Biocontrol characteristics of the fruit fly pupal parasitoid *Trichopria drosophilae* (Hymenoptera: Diapriidae) emerging from different hosts

Jiani Chen¹,², Sicong Zhou¹,², Ying Wang¹,², Min Shi¹,², Xuexin Chen¹,²,³ & Jianhua Huang¹,²

*Trichopria drosophilae* (Hymenoptera: Diapriidae) is an important pupal endoparasitoid of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) and some other fruit fly species, such as *D. suzukii*, a very important invasive and economic pest. Studies of *T. drosophilae* suggest that this could be a good biological control agent for fruit fly pests. In this research, we compared the parasitic characteristics of *T. drosophilae* reared in *D. melanogaster* (*TDₘ*) with those reared in *D. hydei* (*TDₜ*). *TDₜ* had a larger size than *TDₘ*. The number of maximum mature eggs of a female *TDₜ* was 133.6 ± 6.9, compared with the significantly lower value of 104.8 ± 11.4 for *TDₘ*. Mated *TDₜ* female wasp continuously produced female offspring up to 6 days after mating, compared with only 3 days for *TDₘ*. In addition, the offspring female ratio of *TDₜ*, i.e., 82.32%, was significantly higher than that of *TDₘ*, i.e., 61.37%. Under starvation treatment, *TDₜ* survived longer than *TDₘ*. *TDₜ* also survived longer than *TDₘ* at high temperatures, such as 37 °C, although they both survived well at low temperatures, such as 18 °C and 4 °C. Old-age *TDₜ* females maintained a high parasitism rate and offspring female ratio, while they were declined in old-age *TDₘ*. Overall, *TDₜ* had an advantage in terms of body size, fecundity, stress resistance ability and the parasitism rate compared with *TDₘ*. Therefore, *T. drosophilae* from *D. hydei* could improve biocontrol efficacy with enormous economic benefits in the field, especially in the control of many frugivorous Drosophilidae species worldwide.

*Drosophila* is a genus of flies belonging to the family Drosophilidae. Some species of *Drosophila* (also called fruit flies), particularly *D. melanogaster*, have been widely used in the research of genetics, developmental biology and human diseases¹,². However, some *Drosophila* species are destructive pests of agriculture, especially damaging soft fruits such as berries, cherries and wine grapes³. Fruit flies generally lay eggs in decaying fruits, and the larvae feed and develop with the fruits, which causes health risks and economic losses. Traditional chemical control methods for fruit flies have low efficiency and are harmful to public health⁴. Consequently, biological control with parasitoids is more sustainable and is urgently needed. Parasitic wasps constitute a major class of natural enemies of many agriculture pests and have tremendous value as biocontrol agents. Most known parasitoid wasp species attack the egg, larval or pupal stages of their hosts and they carry virulence and some other parasitic factors to modify hosts’ physiology and immunity, to change hosts’ metabolism, to destruct hosts’ endocrine and reproductive structures, and finally kill the hosts for their own development⁵–⁸. Many parasitoids are reported to attack various Drosophilidae species, and the majority of them are larval parasitoids, such as *Leptopilina heterotoma*, *L. boulardi* and *Asobara tabida*⁹,¹⁰. Recently, *Trichopria drosophilae* (Hymenoptera: Diapriidae), an important pupal endoparasitoid of *D. melanogaster* and some other fruit fly species, has been found to be an ideal natural enemy to constrain the fruit fly population because it has extremely high parasitism efficiency¹¹–¹⁴. The life history and

