



## Plasticity of body growth and development in two cosmopolitan pupal parasitoids

Xingeng Wang<sup>a,b,1</sup>, Brian N. Hogg<sup>c</sup>, Antonio Biondi<sup>a,d,2</sup>, Kent M. Daane<sup>a,\*,3</sup>

<sup>a</sup> Department of Environmental Science, Policy and Management, University of California, Berkeley, CA, USA

<sup>b</sup> USDA Agricultural Research Service, Beneficial Insects Introduction Research Unit, Newark, DE, USA

<sup>c</sup> USDA Agricultural Research Service, Invasive Species and Pollinator Health Research Unit, Albany, CA, USA

<sup>d</sup> Department of Agriculture, Food and Environment, University of Catania, Catania, Italy

### HIGHLIGHTS

- *Pachycrepoides vindemiae* and *Trichopria drosophilae* are cosmopolitan pupal parasitoids of *Drosophila suzukii*.
- Host range studies showed remarkable of plasticity in parasitoids' body growth and development.
- Parasitoids benefited from attacking larger hosts, with increased progeny size and fecundity.

### ARTICLE INFO

#### Keywords:

Body size  
Drosophilidae  
Host range  
Parasitoid  
Plasticity

### ABSTRACT

*Pachycrepoides vindemiae* and *Trichopria drosophilae* are cosmopolitan pupal parasitoids of Drosophilidae that attack the invasive *Drosophila suzukii*. This study investigated one aspect of their plasticity – host acceptance and offspring fitness on 25 *Drosophila* species in a phylogenetic framework. Each parasitoid's key biological and ecological traits were compared among the different host species. Results demonstrate that both parasitoid species successfully parasitized and developed from all tested host species. Although the parasitoids' efficiency and offspring fitness varied among host species, effects on life-history characteristics or ecological traits appeared to be unrelated to the phylogenetic position of tested host species. Both parasitoids benefited from attacking larger hosts, with body size of emerging progeny positively correlated to host size and an increased fecundity (mature egg load) of female wasps. Achieving larger body size came at no significant costs in immature development time. Results show remarkable levels of plasticity in the parasitoids' body growth and development. Body size plasticity in *T. drosophilae* and *P. vindemiae* could improve biological control by increasing variation in parasitoid body sizes. Large size may not be advantageous under all conditions, however, and the parasitoids' ecosystem impacts will be influenced not only by their plasticity to hosts but by environmental limitations such as temperature tolerances, habitat location, and host searching behaviors.

### 1. Introduction

Phenotypic plasticity has been discussed with respect to invasive species success and native species adaptation to environmental disturbances such as climate change (Kingsolver and Buckley, 2018; Wilson et al., 2009). Plasticity in host specialization can also impact the success and effectiveness of insect parasitoids that provide ecosystem services

(Biondi et al., 2013; Desneux et al., 2012). An example is a parasitoid's ability to utilize phylogenetically related host species that differ in quality; the ability to use multiple hosts is likely to increase the persistence and abundance of parasitoids (Bribosia et al., 2005), but may affect a parasitoid's key life-history characteristics and ecological traits (Godfray, 1994; Harvey et al., 1994). This is particularly true for parasitoids that attack non-growing host stages, such as pupae, as their

\* Corresponding author.

E-mail address: [kmdaane@berkeley.edu](mailto:kmdaane@berkeley.edu) (K.M. Daane).

<sup>1</sup> ORCID: 0000-0002-8825-2266.

<sup>2</sup> ORCID: 0000-0002-1982-7716.

<sup>3</sup> ORCID: 0000-0001-8052-1954.

<https://doi.org/10.1016/j.biocontrol.2021.104738>

Received 12 November 2020; Received in revised form 26 May 2021; Accepted 3 August 2021

Available online 5 August 2021

1049-9644/© 2021 Elsevier Inc. All rights reserved.

offspring must develop on the host resources present at the time of oviposition (Chen et al., 2018; Ueno, 1998). Within the narrower focus of classical biological control, natural enemies that exhibit plasticity to environmental tolerances are sought after whereas natural enemies that exhibit host species plasticity are rarely purposely released (Heimpel and Cock, 2018; Hoddle et al., 2020).

Here, we report on the plasticity of two insect parasitoids with respect to host size, which is often positively correlated with parasitoid fitness (Eijs and van Alphen, 1999; Ellers and Jervis, 2003; Ellers et al., 1998; Jervis et al., 2003; Kazmer and Luck, 1995; Visser, 1994). Within the range of acceptable host sizes, a parasitoid population often benefits when female wasps oviposit into larger hosts (Charnov and Stephens, 1988; King and Lee, 1994; Napoleon and King, 1999; Otto and Mackauer, 1998; Stephens and Charnov, 1982; Teder et al., 1999). For example, Wang and Messing (2004a) showed that *Dirhinus giffardii* Silvestri, a pupal ectoparasitoid, prefers to attack larger tephritid host species, with numbers of emerged offspring, progeny size, and adult progeny searching efficiency all positively correlated to host size. However, the fitness gain from being larger can come at the cost of other traits, such as developmental time, which often increases with body size (Harvey et al., 1994; Harvey and Strand, 2002; Petersen and Hardy, 1996; Sequeira and Mackauer, 1992). In some cases, host quality may not increase with host size (e.g., Wang and Messing, 2004b), therefore, a parasitoid's plasticity or response to host size may depend on the degree of physiological and nutritional compatibility between parasitoid and host.

The plasticity of the drosophilid parasitoids *Pachycrepoideus vindemiae* (Rondani) (Hymenoptera: Pteromalidae) and *Trichopria drosophilae* (Perkins) (Hymenoptera: Diapriidae) was studied as part of a biological control effort against the invasive spotted wing drosophila, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), which has become a serious pest of various small fruit crops (Asplen et al., 2015). Quarantine studies to determine a parasitoid's suitability for release are, to some extent, an investigation of its plasticity and here the focus was on the host range plasticity of *P. vindemiae* and *T. drosophilae*. The former species oviposits into host pupae, immediately paralyzing the host (typical idiobiont), and then develops as a solitary ectoparasitoid enclosed by a protective puparium formed from the fly's hardened exoskeleton, therefore still hidden from view by the host's puparium (Wang and Messing, 2004c). The latter species also oviposits into host pupae but develops as a solitary endoparasitoid that kills the host after the parasitoid larva begins feeding (Wang et al., 2016b). Like other ectoparasitoids, *P. vindemiae* produces relatively few large eggs, whereas *T. drosophilae* produces high numbers of small eggs and is thus generally more efficient than *P. vindemiae* under suitable laboratory conditions (Kaçar et al., 2017; Rossi Stacconi et al., 2015; Stacconi et al., 2017; Wang et al., 2016a; Wang et al., 2016b). *Pachycrepoideus vindemiae* appears to be more of a generalist than *T. drosophilae* and can act like a hyperparasitoid of other primary fruit fly parasitoids (Wang and Messing, 2004b), whereas the host range of *T. drosophilae* is thought to be more limited (Carton et al., 1986).

To date, *P. vindemiae* and *T. drosophilae* are among the few resident parasitoid species that successfully attack *D. suzukii* in the invaded regions of the Americas and Europe (Lee et al., 2019; Rossi Stacconi et al., 2017; Rossi Stacconi et al., 2019). Both species are efficient parasitoids of *D. suzukii* in laboratory settings (e.g., Kaçar et al., 2017; Wang et al., 2018; Wolf et al., 2020); however, naturally occurring parasitism of *D. suzukii* populations has been generally low, likely due to a lack of host specificity in these parasitoids (e.g., Miller et al., 2015). Recent studies have reported the performance of *P. vindemiae* and *T. drosophilae* against *D. suzukii* and the common host *D. melanogaster* or a few other species (Chen et al., 2018; Wang et al., 2016a; Wang et al., 2016b; Woltering et al., 2019; Yi et al., 2020). Information is lacking, however, on the performance of these two parasitoids across a wide range of *Drosophila* species within a phylogenetic framework – basically, at the fringe of host species acceptance for parasitoids exhibiting plasticity is there an impact

on offspring fitness? Therefore, this study sought to use these parasitoids as model species to investigate the plasticity or response of the parasitoids' body-size plasticity in relationship to different host species, which may be a critical aspect of their use for *D. suzukii* biological control.

