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Life-history and host preference of *Trichopria drosophilae*, a pupal parasitoid of spotted wing drosophila

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Abstract *Trichopria drosophilae* is a cosmopolitan pupal parasitoid that attacks many species of Drosophilidae, including the invasive *Drosophila suzukii*. This study reports on the life-history traits and host preferences of a Californian population of *T. drosophilae* and compares its life-time fecundity with a South Korean population of *T. drosophilae*. Female parasitoids emerge with a high mature egg-load (47.6 ± 2.3 eggs per female). The number of mature eggs of female *T. drosophilae* was affected by the female age and body size but not by the interaction between these two factors. The parasitoid did not show preference among differently aged (1–4 days old) *D. suzukii* pupae and host age did not affect the parasitoid's fitness, except that offspring developmental time slightly increased with host age. In a choice test, more offspring successfully developed from the larger *D. suzukii* than the smaller *D. melanogaster*, and adult females reared from *D. suzukii* were larger than those that were reared from *D. melanogaster*, apparently at no cost in parasitoid fitness. *T. drosophilae* females from the Californian and the South Korean populations survived 27.5 and 20.2 days, produced a total of 63.8 and 52.0 offspring, and had an intrinsic rate of increase of 0.124 and 0.113, respectively, when provided with adult food and *D. suzukii* pupae as host material.

Keywords *Drosophila suzukii* · Biological control · Host preference · Life history

Introduction

The spotted wing drosophila, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), is native to East Asia and has recently expanded its global range to include Europe, North America, and South America (Asplen et al. 2015; Cini et al. 2014; Walsh et al. 2011). The fly can be a devastating pest of various soft- and thin-skinned fruits such as cherries, blueberries, blackberries, raspberries, and strawberries (Burrack et al. 2013; Hamby et al. 2014; Lee et al. 2011). Although *D. suzukii* may be unable to oviposit into fruits with a thick or hard skin such as apples, oranges, and pomegranates, or fuzzy surface, such as peaches, it can complete development when these fruits have

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surface damage or become overripe (Stewart et al. 2014). *D. suzukii* has a short generation time and high fecundity that can result in a rapid population increase (Tochen et al. 2014; Wiman et al. 2014) and significant economic losses to commercial crops (Goodhue et al. 2011; Walsh et al. 2011). Current control efforts in North America rely heavily on the use of insecticides, such as spinosyns, to kill adult *D. suzukii* (Bruck et al. 2011). However, repeated pesticides applications could disrupt established IPM programs, increase chemical residues and insect resistance, and negatively affect pollinators and other beneficial species (Biondi et al. 2012). In addition, chemical control is limited to the cultivated environment leaving unmanaged habitats acting as reservoirs for the fly's reinvasion into treated commercial orchards (Klick et al. 2014; Lee et al. 2015). In this context, developing area-wide management programs is crucial to control this highly polyphagous and mobile pest (Asplen et al. 2015). Biological control, especially by means of parasitoids, may help suppress source populations even in the habitats surrounding crop fields.

Many hymenopteran parasitoids are known to attack various drosophilid species worldwide. The majority of them are larval parasitoids in the genera *Asobara* (Braconidae), *Leptopilina*, and *Ganaspis* (Figitidae) and pupal parasitoids in the genera *Trichopria* (Diapriidae) and *Pachycrepoideus* (Pteromalidae) (Carton et al. 1986). Some larval parasitoids such as *Asobara tabida* Nees, *Leptopilina heterotoma* (Thomson), and *L. boulardi* (Barbotin et al.) were well studied in association with drosophilid larvae infesting fermenting substrates, such as *Drosophila melanogaster* Meigen (Prévost 2009). These parasitoids may play an important role in the regulation of some drosophilid species (e.g., *D. melanogaster*) with one study reporting up to 90 % parasitism of field-collected drosophilids (Fleury et al. 2004). However, information on parasitoid species associated with *D. suzukii* is limited, particularly in its native range, and the few studies available consist mainly of surveys reporting the more common parasitoid species (Mitsui et al. 2007; Nomano et al. 2015). In North America and Europe, several studies have shown that most indigenous larval parasitoid species failed to develop on *D. suzukii* largely due to the strong immune reaction by *D. suzukii* larvae (Chabert et al. 2012; Kacsoh and Schlenke 2012; Poyet et al. 2013). On the other hand, two cosmopolitan pupal parasitoids have been reported to attack and develop from *D. suzukii* in North America and Europe: *Trichopria drosophilae* Perkins and *Pachycrepoideus vindemiae* (Rondani) (Chabert et al. 2012; Gabarra et al. 2015; Rossi Stacconi et al. 2015). We recently surveyed parasitoid species attacking frugivorous drosophilid species in California and found that *T. drosophilae* and *P. vindemiae* were the only two parasitoids that emerged from field-collected *D. suzukii* (Wang, personal observation). *P. vindemiae* is a well-known generalist parasitoid attacking various drosophilids as well as many cyclorrhaphous dipteran species (Wang and Messing 2004a). In the laboratory, *P. vindemiae* can be a highly effective parasitoid of *D. suzukii* (Chabert et al. 2012; Rossi Stacconi et al. 2015). However, field-parasitism levels are typically lower and this species may not provide adequate control of *D. suzukii* in most crop systems (Miller et al. 2015). *T. drosophilae* is an idiobiont parasitoid that also attacks pupae of many frugivorous drosophilid species worldwide (Carton et al. 1986; Fleury et al. 2009). There is, however, limited information on the biology of *T. drosophilae* in general and its association with *D. suzukii* in particular.

