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The ectoparasitic pupal parasitoid, *Pachycrepoideus vindemmiae* (Hymenoptera: Pteromalidae), attacks other primary tephritid fruit fly parasitoids: host expansion and potential non-target impact

Xin-geng Wang* and Russell H. Messing

College of Tropical Agriculture and Human Resources, University of Hawaii, 7370 Kuamoo Road, Kapaa, HI 96746, USA

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Abstract

Pachycrepoideus vindemmiae Rondani is an ectoparasitic idiobiont parasitoid attacking puparia of many cyclorrhaphous Diptera. This study investigated its potential impact as a facultative hyperparasitoid of four other primary tephritid fruit fly parasitoids in Hawaii, *Fopius arisanus* (Sonan), *Diachasmimorpha longicaudata* (Ashmead), *Diachasmimorpha kraussii* Fullaway, and *Psyttalia concolor* (Szépligeti). *F. arisanus* attacks host eggs while the latter three species attack host larvae, and they all emerge as adults from host puparia. *P. vindemmiae* successfully developed from host puparia previously parasitized by all of the other four tephritid parasitoids. There were no significant differences in developmental time or body size of *P. vindemmiae* adults reared from these secondary host species. However, *P. vindemmiae* reared from the secondary hosts were smaller than those from the tephritid hosts *Bactrocera cucurbitae* (Coquillett) or *Bactrocera latifrons* (Hendel); and were larger than those reared from *Drosophila melanogaster* Meigen. Female *P. vindemmiae* developed faster on *D. melanogaster* but slower on *Ceratitis capitata* (Wiedemann) than on the other hosts. *P. vindemmiae* did not prefer to attack unparasitized hosts rather than hosts previously parasitized by *F. arisanus*, and there was no difference in offspring survival and sex ratio between the wasps reared from the primary and secondary host species. Among the three distinctly different size host species, *B. latifrons*, *C. capitata*, and *D. melanogaster*, *P. vindemmiae* preferred to attack the smallest host (*D. melanogaster*), but invested more female offspring on the largest host (*B. latifrons*). There was no difference in offspring survival between those reared on *D. melanogaster* and *C. capitata*, but the adult emergence rate was lower in *B. latifrons* than in the other two species. The flexible body growth and less discriminative nature of *P. vindemmiae* indicate that it has the potential for host range expansion and thus non-target impact to other beneficial parasitoids of Diptera.

Keywords: Biological control; Ectoparasitoid; Fruit fly parasitoids; Hyperparasitism; Non-target impact

1. Introduction

Biological control of insect pests is one of the most cost effective and environmentally sound methods of pest management. However, the use of classical biological control has been subject to increasingly critical scrutiny, and there has been a tightening of regulations against the introduction of exotic species in many countries due to rising concerns about non-target impacts to both endemic and beneficial exotic species (Follett and Duan, 1999; Louda et al., 2002). Several studies expressing these concerns have been reported from Hawaii, mainly due to its long history of extensive biocontrol introductions and highly sensitive Island fauna and flora (Funasaki et al., 1988; Henneman and Memmott, 2001; Howarth, 1991). In this study, we document an example of potential non-target impact by the introduced ectoparasitic pupal fly parasitoid, *Pachycrepoideus vindemmiae* Rondani (Hymenoptera: Pteromalidae).

In Hawaii, the classical biological control of invasive tephritid fruit fly pests using hymenopteran parasitoids has been practiced for over 100 years, and more than 30 species have been introduced from Africa, Asia, and Australia (Purcell, 1998; Wharton, 1989). Successful

* Corresponding author. Fax: 1-808-822-2190.
E-mail addresses: xingeng@hawaii.edu (X.-g. Wang), messing@hawaii.edu (R.H. Messing).

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establishment of several braconids such as the egg–pupal parasitoid, *Fopius arisanus* (Sonan), has resulted in significant suppression of two major tephritid pests, the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and the oriental fruit fly, *Bactrocera dorsalis* (Hendel), becoming one of the most successful examples of classical biological control of fruit fly pests in the world (Purcell, 1998; Wharton, 1989). However, attacks by introduced tephritid fruit fly parasitoids on non-target tephritid flies have recently become a serious concern in Hawaii. For example, Duan et al. (1998) reported that *Diachasmimorpha tryoni* (Cameron), a larval–pupal tephritid fruit fly parasitoid introduced from Australia in the early 1900s, was found to attack a non-target gall-forming tephritid, *Eutreta xanthochaeta* Aldrich, which was itself deliberately introduced from Mexico for control of the weeds, *Lantana camara* L.

