitive ability of *S. invicta* majors against *P. fervens* workers and mixed sizes was not significantly different. The same trend was observed when *S. invicta* mixed sizes were paired with *P. fervens* workers, mixed sizes, and soldiers. In addition, when healthy *S. invicta* minors were paired with *P. fervens* workers, mixed sizes, and soldiers, the competitive ability of *S. invicta* minors against *P. fervens* workers was significantly higher than the *P. fervens* soldiers; however, the competitive ability of *S. invicta* minors against *P. fervens* mixed sizes and soldiers was not significantly different (Fig. 2).

**Table 1. Mortality (percentage) of *P. fervens* against each size category of healthy/SINV-1 infected *S. invicta***

| *P. fervens* pop | *S. invicta* majors[a] | | | *S. invicta* mixed sizes[a] | | | *S. invicta* minors[a] | | |
|---|---|---|---|---|---|---|---|---|---|
| | Healthy | Infected | *P* | Healthy | Infected | *p* | Healthy | Infected | *P* |
| *P. fervens* soldiers | 94 ± 0.9 | 95 ± 0.7 | 1 | 77 ± 1.4 | 83 ± 0.9 | 0.54 | 3 ± 0.4 | 10 ± 0.9 | 0.09 |
| *P. fervens* mixed (soldiers + workers) | 99 ± 0.3 | 100 ± 0 | 1 | 96 ± 0.6 | 94 ± 1.0 | 0.88 | 66 ± 1.7 | 66 ± 1.6 | 0.96 |
| *P. fervens* workers | 100 ± 0 | 100 ± 0 | 1 | 98 ± 0.4 | 99 ± 0.3 | 1 | 98 ± 0.4 | 97 ± 0.6 | 1 |

[a] Wilcoxon–Mann–Whitney test at $P = 0.05$ significance level.

**Table 2. Mean mortality of *M. chinense* against each size category of healthy/SNV-1 infected *S. invicta***

| *S. invicta* pop | Mortality (%) of *M. chinense* caused by *S. invicta*[a] | | |
|---|---|---|---|
| | Healthy | Infected | *P* |
| *S. invicta* majors | 92.2 ± 1.1 | 87.4 ± 2.6 | 0.12 |
| *S. invicta* mixed (majors + minors) | 23.8 ± 2.4 | 18.9 ± 2.4 | 0.19 |
| *S. invicta* minors | 16 ± 2.7 | 17 ± 2.5 | 0.81 |

[a] Wilcoxon–Mann–Whitney test $P = 0.05$ significance level.

When SINV-1–infected *S. invicta* majors were paired with *P. fervens* workers, mixed sizes, and soldiers, the competitive ability of virus infected *S. invicta* majors against *P. fervens* workers, mixed sizes, and soldiers was not significantly different. When virus infected *S. invicta* mixed sizes were paired with *P. fervens* workers, mixed sizes, and soldiers, the competitive ability of virus-infected *S. invicta* mixed sizes against *P. fervens* workers was significantly higher than the *P. fervens* soldiers, and the competitive ability of virus-infected *S. invicta* minors against *P. fervens* mixed sizes and soldiers was not significantly different. When virus-infected *S. invicta* minors were paired with *P. fervens* workers, mixed sizes, and soldiers, the competitive ability of virus-infected *S. invicta* minors against *P. fervens* workers was significantly different than the mixed sizes and soldiers (Fig. 3). The workers of *P. fervens* were more aggressive than the soldiers. The workers actively bite the legs or antenna of *S. invicta*, although such behavior was not successful for killing *S. invicta*. Instead, *S. invicta* were dismembered by *P. fervens* soldiers in most cases.

When healthy or SINV-1–infected *S. invicta* majors were paired with *M. chinense* workers, the competitive ability of healthy or SINV-1–infected *S. invicta* majors was not significantly different against *M. chinense* workers. When healthy or SINV-1–infected *S. invicta* mixed sizes were paired with *M. chinense* workers, the competitive ability of healthy *S. invicta* mixed sizes was significantly higher than the SINV-1–infected *S. invicta* against *M. chinense* workers. Same trend as mixed sizes healthy or SINV-1–infected *S. invicta* also was observed for healthy or SINV-1–infected *S. invicta* minors (Fig. 4). In the controls, no ants were died in any of the sets.

