Population dynamics and ecology of Drosophila suzukii in Central California

Article *in* Journal of Pest Science · July 2016

DOI: 10.1007/s10340-016-0747-6

Population dynamics and ecology of Drosophila suzukii *in Central California*

Xin-Geng Wang, Thomas J. Stewart, Antonio Biondi, Brandy A. Chavez, Chuck Ingels, Janet Caprile, Joseph A. Grant, Vaughn M. Walton, et al.

Journal of Pest Science

ISSN 1612-4758
Volume 89
Number 3

J Pest Sci (2016) 89:701-712
DOI 10.1007/s10340-016-0747-6

J Pest Sci (2016) 89:701–712
DOI 10.1007/s10340-016-0747-6

ORIGINAL PAPER

Population dynamics and ecology of *Drosophila suzukii* in Central California

Xin-Geng Wang[1] · Thomas J. Stewart[1] · Antonio Biondi[1,2] · Brandy A. Chavez[1] · Chuck Ingels[3] · Janet Caprile[4] · Joseph A. Grant[5] · Vaughn M. Walton[6] · Kent M. Daane[1]

Received: 25 October 2015 / Revised: 22 February 2016 / Accepted: 5 March 2016 / Published online: 17 March 2016

Abstract *Drosophila suzukii* is a serious pest of several fruit crop systems in California's Central Valley, which is one of the world's major fruit-growing regions. This study followed *D. suzukii* seasonal population dynamics in multiple cropping and riparian systems in four cherry-producing counties of the Valley. Apple cider vinegar baited traps were used to monitor *D. suzukii* adults weekly, from April 2013 to July 2014, in 28 fields. Results show peak captures in the spring and fall seasons. In cherry orchards, adult trap counts were the highest near harvest (June) and declined thereafter, as fly populations moved to other crop (e.g., citrus) or non-crop habitats. The number of captured adults was positively related between pairs of sampled sites based on their proximity but was negatively related to differences in fruit ripening periods between different crops, suggesting that fly populations moved among crop and/or non-crop habitats during the year or had varying population dynamics on different crops and in different seasons. Mature egg load per female was higher during the fruiting season but lower during the winter season, with the majority of winter-captured females not containing mature eggs. This survey also reports for the first time the presence of trapped *D. suzukii* adults bearing melanized and encapsulated parasitoids in North America, non-target captures of larval drosophilid parasitoids in the traps, as well as the occurrence of larvae in the ovaries of adult female *D. suzukii*.

Keywords Spotted wing drosophila · Population ecology · Egg load · Encapsulation · Ovoviviparity

Special Issue: Spotted Wing Drosophila

Communicated by M. Traugott.

✉ Xin-Geng Wang
xggwang@ucanr.edu

1 Department of Environmental Science, Policy and Management, University of California Berkeley, Berkeley, CA, USA

2 Department of Agriculture, Food and Environment, University of Catania, Catania, Italy

3 University of California Cooperative Extension, Sacramento County, Sacramento, CA, USA

4 University of California Cooperative Extension, Contra Costa County, Pleasant Hill, CA, USA

5 University of California Cooperative Extension, San Joaquin County, Stockton, CA, USA

6 Department of Horticulture, Oregon State University, Corvallis, OR, USA

Key message

- We monitored *Drosophila suzukii* population dynamics in 28 different fields located in California's Central Valley.
- Adult flies captured by apple cider vinegar baited traps showed two peaks of abundance, one in spring and another in fall.
- Higher fly numbers were first caught in host crops early the fruiting season and then in other crop or non-crop habitats later in the season, suggesting population migration.
- Management strategies should then consider suppression of source populations in non-crop habitats.

Introduction

The spotted wing drosophila, *D. suzukii* Matsumura, is native to Asia, but has widely invaded North America and Europe (Asplen et al. 2015; Cini et al. 2014; Walsh et al.

2011), and was more recently found in Brazil (Deprá et al. 2014). In the continental US, the fly is now reported in most fruit production regions since being first detected in California in 2008 (Walsh et al. 2011). *D. suzukii* is unique among Drosophilidae in that adult females have serrated ovipositors (Atallah et al. 2014), allowing them to oviposit in intact (ripening) soft- and thin-skin fruits such as cherries, blueberries, blackberries, mulberries, raspberries, strawberries, and some wine grape cultivars as well as ornamental plant species (Ioriatti et al. 2015; Lee et al. 2015; Poyet et al. 2014; Yu et al. 2013). Although it is unlikely for the fly to oviposit into fruits with thick and hard skin or fuzzy surfaces such as apples, cranberries, oranges, peaches, and pomegranates, it can complete development when these 'suboptimal' hosts are damaged, rotted, or overripe (Kaçar et al. 2016; Steffan et al. 2013; Stewart et al. 2014). Therefore, numerous cultivated and uncultivated fruits can be utilized by *D. suzukii* (Lee et al. 2015).

Pesticide applications have been the primary control tactic against *D. suzukii* in North America (Beers et al. 2011; Bruck et al. 2011; Haye et al. 2016). However, the efficacy of insecticide-based programs could be limited by the abundant non-crop host plants that may act as reservoirs for the fly's reinvasion into the treated commercial crops, resulting in multiple applications per crop season (Pelton et al. 2016; Van Timmeren and Isaacs 2013). *D. suzukii* is a highly mobile pest, even migrating from low to high altitudes between winter and summer seasons in Japan, likely seeking better host sources or climatic conditions (Mitsui et al. 2010). Immigration from unmanaged hosts may support the persistence of *D. suzukii* in commercial orchards, which would otherwise be eliminated by recurrent insecticide applications (Klick et al. 2016). Host plants in unmanaged habitats could then act as sinks or sources of *D. suzukii* populations in commercial crops (Briem et al. 2016). It is therefore critical to understand the pest's seasonal phenology and factors triggering dispersal and persistence of this pest's populations on a landscape-scale in order to develop reduced risk strategies for highly mobile and polyphagous pests such as *D. suzukii* (Carriere et al. 2012; Mazzi and Dorn 2012).