## 2. Materials and methods

### 2.1. Insects

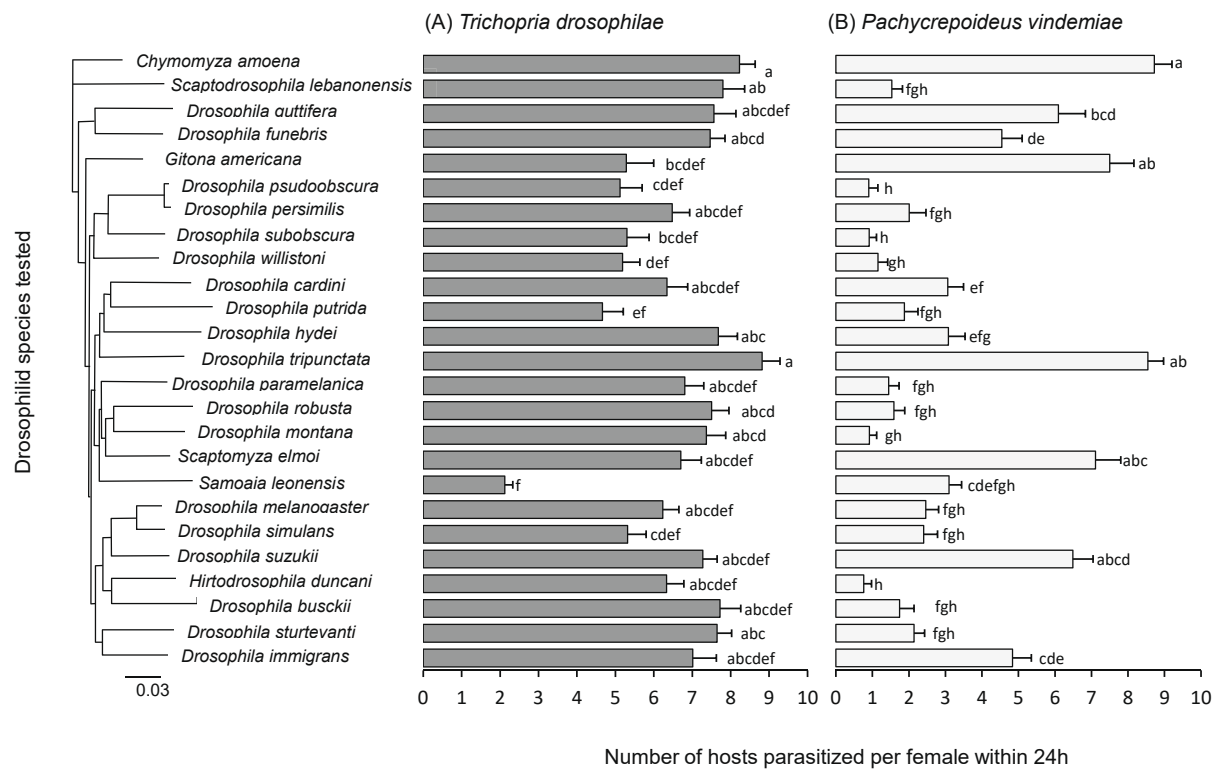
All bioassays and insect rearing were conducted under controlled conditions ( $23 \pm 1$  °C, 16L:8D, 40–60% RH) at the University of California (UC) Kearney Agricultural Research Center in Parlier, California, USA. As described in Wang et al. (2016b), colonies of *D. suzukii*, *P. vindemiae* and *T. drosophilae* were initiated from parasitoids field-collected from nearby farms, with new material periodically introduced to maintain colony vigor. Adult flies were held in Bug Dorm cages (BioQuip Products Inc., Rancho Dominguez, CA), while adult parasitoids were held in screened cages (30 × 30 × 30 cm) (Mega View Science Co. Ltd., Taichung, Taiwan); all insects were supplied with a 20% honey-water solution (*ad libitum*) as food. Parasitoids were reared on *D. suzukii* pupae, whereas fly larvae were reared on a cornmeal-based artificial diet.

### 2.2. Collection of drosophilid species

There are over 2,000 described drosophilid species worldwide (Markow et al., 2006); we selected 25 representative species from two subfamilies, seven genera, nine subgenera and 20 species groups (Table S1). Except for *D. suzukii*, all species were purchased from the UC San Diego Drosophila Stock Center and then reared for two generations on artificial diet (Table S1). Among them, 22 species were originally collected within the USA, one was from American Samoa and one was from Japan. All species except *Gitona americana* Patterson (subfamily Steganinae) belong to the subfamily Drosophilinae. The Japanese species (*Scaptomyza elmoi* Takada) was selected as a close representative of endangered Hawaiian drosophilids. Host species selection considered phylogenetic relatedness, potential sympatry with *D. suzukii*, geographic distribution and occurrence in North America, and ecological diversity (e.g., breeding substrates) (Table S1). Host species phylogenetic relationship was constructed based on available COI gene sequences from the NCBI database. Because gene sequences of *S. elmoi* and *G. americana* were not available, we completed a DNA extraction using DNeasy Blood & Tissue Kit (Qiagen, Germantown, MD), amplifying the COI gene using polymerase chain reaction (PCR) with primer pair LepF1-short/LepR1-short (LepF1-short: 5'-ATTCAACCAATCATAAAGATAT-3' and LepR1-short: 5'-TAAACTTCTGGATGTCCAAAAA-3'). Following target COI amplification, samples were treated with ExoSAP (0.5 µl Exonuclease I, 0.5 µl Shrimp Alkaline Phosphatase, 1.0 µl 10X Exonuclease Reaction Buffer, and 5.0 µl PCR product), and run at 37 °C for 15 min, then at 80 °C for 15 min. Samples were then sequenced using an ABI 3730xl DNA Sequencer (Thermo Fisher Scientific).

### 2.3. Host acceptance, parasitoid fitness and foraging efficiency

No-choice assays were conducted to ascertain the innate potential of *P. vindemiae* and *T. drosophilae* to parasitize a specific host, which could be masked in choice assays by host preference. All tests used 3–6 day old mated female parasitoids and 2–3 day old fly pupae. For each treatment replicate, 10 pupae were placed on a wet tissue paper in a plastic petri dish (1.5 cm high, 8.5 cm diameter) and exposed to a single female wasp for 24 h. Tests had 25–30 replicates for each host species and parasitoid combination, except for *S. elmoi* that had only 5 replicates due to difficulties rearing this species. For each *Drosophila* species, 5 additional replicates of pupae were not exposed to the parasitoids, and these served as a control for natural mortality of unexposed pupae. All treated and



**Fig. 1.** Number of *Drosophila* pupae parasitized by (A) *T. drosophilae* or (B) *P. vindemiae* in various *Drosophila* species. Phylogenetic tree of tested *Drosophila* species was constructed based on COI gene sequences retrieved from the NCBI database except for *S. elmoi* and *G. americana* that were collected from this study. Bars refer to mean  $\pm$  SE and bars bearing different letters are significantly different (Tukey's HSD,  $P < 0.05$ ).

control pupae were checked twice daily, when the gender and developmental time of emerged adults were recorded. After emergence ceased, all dead pupae were reconstituted in water for 1 day and then dissected under a microscope to determine the presence or absence of recognizable fly or parasitoid cadavers (pharate adults, larvae or pupae). Percentage parasitism or host mortality due to parasitism was corrected based on the Schneider-Orelli formula:

$$P = (b - k) \times 100 / (1 - k)$$

where  $P$  is corrected mortality resulting from parasitism, and  $b$  and  $k$  are host mortality in the treatment and control, respectively. Mortality of unexposed host pupae in the controls varied among the various host species ( $F_{24,195} = 4.82$ ,  $P < 0.001$ ), but was  $< 5\%$  for most of tested species, with the exception of two species (*G. americana* and *D. tripunctata*) that had about 30% mortality (Fig. S1). The number of parasitized hosts was estimated based on the corrected mortality, while offspring mortality was estimated based on developed offspring and the total number of parasitized hosts. Offspring sex ratio was estimated based on emerged adult parasitoids.

To estimate the effect of host species on parasitoid fitness, a subsample of 2–5 parasitized pupae were randomly selected from each replicate, their pupal length and width were measured ( $\pm 0.001$  mm), and they were then individually reared in gelatin capsules. Each emerged wasp was monitored for the immature developmental time. Emerged female wasps were held in vials (8 cm high, 2 cm diameter) streaked with 20% honey water and then killed 2 days later and dissected to record the mature egg load. The hind tibia length of each dissected female was also measured to serve as a proxy of female's body size (Wang et al., 2016a). Unemerged pupae were also dissected as described above and these data were included in the calculation of parasitism and offspring survival (i.e., proportion of parasitoids that successfully emerged from hosts). For these measures, a subsample of 18 host species were measured. A total of 30–50 parasitized individual

pupae were tracked for the entire process from exposure to the emergence of wasps for each host and parasitoid combination. Because host shape of different species was slightly different we estimated puparium volume as a measure of size using the formula (Otto and Mackauer, 1998; Wang and Messing, 2004a):

$$V = 4/3\pi \cdot (l/2) \cdot (w/2)^2$$

where  $V$  is the volume of a prolate ellipsoid puparium with length  $l$  and width  $w$ .

To determine the effect of natal host species and female body size on the parasitoids' relative efficiency on *D. suzukii*, a sub-sample of 10–20 female wasps that emerged from various host species were tested for their foraging efficiency by providing each female with twenty 2–3 day old *D. suzukii* pupae using the same methods as described above. After a 24 h exposure, all tested females were killed in the freezer and dissected to measure their hind tibia length and all exposed pupae were reared to determine the number of hosts parasitized.

#### 2.4. Data analysis

All values are presented as mean  $\pm$  SE. Because host size varied even within the same species, depending on the rearing conditions, and because bioassays for both parasitoids were conducted separately, data were analyzed separately for each parasitoid species. Moran's  $I$  was used to test whether fitness parameters of the parasitoids were associated with fly phylogeny, using the PhyloSignal function in the PhyloSignal package of R version 4.0.2 (Team, 2020). Moran's  $I$  varies from  $-1$  to  $+1$ , with more positive values indicating higher similarity between closely related taxa than expected by chance, and is insensitive to tree size and tree balance, and is not based on an evolutionary model (Münkemüller et al., 2012). All subsequent analyses were performed using JMP®, Pro 14 (SAS Institute Inc., Cary, NC, 1989–2019). The number of hosts parasitized, offspring survival, and sex ratio on each

**Table 1**  
Pupal sizes of various *Drosophila* species and offspring fitness of *Trichopria drosophilae* developed from the *Drosophila* species.

