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ORIGINAL ARTICLE

Avoidance of parasitized host by female wasps of *Aphidius gifuensis* (Hymenoptera: Braconidae): The role of natal rearing effects and host availability?

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Abstract Natal rearing experience of animals may affect their behaviors, such as habitat selection and oviposition decision. As part of the overall fitness of insect parasitoids, successful host discrimination (distinguishing parasitized hosts from unparasitized hosts) is of paramount importance. In this study we examined whether and how parasitoids' natal rearing experience would affect their host discrimination ability according to host availability. We established separate colonies of *Aphidius gifuensis* Ashmead by continual rearing on two hosts, *Sitobion avenae* F. and *Myzus persicae* (Suzler), and quantified self superparasitism and self superparasitism versus parasitism ratio for the four combinations of parasitoid colonies and host species (*S. aveane* and *M. persicae*) at four host densities (30, 50, 100 or 150 per plant). Results showed that self superparasitism of *M. persicae* by *A. gifuensis* reared on *S. avenae* was significantly higher than by those reared on *M. persicae*, no matter whether the host densities were 30, 50, 100 or 150. *Aphidius gifuensis* reared on *M. persicae* significantly superparasitized more *S. avenae* than those reared on *S. aveane* only when host density was 30. Self superparasitism versus parasitism ratio of *A. gifuensis* from both colonies was always lower on natal hosts than on new hosts, and the difference was more pronounced as the host density decreased. These results suggested that natal rearing effects is important on host discrimination and oviposition decision of the parasitoid *A. gifuensis*. These effects promoted the parasitoid's host adaptation and made them confer greater fitness.

Key words host discrimination; *Myzus persicae*; self superparasitism; *Sitobion avenae*

Introduction

A popular theory to explain some of the patterns of host affiliation in phytophagous insects is that traits leading to an increased fitness on one host are detrimental on others (Fry, 1996; Henry *et al.*, 2008). Insect parasitoids are excellent model organisms for examining questions about the adaptive behavior and its consequences (Godfray & Shimada, 1999), as host–parasitoid interactions tend to be both complex and unique as a single host harbors the parasitoid's offspring until maturity (Godfray, 1994).

Oviposition decisions have significant fitness consequences for parasitoids. Parasitoids usually lay their eggs in or on other invertebrates, and all the resources they obtain for their development depend on which host female adults select when they oviposit (Rehman & Powell, 2010). Hosts for oviposition may vary in nutrition quality and immune response (Honda & Luck, 2000; Han

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et al., 2013; Hopper *et al.*, 2013; Gagic *et al.*, 2016), or may already contain the eggs of other individuals, of the same or another species (Vinson & Iwantsch, 1980), and parasitoid females' oviposition decisions may affect the survival and fitness of offspring, so female wasps are expected to have the ability to recognize hosts that can best support the development of their progeny. Previous studies suggested that exclusive rearing of a parasitoid on one particular host may negatively affect its host recognition or preference on other hosts (Corrigan & Laing, 1994; Storeck *et al.*, 2000; Morris & Fellows, 2002; Rehman & Powell, 2010). This adaptation on natal host could result from changes in behavioral cues that could influence host recognition, preference and acceptance, or chemical contamination (Vafaie *et al.*, 2013).

Self / conspecific superparasitism indicates that female parasitoid lay eggs on or inside a host, which has already been parasitized by herself or other conspecific individuals, which is frequently observed in both field and experimental studies of parasitoids (Bakker *et al.*, 1985; Gauthier *et al.*, 1996). In solitary parasitoids, only one offspring can complete its life cycle within a given host; superparasitism will increase intraspecific competition (van Alphen & Visser, 1990) and often results in loss of eggs and/or search time of female parasitoids (Bai & Mackauer, 1992; Outreman *et al.*, 2001; Yamada & Sugaura, 2003; Keasar *et al.*, 2006). Further, high rates of superparasitism may adversely affect the efficiency of biological control for targeted pest species (Vinson & Hegazi, 1998; Hubbard *et al.*, 1999; Darrouzet *et al.*, 2002). However, superparasitism has been considered as an adaptive strategy when host density is low (Bakker *et al.*, 1985; Godfray, 1994). According to some theoretical models, adaptive superparasitism is expected to be flexible, with the number of eggs laid per host varying according to the availability of parasitized and health hosts (Reynolds & Hardy, 2004; Hasan & Ansari, 2010). When few hosts are available, many of the hosts encountered by a female parasitoid already are parasitized and/or subsequently visited by other female parasitoids. In this situation, females can gain the greatest payoff by laying eggs into all of the hosts that they encounter. However, theoretically, siblicidal behavior may be adaptive only if clutch size is relatively small (i.e. two to three eggs per host) (Godfray, 1987). Thus, there seems to be a strong selective advantage for female parasitoids to be able to manipulate the number of eggs laid per host according to host availability (Outreman & Pierre, 2005; Cancino *et al.*, 2012).

