Larger olive fruit size reduces the efficiency of *Psyttalia concolor*, as a parasitoid of the olive fruit fly

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1. Introduction

Insect herbivores can potentially escape attacks by parasitoids when feeding within concealed or protected plant structures, such as fruits (Leyva et al., 1991; Sisterson and Gould, 1999; Sivinski, 1991), galls (Brandl and Vidal, 1987; Weis et al., 1985), seeds (Biere et al., 2002), and stems (Freese, 1995). Domesticated crops, with enlarged plant structures, can also protect internal feeders from parasitoids (Chen and Welter, 2003, 2007; Udayagiri and Welter, 2000). For example, the apple maggot fly, *Rhagoletis pomonella* Walsh, gained a structural refuge when it switched from its original wild host, the small Hawthorn fruit, to cultivated apples where its specialized parasitoids were unable to reach a significant proportion of maggots feeding inside the apple fruit (Feder, 1995). Therefore, any morphological enlargement of plant structures may enhance their quality as a refuge for herbivores, and consequently reduce the efficiency of parasitoids for biological control.

Many domesticated plants are strongly selected for larger harvestable fruit to increase their market value (Evans, 1993). Consequently, cultivated fruit may reduce the performance of parasitoids that attack herbivores feeding within relatively small, wild fruit (Kennedy, 2003; Price et al., 1980). Wang et al. (2008b) recently showed that larger olive fruit, resulting from crop domestication, favors the specialist olive fruit fly, *Bactrocera oleae* (Rossi) (Diptera: Tephritidae) as compared with the smaller wild olive fruit in the tephritid’s native range in southern Africa. Within the cultivated olives, female *B. oleae* preferred larger fruit for oviposition and there was no adverse effect on their offspring fitness. In contrast, olive fruit fly parasitoid, *Psyttalia lounsburyi* (Silvestri), was less effective in attacking olive fruit fly larvae within large cultivated olives in California, and this was attributed to its relatively short ovipositor in comparison to the depth of the pulp of mature cultivated olive fruit (Wang et al., 2008b). Sime et al. (2007) also reported that another larval olive fruit fly parasitoid, *Ponera phala* (Silvestri) successfully produced more offspring from smaller than larger cultivated olives.

The olive fruit fly is a major pest of olives in the Mediterranean basin (Tzanakakis, 2006; White and Elson-Harris, 1992). It recently invaded California and within a few years it spread throughout the state to pose a serious threat to the olive industry (Collier and van Steenwyk, 2003; Rice et al., 2003; Yokoyama et al., 2006). A classical biological control program was initiated in California in 2002, and five braconid parasitoids associated with *B. oleae* from Africa or Central Asia have been studied for the control of the olive fruit fly (Daane et al., 2008; Sime et al., 2006a, b, c). In order of
increasing ovipositor length, these are: Utetes africanus (Silvestri), P. lounsburyi, P. ponerophaga, P. concolor (Szépligeti), and Bracon celer Szépligeti (Wang et al., 2008b). Of these, U. africanus, P. lounsburyi, and P. ponerophaga appear to be the most specialized on B. oleae (Danea et al., 2008; Neuenschwander, 1982; Sime et al., 2007; Wharton and Gilstrap, 1983). Psytalla concolor and B. celer were also recorded from other frugivorous tephritid genera (Cope-land et al., 2004; Wharton and Gilstrap, 1983).

Psytalla concolor, the subject of this study, has often been introduced from Africa into the Mediterranean basin for the control of the olive fruit fly, although these efforts have not resulted in successful control of the olive fruit fly (Neuenschwander, 1982; Tzanakakis, 2006). One reason for its common use is that P. concolor can be mass-reared on the Mediterranean fruit fly, Ceratitis capitata (Wiedemann) (Wharton et al., 2000). While it is reported from multiple tephritid host species and is widespread in Africa (Kimani-Njogu et al., 2001; Wharton and Gilstrap, 1983), it likely comprises several genetically or biologically differentiated populations (Cope-land et al., 2004; Karam et al., 2008; Kimani-Njogu et al., 2001; Sime et al., 2006b). The parasitoid examined in this study, P. concolor, has a broader host range than P. lounsburyi (Daane et al., 2008; Wharton and Gilstrap, 2000) but still has a short ovipositor relative to the pulp depth in mature cultivated olives (Wang et al., 2008b).