In the past, evaluation of non-target impacts of introduced tephritid fruit fly parasitoids have not explicitly addressed pupal parasitoids, although several pupal parasitoids were among the earliest introductions into Hawaii and other regions in the world (Ovruski et al., 2000; Purcell, 1998; Wharton, 1989). In general, there is an historical lack of data regarding pupal fruit fly parasitoids, possibly due to the fact that egg and larval-attacking parasitoids (for example, *F. arisanus* and *Diachasmimorpha longicaudata* (Ashmead)) have been more successful and were mass-reared for augmentative release (Bautista et al., 1999; Purcell et al., 1998; Wong and Ramadan, 1992). Most egg and larval-attacking tephritid fruit fly parasitoids are endoparasitic koinobionts, i.e., continue development in host puparia (Wang et al., 2003; Wharton et al., 2003), leaving their pupae open to attack by pupal parasitoids that are often ectoparasitic idiobionts (Guillén et al., 2002; Sivinski et al., 1998). Idiobiont ectoparasitoids usually have a wide host range and are also frequently facultative hyperparasitoids (Godfray, 1994; Quicke, 1997). For example, the chalcid *Dirhinus giffardii* Silvestri was found to attack *B. dorsalis* puparia that were previously parasitized by the larval–pupal parasitoid *Fopius vandenboschi* (Fullaway) in Hawaii (Dresner, 1954), while another chalcid ectoparasitoid, *Spalangia gemina* Boucek, attacked puparia of the Mexican fruit fly, *Anastrepha ludens* (Loew) that had been previously parasitized by *D. longicaudata* (Sivinski et al., 1998). Furthermore, *S. gemina* did not discriminate between parasitized and unparasitized pupae, and could develop into adults on the secondary host (Sivinski et al., 1998).

Pachycrepoideus vindemmiae is another ectoparasitic idiobiont parasitoid attacking puparia of many cyclorrhaphous flies (Crandell, 1939). It is widespread over 60 countries around the world and has been reported to attack over 60 fly species, including many tephritid fruit flies such as the melon fly *Bactrocera cucurbitae* (Coquillett), *B. dorsalis* and *C. capitata*, and several *Drosophila* species (see Noyes, 2002). The parasitoid has been evaluated mainly for the control of stable and house flies (Meyer et al., 1990; Petersen et al., 1992; Wharton, 1989). It was also introduced into Hawaii and several countries in South America for the control of *C. capitata* and *Anastrepha* spp. (Ovruski et al., 2000; Purcell, 1998), and was recently mass-released for the control of *C. capitata* in Costa Rica (see Ovruski et al., 2000). As a facultative hyperparasitoid, *P. vindemmiae* was able to attack two parasitoids of *Drosophila* larvae, *Asobara tabida* Nees and *Leptopilina heterotoma* (Thomson) (Van Alphen and Thunnissen, 1983). Although it was also reported to attack some parasitic tachinid flies and other tephritid fruit fly parasitoids, including *Diachasmimorpha fullawayi* (Slivestri), *D. tryoni*, *Psyttalia humilis* Silvestri (all Braconidae), *Coptera silvestrii* Kieffer (Diapriidae), and *Tetrastichus giffardianus* Silvestri (Eulophidae), these reports are all anecdotal and scattered among the older literature and detailed information is lacking (see Noyes, 2002).

We examined the potential non-target impact of *P. vindemmiae* on four primary tephritid fruit fly parasitoids in Hawaii: *F. arisanus*, *D. longicaudata*, *Diachasmimorpha kraussii* Fullaway, and *Psyttalia concolor* (Szépligeti). *F. arisanus* attacks host eggs while the other three species attack host larvae; they all complete their development on the host pupae within puparia. *F. arisanus* is currently the dominant fruit fly parasitoid in Hawaii (Purcell, 1998), in part due to its competitive superiority against larval parasitoids (Wang and Messing, 2002, 2003, Wang et al., 2003). *D. longicaudata* is one of the most widely established fruit fly parasitoids in the world (Ovruski et al., 2000; Purcell, 1998). With recent development of mass-rearing technology (Bautista et al., 1999; Wong and Ramadan, 1992), both *F. arisanus* and *D. longicaudata* have the potential for augmentative biological control of tephritid fruit fly pests (Messing, 1995; Ovruski et al., 2000; Purcell, 1998; Sivinski et al., 1996). *D. kraussii* and *P. concolor* have both been recently reintroduced into Hawaii from Australia and West Africa, respectively, as part of a renewed effort to improve the biological control of fruit fly pests throughout the islands (Messing and Ramadan, 2000; Wang and Messing, 2002).

Our aim was to determine to what extent *P. vindemmiae* could successfully develop in these four tephritid fruit fly parasitoids as a facultative hyperparasitoid. To understand the ecological and behavioral mechanisms underlying the possibility of host range expansion and non-target impact, we also determined if the parasitoid prefers to attack different size host species, or if it prefers to attack primary hosts (flies) over secondary hosts (braconid parasitoids). We also quantified the potential consequences of secondary host species selection on the parasitoid's offspring fitness, as compared to offspring development in five primary fly species in Hawaii:

C. capitata, *B. cucurbitae*, *B. dorsalis*, the Solanaceous fruit fly, *Bactrocera latifrons* (Hendel), and *Drosphilia melanogaster* Meigen,

2. Materials and methods

2.1. Flies and parasitoids

Ceratitis capitata, *B. cucurbitae*, *B. dorsalis*, and *B. latifrons* were provided by the USDA-ARS Pacific Basin Agricultural Research Center (PBARC), Honolulu, where they were mass-reared on wheat-based artificial diets (Tanaka et al., 1969). Fresh fly eggs incubated on diet in plastic containers ($20 \times 12 \times 4$ cm) or fly puparia were shipped weekly from the rearing laboratory to the Kauai Agricultural Research Center (KARC) where this study was conducted. Fly eggs were reared in containers under laboratory conditions (23 ± 1 °C, $65 \pm 10\%$ RH, and LD 12:12 h, 3500 lux). When the fly larvae started to pupate, each rearing container was placed into a Fiberglas box ($45 \times 30 \times 15$ cm) containing 2 cm of sand, so that fly puparia could be easily collected from the sand. *D. melanogaster* was commonly found as a contaminant in the culture of the tephritid fly species, so *D. melanogaster* puparia were directly collected from the rearing containers of tephritids as needed.