---

¹Institute of Insect Sciences, Zhejiang University, 866 Yuhangtang Road, 310058, Hangzhou, China. ²Ministry of Agriculture Key Lab of Molecular Biology of Crop Pathogens and Insect Pests, Zhejiang University, 866 Yuhangtang Road, 310058, Hangzhou, China. ³State Key Lab of Rice Biology, Zhejiang University, 866 Yuhangtang Road, 310058, Hangzhou, China. Correspondence and requests for materials should be addressed to X.C. (email: xxchen@zju.edu.cn) or J.H. (email: jhhuang@zju.edu.cn)
The biological characteristics of *T. drosophilae* have been well studied by several groups. In 2012, Chabert et al. found that *T. drosophilae* was effective against many fruit fly species, including *D. suzuki*, a well-known invasive pest. Female *T. drosophilae* emerged with a relatively high number of mature eggs, and the egg numbers increased during their first four days after eclosion. This indicates that *T. drosophilae* might maximize reproduction during early adult life. Moreover, the parasitism rate of *T. drosophilae* is higher than that of another well-known cosmopolitan pupal parasitoid, *Pachycrepodeus vinderemmiae* (Diptera: Pteromalidae). Although *T. drosophilae* is reported to be effective against *Drosophila* species under laboratory conditions, it is necessary to find the parasitoids that have the highest parasitism rate, highest female offspring numbers and longest adult longevity and which are resistant to certain stress conditions, such as food deprivation and extreme weather conditions, for the biological control purpose of augmentative release in the field.

To increase the effectiveness of parasitoids as natural enemies, female adult wasps are supplied with extra nutrient sources, such as sugars, to enhance their longevity and fecundity and subsequently, the biocontrol efficacy. However, host quality can also have a major influence on the fitness and parasitic efficiency of offspring. Lampson et al. found that different sizes of the same parasitoid had an effect on several biological characteristics, suggesting that larger parasitoids have a longer life span and greater competitiveness. Another comparative study on the parasitism of *P. vinderemmiae* hatching from housefly and fruit fly pupae showed a positive correlation between the size of the host and the size of the emerged offspring, as well as the longevity, the oviposition duration and other parasitic attributes.

Based on the results of previous studies, *T. drosophilae* reared on a larger sized host could be more advantageous for further biological control. Here, we used *D. hydei* as a substitute host, of which the pupae are significantly larger than those of *D. melanogaster*. Then, we compared the body size, fecundity, stress resistance ability and parasitism efficiency between the two parasitoid populations that emerged from the different hosts.

**Results**

**The parasitoid and host size measurements.** The respective pupal length and width were 4.05 ± 0.13 mm and 1.27 ± 0.04 mm for *D. hydei* (n = 18) and 2.93 ± 0.14 mm and 0.99 ± 0.06 mm for *D. melanogaster* (n = 37). The size of *D. hydei* was significantly larger than that of *D. melanogaster* (length: t = 28.57, df = 53, P < 0.01, width: t = 18.68, df = 53, P < 0.01). To investigate whether there was a correlation between the size of the hosts and their offspring, *T. drosophilae* was used to parasitize *D. melanogaster* and *D. hydei* pupae. The measurements indicated that the body length of TDm was significantly longer than that of TDm, in both females and males (Fig. 1A–C). The body length of female TDh was 2.41 ± 0.12 mm (n = 10), compared with 2.12 ± 0.11 mm (n = 12) for female TDm (t = 5.50, df = 20, P < 0.01). The length of male TDh was 2.21 ± 0.07 mm (n = 16), compared with 1.92 ± 0.11 mm (n = 10) for male TDm (t = 7.94, df = 24, P < 0.01). These results showed that the size of TDh was much larger than that of TDm.

**Parasitism rate and offspring female ratio comparison.** The results showed that this local 4-day old *T. drosophilae* females had an extremely high parasitism rate. Approximately 97% of the *D. melanogaster* pupae were successfully parasitized by TDm, and no significant difference in the parasitism rate was found between TDh and TDm (t = 1.67, df = 4, P > 0.05) females. However, the offspring female ratio of TDh, which averaged 82.32%, was significantly higher than that of TDm, which averaged 61.37% (t = 8.96, df = 4, P < 0.01) (Table 1).