The study reported herein continued investigations, begun with P. ponerophaga (Sime et al., 2007) and P. lounsburyi (Wang et al., 2008b), on how olive fruit size affects parasitoid—in this case P. concolor—performance on olive fruit fly larvae. The two earlier studies examined the effects of either two groups of different sized cultivars on P. ponerophaga (Sime et al., 2007), or the effects of fruit size within the cultivar Sevillano and across different sized cultivars on P. lounsburyi (Wang et al., 2008b); both using picked olives under laboratory conditions. Similar to the earlier investigations (Wang et al., 2008b), this study also examined the effects of fruit size within the cultivar Sevillano and across different sized cultivars on P. concolor in order to make a comparison between the two different parasitoid species. We then conducted a field study that used two olive cultivars with different sized olives to study parasitoid performance under conditions that better reflected actual levels of biological control, as compared with laboratory studies. Picked fruit and laboratory conditions may exert unanticipated effects on parasitoid performance. Finally, we manipulated the ovipositor size of P. concolor adults by using individuals from different tephritid hosts. Body size and ovipositor length of a generalist parasitoid often depends on the size of its host species, with the size of female wasps often positively correlated with the size of the natal hosts (e.g., Wang and Messing, 2004). We used populations of P. concolor reared on either C. capitata or B. oleae to produce individuals that had, relatively, longer or shorter ovipositors, respectively. This allowed studies of fruit size and ovipositor lengths to be conducted within the same species. Our particular interest in this study was to explore the advantage of the generalist parasitoid, P. concolor, for example, through manipulation of rearing hosts for augmentative biological control of B. oleae.

2. Materials and methods

2.1. Insects and olives

Laboratory colonies of B. oleae and P. concolor were maintained in a controlled room (25 ± 2 °C, 16L: 8D h, 40–60% RH) at the University of California Kearney Research and Education Center (KREC), Parlier, California, USA.

The fly colony has been maintained on olive fruit since 2003, with periodic additions of field-collected flies into the colonies. Adult flies were held in organy screened cages (60 × 60 × 60 cm) with water, honey, and protein yeast (Fisher Biotech, Fair-lawn, NJ, USA) provided upon eclosion. Olives were exposed to sexually mature (>2-wk old) female flies in the cages until each fruit had 3–5 oviposition marks. The newly infested olives were then distributed over a fine metal grid that rested 2 cm above a plastic tray (36 × 18 × 10 cm). Larvae matured in 9–12 d and dropped from the fruit into a container placed below, where puparia were later collected and then placed into a new organy screened cage for adult emergence.

The P. concolor colony was established in July 2007 from about 400 wasps that were shipped from the USDA-APHIS-PPQ, MOSCA-MED Parasitoid Rearing Facility at San Miguel Petapa, Guatemala, where the parasitoids were reared on C. capitata in artificial diet. This MOSCAMED P. concolor colony was originally established with parasitoids reared from tephritids infesting coffee in Kenya (Wharton et al., 2000). Previously, this P. concolor population was considered a synonym of P. humilis (Silvestri) (Kimani-Njogu et al., 2001) and has since been described as P. cf. concolor (Wharton et al., 2006). Psytalla concolor may be complex of closely related species (Wharton, pers. comm.). The origin of the P. concolor population used in this study was same as that used by Yokoyama et al. (2008), described as P. cf. concolor, and different from that used by Sime et al. (2006b).

For most experiments, parasitoids used were from the KREC colony maintained on B. oleae infested olives for 1–3 generations. For this colony, adult wasps were held in large, clear acrylic cages (30 × 30 × 30 cm) that had organy screening on three sides for ventilation and water and honey freely available. Infested olives containing second to third B. oleae instars were exposed to the parasitoids in the holding cages. Following exposure, the olives were transferred to plastic trays, as described above, for the rearing of parasitized larvae. To ensure mating, females were randomly chosen from cages that had approximately the same number of males for about 6 d prior to tests. In one set of experiments, P. concolor adults shipped directly from the MOSCAMED colony were used.

The olives used were green, moderately ripe olives collected in August from an untreated orchard at KREC where there were multiple olive cultivars, all fertilized and irrigated similarly. Olive cultivars used were Mission, Manzanillo, Ascolano, and Sevillano, which are the four most common cultivars found in California.

