Innate Olfactory Responses of *Asobara japonica* Toward Fruits Infested by the Invasive Spotted Wing Drosophila

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Abstract Insect parasitoids are often manipulated to improve biological control programs for various arthropod pests. Volatile compounds can be a relevant cue used by most parasitoid hymenoptera for host or host microhabitat location. Here, we studied olfactory responses of the braconid *Asobara japonica* Belokobylskij, an Asiatic endoparasitoid of the invasive pest *Drosophila suzukii* (Matsumura), toward its host and host substrates. Adult *A. japonica* displayed an innate attraction to undescribed volatile cues from infested host fruits irrespectively of the juvenile rearing experience, i.e. they respond to a novel cue subsequently used for microhabitat selection. These data suggest that *A. japonica* parasitoids mass-reared on artificial diet and factitious host (*D. melanogaster*) can successfully locate their hosts. Naïve female parasitoids did not show a preference towards any of the tested host media. However, the enforced adult experience with the rearing host medium modified the olfactory preference patterns toward non-natal host fruits. These findings provide evidence of associative

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learning during the adult stage of *A. japonica*, and demonstrate its plasticity in exploiting the volatiles from various fruits infested by *D. suzukii*.

Introduction

Many hymenopteran parasitoids are known for their role in the regulation of arthropod pests of economic importance (Godfray 1994), and their biology, physiology, evolution, and ecology have been studied to better understand their use in agroecology (Jervis 2005). A parasitoid's host searching behavior is essential for parasitoid-host evolution and population dynamics, thus affecting their biological control efficiency (Vet 2001; Lof et al. 2013). Foraging parasitic wasps often seek out host species at medium and long distances by orienting toward volatile chemicals (Dicke and Sabelis 1988; Vet and Dicke 1992). A parasitoid's olfactory responses may be either innate or acquired and, if acquired, parasitoids must associate fruit odors with host cues (Vet and Groenewold 1990). Therefore, a parasitoid's prior associate learning can modify their responses to odors and, to some level, their effectiveness as biological control agents (Giunti et al. 2015).

The ability to rear hymenoptera parasitoids is a crucial component for studies on parasitoid biology, physiology, and behavior and can also be an important component in biological control programs. Multigenerational laboratory production of parasitoids is needed for these studies, often beginning with a relatively small number of parasitoids collected from the field. Rearing unavoidably results in laboratory adaptation, inbreeding depression, inadvertent selection and adaptation to artificial diets (Canale and Benelli 2012; Gariepy et al. 2015). These adaptations can result in the loss of some of the parasitoid's biological or behavioral traits that are essential for biological control (Sørensen et al. 2012).

Biological control of invasive insect pests of crops can be implemented through natural enemy conservation (Hogg et al. 2011; Zappalà et al. 2013; Haye et al. 2015; Mazzetto et al. 2016a); inoculative or inundative field release(s) (Biondi et al. 2016; Van Lenteren 2012); or classical biological control (Daane et al. 2015; Goldson et al. 2014; Kaser and Heimpel 2015). A recent example of this latter strategy is represented by the ongoing efforts to utilize effective parasitoids of the invasive spotted wing drosophila, *Drosophila suzukii* (Matsumura), hereafter called SWD (Daane et al. 2016; Guerrieri et al. 2016; Haye et al. 2016). This pest is native to South East Asia and it has recently invaded parts of Europe, North America and South American (Asplen et al. 2015; Gutierrez et al. 2016). Significant SWD population outbreaks are frequent and often unpredictable because of the high intrinsic rate of population increase of this species (Hamby et al. 2016; Wiman et al. 2016) and owing to larva's ability to feed and develop on ripening fruits of numerous wild and cultivated species (Arnó et al. 2016; Briem et al. 2016; Kenis et al. 2016; Garantonakis et al. 2016; Wang et al. 2016).