**The fecundity of *T. drosophilae*.** The number of mature eggs in the ovaries of TDh and TDm females was compared among different ages (Fig. 2). The results showed that the number of mature eggs was affected by the female age for TDh (X² = 69.06, df = 7, P < 0.01) and TDm (X² = 51.84, df = 7, P < 0.01). The mean number was further compared among different age classes using ANOVA between two *T. drosophilae* groups. Interestingly,
Parasitoid TDm and TDh represent T. drosophilae that emerged from D. hydei and D. melanogaster, respectively. There was no significant difference in the parasitism rate between TDh and TDm (t = 1.67, df = 4, P > 0.05). The offspring female ratio of TDh was significantly higher than that of TDm (t = 8.96, df = 4, P < 0.01).

| Parasitoid | Number of hosts | Number of emerged flies | Parasitism rate | Average parasitism rate | Number of emerged wasps | Number of emerged female wasps | Offspring female ratio | Average offspring female ratio |
|------------|-----------------|------------------------|----------------|-------------------------|------------------------|-----------------------------|----------------------|-----------------------------|
| TDm        | 200             | 1                      | 99.50%         | 97.06 ± 1.86%          | 171                    | 102                         | 59.65%               | 61.37 ± 2.32%              |
|            | 120             | 6                      | 95.00%         |                         | 99                     | 64                          | 64.65%               |                            |
|            | 120             | 4                      | 96.67%         |                         | 102                    | 61                          | 59.80%               |                            |
| TDh        | 200             | 0                      | 100.00%        | 99.44 ± 0.79%          | 193                    | 164                         | 84.97%               | 82.32 ± 2.35%              |
|            | 120             | 0                      | 100.00%        |                         | 106                    | 84                          | 79.25%               |                            |
|            | 120             | 2                      | 98.33%         |                         | 110                    | 91                          | 82.73%               |                            |

Table 1. Parasitism rate and offspring female ratio of 4-day old female parasitoids that emerged from two different hosts. TDh and TDm represent T. drosophilae that emerged from D. hydei and D. melanogaster, respectively. There was no significant difference in the parasitism rate between TDh and TDm (t = 1.67, df = 4, P > 0.05). The offspring female ratio of TDh was significantly higher than that of TDm (t = 8.96, df = 4, P < 0.01).

The stress resistance ability of T. drosophilae. To determine T. drosophilae stress resistance ability, TDh and TDm were treated with different environmental stresses, including starvation and high and low temperatures. Under food deprivation, the starved TDm wasps had a maximum life span of 216 hours, whereas the TDh wasps had a maximum life span of 288 hours, and half of the wasps could survive at least 216 hours. The TDh wasps had a longer lifespan than the TDm wasps under starvation treatment (Log-rank test X² = 154.40, df = 1, P < 0.01) (Fig. 4).

T. drosophilae parasitism efficiency related to age. In order to evaluate the influence of T. drosophilae age on the parasitism rate, 1-, 5-, 10-, 15-, 20-, 25-, 30- and 40-day-old wasps were used to parasitize the hosts. The results showed that both TDh and TDm had an extremely high parasitism rate at all time points; however, a significant decrease in the parasitism rate was observed for the 40-day-old TDm parasitoids compared with the 40-day-old TDh parasitoids (t = 4.94, df = 4, P < 0.01) (Fig. 6A). In accordance with the results of our fecundity experiment (Table 1, Fig. 3C), the offspring female ratio of TDm was slightly higher than that of TDh; significant differences were found between TDh and TDm at 5 days (t = 3.32, df = 4, P < 0.05), 10 days (t = 3.43, df = 4, P < 0.05) and 40 days (t = 6.87, df = 4, P < 0.01) after eclosion (Fig. 6B).
Assessing the capacity of the *T. drosophilae* parasitoid to attack Drosophilidae species and enhancing its ability to adapt to extreme environments are two of the most important steps for the release of *T. drosophilae* as a biological control agent. In this study, we showed that local *T. drosophilae* was able to successfully attack *D. melanogaster* and *D. hydei* under laboratory conditions. A previous study reported that *T. drosophilae* offspring reared in large hosts such as *D. suzukii* were larger than those reared in *D. melanogaster*\(^14\). Because *D. hydei* had a larger size than *D. melanogaster*.