Diachasmimorpha longicaudata and *F. arisanus* were also provided weekly by PBARC where they were mass-reared according to methods described by Wong and Ramadan (1992) and Bautista et al. (1999), respectively. Parasitized puparia of both species were shipped to KARC. Laboratory populations of *D. kraussii* and *P. concolor* were established and maintained at KARC. *D. kraussii* were recently imported from Australia and were reared on *B. latifrons* larvae, the most suitable host species (Messing and Ramadan, 2000), while *P. concolor* were recently imported from Kenya and were reared on *C. capitata* larvae. For detailed procedures of the culture of both *D. kraussii* and *P. concolor* see Wang and Messing (2002). Emerged wasps of each of the four parasitoid species were maintained with an approximate 1:1 sex ratio in cages ($25 \times 25 \times 25$ cm) with water and honey provided; 7- to 10-day-old female wasps were used to obtain parasitized hosts for later tests.

A laboratory population of *P. vindemmiae* was initially established from collections of adult wasps that naturally infested our laboratory cultures of the other tephritid fruit fly parasitoids at KARC. They were reared on *C. capitata* by exposing about one hundred to two hundred 2- to 3-day-old *C. capitata* puparia on a petri dish (9 cm diameter) to about 50 pairs of 6- to 10-day-old adult wasps of *P. vindemmiae* for 24 h in a cage ($9.5 \times 10.5 \times 13$ cm) with water and honey provided. For later tests we used 1-week-old *P. vindemmiae* females that had been housed with males since their emergence in cages with food but no hosts provided.

All rearing and experiments were conducted under the same laboratory conditions described above.

2.2. Preparation of parasitized puparia

To obtain host puparia parasitized by *F. arisanus*, *C. capitata* eggs were collected by exposing a papaya fruit (8–10 cm diameter) to 100 pairs of 7- to 10-day-old *C. capitata* adults in a cage for 12 h; the infested fruit was then exposed to 100 pairs of *F. arisanus* adults in a cage for 24 h. The exposed fruit was placed over fly diet in a rearing container. When the fly larvae started to pupate, the rearing container was placed into a holding box containing sand. Puparia parasitized by *D. longicaudata*, *P. concolor*, and *D. kraussii* were obtained using a similar procedure. About 300 third instar *C. capitata* (for *D. longicaudata* and *P. concolor*) or *B. latifrons* (for *D. kraussii*) were placed into an oviposition unit (modified petri dish, 9 cm diameter, 0.8 cm deep, with fine screen lid) containing fresh diet, and were exposed to 100 pairs of adult wasps of either species for 24 h in a cage, respectively. The exposed host larvae were transferred to rearing containers using the same methods as for *F. arisanus*. For detailed procedures about exposure and rearing see Wang and Messing (2002, 2003) and Wang et al. (2003).

Pilot tests showed that *P. vindemmiae* can attack all stages of host puparia, but attacks on young puparia in which the fly larvae had not yet formed into a pupa resulted in death of the parasitoid progeny. It took ca. 1–2 days for *C. capitata* and the other fly species, 2–3 days for *F. arisanus*, and 4–5 days for the larval–pupal parasitoids to develop into fully formed pupae within the puparia. Thus, in all experiments we used 2-to 3-day-old unparasitized puparia, 3- to 4-day-old *C. capitata* puparia parasitized by *F. arisanus*, and 6- to 7-day-old *C. capitata* or *B. latifrons* puparia parasitized by larval-pupal parasitoids. The adult appendages of the fly pupae within 2- to 3-day-old unparasitized puparia could be seen clearly under a microscope. In a parasitized puparium when the larval parasitoid has formed a pupa, it created an obvious large gap between the parasitoid pupa and the puparium shell, and the whole pupa was also visible under a microscope. Furthermore, parasitized *C. capitata* puparia were darker and smaller than unparasitized puparia (see results in Table 1). Therefore, it was easy to distinguish unparasitized from parasitized puparia under a microscope.

2.3. Hyperparasitism and effects of host species on the parasitoid's developmental time and size

This experiment was conducted to determine if *P. vindemmiae* could successfully develop on *F. arisanus*, *D. longicaudata*, *D. kraussii* or *P. concolor*. The develop-

Table 1
Comparison of body size among the primary hosts (fruit fly species) and the secondary hosts (fruit fly parasitoids)

Host species	*N*	Length (mm)	Width (mm)	Volume (mm^3)
Primary hosts (flies)				
D. melanogaster	50	2.78 ± 0.03 a	1.12 ± 0.02 a	0.186 ± 0.023 a
C. capitata	50	4.59 ± 0.03 b	2.05 ± 0.01 b	1.018 ± 0.023 b
B. dorsalis	50	4.85 ± 0.03 c	2.26 ± 0.01 c	1.311 ± 0.023 c
B. cucurbitae	50	5.01 ± 0.03 d	2.31 ± 0.02 c	1.430 ± 0.023 d
B. latifrons	50	5.35 ± 0.03 e	2.26 ± 0.03 c	1.486 ± 0.023 d
Secondary hosts (Braconids)				
F. arisanus	50	4.34 ± 0.03 f	1.75 ± 0.02 d	0.708 ± 0.023 e
D. longicaudata	50	4.14 ± 0.03 g	1.86 ± 0.02 e	0.761 ± 0.023 e
P. concolor	50	4.12 ± 0.03 g	1.83 ± 0.02 e	0.734 ± 0.023 e
D. kraussii	50	5.32 ± 0.03 e	2.22 ± 0.02 c	1.418 ± 0.023 d