In this framework, biological control programs targeting this important pest were proposed as a sustainable long-term control strategy and initiated in 2013. For one program, SWD parasitoid explorations were conducted in China and South Korea,

from which parasitoid species were identified as potential candidates and imported for further quarantine studies in the USA (Daane et al. 2016; Guerrieri et al. 2016). Among these, the braconid endoparasitoid *Asobara japonica* Belokobylskij showed to be an efficient SWD parasitoid in quarantine laboratory bioassays (Daane et al. 2016; Biondi et al. in prep.). Nevertheless, its efficacy and biological attributes were not examined in a multitrophic context. The present laboratory study was designed to assess the behavioral responses that might impact field performance of *A. japonica*. A series of dual-choice bioassays were conducted using a two-way olfactometer to test *A. japonica* response to volatiles emitted from different SWD-infested host fruits. The role of juvenile and/or adult experience in determining the response to those volatiles was also determined.

Materials and Methods

Study Insects

The SWD colony was initiated using adults originating from infested cherries collected during spring and summer 2013 near Parlier, California, USA (Wang et al. 2016). The *Drosophila melanogaster* Meigen colony was initiated with pupae and adults purchased at the Drosophila Species Stock Center at the University of California San Diego (San Diego, California, USA); Stock Number 14021–0231.131; wild type obtained from a multifemale collection in La Jolla, CA, USA, on September 2009. For both fly colonies, adults were maintained in large (45 × 45 × 45 cm) BugDorm cages (BioQuip Products Inc., California, USA) provisioned with plastic vials (25 × 95 mm) half filled with a cornmeal and yeast-based diet for adult oviposition and larval rearing (Dalton et al. 2011). A deuterotokous parthenogenetic strain of *A. japonica* was obtained from material collected in Geochang, South Gyeongsang province (South Korea) during a foreign exploration for SWD natural enemies in August 2013 (Daane et al. 2016). All colonies were maintained under controlled conditions (23 ± 1 °C, 16 L: 8D, 50 ± 20% RH); the parasitoid colony was housed in a quarantine facility at the University of California, Berkeley (California, USA) (permit: P526P-11-03867), where the described studies were conducted. There were 10 to 20 parasitoid generations in quarantine prior to initiation of the experiments.

Three additional colonies were established for specific experiments, and maintained for at least three generations prior to their use in any experiment. These colonies used different host and substrate combinations: SWD infesting fresh cherries (*cv* Rainier), strawberries (*cv* Monterey) and blackberries (*cv* Kotata). For each colony, organic fruits were purchased at the local market, immersed in a 2% bleach solution for 3 min, rinsed twice in water, and then examined under the microscope to discover and remove any fruits that were infested by any arthropod or were mechanically damaged. SWD-infested fruits were obtained by exposing the clean fruit to adult SWD in the BugDorm cages for 12 h. Newly infested fruit were then held for 3 to 4 days for the SWD to develop to suitable larval instars for *A. japonica* (Ideo et al. 2008; Hamby et al. 2016). The parasitoids were reared on the infested fruit in small (0.473 L) plastic cups covered with a fine mesh-screened lid; the infested fruit rested on a metallic mesh that supported the fruit above the bottom of the cup, which allowed the parasitoid to forage on most of

the fruit surface. A piece of wet paper towel was also provided as a possible fly pupation substrate.

Olfactometer Dual-Choice Bioassays

To assess the volatile chemical preferences by *A. japonica* females, several dual-choice bioassays were conducted using an olfactometer composed of a Y-shaped Pyrex tube (YTO-A13, ARS Inc., Florida, USA) of 2.5 cm of diameter, with an entry arm (18 cm long) and two side arms (10 cm long). The olfactometer was positioned horizontally in a white-foam box. Each side arm was hermetically connected to an odor-source chamber consisting of a cylindrical glass jar (5 L) with a glass stopper fixed on top. Before reaching the jar, the airflow passed through a hydrocarbon filter and then through two water bubblers to humidify the air. The wind speed was regulated at 0.7 L min^{-1} using a two-channel air delivery system (ARS Inc., Florida, USA). The device was operated in a dark room to minimize exterior light effects. Illumination during the trials was provided by two 22-W cool white fluorescent bulbs placed 1 m above the Y-tube. The bioassays were conducted between 13:00 and 18:00 h, at 23 ± 1 °C and 50 ± 10% RH.