2.2. Fruit size and parasitoid performance—Sevillano cultivar

Fruit on Sevillano trees expressed enough variation in size to collect and categorize fruit into small (1.73 ± 0.02 cm, range 1.55–2.00), medium (2.41 ± 0.03 cm, range 2.05–2.75), and large (3.14 ± 0.03 cm, range 2.90–3.30) treatments, as reported by Wang et al. (2008b). Using these size categories, choice tests were conducted to determine the performance of P. concolor on different sized fruit in the same olive cultivar collected during the same period to provide similar levels of fruit maturity. The effect of host density on parasitoid performance was simultaneously examined during the trials with different sized fruit. This variable was added as B. oleae deposits more eggs on large fruit (Wang et al., 2008b). Two host density categories were created: a ‘variable host distribution’ where tested fruit were exposed to female flies to freely lay eggs, and a ‘uniform host distribution’ where host density was manipulated to be as similar as possible across fruit sizes. To obtain the variable host distribution, sets of the three different sized fruit were exposed to a single female fly for 2 h in a cylindrical acrylic cage (20 × 15 × 15 cm) that had three organy screen holes for ventilation. Uniform host density was obtained by controlling the exposure time of the fly to the different sized fruit to ensure each fruit contained 2–3 oviposition marks. The fly’s ovipositional stings deposited on the green fruit surface were easily visible, allowing us to control host density per fruit.
Experimental trials were conducted in the acrylic cages, described previously. The infested fruit were exposed to the parasitoid when *B. oleae* had developed into young third instars (8–10 d after inoculation). For each trial, a set of three different sized fruit were placed in a Petri dish (8 cm diameter) in the middle of the cage, and one female wasp was released into the cage for 36 h. To compare treatments, the female wasp’s searching efforts were recorded during two observation sessions—morning and afternoon. The location of the wasp on each fruit was recorded at 3 min intervals, for a total of 30 observations. Following exposure, the fruit were individually isolated and the numbers of flies or wasps that emerged were recorded. After which, exposed fruits were dissected and the unemerged or dead puparia were collected, reconstituted in water for 1–2 d, and then dissected under a microscope to determine the presence or absence of immature parasitoid cadavers and pharate adults, which were recorded.

Uniform and variable host density trials were conducted separately. The parasitoids used were mated females, 1–2 weeks old, and without prior oviposition experience. All trials were conducted at 25 ± 2 °C, 16L: 8D h, and 40–60% RH. There were 41 and 47 replicates for the variable and uniform host distribution trials, respectively, with the 30 observations for each wasp used as a single replicate. For data analysis, percentage of visits to each treatment was determined for each wasp so that the relative frequency reflects the wasps’ searching activity on the different fruit size categories. Parasitism was estimated based on the number of emerged and dissected wasps and flies.

2.3. Fruit size and parasitoid performance—multiple cultivars

Fruit from Mission, Manzanillo, Ascolano, and Sevillano cultivars were used to test parasitoid performance in commercial olive cultivars with greatly varying fruit size. Previously, Wang et al. (2008b) showed olives from these cultivars, collected during the same period, significantly varied in fruit pulp thickness (i.e., distance from the epidermis to pit) as follows: Mission (3.06 ± 0.06 mm), Manzanillo (4.05 ± 0.05 mm), Ascolano (4.89 ± 0.04 mm), and Sevillano (5.92 ± 0.04 mm). Choice tests were conducted to determine the performance of *P. concolor* on these four different sized cultivars, infested with variable or uniform host distributions. Methods used were similar to those described previously with the following exceptions. To obtain variable host density, 50 fruit of each of the four cultivars were exposed to 200 *B. oleae* females in a holding cage for 1–2 h. To obtain uniform host density, fruit collected in the holding cages that contained 2–3 oviposition stings were used, as determined by oviposition marks observed on the green fruit. Two female wasps (rather than one) were released into the acrylic and mesh cage, which contained one infested fruit of each of the four cultivars. The wasps were removed after 24 h (rather than 36 h). There were 31 and 37 replicates for the variable and uniform host distribution trials, respectively.