| Host species            | Host pupal size <sup>1</sup> |             |                           | Hind tibia length (mm) <sup>1</sup> |             | Developmental time (day) <sup>1</sup> |              | No. of mature eggs <sup>1</sup> | No. of hosts parasitized <sup>1</sup> |
|-------------------------|------------------------------|-------------|---------------------------|-------------------------------------|-------------|---------------------------------------|--------------|---------------------------------|---------------------------------------|
|                         | Length (mm)                  | Width (mm)  | Volume (mm <sup>3</sup> ) | Male                                | Female      | Male                                  | Female       |                                 |                                       |
| <i>D. busckii</i>       | 2.59 ± 0.03                  | 0.95 ± 0.01 | 0.12 ± 0.00               | 0.49 ± 0.01                         | 0.52 ± 0.01 | 21.54 ± 0.34                          | 19.67 ± 0.49 | 52.71 ± 2.45                    | — <sup>2</sup>                        |
| <i>D. cardini</i>       | 2.84 ± 0.02                  | 1.03 ± 0.01 | 0.16 ± 0.00               | 0.54 ± 0.01                         | 0.57 ± 0.01 | 21.13 ± 0.26                          | 20.05 ± 0.25 | 69.38 ± 2.24                    | 16.90 ± 1.34                          |
| <i>D. funebris</i>      | 3.73 ± 0.04                  | 1.27 ± 0.02 | 0.32 ± 0.01               | 0.56 ± 0.01                         | 0.58 ± 0.01 | 22.50 ± 0.38                          | 19.67 ± 0.44 | 73.29 ± 3.57                    | 17.02 ± 0.69                          |
| <i>D. hydei</i>         | 4.42 ± 0.06                  | 1.29 ± 0.02 | 0.40 ± 0.02               | 0.56 ± 0.01                         | 0.59 ± 0.01 | 25.32 ± 0.55                          | 23.73 ± 0.46 | 70.00 ± 3.65                    | 17.98 ± 0.37                          |
| <i>D. immigrans</i>     | 3.82 ± 0.04                  | 1.36 ± 0.02 | 0.38 ± 0.01               | 0.60 ± 0.01                         | 0.63 ± 0.01 | 22.39 ± 0.51                          | 20.38 ± 0.25 | 73.11 ± 3.96                    | 16.39 ± 0.37                          |
| <i>D. montana</i>       | 4.52 ± 0.11                  | 1.26 ± 0.03 | 0.38 ± 0.03               | 0.60 ± 0.01                         | 0.60 ± 0.02 | 23.50 ± 0.55                          | 21.38 ± 0.72 | 69.29 ± 3.21                    | 18.62 ± 0.23                          |
| <i>D. melanogaster</i>  | 2.76 ± 0.01                  | 0.97 ± 0.01 | 0.14 ± 0.00               | 0.51 ± 0.00                         | 0.54 ± 0.01 | 21.71 ± 0.29                          | 19.97 ± 0.48 | 62.34 ± 1.52                    | 17.45 ± 0.41                          |
| <i>D. persimilis</i>    | 2.94 ± 0.02                  | 1.07 ± 0.01 | 0.18 ± 0.01               | 0.51 ± 0.00                         | 0.55 ± 0.01 | 22.40 ± 0.35                          | 20.50 ± 0.24 | 63.17 ± 1.54                    | 17.04 ± 0.56                          |
| <i>D. paramelanica</i>  | 2.91 ± 0.03                  | 1.09 ± 0.01 | 0.18 ± 0.01               | 0.53 ± 0.00                         | 0.58 ± 0.01 | 21.64 ± 0.43                          | 20.64 ± 0.18 | 64.07 ± 2.10                    | — <sup>2</sup>                        |
| <i>D. pseudoobscura</i> | 2.80 ± 0.03                  | 1.09 ± 0.02 | 0.18 ± 0.01               | 0.53 ± 0.00                         | 0.56 ± 0.01 | 24.38 ± 0.74                          | 22.13 ± 1.00 | 63.50 ± 3.47                    | 14.50 ± 2.05                          |
| <i>D. putrida</i>       | 2.27 ± 0.02                  | 0.78 ± 0.01 | 0.07 ± 0.00               | 0.47 ± 0.01                         | 0.50 ± 0.00 | 23.50 ± 1.02                          | 20.28 ± 0.27 | 48.86 ± 2.19                    | — <sup>2</sup>                        |
| <i>D. robusta</i>       | 4.36 ± 0.04                  | 1.38 ± 0.02 | 0.44 ± 0.02               | 0.60 ± 0.01                         | 0.63 ± 0.01 | 25.00 ± 1.01                          | 20.96 ± 0.56 | 62.79 ± 2.73                    | 17.22 ± 0.42                          |
| <i>D. simulans</i>      | 2.84 ± 0.03                  | 1.02 ± 0.01 | 0.16 ± 0.00               | 0.48 ± 0.00                         | 0.52 ± 0.01 | 21.51 ± 0.19                          | 20.37 ± 0.19 | 54.44 ± 1.78                    | 16.78 ± 0.66                          |
| <i>D. sturtevantii</i>  | 2.99 ± 0.04                  | 1.09 ± 0.02 | 0.19 ± 0.01               | 0.52 ± 0.01                         | 0.54 ± 0.01 | 21.69 ± 0.36                          | 19.75 ± 0.45 | 66.18 ± 2.10                    | 15.78 ± 0.82                          |
| <i>D. subobscura</i>    | 2.98 ± 0.04                  | 1.04 ± 0.02 | 0.17 ± 0.01               | 0.52 ± 0.00                         | 0.57 ± 0.01 | 23.71 ± 0.72                          | 21.43 ± 1.02 | 53.08 ± 4.85                    | 15.00 ± 0.58                          |
| <i>D. willistoni</i>    | 2.52 ± 0.02                  | 0.86 ± 0.01 | 0.10 ± 0.00               | 0.43 ± 0.00                         | 0.47 ± 0.01 | 20.67 ± 0.50                          | 19.39 ± 0.13 | 44.38 ± 1.19                    | 14.66 ± 2.79                          |
| <i>H. duncani</i>       | 2.65 ± 0.05                  | 0.93 ± 0.02 | 0.13 ± 0.01               | 0.50 ± 0.01                         | 0.54 ± 0.01 | 19.46 ± 0.70                          | 19.68 ± 0.59 | 53.00 ± 4.60                    | 15.15 ± 0.56                          |
| <i>S. lebanonensis</i>  | 3.19 ± 0.02                  | 0.97 ± 0.01 | 0.16 ± 0.00               | 0.51 ± 0.00                         | 0.55 ± 0.01 | 21.86 ± 0.24                          | 19.91 ± 0.41 | 55.63 ± 1.08                    | 17.69 ± 0.44                          |

<sup>1</sup> Values are mean ± SE and subject to analyses of multiple factors' effects (see statistical results on Table 4).

<sup>2</sup> Data were excluded from analyses due to small samples (only a few individual wasps emerged).

host species was compared separately for each parasitoid using one-way ANOVA; prior to comparisons percentage data were logit transferred to normalize the variance. If a significant difference was detected, the mean values were further compared by Tukey HSD test. Body size was analyzed using Generalized Linear Model (GLM) with a normal distribution and an identity link function, considering the effects of natal host species, host size, parasitoid sex and the interaction between host species and host size; the developmental time was analyzed also using GLM by considering the effect of natal host, wasp size and sex. Both the mature egg load and relative foraging efficiency of female wasps were analyzed using GLM with a Poisson distribution and a logit identity link function, considering the effect of natal host, female body size and their interaction. The relationships among the mean size of host species and mean number of hosts parasitized, mean offspring survival, or mean sex ratio were analyzed using linear regression. The relationship between host size and female body size was described using a polynomial model ( $y = a + b/x$ ; non-linear regression was used to estimate the parameters) while the relationship between female body size and mature egg load were analyzed using linear regression by pooling all measured female wasps for each parasitoid species.

### 3. Results

Both *T. drosophilae* and *P. vindemiae* attacked all 25 tested host species (Fig. 1). Pupal size varied among the measured *Drosophila* species for *T. drosophilae* (pupal length:  $F_{17,647} = 288.0$ ,  $P < 0.001$ , width:  $F_{17,647} = 97.5$ ,  $P < 0.001$ , volume:  $F_{17,647} = 174.4$ ,  $P < 0.001$ ) and

*P. vindemiae* (pupal length:  $F_{17,629} = 148.2$ ,  $P < 0.001$ , width:  $F_{17,629} = 64.4$ ,  $P < 0.001$ , volume:  $F_{17,629} = 99.3$ ,  $P < 0.001$ ). Large-body species were *D. robusta*, *D. hydi*, *D. immigrans*, *D. montana*, and *D. funebris* ( $>0.32$  mm<sup>3</sup>), small-body species were *D. putrida*, *D. willistoni*, *H. duncani*, *D. busckii*, and *D. melanogaster*, *D. simulans*, and *D. cardini* ( $<0.16$  mm<sup>3</sup>); the other species ranged from 0.16 to 0.19 mm<sup>3</sup> (Tables 1–3).

Tests using Moran's *I* uncovered no associations between any of the parasitoid fitness parameters and fly species phylogeny, except for offspring survival of *T. drosophilae* (Table 4). The number of hosts parasitized varied among host species for *T. drosophilae* ( $F_{24,590} = 5.3$ ,  $P < 0.001$ ) and *P. vindemiae* ( $F_{24,723} = 33.5$ ,  $P < 0.001$ ). Overall, more hosts were parasitized by *T. drosophilae* ( $6.7 \pm 0.1$ ) than by *P. vindemiae* ( $3.0 \pm 0.1$ ) ( $F_{1,1361} = 538.9$ ,  $P < 0.001$ ). Offspring survival was also affected by host species for *T. drosophilae* ( $F_{24,584} = 11.0$ ,  $P < 0.001$ ) and *P. vindemiae* ( $F_{24,487} = 5.2$ ,  $P < 0.001$ ). The survival rate of *T. drosophilae* was similar across the various hosts ( $>50\%$ ), except on *D. tripunctata* (1.5%), *G. americana* (30.3%) and *S. elmoi* (33.3%) (Fig. 2). There was wide variation in the offspring survival of *P. vindemiae* among the different host species; the lowest survival rate was observed in *D. persimilis* (4.9%), *S. elmoi* (5.6%) and *D. tripunctata* (8.8%) (Fig. 2). Overall, offspring survival was higher for *T. drosophilae* ( $62.3 \pm 1.3\%$ ) than for *P. vindemiae* ( $46.0 \pm 1.9\%$ ) ( $F_{1,1119} = 100.7$ ,  $P < 0.001$ ). Offspring sex ratio was similar across all tested species for *T. drosophilae* ( $F_{24,511} = 2.3$ ,  $P < 0.001$ ), but varied among various hosts for *P. vindemiae* ( $F_{23,275} = 4.2$ ,  $P < 0.001$ ) (Fig. 3). Across all species, offspring sex ratio was similar between *T. drosophilae* ( $64.0 \pm 1.4\%$ ) and

**Table 2**  
Pupal sizes of various *Drosophila* species and offspring fitness of *Pachycrepoideus vindemiae* developed from the *Drosophila* species.