To evaluate the potential of *T. drosophilae* as a parasitoid of *D. suzukii*, we used a Californian population of this parasitoid to investigate some of its biological attributes, including the adult female parasitoid's egg maturation dynamics, and preference for and suitability of different *D. suzukii* pupal age categories. We also evaluated its performance with *D. suzukii* as a host in comparison with the more common *D. melanogaster*, in terms of offspring survival, developmental time, and body size. We then compared reproductive performances of *T. drosophilae* from the Californian population with one collected from South Korea. Understanding these basic biological attributes is critical for effective rearing and for further evaluation of this parasitoid in comparison to other *D. suzukii* parasitoid species.

Materials and methods

Study insects

Colonies of *D. suzukii*, *D. melanogaster,* and a Californian population of *T. drosophilae* were initiated from field collections during 2013 in Parlier, California, USA. *D. suzukii* were collected from infested cherries while *D. melanogaster* were collected from overripe cherries and peaches that had fallen to the ground. The *T. drosophilae* were collected from parasitized *D. suzukii* and *D. melanogaster* in sentinel host pupae traps in the field, as well as parasitized hosts from field-collected fruits. The Californian *T. drosophilae* population was initiated from six females and five males, but thereafter, field-collected insects from these same areas were periodically introduced into the insectary colonies to maintain genetic diversity. A colony of South Korean population of *T. drosophilae* was initiated from four specimens (one male reared from *D. suzukii* and two females and one male reared from other drosophilid species) that were collected from fruit-baited traps in Sangju, North Gyeongsang province, South Korea. They were collected by J. Miller, B. Miller, and P. Shearer (Oregon State University, USA) during a foreign exploration trip in 2013. This South Korean colony was maintained in a quarantine facility at the University of California, Berkeley, California, USA.

Fly larvae of both *D. suzukii* and *D. melanogaster* were maintained on a standard cornmeal and yeast-based artificial diet, using similar methods as described by Dalton et al. (2011). Adult flies were held in BugDorm cages (BioQuip Products Inc., Rancho Dominguez, California, USA), provisioned with a 10 % honey-water solution as food. The parasitoid colonies were maintained on *D. suzukii* pupae. Adult parasitoids were held in large (30 × 30 × 30 cm) screened cages (MegaView Science Co., Ltd., Taichung, Taiwan), provisioned with a 10 % honey water solution as food. Two to three-day old *D. suzukii* pupae contained in Petri dishes (1.5 cm high × 11 cm diameter) provisioned with a cornmeal diet were exposed to the adult parasitoids. The exposed host pupae were placed in clean cages, and held until adult parasitoids emerged, which were collected daily for the bioassays.

Unless specifically noted, all female parasitoids used in this study were reared from *D. suzukii* and were 4–6 days old (which had the highest mature egg load; see "Results" section), had been kept with males since emergence, and were naïve with no previous oviposition experience. The Californian population of *T. drosophilae* was used for all bioassays except the evaluation of the parasitoid's reproductive potential where both the Californian and the South Korean populations were compared. All colonies and experiments were carried out under controlled laboratory conditions (23 ± 1 °C, 16:8 L:D, 50 ± 10 % RH).