2.4. Fruit size and parasitoid performance in field cages

*Psyttalia concolor* females were released into field cages from September to November 2007 in the KREC olive orchard in order to determine patterns of parasitism on two olive cultivars (Mission and Sevillano). Ten *B. oleae* females were first released into a cylinder screen cages (45 cm long, 25 cm diameter, Tufpro Nylon Paint Strainers, Warren County, NC) enclosing about 50 fruit. Water and honey were provided for the flies in small vials. To control the resulting fly population, all cages were checked daily and the level of fruit infestation determined on 10 randomly selected fruit. After each fruit contained about 2–3 oviposition stings all adult flies were removed. When the resulting *B. oleae* larvae developed to third instars, in about 2 wks, 20 female wasps were released into each cage. Water and honey were provided for the wasps. Two weeks later, after the resulting flies and wasps were about to pupate, all fruit were collected and then held in the laboratory until adult flies or wasps emerged and were recorded. Additionally, the fruit were dissected and the unemerged or dead puparia were examined to better determine levels parasitism, as described previously. There were 10 replicates (cages) for each cultivar.

2.5. Ovipositor size and parasitoid performance

*Psyttalia concolor* reared on *C. capitata* and imported from the USDA-APHIS-PPQ rearing facility in Guatemala were compared with material that had been reared on *B. oleae* for three generations. The average size of wasps from Guatemala was compared with that of wasps reared from *B. oleae* at KREC by measuring the length of forewing, hind leg tibia, and ovipositor of female wasps using an ocular micrometer. Ovipositors were dissected from the abdomens and held fully stretched and straightened on the sticky side of transparent tape for measurement.

To compare parasitization efficiencies of adult female *P. concolor* reared from *C. capitata* and *B. oleae* a single female wasp was provided with 10 medium sized Manzanillo fruit, containing third instars of *B. oleae* for 24 h in the cylindrical acrylic and mesh cages. To determine the effect of pre-imaginable conditioning (larval and adult wasp’s experience) on oviposition behavior, female wasps reared from *C. capitata* were first exposed to olive fly-infested fruit one day prior to each test. Following above exposure, all exposed fruit were collected and held in the laboratory until flies or wasps emerged. Unemerged or dead puparia were dissected to determine parasitism. Each treatment had 20 replicates.

2.6. Data analysis

Results are presented as means (±SE). Before data analysis, proportional data were arcsine square-root transformed to satisfy the assumptions of ANOVA. Data were analyzed using one-way ANOVA for comparisons of means and Tukey’s HSD test for multiple comparisons of mean values (JMP software, V. 6.0.3, SAS 2006, Cary, NC).

3. Results

3.1. Fruit size and parasitoid performance—Sevillano cultivar

*Bactrocera oleae* density was not significantly different among fruit size categories in the uniform host distribution treatment (*F*$_{2,138}$ = 0.04, *P* = 0.96), while density significantly increased with increasing fruit size category in the variable host distribution treatment (*F*$_{2,120}$ = 47.94, *P* < 0.01) (Fig. 1A). Therefore, the desired treatments were established to compare the impact of fruit size on parasitoid performance, with host density as a covariant. Parasitism by *P. concolor* was significantly different among fruit size categories in both the variable (*F*$_{2,120}$ = 22.62, *P* < 0.01) and uniform (*F*$_{2,138}$ = 20.48, *P* < 0.01) host distributions, with parasitism higher in the small fruit size category than either the medium and large fruit categories, but not difference between the medium and large size categories (Fig. 1B). Foraging time by *P. concolor* did not significantly differ among fruit size category treatments in either variable (*F*$_{2,57}$ = 0.32, *P* = 0.72) or uniform (*F*$_{2,57}$ = 0.70, *P* = 0.50) host distribution treatments (Table 1).

3.2. Fruit size and parasitoid performance—multiple cultivars

Host density was similar among the cultivars in the uniform host distribution (*F*$_{3,144}$ = 0.44, *P* = 0.73); in contrast, there was a
significant treatment effect in the variable host distribution ($F_{3,120} = 66.57, P < 0.01$), with more $B. oleae$ larvae in each of the consecutively larger fruit size categories (Fig. 2A). Therefore, the desired treatments were established to compare the impact of fruit size, represented by different olive cultivars, on parasitoid performance with host density as a covariant.