F. arisanus, *D. longicaudata*, and *P. concolor* were reared using *C. capitata* while *D. kraussii* were reared using *B. latifrons*. All values (means ± SE) followed by the same letter within the same column are not significantly different (ANOVA, Tukey's HSD test, $P = 0.05$).

mental time and size of emerging wasps from these secondary hosts were compared with those reared from *B. cucurbitae*, *B. dorsalis*, *B. latifrons*, *C. capitata*, and *D. melanogaster*. Prior to the test, a sample of 50 puparia of each host species was measured for body length and width using a calibrated binocular microscope. Because the shape of *Bactrocera* was slightly different from *Ceratitis*, we also estimated puparium volume of each species as an additional measure of size using the following formula:

$$V = 4/3\pi \cdot (l/2) \cdot (\omega/2)^2, \quad (1)$$

where V is the volume of a prolate ellipsoid puparium with length l and width w (Otto and Mackauer, 1998).

In a no-choice test, 200–300 puparia of each of the nine hosts were placed in a petri dish and exposed to 100 female *P. vindemmiae* in a cage (9.5 × 10.5 × 13 cm) for 24 h. The exposed puparia were then reared until flies or wasps emerged. The developmental time and sex of all emerged wasps of *P. vindemmiae* were recorded twice each day. All wasps were first chilled in a refrigerator (6–7 °C) for 12 h and then individually measured (for body length) under a microscope. Although head width is often used as an index of body size in *P. vindemmiae* (Phillips, 1993; Van Alphen and Thunnissen, 1983), for simplicity we used body length as a convenient measure of the wasp's size. Mean developmental time and size of *P. vindemmiae* adults reared from different hosts were compared.

2.4. Preference between primary and secondary hosts

Because the size and developmental time of *P. vindemmiae* adults reared from the four different secondary host species were similar (see Section 3), we chose *F. arisanus* as a model species to determine if *P. vindemmiae* prefers to attack unparasitized or previously parasitized *C. capitata* puparia, and to compare the offspring survival and sex ratio of wasps reared from the two kinds of hosts.

This experiment involved a sequential exposure of *C. capitata* first to *F. arisanus* as eggs and then to *P. vindemmiae* as puparia. *C. capitata* eggs were collected by exposing a papaya fruit to 100 pairs of 7- to 10-day-old *C. capitata* adults for 12 h; the infested papaya was then exposed to 100 pairs of *F. arisanus* adults for 24 h in a cage. The exposed fruit was placed over diet in a rearing container until the fly larva pupated. One hundred 2- to 3-day-old puparia recovered from this exposure were placed in a petri dish and exposed to 20 *P. vindemmiae* females in a cage (9.5 × 10.5 × 13 cm) for 24 h with food provided.

Following the exposure, 50 randomly selected puparia were dissected to determine the levels of primary and secondary parasitism. The other 50 exposed puparia were sorted under a microscope into two types: previously parasitized by *F. arisanus* vs. previously unparasitized. Each group was reared separately until flies or wasps emerged. Meanwhile, as a control, 50 unparasitized *C. capitata* puparia and 50 puparia parasitized by *F. arisanus* only were reared under identical conditions. All dead puparia from each group were dissected and the number of unmerged adults was recorded. Adult emergence rate and sex ratio of *P. vindemmiae* were thus estimated based on the emerged and unemerged adults, while the immature mortality rate was estimated based on the following formula:

$$M_{\text{med}} = (N_1 \cdot P_1 - W_1)/(N_1 \cdot M_1), \quad (2)$$

$$M_{\text{Fa}} = (N_2 \cdot P_2 - W_2)/(N_2 \cdot M_2), \quad (3)$$

where M_{med} and M_{Fa} are the estimated immature mortality of *P. vindemmiae* on *C. capitata* and *F. arisanus*; N_1 and N_2 are the total number of puparia reared for each group; P_1 and P_2 are the percentage parasitism by *P. vindemmiae* based on the dissection ($N_1 \cdot P_1$ and $N_2 \cdot P_2$ are thus the expected number of *P. vindemmiae* adults reared from each group); W_1 and W_2 are the actual number of *P. vindemmiae* adults emerged from each group; and M_1

and M_2 are the control mortality of unparasitized and parasitized *C. capitata* puparia by *F. arisanus* only.

The experiment was repeated 15 times. Because the level of primary parasitism by *F. arisanus* varied from 40 to 70%, the test for host preference was analyzed using the model of Greenwood and Elton (1979), which distinguishes between frequency-dependent and frequency-independent host preference:

$$e_1/e_2 = (V \cdot A_1/A_2)^b, \quad (4)$$

where e_1 and e_2 are the number of each group parasitized while A_1 and A_2 are the number of each group presented based on the dissection of 50 puparia. A is a parameter which describes the frequency-independent preference for each host type; when $A = 1.0$ there is no frequent-independent preference. B is a parameter describing the degree of frequency-dependent preference; when $B = 1.0$, there is no frequency-dependent preference.