Female parasitoid egg maturation dynamics

To determine the number of mature eggs in differently aged adult female *T. drosophilae*, groups of 17–25 adult female wasps were dissected at different time periods after their emergence from *D. suzukii*. To obtain differently aged females, newly emerged males and females were collected and placed in small (8 × 11 × 14 cm) cages provisioned with 10 % honey-water, but no host material. Female parasitoids were then collected at seven different time periods (4 h, 1, 2, 3, 4, 6 and 8 days post emergence), killed, and dissected to determine the number of mature eggs. Preliminary observations found that the chorion of a mature egg is smooth, thin and transparent, making the developing embryo visible, while immature oocytes lack these characteristics and attach each another. The body size (hind tibia length) of each dissected female was also measured with an ocular micrometer.

Host pupal stage preference and suitability

A choice test was conducted to assess whether *T. drosophilae* would prefer to attack different age categories of *D. suzukii* pupae, and the effect of host pupal age on the parasitoid's offspring fitness (survival, sex ratio, developmental time and body size). To also determine the possible effect of host density on host age preference, the test included four different age categories of host pupae (1, 2, 3 and 4 days old) at two different host densities (five and ten pupae per host age category). *D. suzukii* adults emerge from newly formed pupae within 5–6 days at 23 °C (Tochen et al. 2014). Therefore, the tested age categories covered most of the pupal development period.

For each replicate, either five or ten pupae from each of the four age categories were placed on wet filter paper and exposed to a single female parasitoid for 30 h. The tests were conducted in Petri dishes (1.5 cm high × 8.5 cm diameter) provisioned with a small streak of 50 % honey-water as food for the adult parasitoids. The pupae of each age category were arranged along one randomly selected cardinal direction from the center of the filter paper. After the 30 h exposure period, the host pupae from the different age categories were placed separately on wet tissue paper in clean Petri dishes and held for adult parasitoid or fly emergence. The number and sex of emerged parasitoids were recorded twice per day (morning and afternoon). For each age category, there were 48 (low host density of five pupae) and 26 (high host density of ten pupae) replicates.

After adult emergence had ceased, all remaining host pupae were reconstituted in water for one day and then dissected under a microscope to determine the presence or absence of recognizable fly or parasitoid cadavers. When it was difficult to distinguish parasitized pupae from unparasitized pupae (e.g., when the fly or parasitoid died in the early stages of development) these cases were categorized as ‘unknown’ as to whether or not they were parasitized. A control consisted of fly pupae without exposure to the parasitoids that were held under the same conditions. The unknown mortality was then corrected by the control mortality of unexposed host pupae, which was 15.0 % under the current test conditions. The number of parasitized hosts was estimated based on emerged adult parasitoids and dissected pupae containing a dead parasitoid, and then adjusted based on the corrected mortality of unknown pupae. Offspring sex ratio was estimated using the sex of the emerged adults, whereas offspring mortality was estimated based on developed offspring and total number of parasitized hosts. These parameters were compared among different host ages and between the two different host densities. The body size of developed female parasitoids and developmental times of both sexes were then compared among the different host pupal stages using data with high host density test only. To compare adult parasitoid size, the hind tibia length was measured using a dissecting microscope fitted with an ocular micrometer on a sub-sample of 24–42 females that emerged from each host age category.

Host species effect on fitness

A choice test was conducted to determine the host species preference and offspring size (a proxy of parasitoid performance) by *T. drosophilae* when *D. suzukii* and *D. melanogaster* were offered as hosts. Two-day-old host pupae of both species were used. For each replicate, 15 pupae of each host species were placed on a wet filter paper inside a Petri dish (1.5 cm high × 8.5 cm diameter), and exposed to a single female parasitoid for 34 h, with a small streak of 50 % honey-water as food for the adult parasitoid. Following the exposure, *D. suzukii* and *D. melanogaster* pupae were kept separately in Petri dishes until the emergence of adult wasps or flies. The number and sex of emerged parasitoids were recorded twice per day (morning and afternoon). Sub-samples of 20 individual puparia for each species were randomly selected prior to the test and each puparium was measured for its maximum body length (l) and width (w) using an ocular micrometer, and the volume (V) of the prolate ellipsoid fly puparium was estimated based on the formula: $V = 4/3\pi\cdot(l/2)\cdot(w/2)^2$ (Wang and Messing 2004b). To compare body size of developed females, sub-samples of 30 and 33 females that emerged from *D. suzukii* and *D. melanogaster* were also measured for their hind tibia length, respectively.