Parasitism of $B. oleae$ was significantly different among treatments in both the variable ($F_{3,120} = 10.57, P < 0.01$) and uniform ($F_{3,144} = 21.99, P < 0.01$) host distribution treatments. In each case, there was significantly more parasitism in the smallest fruit category (Mission olives) than next largest fruit size (Manzanillo olives) that, in turn, had significantly more parasitism than $B. oleae$ in either of the two largest fruit cultivar categories (Ascolano and Sevillano, respectively) (Fig. 2B). Foraging time by $P. concolor$ on the different sized cultivars was not significantly different in either the variable ($F_{3,50} = 0.59, P = 0.61$) or the uniform ($F_{3,70} = 0.11, P = 0.96$) host distribution (Table 1).

### 3.3. Fruit size and parasitoid performance in field cages

There was no difference in host density per cage between small (Mission) and large (Sevillano) olive fruit cultivars ($F_{1,19} = 0.20, P = 0.66$), indicating that the methodologies used successfully established different sized fruit with similar host densities. In contrast, parasitism of $B. oleae$ was significantly higher in the smaller fruit than in the larger fruit ($F_{1,19} = 5.14, P < 0.05$) (Fig. 3).

### 3.4. Ovipositor size and parasitoid performance

Female $P. concolor$ reared from $C. capitata$ were larger than those reared from $B. oleae$ in length of forewing, hind leg tibia, and ovipositor (Table 2). While host density was similar among the three treatments ($F_{2,57} = 1.36, P = 0.26$), parasitism by females reared from $C. capitata$ was significantly higher than those reared from $B. oleae$ ($F_{2,57} = 5.40, P < 0.05$) (Table 3). There was no difference in parasitism between experienced and inexperienced females reared from $C. capitata$ (Table 3). Experienced females laid $0.65 \pm 0.27$ eggs prior to the test.

### 4. Discussion

Structural refuges for insect herbivores exist even in natural systems (Dyer and Gentry, 1999) and play an important part in sustaining multi-trophic interactions by preventing the over-exploitation of hosts by their parasitoids (Hawkins et al., 1993).

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**Table 1**

<table>
<thead>
<tr>
<th>Cultivar trial a</th>
<th>Variable</th>
<th>Uniform</th>
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</thead>
<tbody>
<tr>
<td>Fruit size category</td>
<td>27.0 ± 8.6a</td>
<td>40.9 ± 9.5a</td>
</tr>
<tr>
<td>Medium</td>
<td>33.2 ± 8.4a</td>
<td>23.9 ± 8.2a</td>
</tr>
<tr>
<td>Large</td>
<td>39.6 ± 9.5a</td>
<td>35.2 ± 9.3a</td>
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</table>

**Table 2**

<table>
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<tr>
<th>Cultivar trial b</th>
<th>Variable</th>
<th>Uniform</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fruit size category b</td>
<td>20.8 ± 6.7a</td>
<td>22.8 ± 8.5a</td>
</tr>
<tr>
<td>Medium</td>
<td>28.0 ± 7.3a</td>
<td>23.8 ± 8.2a</td>
</tr>
<tr>
<td>Large</td>
<td>24.2 ± 7.6a</td>
<td>22.9 ± 7.2a</td>
</tr>
<tr>
<td>Extra-large</td>
<td>26.8 ± 7.0a</td>
<td>30.4 ± 9.7a</td>
</tr>
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* a See Figs. 1A and 2A for a description of the variable and uniform host densities in “Sevillano” and “Multiple” cultivar trials.

* b Fruit size categories are Mission = small, Manzanillo = medium, Ascolano = large, and Sevillano = extra-large; using size designation by the California Olive Committee.
The effectiveness of olive fruit fly larval parasitoids on their insect host depends on the match of the parasitoid’s ovipositor with the depth at which their insect host feeds within plant organs (Feder, 1995; Leyva et al., 1985). The success of parasitoid attack on concealed feeders depends inversely on fruit size. Large cultivated olives have a pulp thickness that greatly exceeds the maximum ovipositor length of *P. concolor*. This was hypothesized 90 years ago (Latiere, 1917), and has been experimentally demonstrated in *P. poneroophaga* (Sime et al., 2007), and *P. lounsburyi* (Wang et al., 2008b). This situation limits expectations for the classical biological control of *B. oleae* in large olive cultivars (e.g., Sevillano). Over nearly 100 years, considerable efforts have been made to introduce *P. concolor* from Africa to southern Europe for biological control of *B. oleae*, but they have not proved successful (Greathead, 1976; Wharton, 1989). In most regions, the parasitoid has failed to establish, and elsewhere indifferent releases are required to obtain acceptable levels of control.