A large body of studies suggested that host discrimination is quite common among parasitoids (Bai & Mackauer, 1990; Nelson & Roitberg, 1993; Barrera *et al.*, 1994); 150 to 200 species have demonstrated the ability to discriminate between parasitized and healthy hosts (van Lenteren, 1981). Host discrimination may be achieved by the following ways: first, parasitoids deposit oviposition marking pheromones (OMPs) after egg-laying to mark the parasitized hosts or patches (van Alphen & Visser, 1990; Stelinski *et al.*, 2009); second, the embryo releases marking substance during its embryonic or post-embryonic development, and then this substance is diffused over the host surface; third, host quality changes with parasitoid larval development (Gauthier *et al.*, 1996; Díaz-Fleischer & Aluja, 2003; Outreman & Pierre, 2005); and finally, host defensive response may change when they were previously parasitized. Female parasitoids may recognize these signals and decide whether to lay eggs into an already utilized resource according to host availability. The host discrimination could reduce time spent on the previous utilized hosts and sibling competition for limited host resources.

In the present study, we examined the natal rearing effects on host discrimination of a parasitoid. *Aphidius gifuensis* Ashmead is a solitary koinobiont parasitoid; females often lay more than one egg in one host, even when searching alone (Pan & Liu, 2014). *Sitobion avenae* F. is a main aphid pest on winter wheat, and *Myzus persicae* Sulzer is a generalist aphid pest on various vegetables and crops, and are common hosts for *A. gifuensis*. We separately reared *A. gifuensis* on *S. avenae* and *M. persicae* for 30 months, and examined the self superparasitism and 'self superparasitism versus parasitism ratio' of *A. gifuensis* from two colonies on both *S. avenae* and *M. persicae* under different host densities in a no-choice situation. Our objective was to test the hypothesis that *A. gifuensis* has better host discrimination ability on its natal host than on new hosts.

Materials and methods

Insects and plant cultures

Sitobion avenae and *M. persicae* were collected in May, 2011 in Yangling, Shaanxi, China, and maintained on winter wheat (*Triticum aestivum* L.; var. 'Xiaoyan 22') and pepper plant (*Capsicum annuum* L.; var. 'Xinwangzi'), respectively. Winter wheat and pepper seedlings were planted in plastic pots (10 cm in diameter); about 15 winter wheat seedlings or one pepper plant were planted in each pot. They were allowed to grow for 7 days and 45 days, respectively, before being used in the experiments. All aphids and their host plants were reared in air-conditioned insectaries at 25 ± 2°C, 60% ± 10% relative humidity, and a photoperiod of 16 : 8 (L : D) h.

Aphidius gifuensis is an oligophagous parasitoid that parasitizes *M. persicae*, *S. avenae*, *Acyrthosiphon pisum* (Harris), *Aulacorthum solani* Kaltenbach and *Aphis gossypii* Glove. Previous studies showed that *M. persicae* and *S. avenae* are the most suitable hosts for *A. gifuensis* (Ohta & Honda, 2010; Pan & Liu, 2014). *Aphidius gifuensis* used in this study was field collected from parasitized *M. persicae* on tobacco as mummies in August 2011, and then continuously reared on *S. avenae* and *M. persicae* in the laboratory under the same conditions as mentioned above. Two distinct and separate colonies of *A. gifuensis* were exclusively reared on their respective host for 30 months (approximately 70 generations). *Aphidius gifuensis* that reared on *S. avenae* and *M. persicae* are referred to as *AGS* and *AGM*, respectively, and the rearing host is referred to as the natal host for the parasitoid in the following manuscript.

Host discrimination ability

To test the effect of natal rearing effects on host discrimination ability of *A. gifuensis*, we used self superparasitism versus parasitism ratio (S/P ratio) as a metric. A lower S/P ratio represents a higher host discrimination ability and vice versa. We exposed female *AGS* and *AGM* to each of the two aphid species, *S. avenae* and *M. persicae*, at densities of 30, 50, 100 and 150 per plant (a total of 16 treatments, two natal host species × two offered host species × four host densities, were set in the experiments).