**Figure 3.** The offspring number of single *TD_h* and *TD_m* female wasps. (A) The number of offspring each day (red) was calculated by adding the male (black) and female (purple) offspring numbers. (B) The number of offspring each day (blue) was calculated by adding the male (black) and female (purple) offspring numbers. (C) The total number of offspring for a single *TD_h* and *TD_m* female. In total, 8 *TD_h* and 8 *TD_m* female wasps were used in this experiment, respectively. Values are the means ± SEM. Significant differences using Student's t-test at \( P < 0.05 \) are indicated by asterisks.

**Figure 4.** The survival rate of *TD_h* and *TD_m* during the starvation treatment. *TD_h* had a longer survival lifespan than *TD_m* under the starvation treatment \( (X^2 = 744.30, df = 1, P < 0.01) \). Significant differences based on log-rank test (Mantel-Cox) analysis.

**Discussion**
Assessing the capacity of the *T. drosophilae* parasitoid to attack Drosophilidae species and enhancing its ability to adapt to extreme environments are two of the most important steps for the release of *T. drosophilae* as a biological control agent. In this study, we showed that local *T. drosophilae* was able to successfully attack *D. melanogaster* and *D. hydei* under laboratory conditions. A previous study reported that *T. drosophilae* offspring reared in large hosts such as *D. suzukii* were larger than those reared in *D. melanogaster*\(^14\). Because *D. hydei* had a larger size than *D. melanogaster*. 
Figure 5. The survival rates of TDm (A) and TDh (B) at 4 °C, 18 °C, 25 °C and 37 °C. The results showed that almost all TDh and TDm wasps survived well at 4 °C and 18 °C. However, the survival rates of TDh were higher than those of TDm at 25 °C or 37 °C (25 °C: $X^2 = 23.09, df = 1, P < 0.01$; 37 °C: $X^2 = 14.79, df = 1, P < 0.01$). Significant differences were based on log-rank test (Mantel-Cox) analysis.

Figure 6. (A) The parasitic rate of TDh and TDm at different ages. There was a significant increase in the parasitism rate for the 40-day-old TDh parasitoids compared to TDm ($t = 4.94, df = 4, P < 0.01$) (B) The offspring female ratio of TDh and TDm at different ages. The offspring female ratio of TDh was slightly higher than that of TDm; however, significant differences were found between TDh and TDm at 5 days ($t = 3.32, df = 4, P < 0.05$), 10 days ($t = 3.43, df = 4, P < 0.05$) and 40 days ($t = 6.87, df = 4, P < 0.01$) after eclosion. Values are the means ± SEM. Significant differences based on Student’s t-test at $P < 0.05$ are indicated by asterisks.
melanogaster, we compared the offspring size that emerged from the two different hosts, and found that the size of TDh was much larger than that of TDm.

Parasitoids reared in substitute hosts would help to increase the availability of biocontrol agents. It has also been proven that large parasitoids of the same species have longer life spans, and large females produce approximately twice as many eggs as small females. Thus, we evaluated the different parasitic characteristics of T. drosophilae reared in D. hydei and D. melanogaster pupae. Compared to T. drosophilae populations from California, TDm females in our experiments had a similar number of mature eggs, and the egg load increased during the first four days. However, the number of TDh mature eggs was significantly higher than that of TDm and increased during the first six days. Fecundity is the maximum potential reproductive output of a parasitoid female over its lifetime and represents one of the major parasitic characteristics. Under the test conditions, the daily fecundity of TDd and TDm decreased with increasing female age, and when provided only with D. melanogaster pupae, the adult female TDm only survived for 10 days, which is shorter than the reported T. drosophilae lifespan. However, TDh survived for 26 days and produced more female offspring than TDm. Another interesting phenomenon was that female TDh produced female offspring for 6 days after one mating event, compared with only 3 days for TDm. T. drosophilae has a sex-determination system in which males develop from unfertilized eggs and are haploid, whereas females develop from fertilized eggs and are diploid. The results suggested that size differences of T. drosophilae between males or females from different hosts may influence sperm production or storage. In mosquitos, male size does correlate with total numbers of sperm within a male and the number transferred to females.