Crop infestation and economic loss, in cherries for example, may then depend on the population density, distance, and seasonal movement of *D. suzukii* adults dispersing from alternate hosts, and these traits may largely depend on local climatic and landscape traits. In this framework, this study aimed to determine the seasonal phenology of *D. suzukii* in different landscapes in California's Central Valley, a major fruit-growing region where the agricultural landscape can be a mosaic of various cultivated and unmanaged host fruit crops of *D. suzukii*. Such diverse landscapes result in the inevitable presence of *D. suzukii* populations that are resident near susceptible crops and represent a difficult challenge for the management of this pest. We monitored adult *D. suzukii* trap captures as an estimate of fly population dynamics and fruit risk in four major cherry-producing regions in California's Central Valley, and then analyzed the relationship in the number of captured adults between different fields based on their proximity and differences in fruit ripening periods.

In addition, we dissected a portion of the captured female flies to determine their reproductive status and then analyzed the possible effect of seasonal temperature on mature egg load of adult *D. suzukii*. Many larvae of *Drosophila* species are able to defend themselves from parasitoid eggs placed inside their bodies by surrounding the egg with blood cells that eventually melanize and form a black capsule surrounding the egg, resulting in the immature parasitoid death by asphyxiation (Chabert et al. 2012). Therefore, we examined a portion of captured flies for the possible presence of a black capsule inside the fly's abdomen to determine whether resident parasitoids were attempting to attack *D. suzukii*, but might have been unable to develop from it due to the host's immune response (Chabert et al. 2012; Kacsoh and Schlenke 2012). We also monitored the captures of drosophilid parasitoids in the monitoring traps.

Materials and methods

Monitoring sites

Studies were conducted in four major cherry production regions in California's Central Valley: Brentwood (Contra Costa County), Courtland (Sacramento County), Stockton (San Joaquin County), and Parlier (Fresno County; Table 1).

Cherry is the major tree fruit grown in both the Courtland and Brentwood areas, whereas the agricultural landscape in the Stockton or Parlier area is typically dominated by various nut and stone fruit crops. Monitoring traps for *D. suzukii* were placed in three cherry orchards, one kiwifruit vineyard and one pear orchard in the Courtland area, and in one peach and two cherry orchards in the Stockton area. Near Brentwood, traps were placed in each of four fruit orchards (cherry, apricot, pear, and peach), along a riparian area located at the edge of the fruit orchards, and in a 4.5 ha organic farm with mixed fruit crops. Potential host plants including wild *Rubus*, Klamath plum (*Prunus subcordata* Benth.), cherry plum (*P. cerasifera* Ehrh.), and a prickly pear cactus *Opuntia* sp. were present in the riparian area, while various fruits (apple, fig, loquat, lemon, and persimmon) were grown in the organic farm. In Parlier, traps were placed in 14 different orchard crops

Table 1 Locations and monitoring sites of *D. suzukii* adult in California Central Valley during 2013 and 2014

Locations	Sites	Latitude (N)	Longitude (W)	Fruit or habitat	No. of traps
Courtland[a]	1	38°19′03″	121°34′58″	Cherry-1	2
	2			Kiwi	3
	3	38°17′60″	121°35′03″	Cherry-2	2
	4	38°17′40″	121°35′07″	Cherry-3	2
	5			Pear	1
Stockton[b]	1	37°48′47″	121°06′33″	Cherry-1	3
	2	38°02′05″	121°06′15″	Cherry-2	3
	3			Peach	3
Brentwood[c]	1	37°54′53″	121°42′21″	Cherry	1
	2	37°54′50″	121°42′49″	Peach	1
	3	37°54′18″	121°39′27″	Apricot	1
	4	37°54′37″	121°39′28″	Pear	1
	5	37°54′43″	121°42′54″	Riparian area	3
	6	37°54′07″	121°38′38″	Mixed fruit garden	2
Parlier[d]	1–14	36°35′59″	119°30′56″	Apricot, apple, blackberry, blueberry, Cherry-1, Cherry-2, citrus, fig, grape, kiwi, peach, plum, persimmon, pomegranate	3 per crop

[a] All are conventionally farmed and different insecticides were used for *D. suzukii* during the cherry fruiting seasons. The cherry orchards were 1.0–1.7 km apart, whereas the kiwi and pear orchards were adjacent to the cherry blocks

[b] All crops are organically farmed. The peach orchard was 1.3 km from Cherry-2 and the two cherry orchards were 30 km apart

[c] All crops are organically farmed. The riparian area was 0.3 and 0.8 km to the nearest peach and cherry orchards, respectively, and the mixed fruit garden was located 5 km away from the riparian area and 1.1 and 1.3 km to the nearest apricot and pear orchards, respectively

[d] All crops are conventionally farmed (located within a 330-acre research farm at the University of California, Kearney Station), but did not receive any insecticides for *D. suzukii*. All monitoring orchards were 0.2–3.0 km apart and separated at least by one other crop

within a 330-acre research station at the University of California's Kearney Agricultural Research and Extension Center (Table 1).