One hypothesis to explain its mixed performance is that, with its relatively short ovipositor, *P. concolor* is unable to reach larval larvae feeding in large cultivated fruit, as strongly supported by this study both under laboratory and semi-field conditions. However, many other biotic and abiotic factors might have also contributed their failure outside of their native range, particularly the availability of alternative hosts, such as *C. capitata* (Wharton and Gilstrap, 1983). From a practical standpoint, parasitoid species with shorter ovipositors may still be effective biological control agents of olive fruit fly found in cultivars with smaller fruit, in unmanaged olive trees, or in olive cultivars used for oil production that have smaller fruit. In California, for example, the smaller fruit found in unmanaged olives along roads (e.g., ornamental trees) and in abandoned orchards can support substantial *B. oleae* populations (Wang et al., unpubl. data) as do the wild-type fruit of oleaster in Europe (Bigler and Delucchi, 1981). Parasitoids with relatively short ovipositors may provide indirect control of olive fruit populations in commercial orchards by reducing *B. oleae* dispersal from these unmanaged sites. Field cage studies within olive canopies using *P. concolor* have shown a high level of olive fruit fly control in California coastal areas (Yokoyama et al., 2008), where small olive fruit (Mission cultivar) are predominantly grown for olive oil.

The findings of this study support the continued use of imported parasitoids for biological control of olive fruit fly in California’s coastal regions, which are reservoirs of the pest. While the performance of parasitoids with relatively short ovipositors is clearly reduced in large olive fruit, mature *B. oleae* larvae can be attacked when they perform behaviors associated with pupation and adult eclosion. In preparation for exiting the olive fruit as either third-instar larvae or adult flies, the third-instar larva prepares a ‘window’ within the fruit epidermis that will facilitate their exit. We also observed that when host density per fruit was considerably high (>10 larvae per fruit), the olive fly larvae utilize more of the fruit pulp, thereby putting themselves in range of parasitoids with short ovipositors.

Alternatively, one might consider introducing generalist larval parasitoids that have longer ovipositors or egg parasitoids that can take advantage of *B. oleae’s* placement of eggs near the surface of the fruit, regardless of fruit size. For example, the ovipositors of two generalist parasitoids, *Diachasmimorpha longicaudata* (Ashmead) and *D. kraussii* Fullaway, are more than twice as long with short ovipositors may generally be expected to correlate inversely with fruit size. Large cultivated olives have a pulp thickness that greatly exceeds the maximum ovipositor length of *P. concolor*.

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**Table 2**

<table>
<thead>
<tr>
<th>Host species</th>
<th>n</th>
<th>Forewing (length in mm)</th>
<th>Hind leg tibia (length in mm)</th>
<th>Ovipositor (length in mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>B. oleae</em></td>
<td>20</td>
<td>3.48 ± 0.05a</td>
<td>1.09 ± 0.02a</td>
<td>2.48 ± 0.04a</td>
</tr>
<tr>
<td><em>C. capitata</em></td>
<td>20</td>
<td>4.01 ± 0.03b</td>
<td>1.25 ± 0.01b</td>
<td>2.93 ± 0.03b</td>
</tr>
</tbody>
</table>

Within each column, means (±SE) followed by different letters are significantly different (Tukey’s HSD test after ANOVA, *P* < 0.05).

Our study showed that parasitism of the olive fruit fly by *P. concolor* was inversely related to fruit size, regardless of host density across the different sized fruit. Because larval *B. oleae* prefer to feed deeper inside the fruit pulp with increasing fruit size (Wang et al., 2008b), the reduction in parasitism levels by *P. concolor* in larger fruit is likely due to the parasitoid’s relatively short ovipositor that limits them from reaching the maggots deeper within the fruit pulp. Thus, increased olive fruit size, which is associated with crop domestication, creates a better structural refuge for larval *B. oleae*.