Parasitoid mummies collected from each colony were separately placed in Petri dishes (10 cm in diameter). Male and female parasitoids that emerged from the same host species in the same day were placed in clear plastic cages with screen mesh caps (13 cm diameter, 30 cm height) with 10% honey solution for 24 h to allow them to mate. The female wasps were used in the subsequent experiments. Second- to third-instar *S. avenae* or *M. persicae* were placed on their respective host plants (wheat seedlings or pepper plants) at densities of 30, 50, 100 and 150 per plant, and then enclosed using plastic cages as mentioned above. After the aphids settled on the plants, one female *A. gifuensis*, *AGS* or *AGM*, was introduced into each cage and allowed to parasitize for 48 h, then the female parasitoids were moved out of the cages and the aphid nymphs were kept rearing on their host plants. Another 48 h later, 30 aphid nymphs from each pot were randomly selected and dissected under a dissecting microscope. The number of parasitoid larvae in each dissected aphid was recorded. To minimize observer bias, blinded methods were used during aphid samplpng and dissection. Fifteen replications were conducted in each treatment. Parasitism is defined as the percentage of aphids with parasitoid larvae; self superparasitism is defined as the percentage of aphids with more than one parasitoid larvae.

Data analysis

Self superparasitism of *S. avenae* and *M. persicae* by the parasitoid *A. gifuensis*, and the ratio of self superparasitism to parasitism were first transformed by arcsine function; then two-way analysis of variance (ANOVA) was used to analyze the influence of natal host and host density on the two parameters. Means were separated using Tukey-Kramer Honestly Significant Difference (HSD) test at $P < 0.05$. Independent Student's t-test was used to compare the significant difference in self superparasitism, and the ratio of self superparasitism to parasitism on one aphid species by *AGS* and *AGM*. All data were analyzed using SPSS (version 19.0, SPSS Inc., Chicago, IL, USA).

Results

Self superparasitism and egg distribution

Both host density and natal host significantly affected self superparasitism of *A. gifuensis* on *S. avenae* (host density: $F = 43.438$, df = 3111, $P < 0.0001$; natal host: $F = 24.062$, df = 1111, $P < 0.0001$), and *M. persicae* (host density: $F = 31.942$, df = 3112, $P < 0.0001$; natal host: $F = 52.081$, df = 1112, $P < 0.0001$). Self superparasitism of *A. gifuensis* increased with host density decrease. *AGM* superparasitized fewwer *M. persicae* than *AGS* at host densities of 150 ($t = 2.174$, df = 19, $P = 0.043$) (Fig. 1A), 100 ($t = 2.155$, df = 28, $P = 0.040$) (Fig. 1B), 50 ($t = 4.433$, df = 28, $P < 0.0001$) (Fig. 1C) and 30 ($t = 5.478$, df = 28, $P < 0.0001$) (Fig. 1D). However, *AGS* only showed significantly (both in the number and statistics) higher self superparasitism on *M. persicae* than *AGM* at the host density of 30 ($t = 6.199$, df = 28, $P < 0.0001$) (Fig. 1D). There were significant interactions of host density and natal host on self superparasitism of *A. gifuensis* on both *S. avenae* ($F = 11.336$, df = 3111, $P < 0.0001$) and *M. persicae* ($F = 7.350$, df = 3112, $P < 0.013$).

When host density was high (150 per plant), most *A. gifuensis* females laid only one egg in each host aphid; however, as host density decreased, female parasitoids laid more eggs in each host aphid. For example, when host density was 30, *AGS* laid more than four eggs per aphid in 7.1% of *S. avenae* and 23.2% of *M. persicae* (Fig. 2); and *AGM* laid more than four eggs per aphid in 14.7% of *M. persicae* and 20.9% of *S. avenae* (Fig. 3).