Field monitoring

Adult *D. suzukii* were monitored weekly from April 2013 to May 2014 in Courtland, Stockton and Brentwood, and from April 2013 to July 2014 in Parlier, using traps baited with apple cider vinegar at 5 % acidity (Great Value Apple Cider Vinegar®, Wal-Mart Stores, Inc., Bentonville, AR). Each trap was made of a 750 ml Rubbermaid plastic container (Huntersville, NC) with a 7.5 cm diameter hole cut in the lid that was covered with 0.6 cm hardware cloth, and covered with a Pherocon trap cover (TRÉCÉ, Inc. Adair, OK) to block direct sunlight or rain. In the field, traps were filled with 300 ml of apple cider vinegar. The vinegar bait had one tablespoon of Bon-Ami Free and Clear® unscented soap (Bon-Ami Company, Kansas City, MO) in each gallon (3.8 l) to serve as a surfactant.

In each monitoring site, one–three traps (depending on the monitoring field size) were deployed (Table 1), with each trap 10–20 m apart. The trap(s) were placed in the center of the field (for one trap only), in the northwest and southeast corners of the field (for two traps only), or lined up along a northwest direction in the field (for three traps only), i.e., one trap each in the southeast, center, and northwest sections. Each trap was hung on a tree at a height of 1–1.5 m above the ground and on the north side of the canopy. The liquid contents and insects were collected in separate containers and the traps were refilled with fresh apple cider vinegar during each collection period. The collected samples were taken to the laboratory where the numbers of *D. suzukii*, all other Drosophilidae, and *Drosophila* parasitoids were recorded.

All *D. suzukii* females were preserved in 70 % ethanol for additional processing. From this material, a sub-sample of 5–20 *D. suzukii* females from each trap at the Brentwood, Courtland, and Parlier locations were dissected to determine mature egg load of female flies. Mature eggs have two long respiratory filaments and can be easily distinguished from developing eggs (Burrack et al. 2015; Zerulla et al. 2015). Additionally, adult *D. suzukii* from Courtland and Parlier were examined under a microscope for the presence of a black capsule inside the fly's abdomen to determine possible attack from parasitoids.

Data analysis

The mean numbers of weekly trap catches of adult *D. suzukii* among different crop or site locations monitored cannot be properly statistically compared because of the varying management practices used. Therefore, we report the general trend of seasonal population dynamics across different monitoring sites and geographical regions. To determine whether or not captures of adult *D. suzukii* between different sites in each location is correlated to the site distance or to the difference in seasonal fruit ripening at the Parlier site, simple correlation analysis was used to examine correlation in the trap captures between any two adjacent or close sites in each location or between the trap captures in two different crops over the range of their fruit ripening periods. Data were logit transformed before the analysis to stabilize the variation. We used the statistical association between trap captures in cherry orchards and other surrounding orchards to infer source or sink effects, where a significant negative association indicates a sink effect and a positive association indicates a source effect (Carriere et al. 2012).

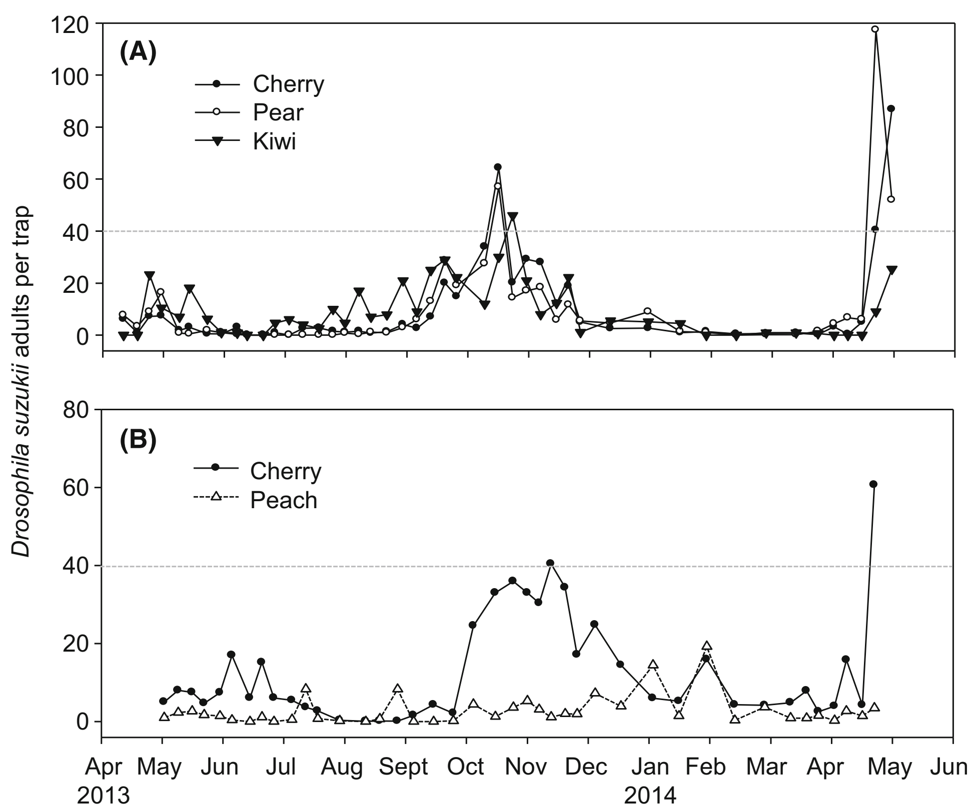
Within each location, adult *D. suzukii* likely move among different crops or sites, thus data on mature egg load per female fly and percentage of females without mature eggs were pooled from different sites in each location and month. The relationship between the mean number of mature egg load per female fly or percentage of females without mature eggs and mean monthly minimum temperature was analyzed using linear regression for each location separately. Climatic data were obtained from the California Irrigation Management Information System stations located nearest to each sampled site: Station 140 (Courtland), Station 47 (Brentwood), and Station 39 (Parlier). All analyses were conducted using JMP software (JMP, V11, SAS 2013, Cary, NC).