| Host species            | Host pupal size <sup>1</sup> |             |                           | Hind tibia length (mm) <sup>1</sup> |                | Developmental time (day) <sup>1</sup> |                | No. of mature eggs <sup>1</sup> | No. of hosts parasitized <sup>1</sup> |
|-------------------------|------------------------------|-------------|---------------------------|-------------------------------------|----------------|---------------------------------------|----------------|---------------------------------|---------------------------------------|
|                         | Length (mm)                  | Width (mm)  | Volume (mm <sup>3</sup> ) | Male                                | Female         | Male                                  | Female         |                                 |                                       |
| <i>D. busckii</i>       | 2.95 ± 0.05                  | 1.08 ± 0.02 | 0.19 ± 0.01               | 0.39 ± 0.00                         | 0.41 ± 0.01    | 20.75 ± 0.14                          | 20.67 ± 0.17   | 13.33 ± 0.98                    | 13.12 ± 0.55                          |
| <i>D. cardini</i>       | 2.67 ± 0.04                  | 1.04 ± 0.02 | 0.15 ± 0.01               | 0.39 ± 0.00                         | 0.41 ± 0.01    | 21.33 ± 0.48                          | 21.38 ± 1.24   | 13.52 ± 0.74                    | 9.42 ± 0.77                           |
| <i>D. funebris</i>      | 3.32 ± 0.07                  | 1.17 ± 0.02 | 0.25 ± 0.01               | 0.44 ± 0.01                         | 0.45 ± 0.01    | 22.02 ± 0.32                          | 21.36 ± 0.58   | 18.50 ± 0.62                    | 12.59 ± 0.68                          |
| <i>D. hydei</i>         | 3.54 ± 0.12                  | 1.14 ± 0.03 | 0.25 ± 0.02               | 0.45 ± 0.02                         | — <sup>2</sup> | 21.90 ± 0.65                          | — <sup>2</sup> | 15.80 ± 1.91                    | 14.50 ± 1.05                          |
| <i>D. immigrans</i>     | 3.82 ± 0.03                  | 1.39 ± 0.02 | 0.40 ± 0.01               | 0.46 ± 0.00                         | 0.47 ± 0.01    | 20.21 ± 0.20                          | 20.22 ± 1.07   | 19.93 ± 0.60                    | 7.68 ± 0.94                           |
| <i>D. montana</i>       | 4.57 ± 0.08                  | 1.25 ± 0.02 | 0.38 ± 0.01               | 0.44 ± 0.00                         | 0.43 ± 0.02    | 21.38 ± 0.28                          | 20.50 ± 0.00   | 18.79 ± 0.82                    | 8.53 ± 0.98                           |
| <i>D. melanogaster</i>  | 2.86 ± 0.03                  | 1.00 ± 0.01 | 0.15 ± 0.00               | 0.41 ± 0.00                         | 0.36 ± 0.05    | 21.99 ± 0.18                          | 21.36 ± 0.37   | 13.32 ± 0.62                    | 11.42 ± 0.69                          |
| <i>D. persimilis</i>    | 2.83 ± 0.05                  | 1.06 ± 0.07 | 0.17 ± 0.02               | 0.45 ± 0.02                         | — <sup>2</sup> | 24.00 ± 0.00                          | — <sup>2</sup> | 15.67 ± 1.45                    | 14.85 ± 1.05                          |
| <i>D. paramelanica</i>  | 2.98 ± 0.02                  | 1.08 ± 0.01 | 0.18 ± 0.00               | 0.42 ± 0.00                         | 0.43 ± 0.00    | 20.91 ± 0.20                          | 20.10 ± 0.40   | 15.31 ± 0.49                    | 7.61 ± 1.04                           |
| <i>D. pseudoobscura</i> | 2.84 ± 0.04                  | 1.01 ± 0.01 | 0.15 ± 0.01               | 0.40 ± 0.01                         | — <sup>2</sup> | 20.35 ± 0.36                          | — <sup>2</sup> | 15.60 ± 0.52                    | 14.46 ± 0.70                          |
| <i>D. putrida</i>       | 2.54 ± 0.02                  | 0.91 ± 0.01 | 0.11 ± 0.00               | 0.36 ± 0.00                         | 0.37 ± 0.01    | 20.71 ± 0.14                          | 20.41 ± 0.24   | 9.68 ± 0.44                     | 7.29 ± 1.34                           |
| <i>D. robusta</i>       | 3.84 ± 0.03                  | 1.22 ± 0.03 | 0.31 ± 0.01               | 0.46 ± 0.01                         | 0.48 ± 0.01    | 22.76 ± 0.46                          | 22.17 ± 1.33   | 16.52 ± 0.78                    | 7.70 ± 1.74                           |
| <i>D. simulans</i>      | 2.52 ± 0.03                  | 0.93 ± 0.02 | 0.12 ± 0.01               | 0.38 ± 0.00                         | 0.39 ± 0.01    | 20.69 ± 0.40                          | 19.75 ± 1.06   | 13.13 ± 0.59                    | 10.01 ± 1.16                          |
| <i>D. sturtevanti</i>   | 2.71 ± 0.03                  | 1.04 ± 0.02 | 0.16 ± 0.01               | 0.42 ± 0.01                         | 0.42 ± 0.01    | 21.30 ± 0.34                          | 20.30 ± 0.80   | 13.71 ± 0.97                    | 6.40 ± 1.30                           |
| <i>D. subobscura</i>    | 2.87 ± 0.03                  | 1.06 ± 0.01 | 0.17 ± 0.01               | 0.41 ± 0.006                        | 0.43 ± 0.008   | 20.63 ± 0.28                          | 18.57 ± 1.03   | 15.78 ± 0.78                    | 13.04 ± 1.06                          |
| <i>D. willistoni</i>    | 2.71 ± 0.04                  | 0.92 ± 0.02 | 0.12 ± 0.01               | 0.34 ± 0.004                        | 0.37 ± 0.008   | 20.67 ± 0.10                          | 20.38 ± 0.21   | 7.38 ± 0.39                     | 8.87 ± 2.38                           |
| <i>H. duncani</i>       | 2.64 ± 0.03                  | 0.96 ± 0.02 | 0.13 ± 0.01               | 0.41 ± 0.004                        | 0.40 ± 0.011   | 19.72 ± 0.25                          | 18.50 ± 0.29   | 17.81 ± 0.85                    | 11.42 ± 0.35                          |
| <i>S. lebanonensis</i>  | 2.69 ± 0.03                  | 0.88 ± 0.01 | 0.11 ± 0.00               | 0.39 ± 0.006                        | 0.40 ± 0.007   | 20.47 ± 0.24                          | 19.88 ± 0.22   | 14.14 ± 0.63                    | 5.08 ± 1.50                           |

<sup>1</sup> Values are mean ± SE and subject to analyses of multiple factors' effects (see statistical results on Table 4).

<sup>2</sup> Data were excluded from analyses due to small samples (only a few individual wasps emerged).

**Table 3**  
Results of General Linear Models analyzing the effects of host species, host size, parasitoid size and/or their interactions on the fitness of *T. drosophilae* and *P. vindemiae*.

| Parameter                           | <i>T. drosophilae</i>         |    |       | <i>P. vindemiae</i> |                               |    |      |         |
|-------------------------------------|-------------------------------|----|-------|---------------------|-------------------------------|----|------|---------|
|                                     | Source                        | Df | F     | P                   | Source                        | Df | F    | P       |
| Offspring developmental time        | Host species                  | 17 | 27.3  | 0.054               | Host species                  | 17 | 18.4 | 0.438   |
|                                     | Body size of female wasp      | 1  | 0.3   | 0.595               | Body size of female wasp      | 1  | 0.8  | 0.381   |
|                                     | Sex                           | 1  | 9.7   | 0.002               | Sex                           | 1  | 2.0  | 0.154   |
| Body size of emerged wasp           | Host species (HS)             | 17 | 113.4 | < 0.001             | Host species (HS)             | 17 | 86.0 | < 0.001 |
|                                     | Host body size (HBS)          | 1  | 65.2  | < 0.001             | Host body size (HBS)          | 1  | 12.3 | < 0.001 |
|                                     | HS × HBS                      | 17 | 71.0  | < 0.001             | HS × HBS                      | 1  | 9.0  | < 0.001 |
|                                     | Sex                           | 1  | 283.7 | < 0.001             | Sex                           | 17 | 54.5 | < 0.001 |
| Mature egg load of female wasps     | Host species (HS)             | 1  | 127.3 | < 0.001             | Host species (HS)             | 17 | 50.2 | < 0.001 |
|                                     | Body size of female wasp (BS) | 17 | 68.2  | < 0.001             | Body size of female wasp (BS) | 1  | 25.2 | < 0.001 |
|                                     | HS × BS                       | 17 | 23.8  | < 0.001             | HS × BS                       | 17 | 23.3 | 0.178   |
| Foraging efficiency of female wasps | Natal host (NH)               | 14 | 49.0  | < 0.001             | Natal host (NH)               | 16 | 62.3 | < 0.001 |
|                                     | Body size of female wasp (BS) | 1  | 0.7   | 0.412               | Body size of female wasp (BS) | 1  | 0.4  | 0.517   |
|                                     | NH × BS                       | 14 | 32.8  | 0.003               | NH × BS                       | 16 | 25.9 | 0.055   |

*P. vindemiae* (76.0 ± 1.8%) ( $F_{1,834} = 3.7, P = 0.052$ ).

Body size of the parasitoids was affected by host species, host size, sex and the interaction between host species and size (Tables 1–3). Developmental time was affected by sex for *T. drosophilae* but was not affected by host species or host size for either species or by sex for *P. vindemiae* (Tables 1–4). Consistent with the regression analyses, mature egg load was affected by host species and female body size and/or their interaction (Tables 1–3). The foraging efficiency of parasitoids (i.e., number of parasitized *D. suzukii* within a 24 h exposure) was not

affected by body size but was affected by the natal host species and/or the interaction between the natal host and female's body size (Tables 1–3).