Odor sources were composed of either 50 g of uninfested or SWD-infested cherries, strawberries or blackberries. Individual *A. japonica* females were released into the base of the Y-tube entry arm, after which each parasitoid was observed until it moved upwind toward the end of one of the side arms (i.e., made a choice) or for a maximum of 5 min (i.e., no choice). The Y-tube was cleaned with 95% alcohol and the odor sources to the olfactometer arms were exchanged to remove any asymmetrical bias in the experimental set-up (Biondi et al. 2015) after every four choices. Each experiment was replicated until 50 independent choices were obtained. The results of each dual-choice test were analyzed by a likelihood chi-square test for comparing the proportion of wasps choosing a given cue.

Effects of Juvenile and Early Adult Experience on Attraction Toward Volatiles

A series of dual-choice tests were carried out to assess the potential effect of *A. japonica* juvenile and early adult rearing experience on adult female olfactory response. We investigated the capacity to detect and distinguish between volatile cues from SWD-infested and uninfested fruits (cherries, blackberries or strawberries). For this, we used naïve 2 to 3 d old *A. japonica* females reared on the respective host fruits infested by SWD. In this case, parasitoids experienced the host- and host-fruit borne cues during their juvenile development. During adult emergence and for the following 0–12 h (newly emerged parasitoids were collected twice a day) parasitoids stayed in contact with the remaining substrate, i.e., dry partial SWD-infested fruit and SWD puparia. Virgin parasitoid females were used in the bioassays because males are rare both in the laboratory (≈ 4%, Biondi et al. in prep.) and in the field (<2%, Daane et al. 2016). Moreover, females were shown to readily attack and oviposit on suitable hosts starting from the first day of adulthood, having a consistent mature egg-load at the emergence (Biondi et al. in prep.).

We also tested parasitoids reared from SWD and *D. melanogaster* on cornmeal diet (i.e., parasitoids that never experienced any kind of fruit cue for at least 10 generations

before the experiment). Newly emerged parasitoids (hereafter called naïve with regard to oviposition) were collected from the rearing tubes or cups twice a day, and then transferred to glass vials (25 × 95 mm) that were provisioned with honey droplets on the foam lid and wet paper. Females were used within 2–6 h after they were collected.

The data generated from the various rearing and volatile cue combinations were analyzed by a generalized linear model (GLM) designed for binomial data. *Rearing substrate* (i.e., cornmeal medium, cherries, strawberries and blackberries), *rearing host species* (i.e., SWD and *D. melanogaster*) and *host fruit volatile* (i.e., cherries, strawberries and blackberries) were the fixed factors. The *type of substrate* (cornmeal diet or fruits) was used as covariate in the model. Type III of sum of squares was used to calculate the Wald Chi-square statistics. A confidence interval level of 95% was used for the significance of all the statistical tests.

Effects of Juvenile and Adult Experience on Preference Among Volatiles

Bioassays were conducted to assess whether parasitoids reared for three generations on a given host fruit species (cherry, strawberry or blackberry) showed any preference toward volatile cues produced by that same (natal) host fruit infested by SWD or for those produced by an alternative SWD-infested fruit species. For parasitoids reared on strawberries and blackberries, the alternative host fruit volatile source was cherries, and for parasitoids reared on cherries the alternative host fruit volatile source was strawberries.

The same experiment was repeated using 8 to 9 d old female parasitoids exposed individually and for 6 d to host fruit infested by 20–30 SWD larvae suitable for oviposition. Such fruit was renewed every 2 d. Although parasitism and/or potential superparasitism activities were not quantified during the conditioning period, we know from a companion study that the oviposition period of *A. japonica* in similar constant host density and environmental conditions averaged to 10.3 d (9 d min; 16 d max) (Biondi et al. in prep.). Consequently, it is likely that tested females were fecund and thus searching for hosts. These older and experienced females, hereafter referred to conditioned, were transferred into clean glass tubes and used within 2–6 h after they were collected.