Results

Adult population dynamics

A total of 4412 traps were deployed and successfully recovered from the field, from which 49,094 *D. suzukii* adults and 1,232,038 other adult Drosophilidae were captured. Mean number of weekly captures varied among geographic locations, host plant ecosystems monitored, and seasonal sampling periods. However, the seasonal capture patterns were similar in different crops or sites and across different regions, with two capture peaks (spring and fall) and dramatically lower numbers of captured flies in the hot summer or cold winter months (Figs. 1, 2, 3). In early-season fruits such as cherry, the spring peak was higher than the fall peak. However, with middle or late season fruits such as apricot, plum, fig, apple, citrus or in the multiple fruit crop garden, the fall capture peak was much higher than the spring peak in all sites (Figs. 1, 2, 3). Similarly high numbers of *D. suzukii* were captured in riparian sites during the spring and fall peak in Brentwood (Fig. 2). In general, more adult *D. suzukii* were captured in

Fig. 1 Weekly mean *D. suzukii* trap captures in cherry and other fruit crop orchards in (**A**) Courtland (Sacramento County) and (**B**) Stockton (San Joaquin County), CA. Data from different cherry orchards were pooled



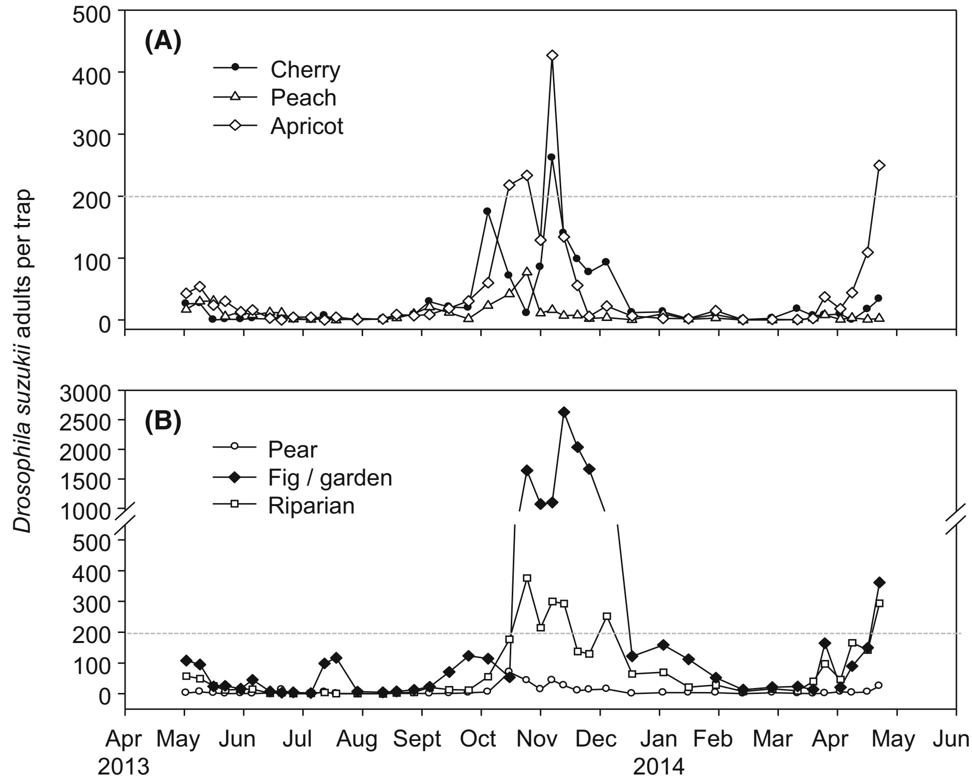


Fig. 2 Weekly mean *D. suzukii* trap captures in (**A**) cherry, peach and apricot, and (**B**) pear, fig/garden and adjacent riparian habitats in Brentwood (Contra Costa County), CA

Brentwood than in Courtland and Stockton, and fewer flies were captured in Parlier than all other locations (Figs. 1, 2, 3). The highest year-long average of *D. suzukii* was at the mixed organic fruit garden near Brentwood with a mean of 342.9 ± 102.1 *D. suzukii* per trap per week. The second largest average was at the riparian sites near Brentwood, with an average 74.9 ± 11.5 *D. suzukii* per trap per week. In contrast, season-long captures of adult *D. suzukii* per trap per week at sampled orchards near Parlier were low, with only 0.4 ± 0.1 in blueberries and only as high as 6.2 ± 1.0 in cherry and 3.4 ± 0.5 in citrus.