2.5. Preference among different size host species

Three distinctly different size host species, *B. latifrons*, *C. capitata*, and *D. melanogaster*, were used to determine if *P. vindemmiae* prefers to attack large rather than small hosts in a choice experiment, and to examine the consequences of host selection on offspring fitness. A single female *P. vindemmiae* (naïve, without oviposition experience) was provided with five 2- to 3-day-old puparia of each of the three species placed together in a petri dish (4 cm diameter) for 24 h in a cage ($9.5 \times 10.5 \times 13$ cm) with water and honey provided. After the exposure the host species were reared separately in containers until wasps or flies emerged. Meanwhile, as a control, 10 unexposed puparia of each host species were reared under the same conditions. The experiment was repeated 26 times.

Mortality of the exposed hosts was low in this experiment. In only 5 *C. capitata*, 21 *B. latifrons*, and 2 *D. melanogaster* did no fly or wasp emerge. These dead puparia were reconstituted in water for 1–2 days before they were dissected under a microscope to determine the presence or absence of recognizable parasitoid cadavers (eggs, larvae, or pharate adults) (Ramadan et al., 1994). In 15 of the 21 unemerged *B. latifrons* puparia, *P. vindemmiae* had developed to the adult stage but failed to successfully emerge from the host puparia. The dead parasitoid eggs and larvae were normally attached to the host surface and were easy to recognize. Parasitism was thus estimated based on both rearing and dissection, while emergence rate and sex ratio were estimated based on the emerged and unemerged adults. In two replicates only did male wasps emerge from all the host species and these two replicates were discarded because of the probability that the female wasps had not mated. Thus, there was at least one female offspring reared from each replicate. Juvenile mortality was corrected based on the control mortality of unparasitized hosts. Because the juvenile mortality was generally low, the sex ratio basically reflects the sex allocation strategy of *P. vindemmiae* in relation to host species, rather than the result of differential sex-specific mortality.

2.6. Data analysis

All comparisons of mean values in host species size, developmental time, mortality, emergence rate, sex ratio, and size of *P. vindemmiae* among different treatments were performed using one-way ANOVA (JMP 4.1, SAS Institute, Cary, NC). All proportional data were transformed by arcsine square root before an analysis of variance. If a significant difference among treatments was detected, the mean values were subjected to multiple comparisons using the Tukey's HSD test. The host preference model was fitted using non-linear least squares (JMP 4.1, SAS Institute, Cary, NC).

3. Results

3.1. Hyperparasitism and effect of natal host species

There were significant differences in puparium size among the tested host species (length: $F_{8,441} = 726.6$, $P < 0.001$; width: $F_{8,441} = 423.8$, $P < 0.001$; volume: $F_{8,441} = 366.7$, $P < 0.001$) (Table 1). The size of fly species decreased according to the order: *Bactrocera* > *Ceratitis* > *Drosophila*. Among the three *Bactrocera* species, *B. latifrons* was longer than *B. cucurbitae*, and *B. cucurbitae* was longer than *B. dorsalis*, but there was no significant difference in width among them. There was also no difference in body volume between *B. latifrons* and *B. cucurbitae*, but both species were larger than *B. dorsalis*. Parasitization of *B. latifrons* by *D. kraussii* did not affect the puparium size. However, *C. capitata* puparia parasitized by *F. arisanus*, *D. longicaudata* or *P. concolor*, were significantly smaller than unparasitized puparia. There was no difference between the size of *C. capitata* puparia parasitized by *D. longicaudata* and *P. concolor*; both were larger than those parasitized by *F. arisanus*.

Pachycrepoideus vindemmiae successfully developed on all the five primary (flies) and all four secondary (braconid parasitoids) hosts tested. Host species significantly influenced the size (female: $F_{8,361} = 40.0$, $P < 0.001$; male: $F_{8,379} = 31.7$, $P < 0.001$) and developmental time (female: $F_{8,361} = 10.2$, $P < 0.001$; male: $F_{8,379} = 3.69$, $P < 0.001$) of *P. vindemmiae* (Table 2). The largest adults of *P. vindemmiae* were reared from *B. cucurbitae* and *B. latifrons*, while the smallest ones were reared from *D. melanogaster*. There was no difference among the size of wasps reared from *B. dorsalis*, *C. capitata* or any of the four secondary host species.

Female *P. vindemmiae* developed faster on *D. melanogaster* but slower on *C. capitata*, and faster on the secondary hosts than on their primary hosts (Table 2). There was no significant difference in developmental time of male wasps among the different hosts, except that those from *C. capitata* developed significantly more slowly than these from the secondary host species (Table 2).

3.2. Preference between primary and secondary hosts

Exposure of *C. capitata* first to *F. arisanus* as eggs and then to *P. vindemmiae* as puparia resulted in $68.8 \pm 6.2\%$ parasitism by *F. arisanus*, 58.9 ± 5.9 parasitism by *P. vindemmiae*, and 35.8 ± 5.5 parasitism by both species ($n = 15$). Model analysis of host preference showed that neither of the two parameters ($b = 1.007 \pm 0.433$; $V = 0.799 \pm 0.483$; mean and 95% confidence limits) was significantly different from 1.0, suggesting no preference by *P. vindemmiae* for previously parasitized or unparasitized hosts.

There were no significant differences in immature morality ($F_{1,28} = 1.1$, $P = 0.27$) (Fig. 1A), adult emergence rate ($F_{1,28} = 0.18$, $P = 0.67$) (Fig. 1B), or sex ratio ($F_{1,28} = 0.16$, $P = 0.69$) (Fig. 1C) of *P. vindemmiae* between offspring developing on unparasitized *C. capitata* puparia and *C. capitata* puparia previously parasitized by *F. arisanus*.