Stress resistance ability is an important factor in evaluating parasitoid fitness and biocontrol efficacy in the field. A larger sized host may provide more nutrients that are vital for parasitoid development, which may be the reason why TDh survived longer than TDm in the starvation experiment. Additionally, our data indicated that both TDh and TDm wasps survived for a long time at lower temperatures (4 °C and 18 °C). The reason for this is that the lower temperature will slow the metabolism of the wasps and can even extend their lifespan.

During the last 10 years, D. suzukii, also known spotted wing drosophila, has become widely distributed from Asia to Europe and North and South America. D. suzukii has spread rapidly to become a serious pest that economically damages soft and thin-skinned fruits in the major fruit production areas. Extensive applications of chemical insecticides will lead to a number of problems, such as pest resistance and chemical residue. Therefore, non-toxic and environmentally friendly biological control methods are urgently needed. Some entomopathogenic nematodes and fungi have been used to kill D. suzukii adults. However, control of D. suzukii populations is very limited. So far, 50 hymenopteran parasitoids are reported to infect various drosophila species which belong to four families including two larval parasitoids, Braconidae and Eucoilidae, and two pupal parasitoids, Pteromalidae and Diapriidae. Some studies have shown that most of these larval parasitoids cannot develop in D. suzukii because of its strong immune response. T. drosophilae is a highly effective pupal parasitoid that can attack D. suzukii and has been proven to be a potential agent for biological control. Our study demonstrates that D. hydei-reared parasitoids show more beneficial parasitic characteristics than D. melanogaster-reared parasitoids. D. hydei has a worldwide distribution and is easy to raise in large numbers. Therefore, rearing of T. drosophilae in D. hydei pupae could be a successful biocontrol strategy, especially for the aim of reducing D. suzukii infestation.

Methods

**Insect collection and rearing.** D. melanogaster, D. hydei and T. drosophilae were collected from traps baited with grape fruits in May 2016 at Zijingang Campus (30.29°N, 120.08°E), Zhejiang University, Hangzhou, China, and were maintained in our laboratory at a temperature of 25 °C, relative humidity of 50–60%, and a photoperiod of 16 h: 8 h (L: D) inside plastic bottles (approximately 10 cm in length and 5 cm in diameter). Both D. melanogaster and D. hydei were maintained on a standard cornmeal/molasses/agar medium. T. drosophilae colonies were maintained on D. melanogaster pupae, and the adult wasps were provided with apple juice/agar medium (27 g agar, 33 g brown sugar and 330 ml pure apple juice in 1000 ml diluted water).

The parasitoid and host size measurements. D. melanogaster and D. hydei pupae, as the different hosts, were parasitized by T. drosophilae. For convenience, T. drosophilae that emerged from D. hydei and D. melanogaster pupae were called TDh and TDm, respectively. The TDh and TDm adults and the pupae of their hosts were imaged using a KEYENCE VHX-2000C digital microscope system (Osaka, Japan). The body length and width of 18 D. hydei pupae and 37 D. melanogaster pupae were measured using KEYENCE VHX-2000C software. The length of the hind tibia or the length of the whole body is usually used as a proxy for the size of parasitoid wasps. Here, body lengths of 10 female and 16 male TDh and 12 female and 10 male TDm were measured.

**Parasitism rate and offspring female ratio comparison.** To compare the parasitism rate and offspring female ratio of TDh and TDm, D. melanogaster pupae were parasitized by 4-day-old TDh and TDm similar to a previous study at a wasp/host ratio of 1:10 for 24 hours. This experiment was performed three times, and 200, 120 and 120 D. melanogaster host pupae were exposed to TDh and TDm. The same approach was applied to compare TDh and TDm at different ages. After eclosion, TDh and TDm adult females were maintained on apple juice wasp food at 25 °C in an incubator without hosts. Then, 1-, 5-, 10-, 15-, 20-, 25-, 30- and 40-day-old TDh and TDm females were parasitized after fully mating with young TDh and TDm males, respectively, for 24 hours. Three replicates were performed for the experiments, and 5 females and 30 host pupae were used in each experiment. After being infected, the host pupae were kept in a 25 °C incubator until the parasitoids emerged. The parasitism rate and offspring female ratio of the wasps were calculated using the following
formulas: parasitism rate = (the number of hosts – the number of emerged flies)/the number of hosts; offspring female ratio = the number of female parasitoids/the number of total emerged parasitoids.