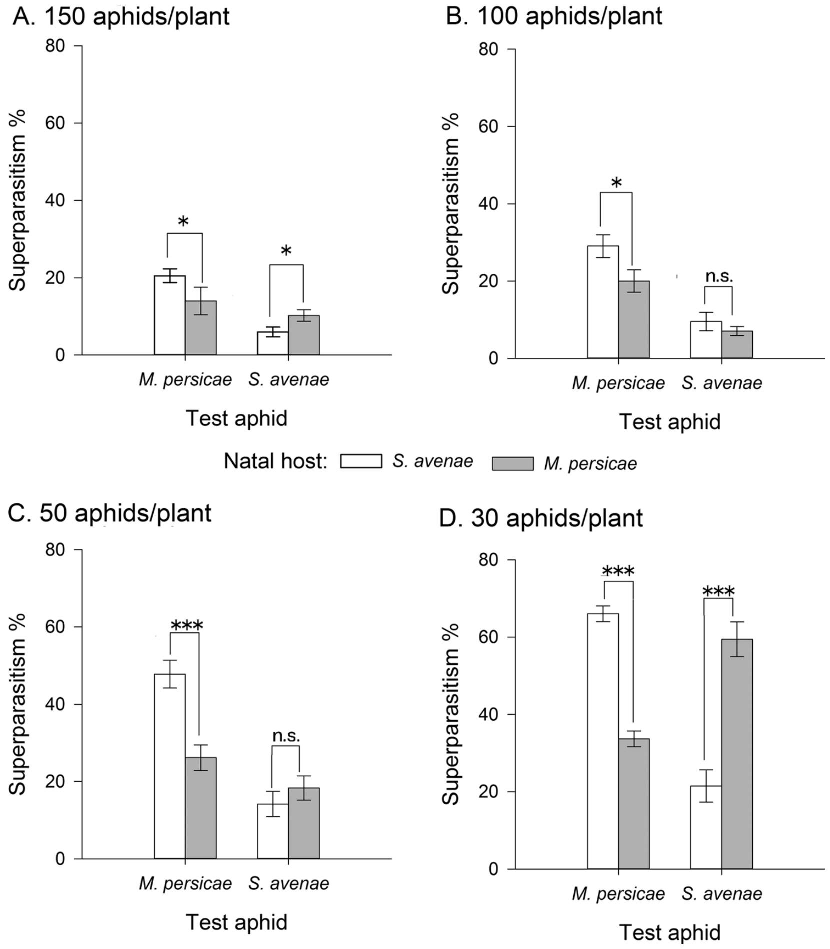

Fig. 1 Mean (± SE) self superparasitism rate of *Myzus persicae* and *Sitobion avenae* by *Aphidius gifuensis* at the host densities of 150 (A), 100 (B), 50 (C) and 30 (D) aphids per plant. Females either originated from *M. persicae* or *S. avenae*. Independent Student's *t*-test, difference between treatments: n.s., no significant difference; *$P < 0.05$, ***$P < 0.001$.

Self superparasitism versus parasitism ratio (S/P ratio)

Both host density and natal host had significant effects on the ratio of self superparasitism versus parasitism (S/P ratio) of *A. gifuensis* on the two host species, *S. avenae* (host density: $F = 31.150$, df = 3111, $P < 0.0001$; natal host: $F = 42.482$, df = 1111, $P < 0.0001$) and *M. persicae* (host density: $F = 35.466$, df = 3112, $P < 0.0001$; natal host: $F = 80.227$, df = 1112, $P < 0.0001$). Interaction effects of host density and natal host on the S/P ratio were also significant (*S. avenae*: $F = 7.113$, df = 3111, $P < 0.0001$; *M. persicae*: $F = 2.726$, df = 3112, $P = 0.048$).

When *M. persicae* was the host, the S/P ratio of *AGS* was significantly higher than that of *AGM*, regardless if host densities were high or low (150: $t = 2.596$, df = 28, $P = 0.015$, Fig. 4A; 100: $t = 5.224$, df = 20, $P < 0.0001$, Fig. 4B; 50: $t = 5.139$, df = 28, $P < 0.0001$, Fig. 4C; and 30: $t = 5.539$, df = 28, $P < 0.0001$, Fig. 4D). When *S. avenae* was the host, *AGM* had higher S/P ratios than *AGS* at host densities of 150 ($t = 4.446$, df = 28, $P < 0.0001$) (Fig. 5A), 50 ($t = 2.142$, df = 28, $P = 0.041$) (Fig. 5C), and 30 ($t = 6.593$, df = 28, $P < 0.0001$) (Fig. 5D), but not at the host density of 100 ($t = 0.438$, df = 28, $P = 0.665$) (Fig. 5B).

Discussion

Natal host affected self superparasitism and S/P ratio of *A. gifuensis* on *S. avenae* and *M. persicae*. *AGS* always showed significantly higher self superparasitism on *M. persicae* than *AGM*, and the difference was more pronounced as the host density decreased. *AGM* showed significantly higher self superparasitism on *S. avenae* than