Reproductive performance of two *Trichopria drosophilae* populations

The age-specific lifetime fertility of *T. drosophilae* females belonging to the Californian and the South Korean populations was determined using two or three days old *D. suzukii* pupae as host. Newly emerged (<24 h after emergence) parasitoid females and males were paired and isolated in Petri dishes (1.5 cm high × 8.5 cm diameter). Each parasitoid pair was provided with ten host pupae and a small streak of 50 % honey-water every two days until the female parasitoid died. After each two-day exposure, the parasitoids were transferred to a new Petri dish and provided with new host pupae and honey-water, while the exposed hosts were reared in the old dish. If the male parasitoid died before the female, it was replaced with another male. After each parasitoid and host individual had fully developed, the number, sex, and the juvenile developmental time were recorded. All female parasitoids were dissected within 24 h of their death and the number of mature eggs were recorded. All host pupae were dissected after adult emergence had ceased, and the number of parasitized hosts was estimated based on emerged adult parasitoids and dissected pupae containing a dead parasitoid, and then adjusted based on the corrected mortality of unknown pupae. Offspring sex ratio and mortality were also assessed as described previously. We tested 50 and 40 *T. drosophilae* females from the Californian and the South Korean populations, respectively.

Female longevity, numbers of parasitized hosts and offspring developed, offspring sex ratio and survival rate, and juvenile developmental time were calculated. Mean number of offspring produced per day was estimated based on the total number of offspring produced during each two-day exposure. From these data, life table fertility parameters were estimated for each population including net reproductive rate (R_o), intrinsic rate of natural increase (r), mean generation time (T), and doubling time (DT). The r was estimated according to the equation:

$$\sum e^{-rx} l_x m_x = 1$$

where, x is female age in days, l_x is the age-specific survival rate, and m_x is the number of daughters produced per female alive at age x (Birch 1948). The R_0 is given by $R_0 = \sum l_x m_x$. The T in days is given by $T = \ln\ R_0/r$, and the TD in days is $DT = \ln\ (2)/r$ (Biondi et al. 2013; Daane et al. 2013; Rojas et al. 2015).

Data analysis

The effects of female parasitoid age and body size on the number of mature eggs, as well as the effects of host density and host pupal age on the number of parasitized hosts were analyzed using a Generalized linear model (GLM) with Poisson distribution and log link function. All percentage data including offspring sex ratio and survival rate were analyzed using GLM with binomial distribution and logit link function. Developmental time from egg to adult emergence was analyzed using analysis of variance (ANOVA), considering the effects of sex and host age or host species, as well as the interaction between these two factors. Host species effect on the number of offspring produced or the body size of developed adult female, as well as performances between the two parasitoid populations were also compared using ANOVA. All analyses were performed using JMP Pro ver13 (SAS 2013, Cary, NC, USA).

Results

Female parasitoid egg maturation dynamics

The number of mature eggs carried by *T. drosophilae* females was affected by the female age ($\chi^2 = 87.9$, df = 6, $P < 0.001$) and body size ($\chi^2 = 168.8$, df = 1, $P < 0.001$), but not by the interaction between these two factors ($\chi^2 = 8.3$, df = 6, $P = 0.213$). The body size (hind tibia length) of dissected individual females varied from 0.36 to 0.60 mm, but the mean length was not significantly different among the seven age classes ($F_{6,148} = 1.8$, $P = 0.110$). Therefore, the mean number of mature egg load was further compared among different age classes using ANOVA. Newly emerged female *T. drosophilae* (<4 h old) contained 47.6 ± 2.3 mature eggs, and the number of mature eggs increased until females were four days old (Fig. 1).