GLM was used, as described above, to study the effects of the *rearing fruit species* and *experience* (naïve and conditioned) factors on the parasitoid choices among the cues from SWD-infested rearing and alternative host fruits. In this case, the *alternative fruit species* tested in the olfactometer was used as covariate in the model.

Results

Effects of Juvenile and Early Adult Experience on Attraction Toward Volatiles

Asobara japonica females reared from SWD-infested fruit (cherry, strawberry or blackberry), cornmeal or *D. melanogaster* reared from cornmeal promptly responded to the tested volatile cues. Per each test, to achieve the 50 choices in the Y-tube, 50 to 54 wasps were used, i.e., very few insects did not make a choice during the 5 min test period (data not shown). This trend was consistent in all the performed tests, and the proportion of wasps that did not make a choice did not vary significantly among the four *rearing substrates* (i.e. cornmeal medium, cherries, strawberries and blackberries)

(χ^2 = 0.691, df = 3, P = 0.875), between the two *rearing host species*, i.e., SWD and *D. melanogaster* (χ^2 = 0.064, df = 1, P = 0.800), and among the three *host fruit volatiles* (χ^2 = 3.083, df = 2, P = 0.214).

In all choice tests, female parasitoids were significantly attracted by the volatiles from SWD-infested fruits compared with healthy fruits (Fig. 1). SWD-infested fruits resulted in 70–96% positive responses. The lowest choice preference percentages were for wasps reared from cornmeal diet infested with either SWD or *D. melanogaster*. GLM analyses showed preference percentages varied significantly among the four *rearing substrates* (χ^2 = 12.730, df = 3, P = 0.005), and not significantly between the two *rearing host species* (χ^2 = 0.079, df = 1, P = 0.779). Parasitoids showed similar levels of response toward tested volatile cues irrespective of the fruit species or given *host fruit volatile* (χ^2 = 0.079, df = 2, P = 0.779) (Fig. 1).

Effects of Juvenile and Adult Experience on Preference Among Volatiles

For each choice assays 51 to 55 wasps were used, and the proportion of wasps that did not make a choice did not vary significantly because of their *experience* (naïve vs
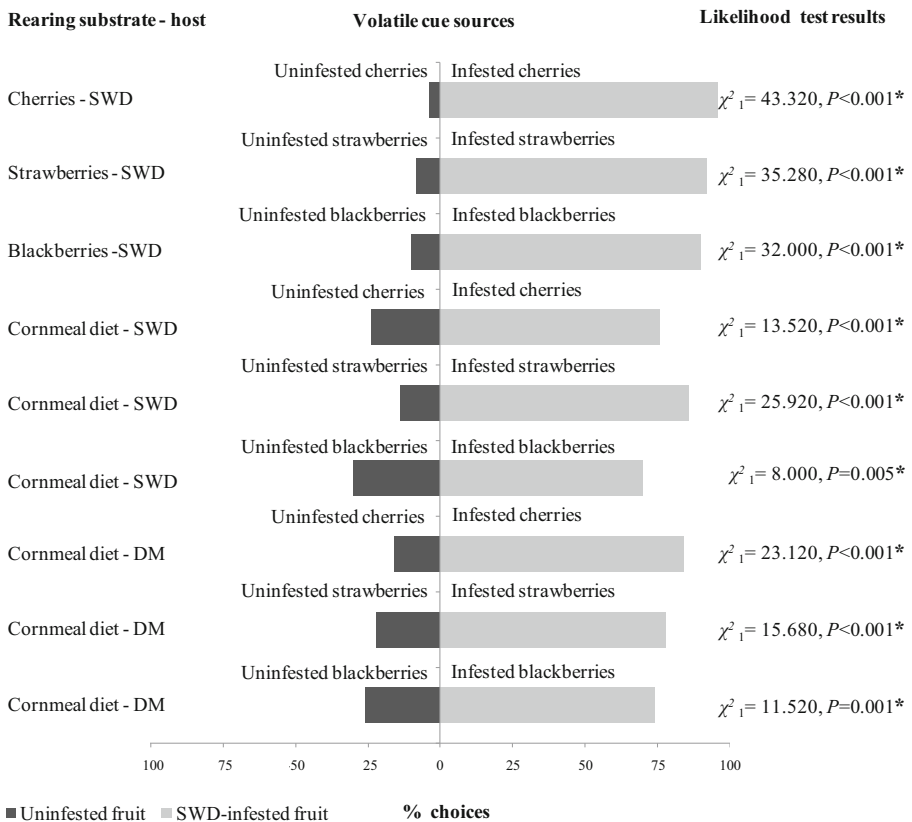