**Colony Interference Experiment.** *P. fervens* were the first to discover food and instantly recruited additional nestmates, whereas most *S. invicta* aggregated in the nest and seldom foraged, resulting in low recruitment numbers, especially for SINV-1–infected *S. invicta*. Subsequently, *P. fervens* quickly entered the *S. invicta* nest and attacked the *S. invicta* workers. When *P. fervens* first explored the central food arena and invaded *S. invicta* nest, *P. fervens* caused higher mortality of *S. invicta* during the first day. However, when *M. chinense* competed with *S. invicta*, *M. chinense* and *S. invicta* took ≈7–10 min and 11–13 min to discover the food, respectively. The *M. chinense* paired with SINV-1–infected *S. invicta* were relatively faster to discover food than the *M. chinense* paired with healthy *S. invicta*.

**Table 3. Mortality of healthy/SNV-1 infected *S. invicta* against *M. chinense***

| *S. invicta* pop | Mortality (%) of *S. invicta* caused by *M. chinense*[a] | | |
|---|---|---|---|
| | Healthy | Infected | *P* |
| *S. invicta* majors | 0 ± 0 | 0 ± 0 | 1 |
| *S. invicta* mixed (majors + minors) | 32 ± 3.7 | 64 ± 2.4 | 0.0079 |
| *S. invicta* minors | 32 ± 4.4 | 81 ± 6.5 | 0.0001 |

[a] Wilcoxon–Mann–Whitney test $P = 0.05$ significance level.

In all observations, *P. fervens* killed *S. invicta* workers by forming a group of five to six *P. fervens* workers and then biting the antennae and legs or dismembering the gaster of *S. invicta*. However, *S. invicta* were more aggressive than *P. fervens* when fighting and always stung *P. fervens*. One *S. invicta* worker would kill more than three *P. fervens* workers. In contrast, *M. chinense* workers always attacked singly, with raised abdomens and they tended to use their stinger against the *S. invicta* workers.

When *S. invicta* were paired against colonies of 20 *P. fervens*, *S. invicta* defeated all *P. fervens* colonies. When comparing SINV-1–infected *S. invicta* with healthy *S. invicta*, we found that healthy *S. invicta* took less time (≈1 d) to eliminate *P. fervens* ($Z = -2.17$, df = 1, $P = 0.03$). However, when the colony size of *P. fervens* was increased to 100 workers, *P. fervens* invaded *S. invicta* nest and killed the *S. invicta* queen in most experiments, and in only two cases were the *P. fervens* colonies eliminated by healthy *S. invicta* after 20 d. In those cases, the time for a healthy or a SINV-1–infected *S. invicta* to eliminate *P. fervens* was not significantly different ($Z = -0.3$, df = 1, $P = 0.75$). When the size of the *P. fervens* colony was increased to 200, they successfully invaded the *S. invicta* colony of 20 workers, regardless of viral infection (Table 4).

When 750 *M. chinense* were paired with 20 *S. invicta*, the mean time for *M. chinense* to kill the SINV-1–infected *S. invicta* queens was significantly less compared with healthy and infected colonies ($Z = -2.1$, df = 1, $P = 0.03$). *M. chinense* took ≈2 d to kill the SINV-1–infected *S. invicta* queen and within 8 d killed the healthy *S. invicta* queen. All *S. invicta* queens, both healthy and the SINV-1–infected, were killed by *M. chinense*. When 150 *M. chinense* were paired with a colony of 20 *S. invicta*, the *M. chinense* took a significantly longer time to eliminate the *S. invicta* colony compared with 750 *M. chinense* workers ($Z = 2.09$, df = 1, $P = 0.02$). There was no significant difference for the time required to kill SINV-1–infected *S. invicta* queen by *M. chinense* compared with healthy *S. invicta* ($Z = -1.74$, df = 1, $P = 0.14$) (Table 5). In the controls, no queens died during the whole study period.