Host stage preference and suitability

In choice tests, *T. drosophilae* did not show a preference among the four different host pupal age categories in either the low (five pupae) or high (ten pupae) host densities. More pupae were parasitized at the higher host density ($\chi^2 = 157.0$, df = 1, $P < 0.001$), regardless of the host age category ($\chi^2 = 0.7$, df = 3, $P = 0.871$) or the interaction of these two factors ($\chi^2 = 1.3$, df = 3, $P = 0.729$) (Fig. 2a). Offspring juvenile mortality was higher at

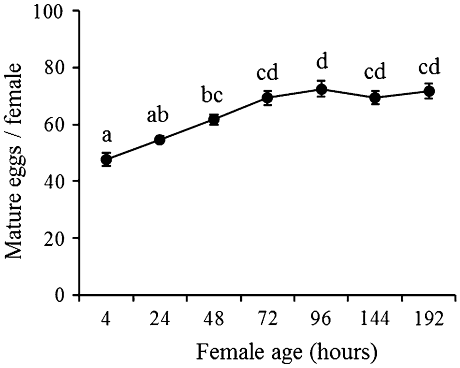

Fig. 1 Egg maturation dynamics of female *T. drosophilae* when deprived of host but provided with food. Values are mean ± SE (n = 17–25 for each age group) and different letters above the *standard error bars* indicate significant differences (Tukey's HSD, $P < 0.05$)

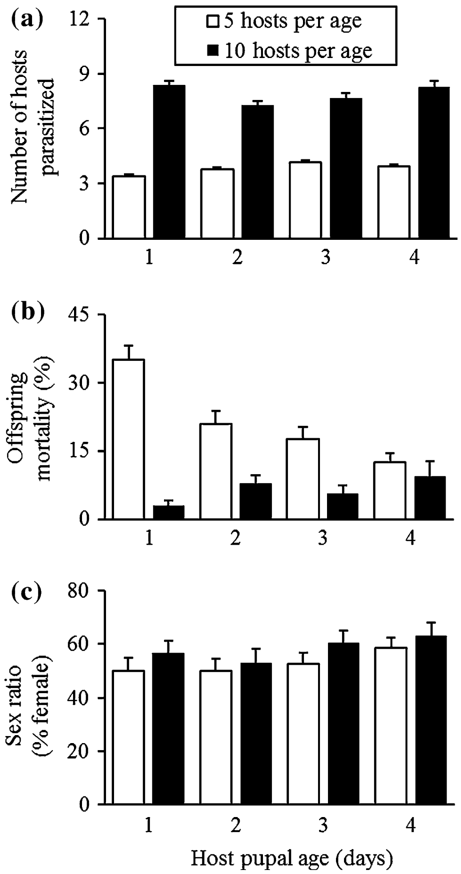

Fig. 2 *Trichropria drosophilae* preference and suitability for four different age categories of *D. suzukii* pupae under two different host densities (five or ten host pupae per age class) showing the (**a**) number of hosts parasitized during a 30 h exposure period, (**b**) juvenile mortality, and (**c**) offspring sex ratio (% female); values are mean + SE

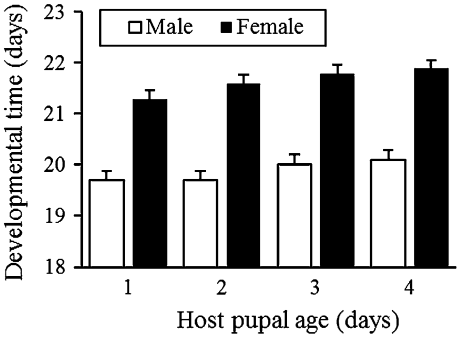

Fig. 3 *Trichropria drosophilae* juvenile developmental time when reared from four different age classes of *D. suzukii* pupae; values are mean + SE

the low host density ($\chi^2 = 11.5$, df = 1, $P < 0.001$), but was not affected by host age ($\chi^2 = 0.2$, df = 3, $P = 0.974$) or their interaction ($\chi^2 = 3.9$, df = 3, $P = 0.278$) (Fig. 2b). Percentage of female progeny was not affected by host density ($\chi^2 = 1.5$, df = 1, $P = 0.691$), by host age ($\chi^2 = 0.9$, df = 3, $P = 0.344$), or by their interaction ($\chi^2 = 0.1$, df = 3, $P = 0.994$) (Fig. 2c).

Body size (hind tibia length) of the developed female was not affected by host age ($F_{1,128} = 1.2$, $P = 0.309$). Juvenile developmental time was affected by host age ($F_{3,732} = 5.1$, $P = 0.002$) or sex ($F_{1,732} = 219.2$, $P < 0.001$), but not by the interactions between the host age and sex ($F_{3,732} = 0.6$, $P = 0.636$) (Fig. 3). Males developed significantly faster than females in all host age classes and offspring developmental time in both sexes slightly increased with host age.