Fig. 1 Percent *Asobara japonica* female adults showing a response toward the volatile cues produced by *Drosophila suzukii* (SWD)-infested and uninfested cherries. Tested parasitoids were reared on SWD-infested fruits, SWD or *Drosophila melanogaster* (DM)-infested cornmeal diet. The results of the likelihood chi-square tests are reported per each test. Asterisks indicate statistical significance at confidence interval level of 95%

conditioned, $\chi^2 = 2.582$, df = 1, $P = 0.108$) nor of the *rearing fruit medium* ($\chi^2 = 0.763$, df = 2, $P = 0.682$).

The *rearing fruit species* significantly influenced the preferences of *A. japonica* toward the volatiles from rearing vs. alternative host fruits ($\chi^2 = 15.376$, df = 2, $P < 0.001$). Naïve and young *A. japonica* females reared from cherries and blackberries did not show a preference between the volatiles from the rearing host and the alternative host fruits. However, naïve females reared from strawberries were significantly more attracted by the volatiles from the same rearing host (Fig. 2). The *experience* factor ($\chi^2 = 27.069$, df = 1, $P < 0.001$), but not its interaction with the *rearing fruit species* factor ($\chi^2 = 2.442$, df = 2, $P = 0.295$), significantly influenced the preferences of *A. japonica* toward the volatiles from the rearing or alternative host fruits. Older females that experienced oviposition in blackberries preferred the volatiles from cherries, while those that experienced oviposition in cherries preferred the volatiles from strawberries. Female with prior oviposition experience in strawberry and cherries showed no difference in preference toward any specific fruit (Fig. 2).

Discussion

Asobara japonica is a sympatric parasitoid of SWD in this pest's native range (Mitsui et al. 2007; Daane et al. 2016; Guerrieri et al. 2016); in quarantine studies, it showed potential as an effective parasitoid and for this reason was examined as a potential biological control agent, including studies of its olfactory responses. Parasitoids attacking larvae of various Drosophilidae will encounter a variety of microhabitats
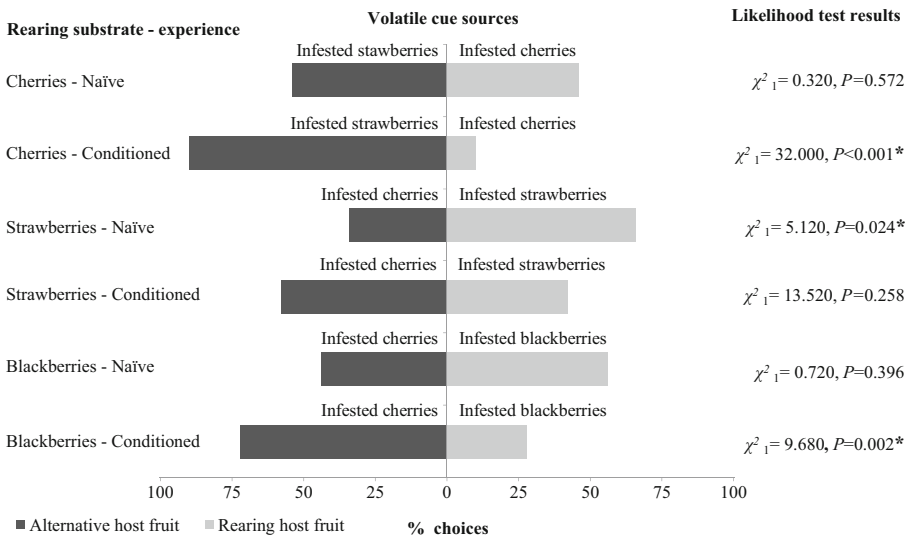