The percentages of *S. invicta* workers killed were increased when the number of *P. fervens* workers was increased from 20 to 200 against 20 SNV-1–infected or healthy *S. invicta*. When the *P. fervens* population was increased 10-fold, the percentage of 20 SNV-1–infected and healthy *S. invicta* workers killed was in-

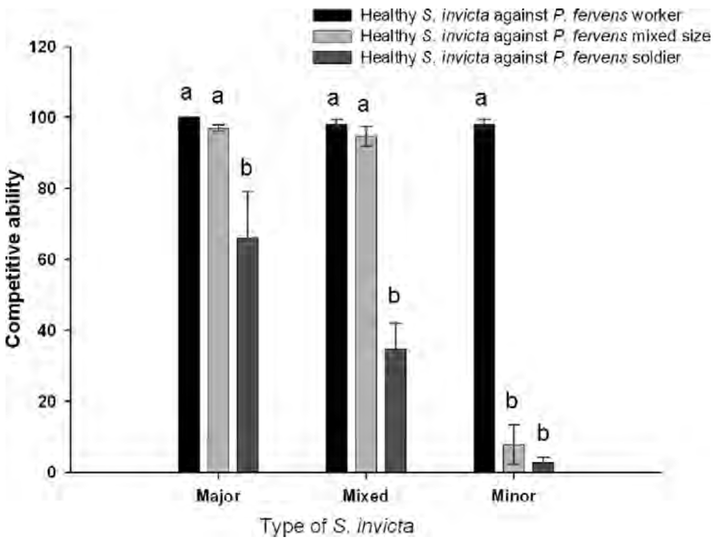

**Fig. 2.** Competitive ability of healthy *S. invicta* against *P. fervens* as a function of the *S. invicta* worker size in individual interference confrontations. Different letters above error bars indicate that there are significant differences in competitive ability of *S. invicta* for three categories of *P. fervens* ($P < 0.05$; Wilcoxon–Mann–Whitney *U* test).

creased by 4.8 and 2.2 times, respectively. The same trend also was observed when *M. chinense* population was increased from 150 to 750 against SNV-1–infected or healthy *S. invicta.* When the *M. chinense* population was increased five-fold, the percentage of 20 SNV-1–infected and healthy *S. invicta* killed was increased 1.9- and 1.96-fold, respectively (Table 6).

## Discussion

The ant's body size is an important factor during interspecific competition. Ants with a larger body size have a better chance of defeating the smaller ones (Persson 1985, Morrison 2000, Kabashima et al. 2007). Compared with *P. fervens* soldiers, *P. fervens* workers were at a disadvantage to *S. invicta*, regardless of the size of *S. invicta.* Although *P. fervens* workers were able to fight with *S. invicta*, they could not kill all the *S. invicta* workers due to their smaller size and lack of chemical defense (Kugler 1979). Thus, *P. fervens* worker fought cooperatively in groups to grasp the antennae and legs of *S. invicta* workers and dismember their gaster. By fighting in groups, *P. fervens* were able to kill *S. invicta.* Because

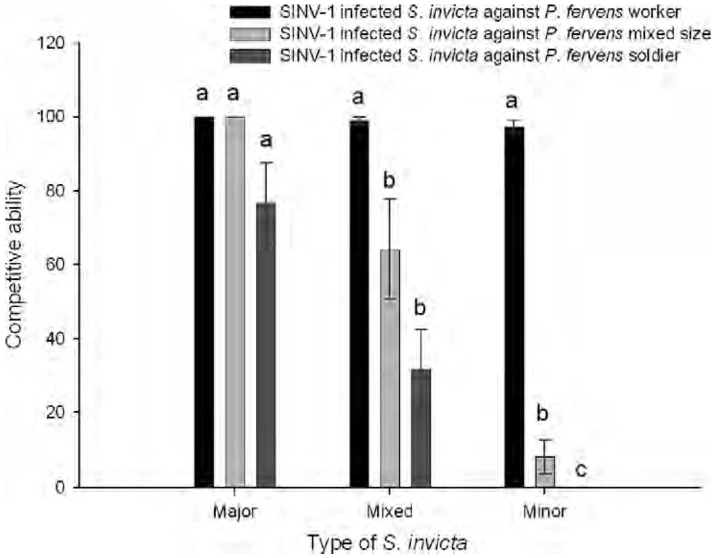

**Fig. 3.** Competitive ability of SINV-1–infected *S. invicta* against *P. fervens* as a function of the *S. invicta* worker size in individual interference confrontations. Different letters above error bars indicate that there are significant differences in competitive ability of *S. invicta* for three categories of *P. fervens* ($P < 0.05$; Wilcoxon–Mann–Whitney *U* test).