Host species effect on fitness

The mean ± SE maximum pupal body length and width were 3.22 ± 0.03 and 1.23 ± 0.01 mm for *D. suzukii* and 2.63 ± 0.02 and 1.06 ± 0.02 mm for *D. melanogaster*. As a result, the estimated volume of *D. suzukii* (0.261 ± 0.005 mm^3) was larger than that of *D. melanogaster* (0.159 ± 0.005 mm^3) ($F_{1,38} = 174.8$, $P < 0.001$). In the choice test, after the 24 h exposure period to 15 *D. suzukii* and 15 *D. melanogaster* pupae, more *T. drosophilae* adults were reared from the larger *D. suzukii* pupae ($F_{1,60} = 633.9$, $P < 0.001$) (Fig. 4a). Offspring sex ratio was not affected by host species ($\chi^2 = 1.5$, df = 1, $P = 0.225$) (Fig. 4b), but the female offspring reared from *D. suzukii* were larger than those reared from *D. melanogaster* ($F_{1,64} = 44.8$, $P < 0.001$) (Fig. 4c). Developmental time from egg to adult emergence was affected by sex ($F_{1,455} = 64.3$, $P < 0.001$), but not affected by host species ($F_{1,455} = 3.1$, $P = 0.081$) or the interaction of both factors ($F_{1,455} = 3.6$, $P = 0.058$) (Fig. 4d).

Reproductive potential of two *Trichopria drosophilae* populations

At 23 °C, female *T. drosophilae* started oviposition within two days after emergence and the number of offspring produced by the parasitoid decreased with increasing age (Fig. 5). When provided with honey-

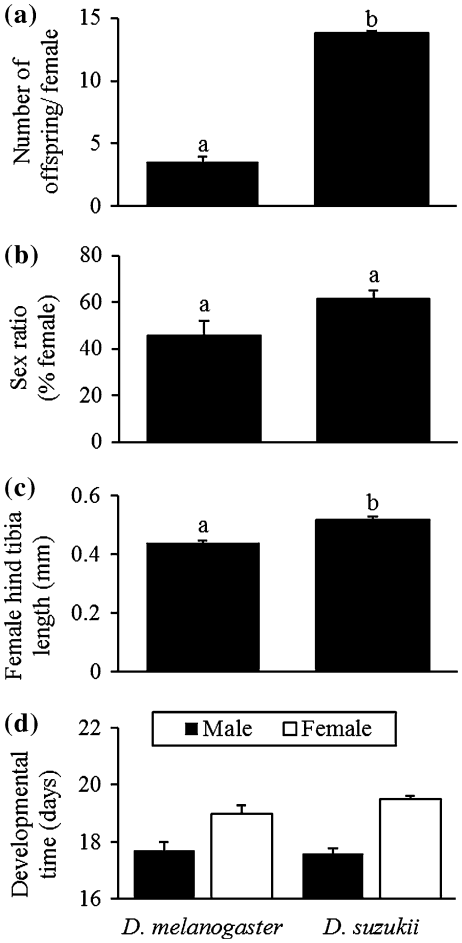

Fig. 4 Host selection and performance by *T. drosophilae* parasitizing *D. suzukii* and *D. melanogaster* in a choice test. (**a**) Number of offspring produced; (**b**) offspring sex ratio (% female); (**c**) female body size (hind tibia length), and (**d**) offspring developmental time. Values are mean + SE and bars bearing *different letters* are significantly different (Tukey's HSD, $P < 0.05$)

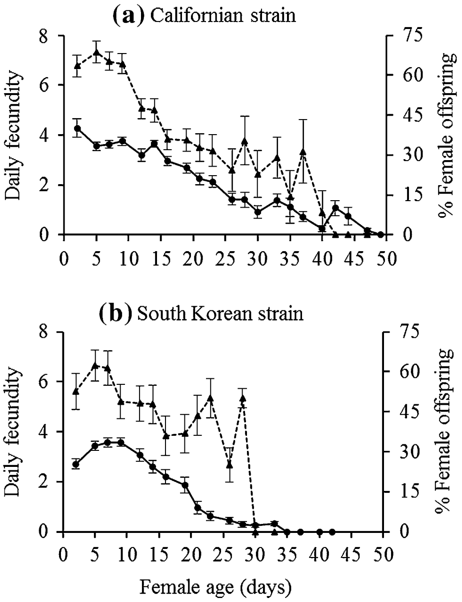

Fig. 5 Lifetime fecundity of female *T. drosophilae* of the Californian (**a**) and the South Korean (**b**) populations when parasitizing *D. suzukii* pupae at 23 °C; values are mean (±SE) and *solid* and *dash lines* refer to daily fecundity and sex ratio (% female offspring), respectively