Fig. 2 Percent *Asobara japonica* female adults showing a response toward the volatile cues from SWD-infested natal and alternative host fruits. Tested parasitoids were reared on three host fruit species and subjected to two different host-exposure experiences: (i) *naïve*, which experienced the host fruit as juvenile and during adult emergence, and (ii) *conditioned*, which spent seven additional days foraging and parasitizing SWD larvae on the same host microhabitat. The results of the likelihood chi-square tests are reported per each test. Asterisks indicate statistical significance at confidence interval level of 95%

(Vet and van Opzeeland 1984), and efficient host seeking behaviors will undoubtedly contribute in field success (Vet 2001; Lof et al. 2013). Here, we demonstrated that *A. japonica* females reared in the laboratory for many generations respond to volatiles emitted by SWD and host fruit complex. In all trials, female *A. japonica* oriented toward SWD-infested as opposed to uninfested fruits. Some studies predict that specialists, more than generalists, will respond to cues specific to their hosts and immediate microhabitats, whereas generalists, other than specialists, more often respond to higher trophic level stimuli, i.e., the host plant (Vet and Groenewold 1990). This could be important feature of *A. japonica* as a SWD natural enemy. Within a given season, each generation of *A. japonica* may occupy a different host microhabitat because SWD will likely infest different fruit species as the season progresses (Diepenbrock et al. 2016; Pelton et al. 2016; Wang et al. 2016).

Other studies have demonstrated that natural enemy species can be attracted by volatile compounds originating directly from hosts or host products, such as host feces, silk, exuvia or emitted pheromones (Wertheim et al. 2003; Benelli et al. 2013, 2014); from the host food plant or plant parts (Wertheim et al. 2003; Wäschke et al. 2014); or from the chemical emitted because of the host feeding on the plant (Kaplan 2012; Pérez-Hedo et al. 2015). In this study, we did not aim at identifying the chemicals produced by SWD-infested fruits. It is possible that the strong attraction to infested-fruits compared with uninfested fruits could be from the pest itself – either from the adults leaving a cue during oviposition or from the activity of fly larvae inside the fruit – and/or by the SWD symbiotic microbioma (Dekker et al. 2015; Hamby and Becher 2016; Mazzetto et al. 2016b). Previous studies showed that another group of drosophilid parasitoids, *Leptopilina* spp. (Hymenoptera: Figitidae), exploit aggregation pheromones for host location, although this was not the case for the more closely related *Asobara tabida* (Nees) (Wertheim et al. 2003; Wäschke et al. 2014). Further specific studies with *A. japonica* and its SWD-susceptible fruit complexes are needed to clarify this specific aspect.

Innate stimuli are thought to be preprogrammed response patterns more typical of specialized natural enemies (Hedlund et al. 1996), although we are not suggesting here that *A. japonica* is a specialist. The innate preference for the volatiles emitted by SWD-infested fruits was consistently exhibited by naïve females (i.e., with no oviposition experience) reared on artificial diet infested by larvae of a factitious hosts (*D. melanogaster*), thus without any experience with host fruit-associated cues. In our trials, *A. japonica*'s response to SWD-fruit was not affected by the fly species used during the insectary rearing. We previously found that *A. japonica* adults that developed as larvae on *D. melanogaster* are smaller than those reared from SWD (Daane et al. 2016), and thus potentially less fecund or effective in host foraging (Jervis 2005). Nevertheless, *D. melanogaster* is an iconic laboratory test subject that is well adapted to artificial rearing and has a *mean generation time* (T) that is 1 week shorter than that of SWD (Lin et al. 2014; Hamby et al. 2016). We thus suggest that *A. japonica* could be more efficiently mass-reared on *D. melanogaster* for use in biological control because searching behavior would not be altered. In addition to the innate *A. japonica* response toward SWD-infested fruits, we noticed a small effect of the larval and/or early adult experience with host fruit cues, including higher preference for SWD-infested fruits from parasitoids reared from SWD-infested fruits compared with