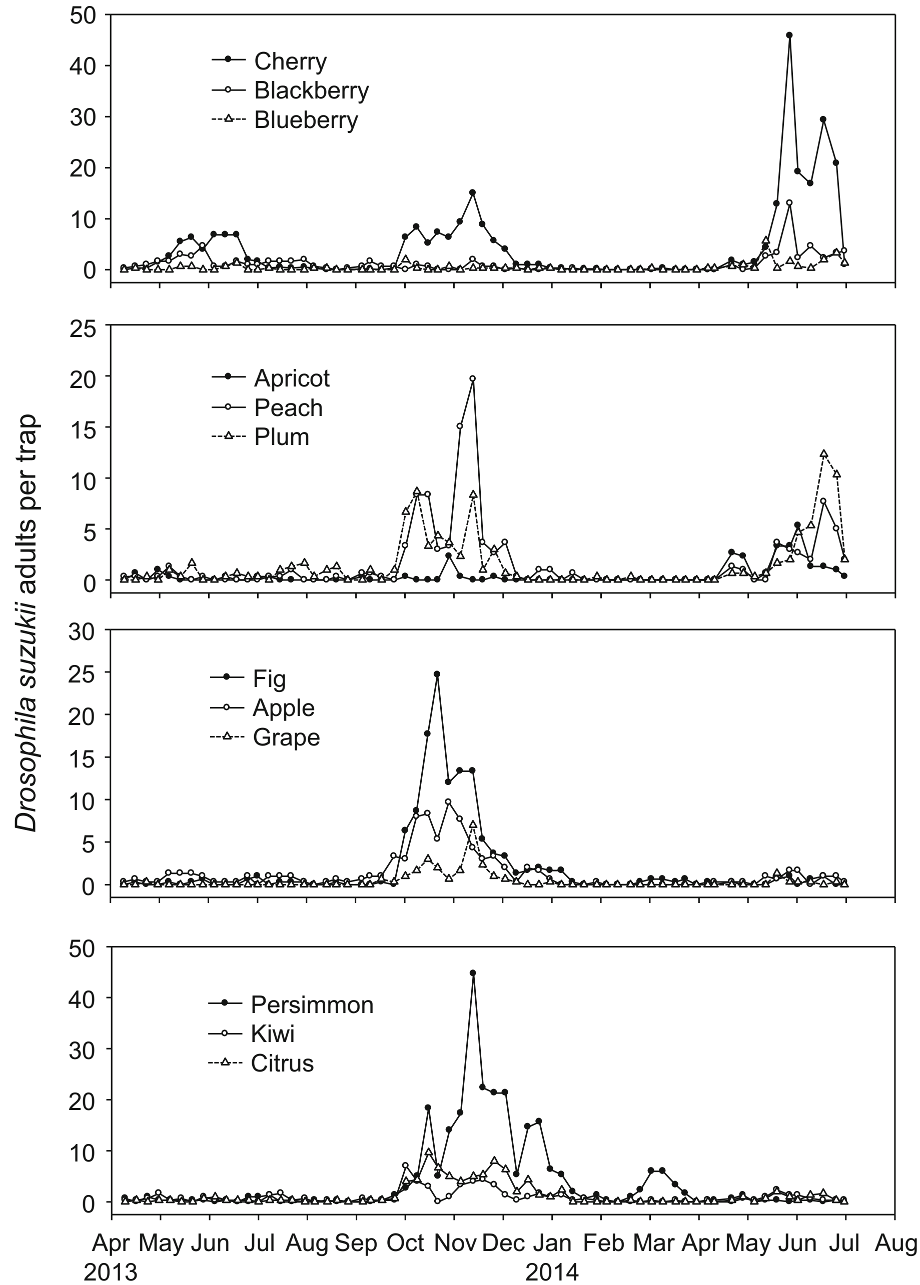
Correlation analyses showed that numbers of captured *D. suzukii* were positively correlated between sites based on their proximity (<2 km, Table 2). For example, in Courtland, the numbers of captured *D. suzukii* between the cherry and the adjacent pear orchard were highly correlated. However, the correlation relationship shifted from positive to negative with the increasing time gap between fruit ripening periods based on the analyses of captured *D. suzukii* in 14 different crops in Parlier (Fig. 4).

Among the *D. suzukii* captured in Courtland and Parlier (flies from Brentwood and Stockton were not examined), 10 adults (5 from each location) were found containing a black capsule in their abdomen (Fig. 5), i.e., field evidence of the immune capacity of *D. suzukii* against some resident larval parasitoids. The apple cider vinegar traps also captured adults of two common larval drosophilid parasitoids, *Leptopilina boulardi* Barbotin et al. and *L. heterotoma* (Thomson) (Fig. 6), and the seasonal capture patterns of parasitoids also had two capture peaks in the spring and fall (Fig. 6). Laboratory tests of both parasitoid species collected from field in California with *D. suzukii* further confirmed the presence of a black capsule in their abdomen of emerged adult flies.

Mature egg load

Dissections were made on 1992, 1331, and 1785 *D. suzukii* adult females from Brentwood, Courtland, and Parlier, respectively. In all three locations, the mature egg load increased from early (April–May) to late (August–September) fruit seasons, and then decreased during late summer and fall and was the lowest from late fall to early spring during the colder weather period (November–March), when the majority of females did not contain mature eggs (Fig. 7). The mean number of mature egg load per female (y) was positively related to minimum daily temperature (x) (Brentwood: $y = -0.934 + 0.699x$, $r^2 = 0.599$, $P < 0.001$, Courtland: $y = -2.983 + 0.950x$, $r^2 = 0.662$, $P < 0.001$, Parlier: $y = 0.846 + 0.584x$, $r^2 = 0.640$, $P < 0.001$), while the percentage of females without mature eggs (y) was negatively related to minimum daily temperature (x) (Brentwood: $y = 94.1 - 5.4x$, $r^2 = 0.639$, $P < 0.001$, Courtland: $y = 93.2 - 5.6x$, $r^2 = 0.822$, $P < 0.001$,

Fig. 3 Weekly mean *D. suzukii* trap captures in different crop orchards within a 330-acre research farm at the University of California Kearney Agricultural Research and Extension Center in Parlier (Fresno County), CA. Data are grouped based on the fruiting seasons of monitored crops



Parlier: $y = 80.2 - 3.7x$, $r^2 = 0.710$, $P < 0.001$; Fig. 7). Of interest is that from these dissected females, 61, 50, and 51 females (Brentwood, Courtland, and Parlier, respectively) had at least one hatched live larva in the uterus, suggesting facultative ovoviviparity.