The fecundity and stress resistance ability of *T. drosophilae*. The egg load of a female parasitoid wasp. The newly emerged male and female wasps were collected and placed in plastic bottles containing apple juice wasp food without hosts. To compare the maximum egg load between TDh and TDm, ovaries of 12-, 24-, 48-, 72-, 96-, 144-, 192- and 240-h-old female *T. drosophilae* adults were dissected in 1 × PBS buffer, pH 7.4. Ten female wasps for each category were dissected, and the mature eggs were counted at each time point. An egg was considered mature based on criteria used in a previous study: the chorion of a mature egg is smooth, thin and transparent, and the developing embryo is visible, while immature eggs lack these characteristics and are attached to each other.

The offspring of a single female wasp. To compare the offspring numbers of TDh and TDm, a fully mated female was allowed to parasitize 150 two-day old *D. melanogaster* pupae for 24 hours at 25 °C. Then, the host pupae were replaced by a new batch of 150 pupae the following day until the female adult died. The total number of offspring from single females was counted as the number of emerged wasps, including males and females. In total, 8 TDh and 8 TDm female wasps were used in this experiment, respectively.

Starvation and high and low temperature tolerances. One hundred newly emerged wasps of TDh and TDm (50 females, 50 males) were reared in an empty plastic bottle without any food at 18 °C for the starvation treatment. For the high and low temperature tolerance experiment, 100 newly emerged wasps of TDh and TDm (50 females, 50 males) were reared on apple juice wasp food in incubators at 4 °C, 18 °C, 25 °C and 37 °C. The survival rate (the number of surviving wasps/100) was calculated every 12 hours for the starvation treatment and daily for the high and low temperature tolerance analysis. Three replicates were performed for each experiment.

Data analysis and statistics. The effects of female age on the number of mature eggs were analysed using a generalized linear model (GLM) and the mean number of mature eggs in different age classes were further compared using analysis of variance (ANOVA). Log-rank tests (Mantel-Cox) were performed to analyse trends in the survival rate during the environmental stresses, i.e., starvation and high and low temperatures. Student’s t-test was used to compare the body length or body width of parasitoids and hosts, the parasitism rate and offspring female ratio, as well as the fecundity of female parasitoid wasps. Statistical analyses were performed using GraphPad Prism version 7.0a (Graphpad Software, San Diego, CA) and SPSS software 25.0 (SPSS Inc., Chicago, IL). Error bars indicate the standard error of the mean (SEM), and all data sets are expressed as the mean ± SEM. Significant differences between groups were determined by the P-value and are marked with one asterisk for *P* < 0.05 and two asterisks for *P* < 0.01.