3.3. Host species selection and its consequences

Pachycrepoideus vindemmiae preferred to attack *D. melanogaster* puparia over *B. latifrons* or *C. capitata* puparia, and preferred *C. capitata* to *B. latifrons* puparia when provided a choice among the three host species ($F_{2,69} = 15.7$, $P < 0.001$) (Fig. 2A). Immature mortality was generally low in this experiment, but it was higher on *B. latifrons* and *C. capitata* than on *D. melanogaster* ($F_{2,56} = 4.1$, $P < 0.02$) (Fig. 2B). There was no difference

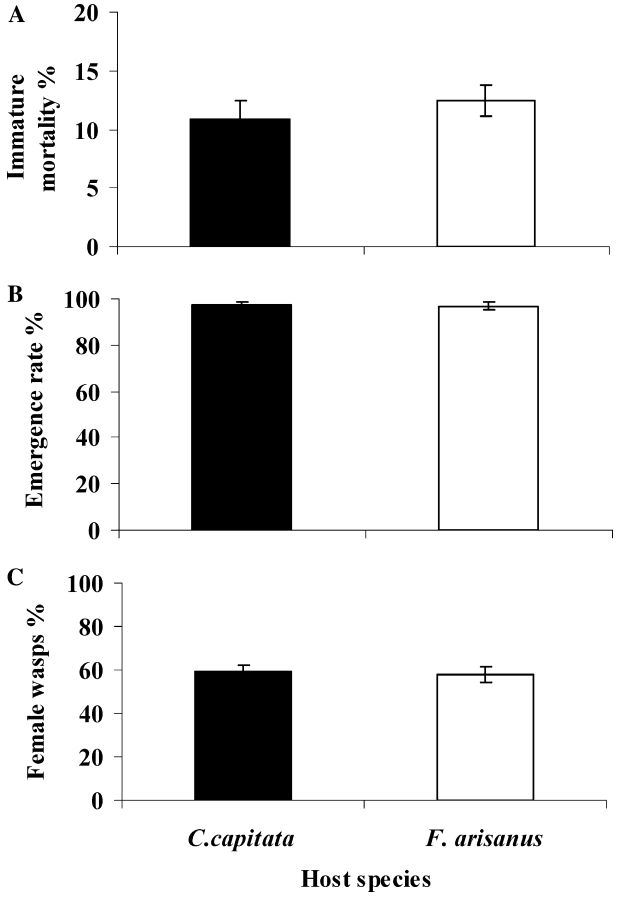

Fig. 1. Comparison of offspring sex ratio and survival rate of *P. vindemmiae* developed from its primary host (*C. capitata*) and a secondary host (*F. arisanus*). (A) Immature mortality; (B) adult emergence rate; and (C) sex ratio. Bars refer to means ± 1 standard error ($n = 15$).

in the emergence rate of adult wasps between the offspring reared from *C. capitata* and *D. melanogaster*; the emergence rates from these two host species were significantly higher than those from *B. latifrons* ($F_{2,55} = 25.7$, $P < 0.001$) (Fig. 2C). However, the parasit-

Table 2
Effect of natal host species on the size and developmental time of *P. vindemmiae*

Host species	Size (mm)		Developmental time (day)	
	Female	Male	Female	Male
Primary hosts				
D. melanogaster	1.66 ± 0.01(41) a	1.52 ± 0.01(63) a	20.8 ± 0.28 a	20.1 ± 0.21 a
C. capitata	1.80 ± 0.01(44) b	1.68 ± 0.01(48) bc	23.6 ± 0.27 b	21.2 ± 0.23 b
B. dorsalis	1.82 ± 0.01(35) b	1.66 ± 0.01(40) b	22.4 ± 0.30 c	20.5 ± 0.26 ab
B. cucurbitae	1.88 ± 0.01 (39) c	1.74 ± 0.02(24) c	22.5 ± 0.29 c	20.8 ± 0.33 ab
B. latifrons	1.84 ± 0.01(32) bc	1.71 ± 0.02(20) c	22.7 ± 0.32 bc	20.5 ± 0.36 ab
Secondary hosts				
F. arisanus	1.82 ± 0.01(58) b	1.66 ± 0.01(63) b	21.5 ± 0.23 d	20.0 ± 0.20 a
D. longicaudata	1.80 ± 0.01(35) b	1.61 ± 0.01(41) b	21.5 ± 0.30 d	19.9 ± 0.25 a
P. concolor	1.81 ± 0.01(48) b	1.62 ± 0.01(44) b	21.3 ± 0.26 d	20.3 ± 0.25 a
D. kraussii	1.81 ± 0.01(38) b	1.65 ± 0.01(47) b	21.3 ± 0.29 d	19.8 ± 0.24 a

All values (means ± SE) followed by the same letter within each column are not significantly different (ANOVA, Tukey's HSD test, $P = 0.05$). Figures in parentheses are sample size. The sample size for the developmental time is the same as for the measure of body size within the same sex.