Linear regressions found that the body size of emerged female parasitoids increased positively with the size of host pupa (Fig. 4), and that the number of mature eggs increased positively with the body size of female wasps (Fig. 5). However, there were no significant relationships between mean host size (volume, measured only for 18 species) and the number of hosts parasitized (*P. vindemiae*:  $F_{1,17} = 2.6, P = 0.128$ ),



**Table 4**  
Phylogenetic signal in fitness traits of the two parasitoid species as measured by Moran's I.

| Parameter                          | <i>T. drosophilae</i> |       | <i>P. vindemiae</i> |       |
|------------------------------------|-----------------------|-------|---------------------|-------|
|                                    | I                     | P     | I                   | P     |
| Female offspring development time  | -0.044                | 0.302 | -0.171              | 0.985 |
| Male offspring development time    | -0.050                | 0.359 | -0.081              | 0.085 |
| Offspring survival                 | 0.054                 | 0.014 | -0.008              | 0.106 |
| Offspring per day per female       | -0.036                | 0.287 | -0.043              | 0.296 |
| Female offspring hind tibia length | -0.050                | 0.373 | -0.076              | 0.732 |
| Male offspring hind tibia length   | -0.053                | 0.444 | -0.050              | 0.063 |
| Sex ratio                          | -0.085                | 0.801 | -0.090              | 0.992 |
| Mature eggs per female             | -0.056                | 0.449 | -0.054              | 0.408 |

offspring survival (*T. drosophilae*:  $F_{1,17} = 1.8$ ,  $P = 0.202$ ; *P. vindemiae*:  $F_{1,17} = 0.1$ ,  $P = 0.776$ ) or sex ratio (*T. drosophilae*:  $F_{1,17} = 3.9$ ,  $P = 0.064$ ; *P. vindemiae*:  $F_{1,17} = 3.8$ ,  $P = 0.067$ ), except that the number of hosts parasitized by *T. drosophilae* increased with host size ( $F_{1,17} = 8.8$ ,  $P = 0.009$ ).

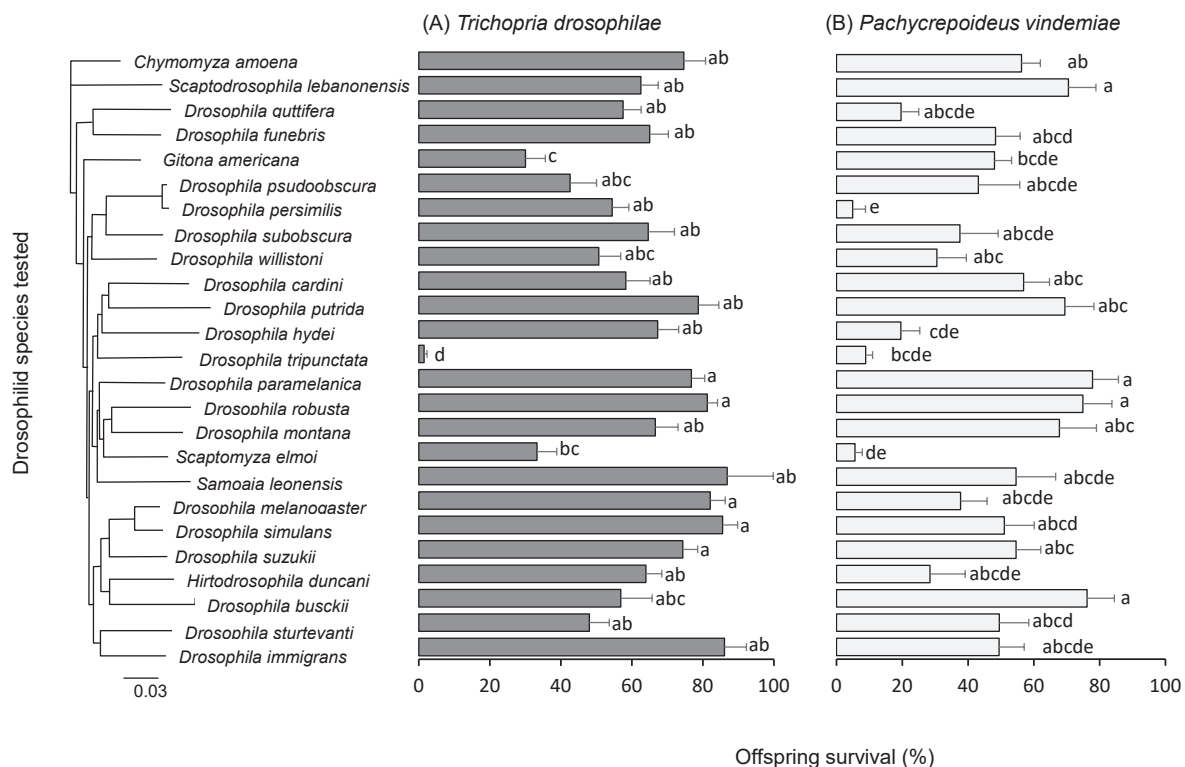
**4. Discussion**

Body size is a central element in theories of life-history evolution (Fox and Czesak, 2000; Lafferty and Kuris, 2002) and for parasitoid-host size models there often exist trade-offs for the use of smaller or larger hosts (King and Charnov, 1988; Sagarra et al., 2001; Teder et al., 1999). In this study, both *P. vindemiae* and *T. drosophilae* were able to parasitize and develop from all 25 tested *Drosophila* species. Although parasitism efficiency and offspring fitness varied among the different host species, the parasitoids showed remarkable levels of plasticity in body growth and development. Overall, host species-related effects on the key life-history traits (survival, development time, sex ratio and body size) of both parasitoids appeared to be unrelated to the phylogenetic position of

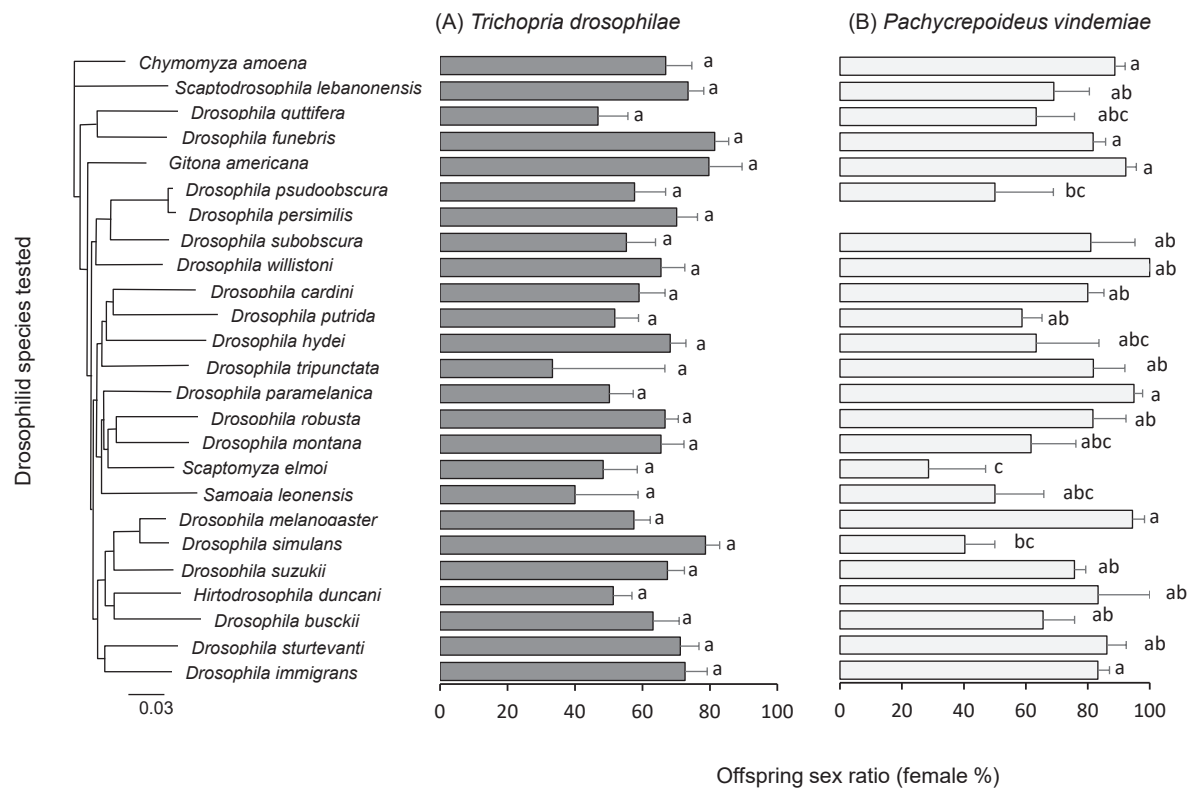
tested host species.

The quality and quantity of different host species available to a parasitoid will inevitably vary, and host suitability may depend on a parasitoid's ability to adjust to variation in host resources. Here, there were positive correlations between host and parasitoid-progeny size. Previous studies showed that *T. drosophilae* reared from the larger *D. suzukii* (Woltering et al., 2019) or *D. hydei* (Chen et al., 2018) had a larger body size than those reared on the smaller *D. melanogaster*, and *T. drosophilae* showed a preference for *D. suzukii* over *D. melanogaster* in choice tests (Woltering et al., 2019; Yi et al., 2020). Wang and Messing (2004b) showed that *P. vindemiae* successfully developed on several tephritid hosts, including *Bactrocera cucurbitae* (Coquillett) and *B. latifrons* (Hendel), as well as on puparia of these species that had been parasitized by their primary tephritid parasitoids, although *P. vindemiae* reared from these secondary hosts were smaller than those reared from the tephritid hosts or from *D. melanogaster*. It was observed that *P. vindemiae* could only consume a small part of the host resources when attacking a tephritid host (Wang and Messing, 2004b), but in the current study parasitoid larvae consumed almost all the host resources prior to pupation. There seems to be no obvious physiological constraint on the maximal use of *Drosophila* host resources by these parasitoids.

According to the "adult size-fitness hypothesis", fitness increases with body size (Kazmer and Luck, 1995). A positive relationship between body size and fitness has been found in both vertebrates and invertebrates, including parasitoids (Ellers and Jervis, 2003; Jervis et al., 2003; Segoli and Rosenheim, 2013). The results of the current study are in line with these past findings. Although the 24 h fecundity of female wasps was not significantly affected by the female's size in either parasitoid, female body size of both parasitoids was positively correlated with host size and was in turn associated with increased mature egg load. Chen et al. (2018) similarly reported that *T. drosophilae* females reared from the larger *D. hydei* had a higher mature egg load, percentage of female offspring and longevity than those reared from the smaller



**Fig. 2.** Offspring survival (%) of (A) *T. drosophilae* or (B) *P. vindemiae* on various *Drosophila* species. Phylogenetic tree of tested *Drosophila* species was constructed based on COI gene sequences retrieved from the NCBI database except for *S. elmoi* and *G. americana* that were collected from this study. Bars refer to mean + SE and bars bearing different letters are significantly different (Tukey's HSD,  $P < 0.05$ ).