References

1. Mackay, T. F. C. Mutations and quantitative genetic variation: lessons from Drosophila. *Philos. Trans. R. Soc. Lond B Biol. Sci*. **365**, 1229–1239 (2010).
2. Hales, K. G., Koresy, C. A., Larracuente, A. M. & Roberts, D. M. Genetics on the fly: a primer on the Drosophila model system. *Genetics* **201**, 815–842 (2015).
3. Lee, J. C. *et al.* The susceptibility of small fruits and cherries to the spotted-wing drosophila, *Drosophila suzukii*. *Pest Manage. Sci.* **67**, 1358–1367 (2011).
4. Bruck, D. J. *et al.* Laboratory and field comparisons of insecticides to reduce infestation of *Drosophila suzukii* in berry crops. *Pest Manage. Sci.* **67**, 1375–1385 (2011).
5. Pennacchio, F. & Strand, M. R. Evolution of developmental strategies in parasitic hymenoptera. *Annu. Rev. Entomol.* pp. 233–258 (2006).
6. Shi, M. & Chen, X. X. Progress in study on regulation of insect host physiology by parasitoids in China. *Chin. J. Biol. Control* **31**, 620–637 (2015).
7. Zhao, W. *et al.* Comparative transcriptome analysis of venom glands from *Cotesia vestalis* and *Diaeratus collaris*, two endoparasitoids of the host *Plutella xylostella*. *Sci. Rep.* **7**, 1298, https://doi.org/10.1038/s41598-017-01383-2 (2017).
8. Gao, F. *et al.* *Cotesia vestalis* teratocites express a diversity of genes and exhibit novel immune functions in parasitism. *Sci. Rep.* **6**, 26967, https://doi.org/10.1038/srep26967 (2016).
9. Carton, Y. *et al.* The susceptibility of small fruits and cherries to the spotted-wing drosophila, *Drosophila suzukii*. *In: Ashburner, M., Carson, H.* (eds) The genetics and biology of Drosophila, vol 3. Academic Press, London, pp 347–394 (1986).
10. Fleury, F., Gibeau, R., Ris, N. & Allemand, R. Ecology and life history evolution of frugivorous Drosophila parasitoids. In: Prevost, G. (Ed.), Advances in Parasitology, Vol 70: Parasitoids of Drosophila, pp. 3–44 (2009).
11. Schlenke, T. A., Morales, J., Govind, S. & Clark, A. G. Contrasting infection strategies in Generalist and specialist wasp parasitoids of *Drosophila melanogaster*. *PLoS Path.* **3**, 1345–1351 (2007).
12. Chabert, S., Allemand, R., Poyet, M., Edin, P. & Gibeau, R. Ability of European parasitoids (Hymenoptera) to control a new invasive Asian pest. *Drosophila suzukii*. *Biol. Control* **63**, 40–47 (2012).
13. Rossi Stacconi, M. V. *et al.* Host stage preference, efficacy and fecundity of parasitoids attacking *Drosophila suzukii* in newly invaded areas. *Biol. Control* **84**, 28–35 (2015).
14. Wang, Y.-G., Kacar, G., Biondzi, A. & Daane, K. M. Life-history and host preference of *Trichopria drosophilae*, a pupal parasitoid of spotted wing drosophila. *Biol Control* **61**, 387–397 (2016).
15. Tian, J. C. *et al.* Host preference of *Trichogramma* *Hymenoptera: Trichogrammatidae*. Species Feeding on Sugars. *Environ Entomol.* **45**, 1316–1321 (2016).
16. Harvey, J. A. *et al.* The effect of different dietary sugars and honey on longevity and fecundity in two hyperparasitoid wasps. *J Insect Physiol.* **58**, 816–823 (2012).
17. Liu, L. D., Xu, B. B., Li, L. & Sun, J. H. Host-size mediated trade-off in a parasitoid *Sleroderma harmandii*. *Plos One* **6**(8), e23260 (2011).
18. Lampson, L. J., Morse, J. G. & Luck, R. F. Host selection, sex allocation, and host feeding by *Metaphycus helvolus* (Hymenoptera: Encyrtidae) on *Saissetia oleae* (Homoptera: Coccidae) and its effect on parasitoid size, sex, and quality. *Environ. Entomol.* **25**, 283–294 (1996).
19. Zhou, H. F. et al. Comparative studies on parasitism of Pachycercoides vinicinniae (Rondani) reared on houssely and fruit fly pupae. Chin. J. Appl. Entomol. 51, 194–199 (2014).
20. Powell, W. & Wright, A. F. The abilities of the aphid parasitoids Aphidius ervi Haliday and A. rhopalosiphi De Stefani Perez (Hymenoptera: Braconidae) to transfer between different known host species and the implications for the use of alternative hosts in pest control strategies. Bull. Entomol. Res. 78, 683–693 (1988).