water and *D. suzukii* pupae, *T. drosophilae* adult females survived 27.5 ± 1.5 days (range: 12–49 days) and 20.2 ± 1.0 days (range: 8–40 days) for the Californian and the South Korean populations, respectively ($F_{1,88} = 15.3$, $P < 0.001$). The lifetime number of parasitized hosts ($F_{1,88} = 15.1$, $P < 0.001$) and emerged progeny ($F_{1,88} = 10.8$, $P < 0.05$) were higher for the Californian population (73.5 ± 2.4 parasitized host pupae and 63.8 ± 2.7 offspring per female) compared with the South Korean population (61.6 ± 2.2 parasitized host pupae and 52.0 ± 2.2 offspring per female). The percentage of female progeny (females per total progeny) showed a decreasing tendency over the maternal age in both populations, although this trend was more marked for the Californian population (Fig. 5). Overall, the lifetime percentage of female progeny was 53.6 ± 2.6 for the Californian population and 48.4 ± 4.2 for the South Korean one ($\chi^2 = 0.2$, df = 1, $P = 0.621$). The residual mature egg load at the end of the experiment was low for both populations: 1.7 ± 1.4 and 2.1 ± 0.5 eggs were found in the ovaries of deceased Californian and South Korean females, respectively. Thus, most females laid almost all their eggs before death. The estimated demographic parameters of the Californian population were all higher than those of the South Korean one. Net reproduction rate was 31.5 and 22.8; intrinsic rate of increase was 0.124 and 0.113; mean generation time was 27.8 and 27.7 days; doubling time was 5.6 and 6.1 days for the Californian and the South Korean populations, respectively.

Discussion

Adult female *T. drosophilae* did not show a preference for different ages of *D. suzukii* pupae, regardless of the tested low (five host pupae) and high (ten host pupae) densities provided. For parasitoids attacking static developmental stages such as pupa, younger hosts generally offer nutrition of higher quality for the parasitoids' development because less and less host resources would be available as the hosts undergo physiological and morphological changes towards aging (Quicke 1997). Indeed, many pupal parasitoid species prefer to attack younger hosts and consequently their offspring perform better than those that developed from older hosts (Wang et al. 1999). In *T. drosophilae*, however, host age did not significantly affect the parasitoid's foraging efficiency and offspring fitness, except that offspring developmental time slightly increased with host age, which may preclude the necessary selection for particular pupal host age categories. Juvenile parasitoid mortality was relatively higher at the lower than the higher host densities tested, regardless of host age, and the high mortality likely resulted from a higher rate of superparasitism at the lower host density.

It is critical to understand the rate of egg maturation of parasitoids in response to changing host availability (Quicke 1997). Female *T. drosophilae* emerged with a relatively high number of mature eggs (e.g., high egg load), and their egg load increased during the first four days. Many frugivorous *Drosophila* larvae breed on fallen or decaying fruits, where there is often found a clumped pattern in terms of host availability, with many fruits containing high numbers of hosts and others not infested. Parasitoids with a high available mature egg load might maximize their reproductions at their early life stages. The reproduction strategies of *T. drosophilae* appear to be well adapted to the distribution and availability of typical drosophila hosts. As shown in this laboratory study, *T. drosophilae* was quite effective: parasitizing as many as 30 hosts per 30 h at the high host density. However, unlike most drosophilid species, *D. suzukii* commonly deposits only one or a few eggs in each fruit, and its eggs are therefore more randomly distributed across fruits in the field (Mitsui et al. 2006). Thus, its parasitoids would unlikely encounter single fruit with a high host density in the field if they selectively forage for *D. suzukii* pupae. The host density tested (ten pupae per two days) in this study may better reflect this scenario of fewer hosts per fruit, but the test conditions would also likely underestimate the parasitoid's fecundity at least during their early adult life stages. Under the current test conditions, the daily fecundity of *T. drosophilae* decreased with increasing female age, suggesting that the mature egg load was depleted with increasing adult age. The lower fecundity in female's early life could be compensated for by either an increase in oviposition later in life or an extension of the reproductive life under the current test conditions. In the field, the realized fecundity of *T. drosophilae*, a synovigenic parasitoid, could be influenced by egg supply when foraging for patchily distributed hosts or in a host-rich habitat, and limited by searching efficiency when foraging in a host-poor habitat.