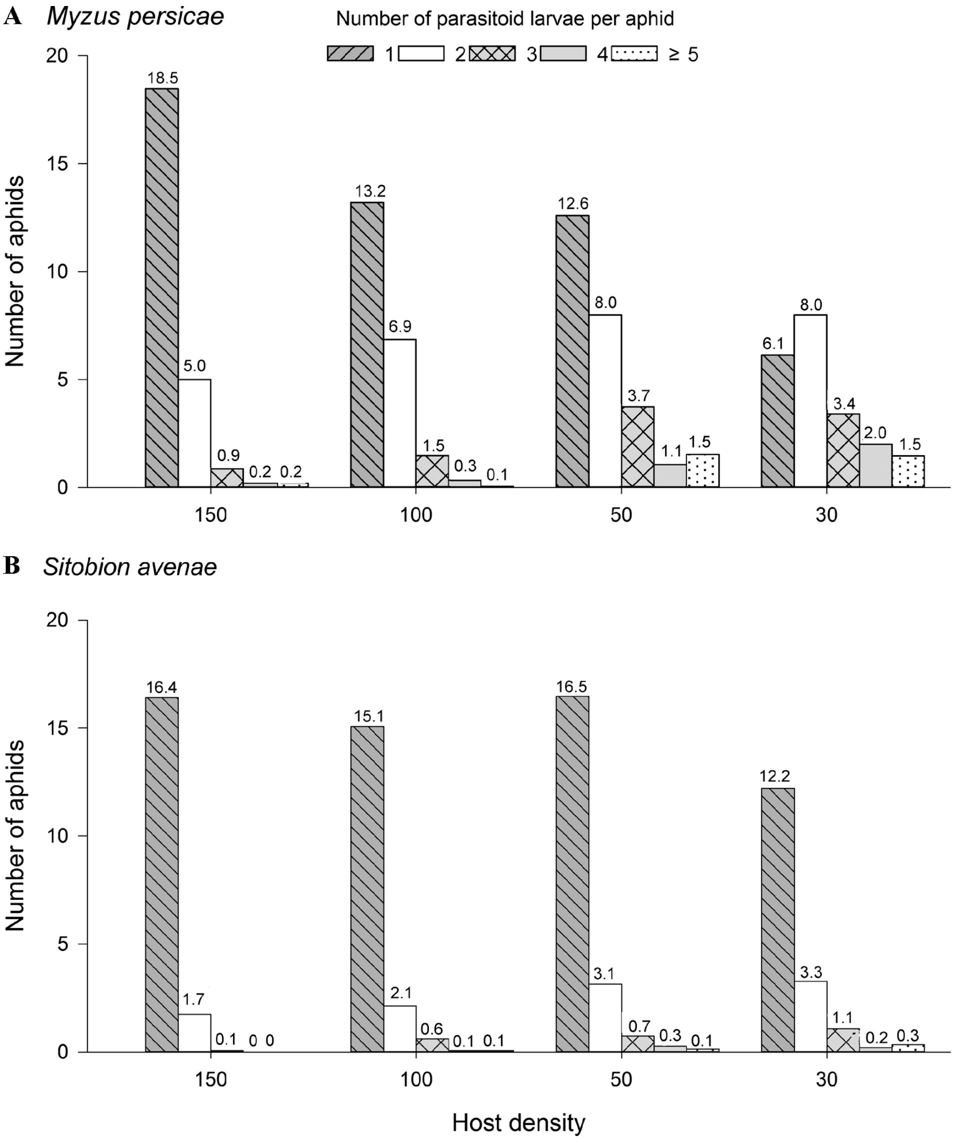

Fig. 2 Egg distribution of *Sitobion avenae* reared *Aphidius gifuensis* on *Myzus persicae* (A) and *Sitobion avenae* (B) at different host densities. Numbers on each bar are the mean number of aphids with certain numbers of parasitoid larvae.

AGS only when host densities were 150 and 30 aphids per host; however, the S/P ratio of *AGS* was lower on natal host *S. avenae* than on new host *M. persicae* except when host density was 100.

There are several factors that could influence the oviposition decision of parasitoids on self-parasitized hosts, such as host availability and host discrimination ability; we investigated whether the natal host of *A. gifuensis* would have impact on their self superparasitism under different host densities. *Aphidius gifuensis* females were observed to lay eggs on self-parasitized hosts when there were enough healthy hosts available (host density was 150); the results suggested that *A. gifuensis* females could not perfectly discriminate parasitized hosts from unparasitized hosts. As a solitary parasitoid, only one offspring could survive to adult in a host. Self superparasitism will increase competition among siblings (Darrouzet *et al.*, 2007; Böckmann *et al.*, 2012), so it often means a waste of time and eggs for *A. gifuensis* females when enough healthly hosts are available; further, hosts that had already been parasitized are generally of low host quality, and in turn, cause low quality offspring. Self superparasitism rate of *A. gifuensis* on two hosts increased as the host density decreased. This result was consistent with the study of