**Fig. 3.** Offspring sex ratio (females %) of (A) *T. drosophilae* or (B) *P. vindemiae* developed from various *Drosophila* species. *P. vindemiae* produced only a few female offspring on *D. persimilis* and the data were excluded from the analyses due to small samples. Phylogenetic tree of tested *Drosophila* species was constructed based on COI gene sequences retrieved from the NCBI database except for *S. elmoi* and *G. americana* that were collected from this study. Bars refer to mean + SE and bars bearing different letters are significantly different (Tukey's HSD,  $P < 0.05$ ).

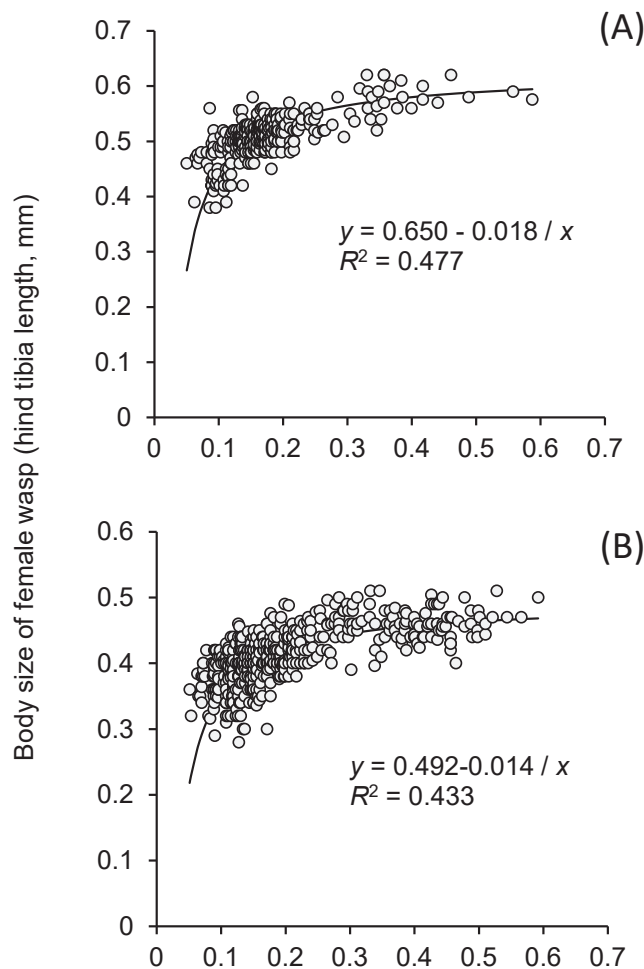
*D. melanogaster*. It was suspected that smaller females would suffer more from egg limitation than larger females in terms of life-time fecundity (Wang and Messing, 2004a), as was recently shown for *T. drosophilae* where large females had higher life-time fecundity and longevity, possibly due to larger energy reserves (Chen et al., 2018). Also, *P. vindemiae* reared from the muscid host *Musca domestica* L. were larger and had higher attack rates than those reared from *D. melanogaster* (Morris and Fellowes, 2002).

Importantly, we did not observe trade-offs between body size and other fitness traits. Although body size of both parasitoid species was correlated with host size, and both offspring survival and sex ratio varied among host species, this variation was unrelated to host size or the host's phylogenetic position, with the exception of offspring survival for *T. drosophilae* (Figs. 2 and 3; Table 1). Furthermore, offspring developmental time was not affected by host species in either parasitoid. Often, the fitness gained from being large comes at the cost of prolonged developmental time (Harvey and Strand, 2002; Sequeira and Mackauer, 1992). The lack of a relationship between developmental time and body size in both parasitoids in the current study suggests that they grow faster on larger host species, as predicted for parasitoids developing in a fixed resource system (Otto and Mackauer, 1998). This reflects the plasticity of body growth in both parasitoids, suggesting that host quality seems to be correlated with host size in both parasitoids, and that both can adjust their growth rates to maximize body size. These results suggest that larger hosts are likely to be more suitable for mass-rearing programs.

*Pachycrepoideus vindemiae* and *T. drosophilae* are generalist parasitoids (Chabert et al., 2012; Fleury et al., 2004), which has both advantages and disadvantages for aspects of ecosystem services (Stiling and Cornelissen, 2005). A lack of physiological immunity against these pupal parasitoids may explain, in part, their broad host ranges (Kacsoh et al., 2012). Physical immunity may influence host susceptibility to the

parasitoids, however; for successful parasitism, *P. vindemiae* and *T. drosophilae* must drill through the host puparial wall before injecting venom or laying eggs. Thus, host acceptance may be contingent on the puparial wall thickness, which likely varies among drosophilid species. We found that *T. drosophilae* accepted all tested host species relatively equally, whereas there was wide variation in hosts parasitized by *P. vindemiae*. The larger body size of *T. drosophilae* relative to *P. vindemiae* might make it easier for the former to penetrate the puparial wall of some host species. Larger *P. vindemiae* may be more able to drill through the thicker protective outer layer of some host pupae (Morris and Fellowes, 2002). Host acceptance might then be a dynamic process (Hopper et al., 2013), as oviposition into larger hosts results in larger progeny that might be more capable of ovipositing into larger hosts.

The "host-ecology hypothesis" of host range evolution assumes that parasitoid species can broaden their host ranges by utilizing new hosts that exist within the parasitoid's searching niche. Parasitoids may attack hosts that are closely phylogenetically related and that share similar physiological properties and defense mechanisms, and more importantly, overlapping niches (Godfray, 1994). Therefore, phylogenetic concordance would be expected if host ranges evolve according to the host-ecology hypothesis, as appears to be the case for larval parasitoids of *D. sukuzii* (Daane et al., 2021). In contrast, the two pupal parasitoids tested in the current study are physiologically capable of developing from various host species regardless of phylogenetic position. Plasticity towards host species and host size in *P. vindemiae* and *T. drosophilae* indicates their potential for host range and geographic range expansion. In nature, these pupal parasitoids likely switch from one host species to another, as a consequence of temporal or spatial variation in host community composition, or they may colonize new hosts via novel associations. It seems plausible that the lack of fitness costs associated with parasitizing larger hosts would select for larger progeny. However, the diverse array of *Drosophila* species in various habitats (Gleason et al.,

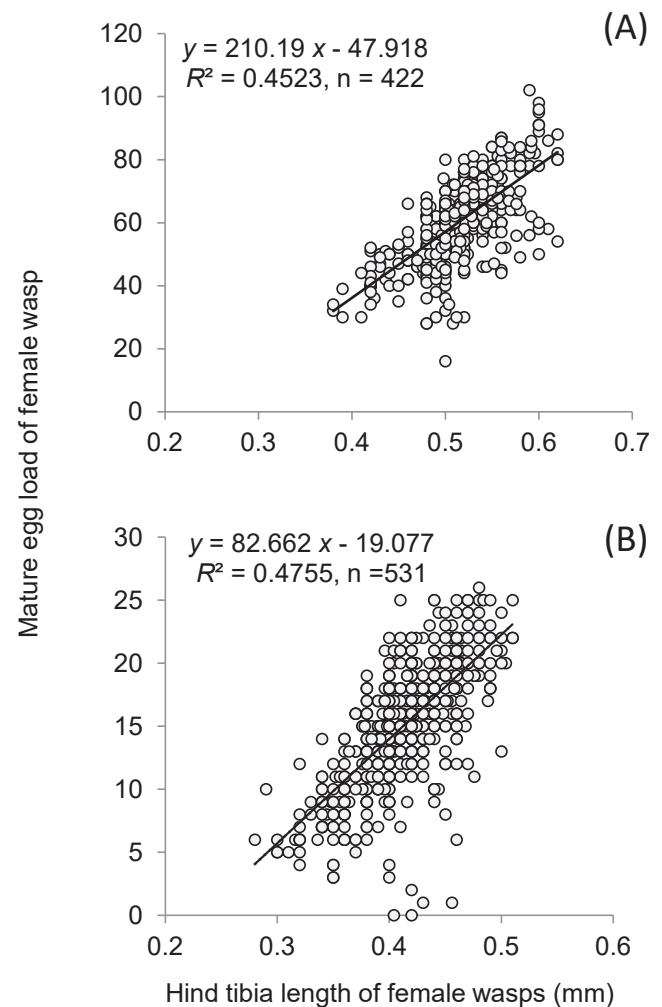


**Fig. 4.** The relationship between host body size (pupal volume) and the body size (hind tibia length) of female (A) *T. drosophilae* or (B) *P. vindemiae*. Data were pooled from all measured individuals developed from various species (see Tables 1, 2) and were fitted to a polynomial model,  $y = a + b / x$ ). Points are observed values and the lines the best-fit curves for the predicted values.

2019) might counterbalance selective forces. Host availability for parasitoids may vary stochastically, as they typically sample only a few patches in their lifetime (Ellers and Jervis, 2003). Although a narrow host range makes a parasitoid from the pest's native range an attractive candidate for importation in classical biological control, the ability to switch between hosts is likely to increase the persistence and abundance of generalist parasitoids (Bribosia et al., 2005).

As generalists, these pupal parasitoids might contribute to *D. suzukii* control by being more common in a diverse range of habitats, as generally appears to be the case for natural enemies that move across habitat boundaries (Tschamntke et al., 2007). *Drosophila suzukii* has been shown to utilize a wide variety of host plants and habitats (Haye et al., 2016; Kenis et al., 2016; Poyet et al., 2015; Sautoiemma et al., 2019). The apparent lack of costs associated with being large in *P. vindemiae* and *T. drosophilae* could further increase their ability to disperse between host patches and habitats. Larger parasitoids may possess superior dispersal ability at the local and/or landscape scale; they may be able to move more efficiently between host or habitat patches and be less vulnerable to changes in environmental conditions among habitats and over time (Abram et al., 2016).