Host selection behavior has important consequences for the size-fitness relationship in generalist parasitoids. There was a positive correlation between the size of emerged *T. drosophilae* and the size of host fly species. The large body comes apparently at no obvious cost of developmental time or offspring survival. This reflects the plasticity of body growth for *T. drosophilae*, and also suggests that it grows faster on *D. suzukii* than on *D. melanogaster*. It seems plausible for generalist parasitoids like *T. drosophilae*, that such plasticity in offspring size (e.g., no fitness costs) combined with a possible fitness advantage of being large, should drive the evolution of body size, and eventually result in selection of large host species (Otto and Mackauer 1998). However, many other factors could impose constraints on host species selection. The existence of flexibility in body growth, on one hand, can allow generalist parasitoids to attack an expanded host range, but on the other hand, favoring a large host species can narrow host availability. Also, physiological or physical capacity may impose limits on the minimum size of hosts and the maximum size of parasitoids (Morris and Fellowes 2002; Wang and Messing 2004b). More detailed studies with a range of differently sized host species are needed to determine possible physiological or physical capacity of *T. drosophilae* and how or to what extent host species selection affects fitness by this parasitoid. Due to its behavioral simplicity, this generalist parasitoid could provide a model system in which it is feasible to quantify the fitness consequence of body size-dependent host species selection, and will contribute to our understanding of the evolution and ecology of host selection.

Ideally, introduction of specialized parasitoids is desirable for *D. suzukii* control because of the lack of specialized indigenous parasitoids in its invaded regions (Asplen et al. 2015). Although successful biological control programs have been achieved by the introduction of specialist natural enemies, there is increasing interest in promoting the use of indigenous generalist natural enemies even for exotic pests (van Lenteren 2012; Zappala et al. 2013). Indigenous parasitoids have already adapted to local ecological conditions, and if they can overcome behavioral and physiological limitations as shown in *T. drosophilae*, they may contribute to the regulation of exotic pests. At present, the field abundance and distribution of *T. drosophilae* is largely unknown in California and elsewhere, partly because it is often difficult to assess field parasitism of pupal parasitoids as this would require extensive samples of soil, rather than infested fruits.

In summary, as one of only a few extant parasitoid species readily attacking *D. suzukii* in this pest's invaded regions in North America and Europe, *T. drosophilae* is effective on *D. suzukii* under laboratory conditions. Although the efficiency of *T. drosophilae* for control of *D. suzukii* has yet to be proved in the field, augmentative releases of this parasitoid might substantially contribute to suppression of *D. suzukii* populations, especially in habitats that surround host crops and may sever as refuges for or sources of *D. suzukii* populations. Our study also showed that this parasitoid can be easily reared on any stage of *D. suzukii* pupae, which makes insectary operations easier for the mass production of material to be used in augmentative release. In a companion study, we tested a range of different drosophilid species as rearing hosts for *T. drosophilae* and found that the parasitoid could develop from all tested hosts but *D. suzukii* and *D. melanogaster* are among the favorable hosts for the rearing of this parasitoid (Wang, personal observation). However, *T. drosophilae* prefers to attack the large *D. suzukii* over the small *D. melanogaster* as showed in this study. The preference for large hosts may result in increasing attack of this parasitoid on *D. suzukii* in long-term and eventually lead to an increased impact on *D. suzukii*. Overall, the Californian population seems to perform better than the South Korean population of *T. drosophilae* in terms of their reproductive potential. However, it is possible that, because the South Korean colony was initiated with only four specimens, inbreeding might have resulted in low fitness of the parasitoid population. While this was not the case of the Californian strain for which field-collected specimens were added to the laboratory colony periodically, further evaluations are needed to determine the relative performance of different geographical populations of this parasitoid on *D. suzukii*. In the near future, we intend to document the control potential of *T. drosophilae* on *D. suzukii* in the field as augmentative biological control agent, as well as its interaction with other extant parasitoids and Asian parasitoids that are presently been considered for introduction into North America.

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