The success of parasitoid attack on concealed feeders depends on the match of the parasitoid’s ovipositor with the depth at which their insect host feeds within plant organs (Feder, 1995; Leyva et al., 1991; Lopez et al., 1999; Sivinski and Aluja, 2003; Weis et al., 1985). The effectiveness of olive fruit fly larval parasitoids when the parasitoids tested were reared from two different host species.

**Table 3**

| Rearing host species | Experience with infested olive | n | Host density | Parasitism %
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</thead>
<tbody>
<tr>
<td><em>B. oleae</em></td>
<td>No*</td>
<td>20</td>
<td>12.75 ± 0.86a</td>
<td>6.87 ± 2.23a</td>
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<tr>
<td><em>C. capitata</em></td>
<td>No*</td>
<td>20</td>
<td>13.80 ± 0.96a</td>
<td>15.74 ± 3.71b</td>
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<tr>
<td><em>C. capitata</em></td>
<td>Yes*</td>
<td>20</td>
<td>11.90 ± 0.58a</td>
<td>16.54 ± 4.12b</td>
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</table>

* Female wasps had no prior experience on olive infested with *B. oleae*.
* Female wasps were exposed to infested olives for 24 h prior to test.
* Total number of host larvae per 10 infested olives based on the numbers of emerged wasps, flies and dead puparia.
* Data were compared between the two different rearing hosts and between experience and inexperienced wasps reared from *C. capitata*. Within each column, means (±SE) followed by different letters are significantly different (Tukey’s HSD test after ANOVA, *P* < 0.05).
as that of P. concolor (Wang et al., 2008b), and both can be readily reared on B. oleae in the laboratory (Sime et al., 2006c). However, they have relatively broad host ranges and may not be suitable for release in California due to concerns about non-target impacts (Sime et al., 2006c). Fopius arisanus (Sonan), native to Southeast Asia, was the only egg parasitoid species that has been reported to attack B. oleae (Calvitti et al., 2002; Sime et al., 2008). F. arisanus is a highly effective parasitoid against many tephritid fruit flies and has been introduced widely to control other pestiferous tephritids worldwide (Rousse et al., 2005). Although the parasitoid is unlikely to attack non-target beneficial tephritids (i.e., biological control agents of weeds) (Sime et al., 2008; Wang et al., 2004), it did have a competitive advantage over species of larval parasitoids including P. concolor (Wang and Messing, 2002), D. longicaudata and D. kraussii (Sime et al., 2008; Wang and Messing, 2003; Wang et al., 2003). The egg-attacking parasitoid invariably eliminates these larval parasitoids through physiological suppression of the later-attacking parasitoid’s egg development, i.e., the early-acting competitive superiority (Wang et al., 2003, 2008a). Thus, there may be a tradeoff between parasitoid efficiency and direct or indirect non-target risk. Further evaluation of these issues is obviously needed for considering the release of these parasitoid species.

A large-sized host species for insectary rearing of P. concolor may be beneficial for augmentative biological control. Besides C. capitata, P. concolor can attack other large tephritid hosts such as B. latrond (Hendel) (Wang et al., unpublished data) and Anastrepha (P. Rendon, personal comm.). As shown in this study, large P. concolor females reared from C. capitata were more efficient in attacking olive fly larvae than smaller females reared from B. oleae. Rearing P. concolor on C. capitata larvae also results in relatively large parasitoid offspring (Billah et al., 2005). Our study on P. concolor also showed that the preimaginal conditioning by larval ovaries and adult experience did not affect parasitism by female wasps reared from C. capitata. The parasitoid may be able to obtain experience or learn quickly. On average, an experienced female wasp laid 0.65 eggs per female, and small female carried an average >30 mature eggs (n = 10), thus egg limitation is unlikely to be a factor on the low parasitization efficiency. A high degree of co-adaptation often exists between plants, specialized herbivores, and their specialized natural enemies in native ecosystems (Price et al., 1980). In this case, selection for larger olive as a result of crop domestication limits the accessibility of specialized larval parasitoids with short ovipositors in large commercial olive fruit. This may present challenges for efforts to manage B. oleae using introduced specialist parasitoids in cultivated large olives. However, the generalist parasitoid may have an advantage over specialists through manipulation of rearing hosts for augmentative biological control.

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