Discussion

The temporal and spatial distribution of the pest population must be understood to implement sustainable pest management strategies. The current study reports the seasonal occurrence of adult *D. suzukii* in major fruit crops and adjacent non-crop habitats in California's Central Valley. Adult trap captures showed a population peak in the spring and another in the fall. High trap captures early in the season were the most common in favorable host crops, such as cherries. The adult trap captures indicate the fly population utilized other crop systems (e.g., apricot, fig and pear) in mid-summer and early fall periods before moving to citrus and non-crop habitats in late fall through early spring. Therefore, the source or sink potential of particular habitats could vary during the seasons due to changes in host suitability or fruit preference.

Table 2 Correlation coefficients in the relationship between trap captures of adult *D. suzukii* in two closely located sites in different geographical locations in California Central Valley

Locations	Site A	Site B	Site distances (km)	*n*	*R*	*P*
Courtland	Cherry-1	Kiwi	Adjacent	45	0.896	<0.001
	Cherry-3	Pear	Adjacent	45	0.618	<0.001
Stockton	Cherry-2	Peach	1.3	40	0.330	0.036
Brentwood	Riparian	Cherry	0.8	40	0.659	<0.001
		Peach	0.3	40	0.386	0.013
	Garden	Apricot	1.1	40	0.636	<0.001
		Pear	1.3	40	0.672	<0.001
Parlier	Cherry	Apricot	0.4	64	0.709	<0.001
		Fig	1.1	64	0.424	<0.001
		Pomegranate	1.2	64	0.435	<0.001
	Apricot	Fig	1.1	64	0.730	<0.001
		Pomegranate	1.2	64	0.676	<0.001
	Fig	Citrus	Adjacent	64	0.785	<0.001
	Pomegranate	Citrus	Adjacent	64	0.556	<0.001

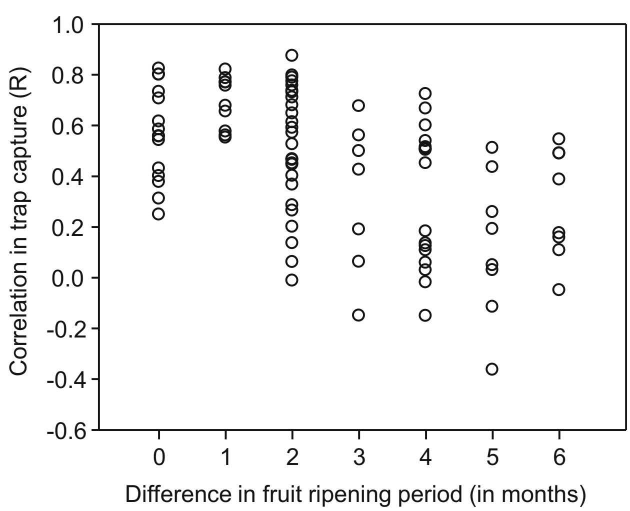


Fig. 4 Shifting correlations between the trap captures of *D. suzukii* in two different crops in Parlier, CA, over a range of gap between fruit ripening seasons ($y = 0.635 - 0.076x$, $r^2 = 0.252$, $P < 0.0001$)

Fig. 5 An encapsulated adult female *D. suzukii*. *Arrow* shows the presence of a melanized parasitoid *larva* in the fly's *abdomen*

Many climate and density-dependent factors may play an important role in sustaining *D. suzukii* populations and dictate their local movement patterns in agricultural landscapes, and the relative importance of those factors could depend on local condition as well as other factors (e.g., harvesting, use of pesticides in and around the orchard). Captures of higher numbers in spring and fall across all geographic regions suggest that adult abundance was associated with seasonal temperatures as also reported in several other studies in North America (Harris et al. 2014; Wiman et al. 2014) or Europe (Mazzetto et al. 2015; Zerulla et al. 2015). Temperature is not only known to affect the abundance of *D. suzukii* (Wiman et al. 2014), but could also affect the fly's dispersal as adult *D. suzukii* reduce or cease their activity when temperatures are lower than 10 °C or exceed 30 °C (Kinjo et al. 2014; Tochen et al. 2014). The average maximum summer temperatures from July to September in 2013 in Brentwood, Courtland, and Stockton were 31.1, 29.6, and 31.0 °C, respectively, whereas it was a warmer 34.5 °C in Parlier. It is not uncommon for daily maximum temperatures exceed 30 °C during the summer in the Central Valley (Wang et al. 2009). This is probably one of the major factors contributing to low total capture numbers throughout the summer seasons, especially in Parlier. However, there were always a few warm hours during the winter and cool hours

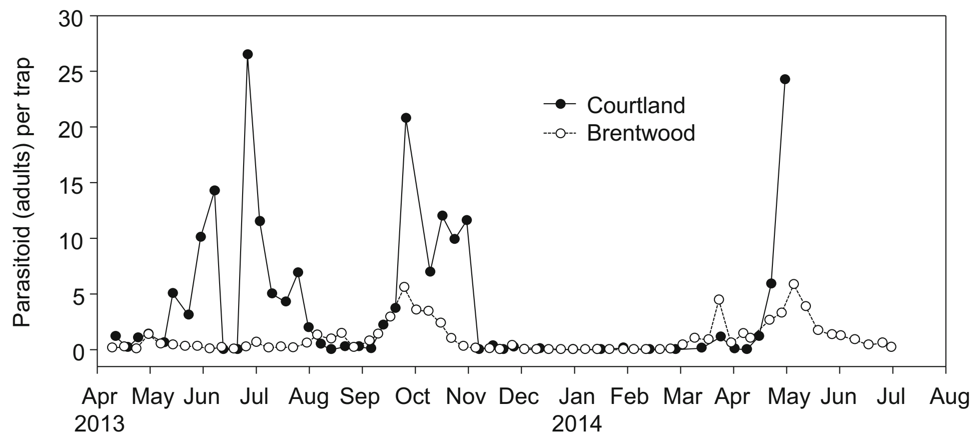


Fig. 6 Weekly mean trap captures of drosophilid parasitoids (*Leptopilina* spp.) in cider vinegar traps for *D. suzukii* in Courtland and Parlier, CA. Data were pooled from all traps in different fruit orchards for each location