Large size may not be advantageous under all conditions, however, and body size plasticity in *T. drosophilae* and *P. vindemiae* could actually improve biological control by increasing variation in parasitoid body sizes. Although host-limited environments may favor larger individuals



**Fig. 5.** The relationship between female's body size (hind tibia length) of (A) *T. drosophilae* or (B) *P. vindemiae* and mature egg load. Data were pooled from all measured individuals developed from various species (see Tables 1, 2).

that can move more efficiently between widely separated host patches (Ellers et al., 1998), smaller individuals may have an advantage in host-rich environments where dispersal capacity is less important, and may escape predators more easily when predation pressure is high (Ellers et al., 2001). In the field, environmental conditions such as host density and stochasticity will ultimately determine the realized fitness of different parasitoid sizes, and the relative frequencies of parasitoid sizes are likely to vary over time as conditions change (Ellers et al., 2001).

## 5. Conclusions

In this study we show that *P. vindemiae* and *T. drosophilae* are likely to attack multiple drosophilid species in invaded regions, but it is still unknown if they will host shift in response to increasing or decreasing *D. suzukii* numbers. Field surveys in Asia found that specialized larvae parasitoids had a greater impact on *D. suzukii* (Daane et al., 2016; Giorgini et al., 2019; Girod et al., 2018). The parasitoids' ecosystem service impact will be influenced not only by their plasticity to hosts but by environmental limitations such as temperature tolerances, habitat location, and host searching behaviors. The estimated volume of *D. suzukii* pupae ( $0.261 \pm 0.005 \text{ mm}^3$ ) (Wang et al. 2016b) was larger than most of tested drosophila species in this study (Table 1,2). From an applied perspective, it is important to determine which host species show the most potential for the mass-rearing of these parasitoids for augmentative biological control of *D. suzukii*. This study shows that



larger hosts are likely to be more suitable for rearing these parasitoids, because they should increase mature egg loads of females, and possibly other traits, through increases in female body size. The survival rates were extremely low (<10%) for *T. drosophilae* on *D. tripunctata* or for *P. vindemiae* on *D. persimilis*, *S. elmoi* and *D. tripunctata*, suggesting these host species are not suitable for optimal rearing of both parasitoids under the tested conditions in this study.

#### CRedit authorship contribution statement

**Xingeng Wang:** Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Writing – original draft. **Brian N. Hogg:** Formal analysis, Writing - review & editing. **Antonio Biondi:** Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Writing - review & editing. **Kent M. Daane:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing - review & editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Acknowledgements

We thank Valeria Hochman-Adler, Pahoua Yang, May Yang and Robert Straser (University of California, Berkeley) for laboratory assistance, and Kei-Li Ooi (University of California, Berkeley) for the collection of COI gene sequences for two species and the construction of the phylogeny of all tested host species. This work was supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture Specialty Crops Research Initiative under Agreement No. 2015-51181-24252 and 2020-51181-32140, USDA APHIS (Farm bill, fund 14-8130-0463), the California Cherry Board, and the University of California's Agricultural and Natural Resources Competitive Grants Program. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture (USDA). USDA is an equal opportunity provider and employer. We confirm that we have no conflicts of interest.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2021.104738>.

#### References

- Abram, P.K., Parent, J.-P., Brodeur, J., Boivin, G., 2016. Size-induced phenotypic reaction norms in a parasitoid wasp: an examination of life-history and behavioural traits. *Biol. J. Linn. Soc.* 117 (3), 620–632.
- Asplen, M.K., Anfora, G., Biondi, A., Choi, D.-S., Chu, D., Daane, K.M., Gibert, P., Gutierrez, A.P., Hoelmer, K.A., Hutchison, W.D., Isaacs, R., Jiang, Z.-L., Kárpáti, Z., Kimura, M.T., Pascual, M., Phillips, C.R., Plantamp, C., Ponti, L., Véték, G., Vogt, H., Walton, V.M., Yu, Y.i., Zappala, L., Desneux, N., 2015. Invasion biology of spotted wing drosophila (*Drosophila suzukii*): a global perspective and future priorities. *J. Pest Sci.* 88 (3), 469–494.
- Biondi, A., Desneux, N., Amiens-Desneux, E., Siscaro, G., Zappala, L., 2013. Biology and developmental strategies of the Palaearctic parasitoid *Bracon nigricans* (Hymenoptera: Braconidae) on the Neotropical moth *Tuta absoluta* (Lepidoptera: Gelechiidae). *J. Econ. Entomol.* 106, 1638–1647.
- Bribosia, E., Bylemans, D., Migon, M., Impe, G.V., 2005. In-field production of parasitoids of *Dysaphis plantaginea* by using the rowan aphid *Dysaphis sorbi* as substitute host. *Biocontrol* 50 (4), 601–610.
- Carton, Y., Bouléreau, B., van Alphen, J.J.M., van Lenteren, J.C., 1986. The *Drosophila* parasitoid wasps. In: Ashburner, M., Carson, H.L., Thompson, J.N. (Eds.), *The Genetics and Biology of Drosophila*. Academic Press, London, pp. 347–394.
- Chabert, S., Allemand, R., Poyet, M., Eslin, P., Gibert, P., 2012. Ability of European parasitoids (Hymenoptera) to control a new invasive Asiatic pest. *Drosophila suzukii*. *Biol. Control* 63 (1), 40–47.
- Charnov, E.L., Stephens, D.W., 1988. On the evolution of host selection in solitary parasitoids. *Am. Nat.* 132, 707–722.
- Chen, J., Zhou, S., Wang, Y., Shi, M., Chen, X., Huang, J., 2018. Biocontrol characteristics of the fruit fly pupal parasitoid *Trichopria drosophilae* (Hymenoptera: Diapriidae) emerging from different hosts. *Sci. Rep.* 8 (1) <https://doi.org/10.1038/s41598-018-31718-6>.
- Daane, K.M., Wang, X.-G., Biondi, A., Miller, B., Miller, J.C., Riedl, H., Shearer, P.W., Guerrieri, E., Giorgini, M., Buffington, M., van Achterberg, K., Song, Y., Kang, T., Yi, H., Jung, C., Lee, D.W., Chung, B.-K., Hoelmer, K.A., Walton, V.M., 2016. First exploration of parasitoids of *Drosophila suzukii* in South Korea as potential classical biological agents. *J. Pest Sci.* 89 (3), 823–835.
- Daane, K.M., Biondi, A., Wang, X.G., Hogg, B.A., 2021. Potential host ranges of *Drosophila suzukii*. *J. Pest Sci.* [doi.org/10.1007/s10340-021-01368-1](https://doi.org/10.1007/s10340-021-01368-1).
- Desneux, N., Blahnik, R., Delebecque, C.J., Heimpel, G.E., 2012. Host phylogeny and specialisation in parasitoids. *Ecol. Lett.* 15, 453–460.
- Eijs, I.E.M., van Alphen, J.J.M., 1999. Life history correlations: why are hymenopteran parasitoids an exception? *Ecol. Lett.* 2 (1), 27–35.
- Ellers, J., Bax, M., Van Alphen, J.J.M., 2001. Seasonal changes in female size and its relation to reproduction in the parasitoid *Asobara tabida*. *Oikos* 92 (2), 209–314.
- Ellers, J., Jervis, M., 2003. Body size and the timing of egg production in parasitoid wasps. *Oikos* 102 (1), 164–172.
- Ellers, J., Van Alphen, J.J.M., Sevenster, J.G., 1998. A field study of size-fitness relationships in the parasitoid *Asobara tabida*. *J. Anim. Ecol.* 67, 318–324.
- Fleury, F., Ris, N., Allemand, R., Fouillet, P., Carton, Y., Bouléreau, M., 2004. Ecological and genetic interactions in *Drosophila*-parasitoids communities: a case study with *D. melanogaster*, *D. simulans* and their common *Leptopilina* parasitoids in south-eastern France. *Genetica* 120, 181–194.
- Fox, C.W., Czesak, M.E., 2000. Evolutionary ecology of progeny size in arthropods. *Annu. Rev. Entomol.* 45 (1), 341–369.
- Giorgini, M., Wang, X.-G., Wang, Y., Chen, F.-S., Hougardy, E., Zhang, H.-M., Chen, Z.-Q., Chen, H.-Y., Liu, C.-X., Cascone, P., Formisano, G., Carvalho, G.A., Biondi, A., Buffington, M., Daane, K.M., Hoelmer, K.A., Guerrieri, E., 2019. Exploration for native parasitoids of *Drosophila suzukii* in China reveals a diversity of parasitoid species and narrow host range of the dominant parasitoid. *J. Pest Sci.* 92 (2), 509–522.
- Girod, P., Borowiec, N., Buffington, M., Chen, G., Fang, Y., Kimura, M.T., Peris-Felipo, F. J., Ris, N., Wu, H., Xiao, C., Zhang, J., Aebi, A., Haye, T., Kenis, M., 2018. The parasitoid complex of *D. suzukii* and other fruit feeding *Drosophila* species in Asia. *Sci. Rep.* 8 (1) <https://doi.org/10.1038/s41598-018-29555-8>.
- Gleason, J.M., Roy, P.R., Everman, E.R., Gleason, T.C., Morgan, T.J., Desneux, N., 2019. Phenology of *Drosophila* species across a temperate growing season and implications for behavior. *Plos One* 14 (5), e0216601.
- Godfray, H.C.J., 1994. *Parasitoids: behavioral and evolutionary ecology*. Princeton University Press, Princeton, New Jersey.
- Harvey, J.A., Harvey, I.F., Thompson, D.J., 1994. Flexible larval growth allows use of a range of host sizes by a parasitoid wasp. *Ecology* 75, 1420–1428.
- Harvey, J.A., Strand, M.R., 2002. The developmental strategies of endoparasitoid wasps vary with host feeding ecology. *Ecology* 83 (9), 2439–2451.
- Haye, T., Girod, P., Cuthbertson, A.G.S., Wang, X.G., Daane, K.M., Hoelmer, K.A., Baroffio, C., Zhang, J.P., Desneux, N., 2016. Current SWD IPM tactics and their practical implementation in fruit crops across different regions around the world. *J. Pest Sci.* 89 (3), 643–651.
- Heimpel, G.E., Cock, M.J.W., 2018. Shifting paradigms in the history of classical biological control. *Biocontrol* 63 (1), 27–37.
- Hoddle, M.S., Lake, E.C., Minter, C.R., Daane, K.M., 2020. Chapter 2, Importation Biological Control. In: Mason, P.G., Dennis, N. (Eds.), *Biological Control: A Global Initiative*. CSIRO Publishing, Canberra, Australia (in press).
- Hopper, K.R., Prager, S.M., Heimpel, G.E., Carroll, S., 2013. Is parasitoid acceptance of different host species dynamic? *Funct. Ecol.* 27 (5), 1201–1211.
- Jervis, M.A., Ferns, P.N., Heimpel, G.E., 2003. Body size and the timing of egg production in parasitoid wasps: a comparative analysis. *Funct. Ecol.* 17, 375–383.
- Kaçar, G., Wang, X.-G., Biondi, A., Daane, K.M., Desneux, N., 2017. Linear functional response by two pupal *Drosophila* parasitoids foraging within single or multiple patch environments. *PLoS One* 12 (8), e0183525.
- Kacsoh, B.Z., Schlenke, T.A., DeSalle, R., 2012. High hemocyte load is associated with increased resistance against parasitoids in *Drosophila suzukii*, a relative of *D. melanogaster*. *PLoS One* 7 (4), e34721.
- Kazmer, D.J., Luck, R.F., 1995. Field test of the size fitness hypothesis in the egg parasitoid *Trichogramma pretiosum*. *Ecology* 76, 412–425.
- Kenis, M., Tonina, L., Eschen, R., van der Sluis, B., Sancassani, M., Mori, N., Haye, T., Helsen, H., 2016. Non-crop plants used as hosts by *Drosophila suzukii* in Europe. *J. Pest Sci.* 89 (3), 735–748.
- King, B.H., Charnov, E.L., 1988. Sex-ratio manipulation in response to host size by the parasitoid *Spalangia cameroni*: a laboratory study. *Evolution* 42, 1190–1198.
- King, B.H., Lee, H.E., 1994. Test of the adaptiveness of sex-ratio manipulation in a parasitoid wasp. *Behav. Ecol. Sociobiol.* 35, 437–443.
- Kingsolver, J.G., Buckley, L.B., 2018. How do phenology, plasticity, and evolution determine the fitness consequences of climate change for montane butterflies? *Evol. Appl.* 11 (8), 1231–1244.
- Lafferty, K.D., Kuris, A.M., 2002. Trophic strategies, animal diversity and body size. *Trends Ecol. Evol.* 17, 507–513.
- Lee, J.C., Wang, X.G., Daane, K.M., Hoelmer, K.A., Isaacs, R., Sial, A.A., Walton, V.M., 2019. Biological control of spotted-wing drosophila (Diptera: Drosophilidae): Current and pending tactics. *J. Integ. Pest Manage.* 10, 13.
- Markow, T.A., O'Grady, P.M., Markow, T.A., Ogrady, P.M., 2006. Key to species. A Guide to Species Identification and Use. Academic Press, London, *Drosophila*, pp. 85–142.