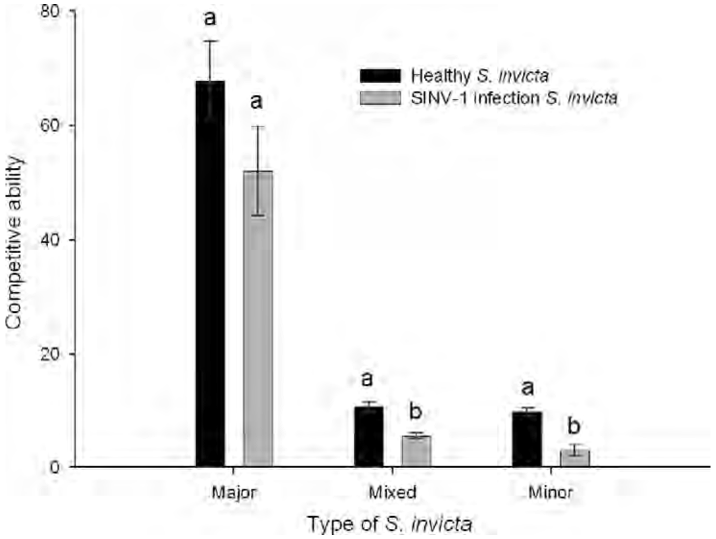

**Fig. 4.** Competitive ability of healthy and SINV-1–infected *S. invicta* against *M. chinense* as a function of the *S. invicta* worker size in individual interference confrontations. Different letters above error bars indicate that there are significant differences in competitive ability of between virus-infected and healthy *S. invicta* ($P < 0.05$; Wilcoxon–Mann–Whitney *U* test).

of their numerical advantage, *P. fervens* had a better chance to overcome *S. invicta.*

*Pheidole* spp. use a group defense; they specialize in the alarm–recruitment system where some scouts directly attack the enemy while others withdraw to the nest to recruit more ants to defending their colony. A numerical advantage is necessary for *P. fervens* to compete with their adversaries because only 8–20% of individuals are soldiers in a *Pheidole* nest (Wilson 1971). During this test, using equal worker numbers, *P. fervens* were not able to defend their colony and were defeated by *S. invicta.* Thus, many *P. fervens* soldiers were killed during a battle, and the *P. fervens* colony collapsed quickly.

*M. chinense* used a chemical defense and killed S. *invicta* even when they encountered *S. invicta.* After *S. invicta* majors were stung by *M. chinense, S. invicta* showed a seizure-like behavior and died soon afterward. The *S. invicta* also secrete a toxic venom from their stinger apparatus. This venom consists of alkaloids and a small amount of venom protein that is used to kill a competitor or prey by injection (Tschinkel 2006). Unlike *S. invicta* minors that suffered high mortality against *M. chinense, S. invicta* major workers seem to be able to better tolerate the chemical defense of *M. chinense.* However, a detailed study to confirm and quantify the involvement of venom or other chemicals during the individual or colony inferences needs to be conducted.

The changes in host behavior are hypothesized to be a kind of adaptation for either host ants or parasite. The parasites may alter their host response to environmental stimuli to make it more likely to facilitate their transmission (Poulin 1994, 1995).

We had observed during this study that once native ants recruited a large number of nestmates or invaded the SINV-1–infected *S. invicta* nest, the SINV-1–infected *S. invicta* stayed in their nest. This is a self-defense behavior to ensure that weaker individuals can avoid having to fight with the attackers. Even in the control experiments when competitive ant species were absent, SINV-1–infected *S. invicta* recruited fewer workers than healthy *S. invicta* would. This shows that the viral infection affected the foraging activity of *S. invicta.*

*S. invicta* minors from SINV-1–infected colonies were less competitive with *M. chinense.* Keck et al. (2005) found that the microsporidium *Thelohania*

**Table 4. Average time (days) required to kill queen by competing species, *P. fervens* and *S. invicta* (no. of trials are in parentheses)**

| Confrontation ratio | *S. invicta* queen killed by *P. fervens*[a] | | | *P. fervens* queen killed by *S. invicta*[a] | | |
|---|---|---|---|---|---|---|
| | Healthy | Infected | *P* | Healthy | Infected | *P* |
| 20 *S. invicta* vs. 20 *P. fervens* | —[b] | —[b] | | 0.82 ± 0.27 (5) | 12.75 ± 1.44 (5) | 0.02 |
| 20 *S. invicta* vs. 100 *P. fervens* | 13 ± 3.51 (3) | 13.8 ± 1.99 (3) | 0.75 | 21.25 ± 0.25 (2)[c] | | |
| 20 *S. invicta* vs. 200 *P. fervens* | 4.75 ± 1.43 (5) | 4.88 ± 1.39 (5) | 1 | —[d] | —[d] | |

[a] Wilcoxon–Mann–Whitney test at $P = 0.05$ significance level.