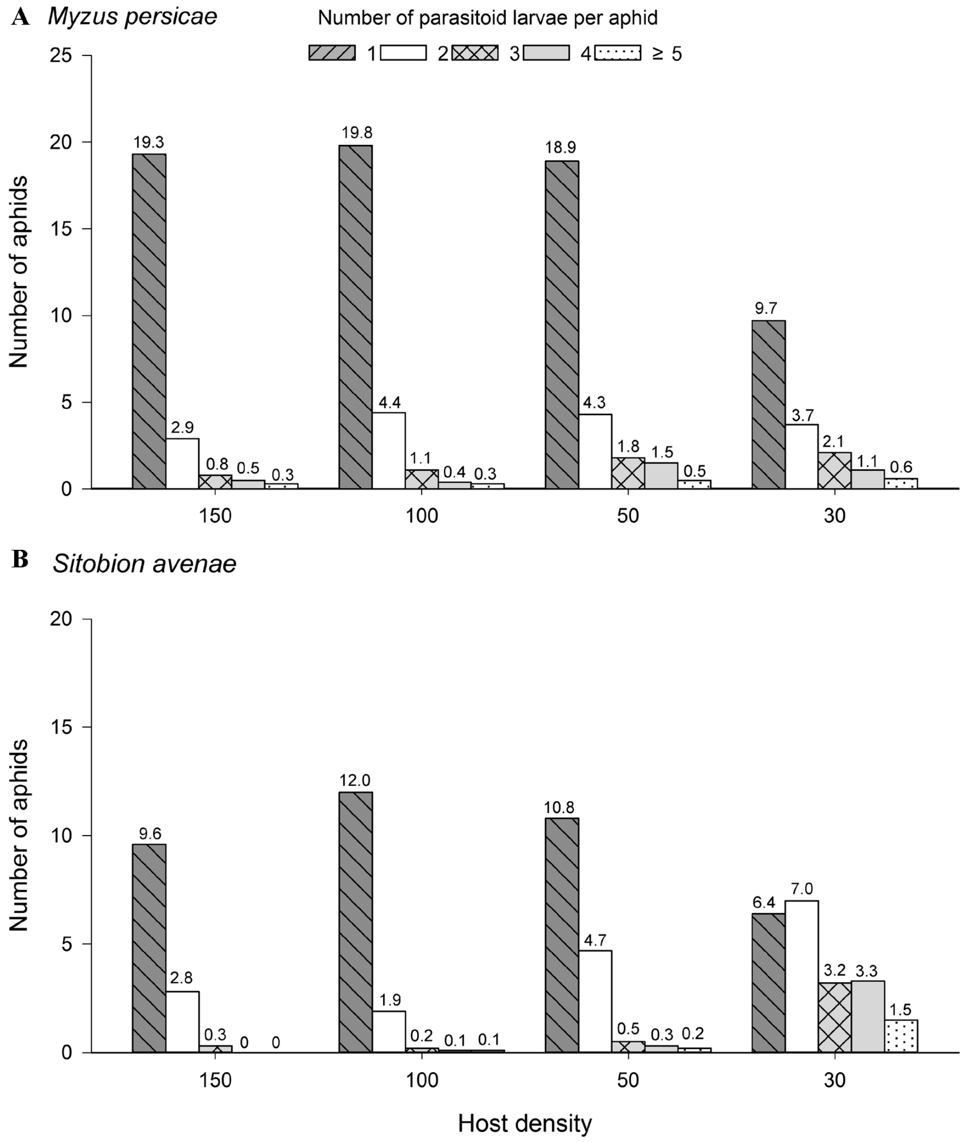

Fig. 3 Egg distribution of *Myzus persicae*-reared *Aphidius gifuensis* on *Myzus persicae* (A) and *Sitobion avenae* (B) at different host densities. Numbers on each bar are the mean number of aphids with certain numbers of parasitoid larvae.

Chen (2013) who found that superparasitism of *Diaphorina citri* Kuwayama by *Tamarixia radiata* (Waterston) decreases with increasing host density over a range from 10 to 60 per parasitoid.

Mostly, fewer aphids were self superparasitized by female parasitoids originating from the same host species than by those from other hosts, but host density plays a role. As there is usually a positive relationship between self superparasitism and parasitism in *A. gifuensis* (Fig. S1), the S/P ratio seemed to be a better metric of host discrimination than self superparasitism. Generally, the S/P ratio of *A. gifuensis* was lower on natal hosts than on the new host. The most significant differences in S/P ratio between *AGS* and *AGM* were observed when host density was 30, no matter on *S. avenae* or on *M. persicae*. The results indicate that *A. gifuensis* maybe have stronger host discrimination abilities on their natal host. Female parasitoids discriminate parasitized hosts from unparasitized hosts by themselves in many ways, such as marking pheromones released by themselves or the embryo, and physiological and behavioral changes of hosts as the parasitoids' larvae develop (Gauthier *et al.*, 1996; Díaz-Fleischer & Aluja, 2003; Outreman & Pierre, 2005; Benelli *et al.*, 2013). These marks and/or changes