- Miller, B., Anfora, G., Buffington, M., Daane, K.M., Dalton, D.T., Hoelmer, K.M., Stacconi, M.V.R., Grassi, A., Ioriatti, C., Loni, A., Miller, J.C., Ouantar, M., Wang, X. G., Wiman, N.G., Walton, V.M., 2015. Seasonal occurrence of resident parasitoids associated with *Drosophila suzukii* in two small fruit production regions of Italy and the USA. *Bull. Insectology* 68, 255–263.
- Morris, R.J., Fellowes, M.D.E., 2002. Learning and natal host influence host preference, handling time and sex allocation behaviour in a pupal parasitoid. *Behav. Ecol. Sociobiol.* 51, 386–393.
- Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffrers, K., Thuiller, W., 2012. How to measure and test phylogenetic signal. *Methods Ecol. Evol.* 3, 743–756.
- Napoleon, M.E., King, B.H., 1999. Offspring sex ratio response to host size in the parasitoid wasp *Spalangia endius*. *Behav. Ecol. Sociobiol.* 46, 325–332.
- Otto, M., Mackauer, M., 1998. The developmental strategy of an idiobiont ectoparasitoid, *Dendrocercus carpenteri*: influence of variations in host quality on offspring growth and fitness. *Oecologia* 117, 353–364.
- Petersen, G., Hardy, I.C.W., 1996. The importance of being larger: Parasitoid intruder-owner contests and their implications for clutch size. *Anim. Behav.* 51, 1363–1373.
- Poyet, M., Le Roux, V., Gibert, P., Meirland, A., Prevost, G., Eslin, P., Chabrerrie, O., 2015. The wide potential trophic niche of the Asiatic fruit fly *Drosophila suzukii*: The key of its invasion success in temperate Europe? *PLoS One* 10, e0142785.
- Rossi Stacconi, M.V., Buffington, M., Daane, K.M., Dalton, D.T., Grassi, A., Kaçar, G., Miller, B., Miller, J.C., Baser, N., Ioriatti, C., Walton, V.M., Wiman, N.G., Wang, X., Anfora, G., 2015. Host stage preference, efficacy and fecundity of parasitoids attacking *Drosophila suzukii* in newly invaded areas. *Biol. Control* 84, 28–35.
- Rossi Stacconi, M.V., Grassi, A., Ioriatti, C., Anfora, G., 2019. Augmentative releases of *Trichopria drosophilae* for the suppression of early season *Drosophila suzukii* populations. *Biocontrol* 64, 9–19.
- Sagarra, L.A., Vincent, C., Stewart, R.K., 2001. Body size as an indicator of parasitoid quality in male and female *Anagyrus kamali* (Hymenoptera : Encyrtidae). *Bull. Entomol. Res.* 91, 363–367.
- Santoiemma, G., Trivellato, F., Caloi, V., Mori, N., Marini, L., 2019. Habitat preference of *Drosophila suzukii* across heterogeneous landscapes. *J. Pest Sci.* 92, 485–494.
- Segoli, M., Rosenheim, J.A., 2013. The link between host density and egg production in a parasitoid insect: comparison between agricultural and natural habitats. *Funct. Ecol.* 27, 1224–1232.
- Sequeira, R., Mackauer, M., 1992. Covariance of adult size and development time in the parasitoid wasp *Aphidius ervi* in relation to the size of its hosts, *Acyrtosiphon pisum*. *Evol. Ecol.* 6, 34–44.
- Stacconi, M.V.R., Panel, Baser, A., N., Ioriatti, C., Pantezzi, T., Anfora, G., 2017. Comparative life history traits of indigenous Italian parasitoids of *Drosophila suzukii* and their effectiveness at different temperatures. *Biol. Control* 112, 20–27.
- Stephens, D.W., Charnov, E.L., 1982. Optimal foraging - some simple stochastic models. *Behav. Ecol. Sociobiol.* 10, 251–263.
- Stiling, P., Cornelissen, T., 2005. What makes a successful biocontrol agent? A meta-analysis of biological control agent performance. *Biol. Control* 34, 236–246.
- Team, R.D.C., 2020. R Development Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Teder, T., Tamaru, T., Pedmanson, R., 1999. Patterns of host use in solitary parasitoids (Hymenoptera, Ichneumonidae): field evidence from a homogeneous habitat. *Ecography* 22, 79–86.
- Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhuys, S., Vidal, S., 2007. Conservation biological control and enemy diversity on a landscape scale. *Biol. Control* 43, 294–309.
- Ueno, T., 1998. Adaptiveness of sex ratio control by the pupal parasitoid *Itopectis naranyae* (Hymenoptera : Ichneumonidae) in response to host size. *Evol. Ecol.* 12, 643–654.
- Visser, M.E., 1994. The importance of being large: The relationship between size and fitness in females of the parasitoid *Aphaereta minuta* (Hymenoptera: Braconidae). *J. Anim. Ecol.* 63, 963–978.
- Wang, X.G., Kaçar, G., Biondi, A., Daane, K.M., 2016a. Foraging efficiency and outcomes of interactions of two pupal parasitoids attacking the invasive spotted wing drosophila. *Biol. Control* 96, 64–71.
- Wang, X.G., Kaçar, G., Biondi, A., Daane, K.M., 2016b. Life-history and host preference of *Trichopria drosophilae*, a pupal parasitoid of spotted wing drosophila. *BioControl* 61, 387–397.
- Wang, X.G., Messing, R.H., 2004a. Fitness consequences of body-size-dependent host species selection in a generalist ectoparasitoid. *Behav. Ecol. Sociobiol.* 56, 513–522.
- Wang, X.G., Messing, R.H., 2004b. The ectoparasitic pupal parasitoid, *Pachycrepoideus vindemmiae* (Hymenoptera : Pteromalidae), attacks other primary tephritid fruit fly parasitoids: host expansion and potential non-target impact. *Biol. Control* 31, 227–236.
- Wang, X.G., Messing, R.H., 2004c. Two different life-history strategies determine the competitive outcome between *Dirhinus giffardii* (Chalcididae) and *Pachycrepoideus vindemmiae* (Pteromalidae), ectoparasitoids of cyclorrhaphous Diptera. *Bull. Entomol. Res.* 94, 473–480.
- Wang, X.G., Serrato, M.A., Son, Y., Walton, V.M., Hogg, B.N., Daane, K.M., 2018. Thermal performance of two indigenous pupal parasitoids attacking the invasive *Drosophila suzukii* (Diptera: Drosophilidae). *Environ. Entomol.* 47, 764–772.
- Wilson, E.E., Mullen, L.M., Holway, D.A., 2009. Life history plasticity magnifies the ecological effects of a social wasp invasion. *P. Natl. Acad. Sci. USA* 106, 12809–12813.
- Wolf, S., Boycheva-Wolterling, S., Romeis, J., Collatz, J., 2020. *Trichopria drosophilae* parasitizes *Drosophila suzukii* in seven common non-crop fruits. *J. Pest Sci.* 93, 627–638.
- Wolterling, S.B., Romeis, J., Collatz, J., 2019. Influence of the rearing host on biological parameters of *Trichopria drosophilae*, a potential biological control agent of *Drosophila suzukii*. *Insects* 10, 183.
- Yi, C.D., Cai, P.M., Lin, J., Liu, X.X., Ao, G.F., Zhang, Q.W., Xia, H.M., Yang, J.Q., Ji, Q. G., 2020. Life history and host preference of *Trichopria drosophilae* from Southern China, one of the effective pupal parasitoids on the *Drosophila* species. *Insects* 11, 103.