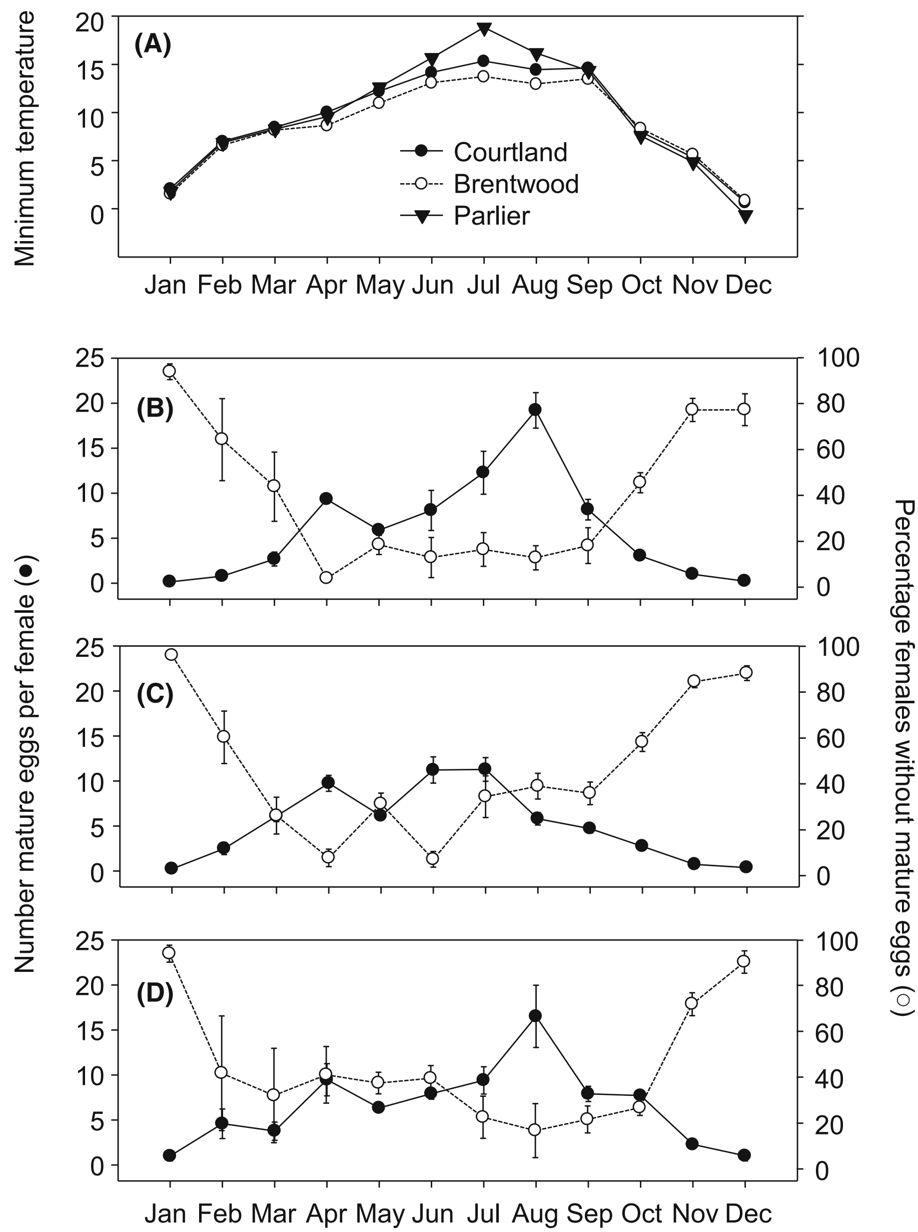


Fig. 7 Monthly mean minimum daily temperature (°C) in three different regions (**A**) and mean ± SE number of mature eggs per female *D. suzukii* and percentage of captured females without mature eggs in Courtland (**B**), Brentwood (**C**), and Parlier (**D**), CA. Data were pooled from different sites in each location for each month

Table 3 Periods of ripening and fruit availability of monitored crops in California Central Valley, where dark cells denote the monthly ripening period and light gray cells denote ripe or overripe fruit may be available post-harvest period

Fruit monitored	Fruit ripening and availability period (by month)[1]											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Cherry (*Prunus avium*)												
Blueberry (*Vaccinium* sp.)												
Blackberry (*Rubus* sp.)												
Peach (*Prunus persicae*)												
Apricot (*Prunus armeniaca*)												
Plum (*Prunus domestica*)												
Pear (*Pyrus domestica*)												
Fig (*Ficus carica*)												
Grape (*Vitis vinifera*)												
Apple (*Pyrus malus*)												
Pomegranate (*Punica granatum*)												
Persimmon (*Diospyros kaki*)												
Kiwi (*Actinidia chinensis*)												
Orange (*Citrus C. sinensis*)												

[1] Fruit ripening period was determined based on our field observation during the trapping periods and the fruiting chart by Dave Wilson Nursery (http://www.davewilson.com)

during the summer that provided favorable daily temperatures for adult *D. suzukii* flight to find available food sources and survive these periods with extreme temperatures (Kaçar et al. 2016).