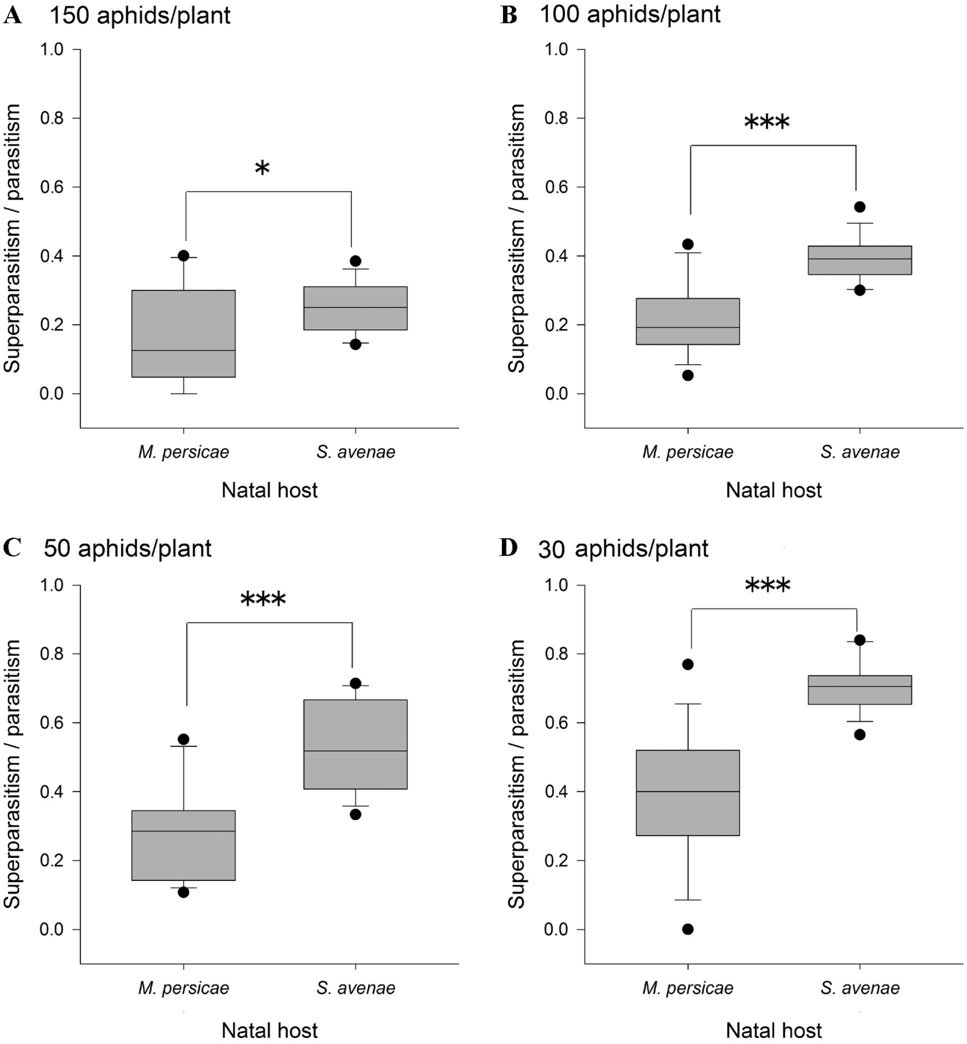

Fig. 4 The self superparasitism versus parasitism ratio of *Myzus persicae* by two colonies of *Aphidius gifuensis* at host densities of 150 (A), 100 (B), 50 (C) and 30 (D) aphids per plant. Parasitoids either originated from *M. persicae* or *Sitobion avenae*. Independent Student's *t*-test, difference between treatments: $^{*}P < 0.05$, $^{***}P < 0.001$.

may vary between parasitoid individuals and hosts (Nufio & Papaj, 2001). *Aphidius gifuensis* females may learn and adapt these specific changes of their natal hosts through positive associative learning, and use it to distinguish unparasitized hosts from parasitized ones. This adaptive is expected to confer greater fitness for parasitoid individuals (Davis, 2008; Zepeda-Paulo *et al.*, 2013). However, it is possible that this could be influenced by the host plant that the aphids feed on. Host plants could directly and indirectly affect suitability and behaviors of natural enemies (Frank *et al.*, 2011; Pan *et al.*, 2014). Further experiments would be needed to examine whether host plants affect host discrimination of *A. gifuensis* females.

Host discrimination does not always imply avoidance of superparasitism; sometimes self superparasitism is considered as an adaptive strategy under certain circumstances. When few hosts are available, there is a high probability that female parasitoids encounter hosts that have been parasitized by themselves. In this situation, females can gain the greatest payoff by laying eggs into all of the hosts that they encounter (Bakker *et al.*, 1985). However, theoretically, siblicidal behavior may be adaptive if clutch size is relatively small (i.e. females deposit only two to three eggs per host) (Godfray, 1987). Laying four or more eggs in one host would increase competition between siblings and mortality of hosts. As we observed,