[b] *S. invicta* posed all threat to *P. fervens.*

[c] In two trails, the *P. fervens* queen was never killed by *S. invicta.*

[d] *S. invicta* never posed a threat to *P. fervens.*

**Table 5. Average time (days) required to kill the queen of the opposite species *M. chinense* and *S. invicta* (number of trials are in parentheses)**

| Confrontation ratio | *S. invicta* queen killed by *M. chinense*[a] | | | *M. chinense* queen killed by *S. invicta*[a,b] | | |
|---|---|---|---|---|---|---|
| | Healthy | Infected | *P* | Healthy | Infected | *P* |
| 20 *S. invicta* vs. 150 *M. chinense* | 13.33 ± 0.88 (3) | 24.33 ± 2.4 (3) | 0.14 | | | |
| 20 *S. invicta* vs. 750 *M. chinense* | 7.8 ± 1.82 (5) | 1.61 ± 0.68 (5) | 0.03 | | | |

[a] Wilcoxon–Mann–Whitney test at $P = 0.05$ significance level.

[b] *M. chinense* queen was never killed by *S. invicta.*

*solenopsae* had a very harmful effect on the competitive ability of *S. invicta* against *Monomorium minimum* (Buckley). This may contribute to the loss of defensive abilities to prevent *M. minimum* from invading.

Owing to the small body size of *M. chinense,* an equal biomass was selected for the experiments. Thus, *M. chinense* had a numerical advantage thereby increasing their chance to defeat *S. invicta.* Similarly, when 150 *M. chinense* invaded the nest of *S. invicta,* it took more time to annihilate than when there were 750 *M. chinense.* In this competition, both *S. invicta* and *M. chinense* were observed that they were foraging less, hence reducing the frequencies of their encounters. Consequently, the *S. invicta* had a lower mortality and managed to increase their survival time as a result of their low foraging behavior.

The *Monomorium* species were the most abundant ant species in the fire ant-infested areas in Taiwan (Tsai et al. 2009). *M. chinense* are the most likely species to encounter with *S. invicta.* The ant population monitoring program in Taiwan the population density of *M. chinense* was not affected by the broadcasting of pyriproxyfen bait, suggesting that the use of native ants integrating with bait control strategy for *S. invicta* might be feasible.

The incipient *S. invicta* colonies can be killed by the native ant species. The findings of this study support the general theory that native ants are a biotic resistance to the survival and establishment of invasive ant species (Wilson 1971, Nickerson et al. 1975, Hölldobler and Wilson 1990, Walters and Mackay 2005). However, a detailed field study need to be conducted to confirm this small-scale experiment conducted under the laboratory conditions.

**Table 6. Mortality (percentage) of healthy/SNV-1 infected *S. invicta* workers against different pop size of *M. chinense* and *P. fervens***

| Confrontation ratio | *S. invicta*[a] | | *P* |
|---|---|---|---|
| | Healthy | Infected | |
| 20 *S. invicta* vs. 20 *P. fervens* | 12 ± 5.61 | 35 ± 2.24 | 0.005 |
| 20 *S. invicta* vs. 100 *P. fervens* | 33 ± 1.77 | 50 ± 1.22 | 0.0001 |
| 20 *S. invicta* vs. 200 *P. fervens* | 58 ± 4.1 | 76 ± 1.2 | 0.003 |
| 20 *S. invicta* vs. 150 *M. chinense* | 30 ± 2.89 | 38 ± 2.73 | 0.1 |
| 20 *S. invicta* vs. 750 *M. chinense* | 56 ± 0.71 | 75 ± 4.96 | 0.007 |

[a] Wilcoxon–Mann–Whitney test at $P = 0.05$ significance level.

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