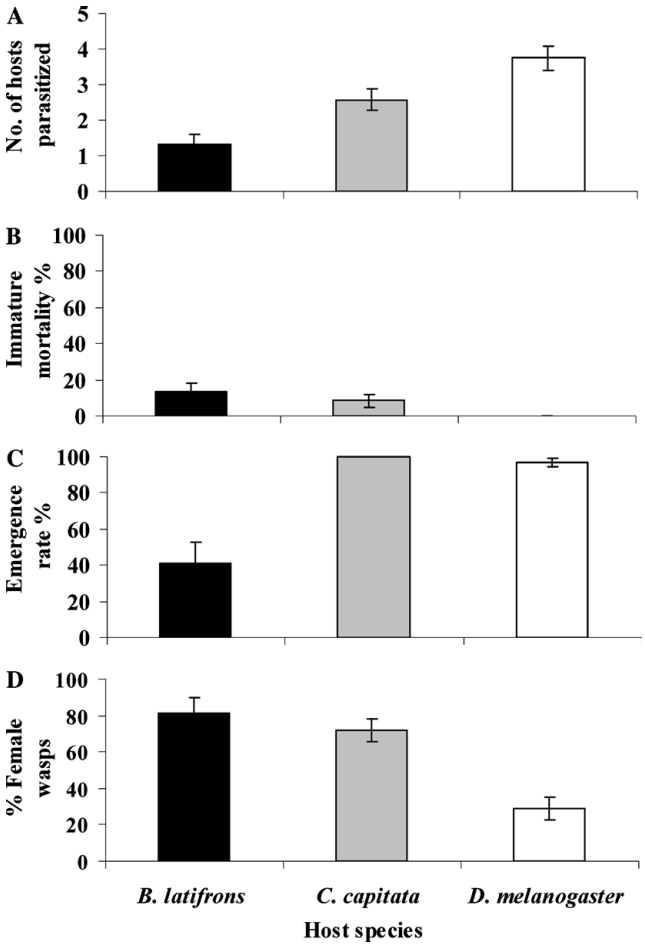

Fig. 2. Host species selection and its effect on offspring fitness of *P. vindemmiae*. (A) Number of each host species parasitized; (B) immature mortality (no mortality from *D. melanogaster*); (C) adult emergence rate; and (D) sex ratio. Bars refer to means ± 1 standard error ($n = 24$).

oid invested significantly more female offspring in the larger *B. latifrons* and *C. capitata* puparia than in *D. melanogaster* ($F_{2,45} = 6.4$, $P < 0.005$) (Fig. 2D).

4. Discussion

Pachycrepoideus vindemmiae can successfully develop on all four braconid host species tested in this study: *F. arisanus*, *D. longicaudata*, *D. kraussii*, and *P. concolor*. To our knowledge this is the first report that *P. vindemmiae* can also develop on *B. latifrons*, a relatively recent invasive tephritid fruit fly pest in Hawaii. The parasitoid has also been reared from host puparia previously parasitized by three other fruit fly parasitoids, *D. tryoni*, *P. humilis*, and *D. giffardii* (Wang and Messing, unpublished data). Because *P. vindemmiae* was also reported to attack two larval parasitoids of *Drosophila* and five other fruit fly parasitoids (see Section 1), it seems reasonable to predict that this parasitoid poses an impact to other beneficial parasitoids of Diptera.

Like other typical idiobiont ectoparasitoids (Godfray, 1994; Quicke, 1997), *P. vindemmiae* has characteristics that may explain its expanded host range and thus the non-target impact. First, it is a physiological generalist, and can develop on either the largest (*Bactrocera*) or the smallest (*Drosophila*) hosts, and on non-co-evolved (*B. atifrons*) host species when colonized in a new region. This flexibility in body growth allows this generalist parasitoid to attack an expanded host range. In general, offspring size was positively correlated with host size, suggesting that the parasitoid is able to adjust growth rate to maximize body size. The wasps were small when reared from the small host *D. melanogaster* with a rapid developmental time, agreeing with the prediction of parasitoid development models (Mackauer and Sequeira, 1993; Otto and Mackauer, 1998). However, the effect of host size on the parasitoid's size was not straightforward in this case. It was observed that the parasitoid could only consume a small part of the host resources provided in a tephritid fly puparium, but consumed almost all the host resources in a *D. melanogaster* puparium. Thus, there may be a physiological constraint on the maximum use of host resources when they are in surplus supply. In such cases, the size of natal hosts may not be a good prediction of the wasp's size. For example, there was no difference in the size of *P. vindemmiae* wasps that developed in unparasitized *C. capitata* puparia vs. puparia previously parasitized by the three other parasitoids, although these parasitized puparia were smaller than unparasitized ones (Tables 1 and 2). The parasitized puparia should contain less food resources than the unparasitized puparia of the same hosts, because the conversion of host-biomass into the parasitoid-biomass requires energy. In addition, *C. capitata* larvae parasitized as eggs by *F. arisanus* were significantly smaller than unparasitized ones (Wang and Messing, 2003). Parasitization by the larval parasitoids occurs at a relatively late stage of host larval development, and thus its effect on puparium size is relatively small. Overall, parasitized *C. capitata* puparia were obviously smaller, while parasitized *B. latifrons* puparia were not.

Secondly, *P. vindemmiae* is also a superior competitor against other pupal parasitoids of tephritids. We recently investigated the detailed life history strategy with regard to host killing by this parasitoid. *P. vindemmiae* injects toxic venom at the time of oviposition, and the venom has a paralytic action on its primary host, as well as on competitors of other species. For example, *P. vindemmiae* always wins in competition against *D. giffardii*, no matter which species occupies the host first (Wang and Messing,unpublished data). This form of host killing strategy is a particularly efficient way of competing with another parasitoid, as no special adaptations are needed to attack competing parasitoids in addition to the host.