parasitoids from SWD in cornmeal diet. In these experiments, the tested parasitoids may have experienced host-fruit cues during juvenile development and adult emergence. Plants can mediate multitrophic interactions between herbivores and their insect parasitoids and understanding these effects may improve crop or environmental manipulation to increase the levels of biological control and reduce pest crop damage. Pre-treatment with odor of a target crop may enhance the foraging efficiency of mass-reared and released parasitoids from hosts cultured in artificial diet (Canale et al. 2014; Giunti et al. 2015). In this specific case, *A. japonica* at their early adult stage could be trained to recognize the odor of a given fruit species.

Parasitoid learning may take place during all developmental stages (Vet and Groenewold 1990). In this study, we were not able to distinguish between pre-imaginal and early adult learning. However, our results suggest that choice patterns could be changed through adult enforced experience on the natal hosts. In this case, host cue associative learning took place through contact with kairomones and/or the reward of successful oviposition (Turlings et al. 1993). Surprisingly, in our study this learning process caused a switching of preference pattern, from the rearing host fruit to the alternative one. Naïve females reared on a given fruit were always significantly more attracted by their natal host fruit. Interestingly, conditioned and older females that had a 6 d experience ovipositing on the natal host fruit, preferred the alternative one, in the case of wasps reared on cherries or blackberries, or did not show anymore the preference toward the natal host fruit, in the case of strawberry-reared parasitoids.

These results suggest a potential plasticity of host microhabitat location by *A. japonica* and that enforced adult experience, rather than larval and early adult experience, can play a key role in determining the adult's behavioral plasticity. The parasitoids used in our experiment were, however, removed from their natal host fruit 2–6 h before experiments were initiated, and further experiments are therefore needed to determine for how long memory of this modification can be retained. For parasitoids attacking hosts using a variety of different plant species, such associative learning has been speculated to favor the evolution of learning by the parasitoid to deal with the variability of plant cues or diverse connections between the herbivore and its host plants (Vet and Groenewold 1990). In this specific case, we show only the variability in olfactory response by *A. japonica* females with enforced experience, whereas we do not know what impact this learning might have on host searching behaviors in the field. We can speculate, however, that *A. japonica* populations could succeed in a multi-crop agroecosystem in which different SWD-susceptible host fruits are simultaneously present. Preference switching patterns toward non-natal microhabitats following enforced adult experience were found by Vet and van Opzeeland (1984) studying two other *Asobara* species, *A. tabida* and *A. rufescens* (Foerster), parasitoids of drosophilae infesting fermenting fruits and decaying plant material, respectively. Here, we only investigated the *A. japonica* response to the volatile of a single microhabitat, i.e., SWD-infested fresh fruits that are the target of the biological control program, but further studies investigating the behavioral effects of volatiles from other microhabitats could provide a clearer picture on learning capacity and host specificity of this parasitoid species, as well as other important traits of exotic natural enemies such as non-target impacts and climatic tolerances.

Conclusions

The results from this study confirm that *A. japonica* orients towards volatile cues for host habitat location. These findings highlight the innate ability of *A. japonica* to find and exploit SWD-infested fruit. Parasitoid females reared in quarantine for several generations did not lose their foraging capacity toward volatiles from plant food infested by host insects. This was valid even for parasitoids reared on the artificial substrate and on a factitious host, thus supporting the idea of mass rearing *A. japonica* on the more laboratory-adapted host, *D. melanogaster*. The behavioral consequences of enforced adult experiences on host volatile preferences were also noticed. Moreover, this parasitoid showed the plasticity to exploit the volatiles from various host fruits being able, after some experience on the natal microhabitat, to switch its pattern of preferences toward non-natal host fruits.

Compliance with Ethical Standards

Conflict of Interests   The authors declare that there is no conflict of interests regarding this paper and that they have no competing financial interests.

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