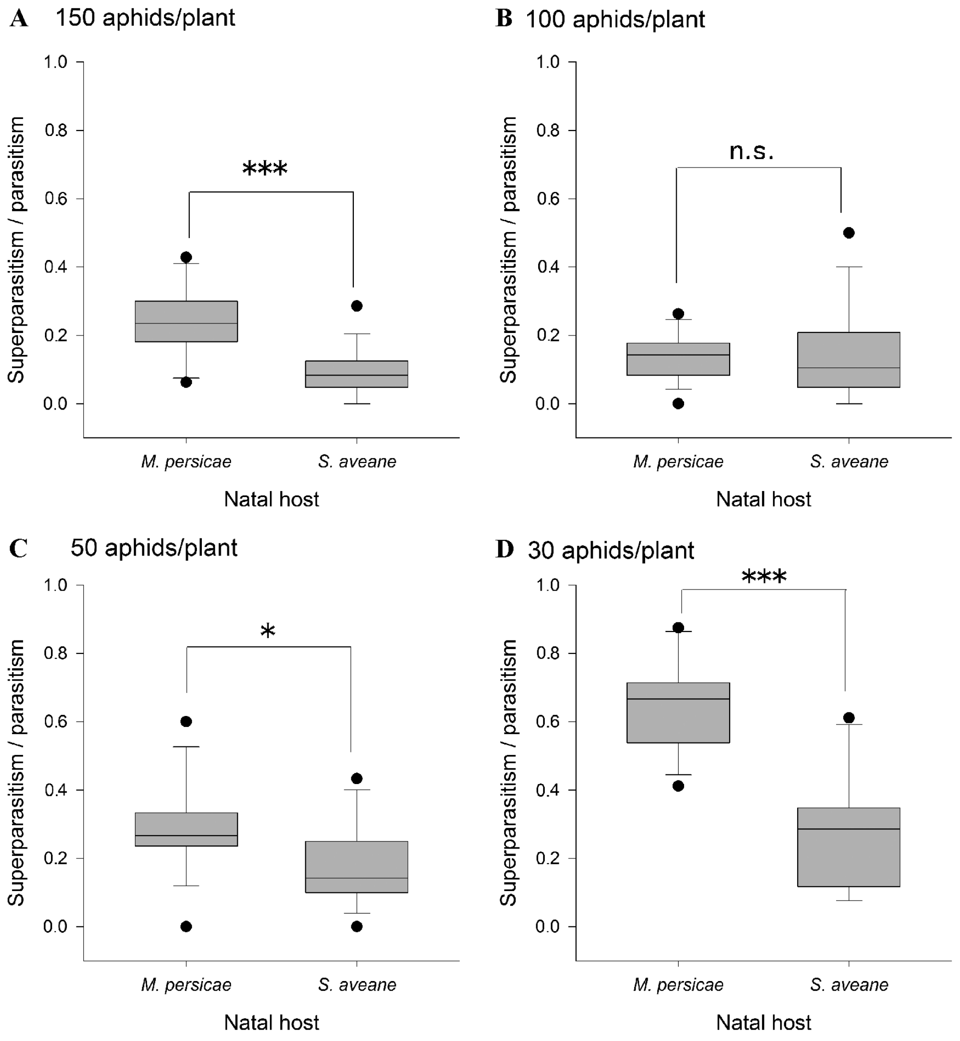

Fig. 5 The self superparasitism versus parasitism ratio of *Sitobion avenae* by two colonies of *Aphidius gifuensis* at host densities of 150 (A), 100 (B), 50 (C) and 30 (D) aphids per plant. Parasitoids either originated from *Myzus persicae* or *S. avenae*. Independent Student's *t*-test, difference between treatments: n.s., no significant difference; $^{*}P < 0.05$, $^{***}P < 0.001$.

female parasitoids sometimes laid more than four eggs in one host when the host density was 30; this was more likely to occur on new hosts than on natal hosts. The result further confirmed that female *A. gifuensis* may have better host discrimination abilities on their natal host than on new hosts; further, they might also distinguish between hosts containing different numbers of eggs, and gain the greatest payoff by manipulating the number of eggs laid per host.

In conclusion, our study demonstrates adaptive natal rearing effects on host discrimination abilities of *A. gifuensis*. *Aphidius gifuensis* females could manipulate the number of eggs according to host availability on their natal host. Our findings could contribute to a better understanding of the evolutionary mechanisms of this host adaptation in parasitoids when exclusive rearing of parasitoids using one host species. However, the questions remain: (i) what are the proximate cues used by female *A. gifuensis* to discriminate parasitized hosts and unparasitized hosts; and (ii) are female parasitoids able to distinguish between hosts containing different numbers of eggs? These questions need to be further studied.

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Disclosure

The authors declare that they have no conflicts of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Fig. S1 Relationship between self superparasitism and parasitism of *Aphidius gifuensis* when attacked *Myzus persicae* and *Sitobion avenae* (*Myzus persicae*: $y = 0.1912x–2.8399$, $R = 0.9906$, $P = 0.0094$; *Sitobion avenae*: $y = 0.0736x - 2.3049$, $R = 0.8526$, $P = 0.1474$).