Adaptive host selection behavior in parasitoids is hypothesized to affect fecundity-related outcomes mainly through the action of progeny mortality (Godfray, 1994). In general, theories predict that a parasitoid should favor selection of large hosts and invest more female offspring in large hosts, particularly in ectoparasitoids attacking quiescent host stages such as pupae (Charnov et al., 1980; Charnov and Stephens, 1988; Heinz, 1993; King and Charnov, 1988; Napoleon and King, 1999; Ueno, 1998). The present study shows a conflict between host preference and offspring sex allocation in *P. vindemmiae*. The parasitoid preferred to attack the small host *D. melanogaster*, but invested more female offspring in the large host *B. latifrons*. Wasps developed from *B. latifrons* were large, and it is known that in *P. vindemmiae* larger size improves a female's ability to search and a male's ability to mate (Morris and Fellowes, 2002). However, a high percentage of adult wasps were unable to successfully emerge from *B. latifrons*, possibly due to the especially hard shell of *B. latifrons* puparia as we noticed in this study. Thus, there is a trade-off between offspring size and survival of *P. vindemmiae* on *B. latifrons*.

There was no significant difference in offspring survival of *P. vindemmiae* that developed in *C. capitata* vs. *D. melanogaster*. Attacking *C. capitata* gave the wasps the advantage of larger body size. Why then did *P. vindemmiae* not prefer to attack *C. capitata* rather than *D. melanogaster* (although it also invested more female offspring in *C. capitata* than in *D. melanogaster*)? There may be other trade-offs. First, *P. vindemmiae* developed faster on *D. melanogaster* than on *C. capitata*. Second, it was observed that when a single female *P. vindemmiae* searched in a patch containing both *C. capitata* and *D. melanogaster* puparia, on average it took 331 s to finish one oviposition in *C. capitata*, with an average of 4.1 repeated visits to the same puparium before leaving the host after a single oviposition. In contrast, it took only 124 s to lay an egg into a *D. melanogaster* puparium and the wasp left the puparium immediately after one visit (Wang and Messing, unpublished data). It is known that a small host such as *D. melanogaster* has a thinner (0.02 mm) puparium shell than that of a large host such as *Musca domestica* (0.06 mm) (Morris and Fellowes, 2002). It may take a longer for *P. vindemmiae* to drill through a larger than a small host puparium. Thus, physical capacity and searching costs may offset size-dependent host species selection. These interactions would be further complicated by natal host species, for example, *P. vindemmiae* reared from *M. domestica* tended to be larger and had higher attack rates than those reared from *D. melanogaster* (Morris and Fellowes, 2002).

Adaptive host discrimination in parasitoids is also related to their offspring survival chances (Van Alphen and Visser, 1990). Van Alphen and Thunnissen (1983) reported that *P. vindemmiae* did not show any preference between unparasitized *D. melanogaster* puparia and puparia previously parasitized by *A. tabida*, in which the larval parasitoid had fully formed within the host puparia. However, when the secondary hosts had not yet formed into pupae *P. vindemmiae* preferred to attack unparasitized hosts, in which its offspring had higher levels of survival. Because there was no significant difference in offspring survival or body size of *P. vindemmiae* developing in unparasitized *C. capitata* puparia or puparia previously parasitized by *F. arisanus*, the selective acceptance of both host types by this parasitoid is adaptive and agrees with the prediction of the 'dynamic diet model' (Van Alphen and Visser, 1990). It was also found that *P. vindemmiae* did not discriminate between unparasitized puparia and puparia parasitized by *D. giffardii*, while the latter intended to avoid multi-parasitism (Wang and Messing, unpublished data). Thus, the observed results for *P. vindemmiae* support the notion that the decision to attack previously parasitized hosts reflects larval survival probabilities.

The current study supports the hypotheses that ectoparasitic idiobiont parasitoids tend to be generalists, and it provides indications as to why *P. vindemmiae* has the potential to expand its host range to include other parasitoid species associated with Diptera hosts. *P. vindemmiae* has been mass-reared and released against several tephritid fruit fly pests for several decades in South America, where augmentative releases of other fruit fly parasitoids such as *F. arisanus*, *D. longicaudata*, and *A. indica* were also made during the same period (Guillén et al., 2002; Ovruski et al., 2000). In view of its potential impacts against other principal fly parasitoids, *P. vindemmiae* should probably not be used in augmentative or classical biological programs. Furthermore, Guillén et al. (2002) recently compared the performance between *P. vindemmiae* and the host-specific pupal endoparasitoid of tephritids, *Coptera haywardi* (Oglobin), and recommended that the latter species was a better candidate.

There is a diverse array of *Drosophila* species that breed on fruits such as strawberry guava in the lowland forests of Hawaii. It is possible that increasing attack of these *Drosophila* populations by *P. vindemmiae* could increase the wild population size of this parasitoid, and this could eventually lead to an increased impact on other principle fruit fly parasitoids through apparent competition or direct interference. However, the field abundance and distribution of *P. vindemmiae* is unknown in Hawaii and elsewhere, because in the past field surveys of tephritid fruit fly parasitoids have largely ignored the pupal parasitoids (infested fruits rather than soil samples were usually collected from the field, see Ovruski et al., 2000). In the near future, we intend to document the potential non-target impact of *P. vindemmiae* through hyperparasitism on other primary tephritid fruit fly parasitoids in the field.

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