21. Briët, E., Bylemans, D., Migon, M. & Van Impe, G. In-field production of parasitoids of Dysaphis plantaginea by using the rowan aphid Dysaphis sorbit as substitute host. Bio Control 50, 601–610 (2005).
22. Tunca, H., Venard, M., Colombel, E.-A. & Tabone, E. A new substitute host and its effects on some biological properties of Ooencyrtus kuvanae. Bull. Entomol. Res. 107, 742–748 (2017).
23. Weiblen, G. D. How to be a fig wasp. Annu. Rev. Entomol. 47, 299–330 (2002).
24. Beukeboom, L. W. & van de Zande, L. Genetics of sex determination in the haplodiploid wasp. Development 144, 2584–2594 (2017).
25. Ponlawat, A. & Harrington, L. C. Factors associated with male mating success of the dengue vector mosquito, Aedes aegypti. Am. J. Trop. Med. Hyg. 80, 395–400 (2009).
26. Colinet, H., Boivin, G. & Hance, T. Manipulation of parasitoid size using the temperature-size rule: fitness consequences. Oecologia 152, 425–433 (2007).
27. Colinet, H., Boivin, G. & Hance, T. Manipulation of parasitoid size using the temperature-size rule: fitness consequences. Oecologia 152, 425–433 (2007).
28. Hauser, M. A historic account of the invasion of Drosophila suzukii (Matsumura) (Diptera: Drosophilidae) in the continental United States, with remarks on their identification. Pest Manage. Sci. 67, 1352–1357 (2011).
29. Cini, A. et al. Tracking the invasion of the alien fruit pest Drosophila suzukii in Europe. J. Pest Sci. 87, 559–566 (2014).
30. Woltz, J. M., Donahue, K. M., Bruck, D. J. & Lee, J. C. Efficacy of commercially available predators, nematodes and fungal entomopathogens for augmentative control of Drosophila suzukii. J. Appl. Entomol. 139, 759–770 (2015).
31. Asplin, M. K. et al. Invasion biology of spotted wing Drosophila (Drosophila suzukii): a global perspective and future priorities. J. Pest Sci. 88, 469–494 (2015).
32. Rota-Stabelli, O., Blaxter, M. & Anfora, G. Drosophila suzukii (Diptera: Drosophilidae) to entomopathogenic fungi. Bio Control 50, 601–610 (2015).
33. Atallah, L. T., Teixeira, L., Salazar, R., Zaragoza, G. & Kopp, A. The making of a pest: the evolution of a fruit-penetrating ovipositor in Drosophila suzukii. J. Pest Sci. 89, 605–619 (2016).
34. Naranjo-Lazaro, J. M. et al. Susceptibility of Drosophila suzukii Matsumura (Diptera: Drosophilidae) to entomopathogenic fungi. Southwest. Entomol. 39, 291–293 (2014).
35. Mazzetto, F. et al. Drosophila parasitoids in northern Italy and their potential to attack the exotic pest Drosophila suzukii. J. Pest Sci. 89, 837–850 (2016).
36. Rossi Stacconi, M. V. et al. Comparative life history traits of indigenous Italian parasitoids of Drosophila suzukii and their effectiveness at different temperatures. Biol. Control 112, 20–27 (2017).
37. Huang, J., Releim, A. & Kalderon, D. Y orkie and Hedgehog independently restrict BMP production in escort cells to permit germline differentiation in the Drosophila ovary. Development 144, 2584–2594 (2017).
38. Gao, S. et al. Relationships between Body Size and Parasitic Fitness and Offspring Performance of Sclerochrus papuariae Yang et Yao (Hymenoptera: Bethylidae). PlOS One. 11, e0156831 (2016).

Acknowledgements
We thank the anonymous reviewers for many useful comments. This research was supported by the National Key R&D Program of China (2017YFD0200400), the National Science Fund for Excellent Young Scholars (31622048), the National Science Foundation of China (31672079) and the National Thousand-Young-Talents Program of China.

Author Contributions
J.N.C. and J.H.H. conceived and designed the experiments; J.N.C., S.C.Z., Y.W. and M.S. performed the experiments and analysed the data; J.N.C., J.H.H. and X.X.C. wrote and revised the manuscript. All authors reviewed the manuscript.

Additional Information
Competing Interests: The authors declare no competing interests.

Publisher’s note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2018