Trends in catches in fruit trees that had similar fruiting seasonality were similar in different regions (Figs. 1, 2, 3), which suggest the availability of host fruits may affect the number of captured *D. suzukii*. Many fruits may provide *D. suzukii* not only an ovipositing host, but also adult food sources, breeding hosts, or shelter for overwintering. Adult *D. suzukii* can be also attracted to leaf or fruit odors (Abraham et al. 2015; Keesey et al. 2015). Plant leaves, such as those of cherries, produce extra floral nectaries that may provide a resource for adult fruit flies (Yee and Chapman 2008). In California's Central Valley, a wide variety of fruit crops such as apple, cherry, fig, grape, kiwifruit, nectarine, peach, pear, persimmon, plum, and pomegranate are grown commercially or as ornamental plants. Moreover, the southern Central Valley is a major citrus production region and not all citrus fruits are commonly harvested, making some fruit available to fruit flies almost year round, albeit in various stages of ripeness and decay (Table 3). *D. suzukii* can complete development in most of these cultivated fruits (Bellamy et al. 2013; Kaçar et al. 2016; Stewart et al. 2014; Wang et al. unpublished data). Captures of other abundant Drosophilidae in those orchards provided indirect evidence of the presence of breeding hosts. Juices from split, damaged, or overripe fruits could seep from wounds and provide food for adult *D. suzukii* (Kaçar et al. 2016). Higher winter trap catches of adult *D. suzukii* in citrus also suggest that citrus orchards are likely a key overwintering site for *D. suzukii* in California's Central Valley, potentially increasing the early-season *D. suzukii* risk in other fruiting crops (Harris et al. 2014; Kaçar et al. 2016).

Many within and outside crop factors (i.e., climate and geography) and landscape traits (i.e., crop arrangement, connectivity, quality of habitat patches) can essentially affect insect dispersal (Mazzi and Dorn 2012; Zappalà et al. 2012). Adult catches do indicate the temporal distribution of adult flies or aggregation patterns over the seasons, although they do not necessarily reflect population movement among different sites. However, strong correlation of catches between subsequently fruiting and adjacent orchards or between orchard and adjacent non-crop habitats do reflect local population movement. Our results from the Brentwood sites (riparian area and orchards) indicated a shift in *D. suzukii* adult location out of crop fields and toward adjacent non-agricultural habitats. On a micro-geographic scale, for example in Parlier, positive correlations among trap catches were clearly related to proximity of fruiting as it was significant for crops fruiting subsequently, whereas this relationship was quite weak between the early fruiting (cherry) and late fruiting (citrus) crops. Other approaches, such as the use of distinct protein markers (Klick et al. 2016) or genetic markers with the recent availability of *D. suzukii* genome (Murphy et al. 2016), may aid to the understanding of local dispersal or long distance movement patterns of the fly in the future.

We found that captured *D. suzukii* females during the winter season had low mature egg loads and a high proportion of females did not contain mature eggs at all. This supports an early hypothesis that adult female *D. suzukii* may enter reproductive diapause when host fruit is not available during the later fall and winter seasons (Mitsui et al. 2010; Zerulla et al. 2015). In Japan, Mitsui et al. (2010) found that *D. suzukii* populations migrated to higher altitudes for better host sources during the summer and were mostly composed of reproductively mature individuals, while those that returned to lower altitudes for overwintering were mainly composed of sexually immature individuals, suggesting that they entered a winter reproductive diapause. Most females captured during the crop fruiting periods had mature egg loads. An alternative explanation may be that *D. suzukii* migrates into the orchards from other host crops. This also suggests that many fruit crops, especially cherries, can be very vulnerable as most *D. suzukii* females contained mature eggs during the fruiting seasons. Many other factors, such as different oviposition rate in different crops, may affect mature egg load as flies would form mature eggs in advance of host availability (Burrack et al. 2015). Thus, the degree of depletion could largely depend on the host availability.

The apple cider vinegar traps were still commonly used for monitoring adult *D. suzukii* (Harris et al. 2014; Mazzetto et al. 2015; Zerulla et al. 2015), although various other traps are available (Burrack et al. 2015; Lee et al. 2012). However, this attractant was non-specific. As we showed in this study, high numbers of two beneficial parasitoids (*L. boulardi* and *L. heterotoma*) were found in the traps. These are the two most common resident larval drosophilid parasitoids that readily attack other Drosophilidae such as *D. melanogaster* (Hertlein 1986), but are unable to develop from *D. suzukii* due to the host's immune response (Chabert et al. 2012; Kacsoh and Schlenke 2012). Although the presence of a black capsule in the abdomen of captured *D. suzukii* was rare, it provides field-drawn evidence of the immune capacity of the *D. suzukii* Californian populations against resident larval parasitoids. However, the traps did not capture two common resident pupal drosophilid parasitoids, *Pachycrepoideus vindemiae* (Rondani) (Hymenoptera: Pteromalidae) and *Trichopria drosophilae* Perkins (Hymenoptera: Diapriidae) that readily attack *D. suzukii* in California's Central Valley (Wang et al. 2016). The results suggest that the apple cider vinegar traps may cause non-target impacts especially on larval parasitoids that are presently being considered for introduction from Asia into North America (Daane et al. 2016).

Ovoviviparity occurs when fertilized eggs remain within the mother until they hatch or are about to hatch and is common in Diptera including Drosophilidae (Markow et al. 2009; Meier et al. 1999). The majority of dissected female *D. suzukii* were found to be oviparous (i.e., contained only eggs), but some dissected female *D. suzukii* exhibited retention of larvae and eggs, clearly showing facultative ovoviviparity, although it is unknown if a live larva could be successfully deposited into host plant material. However, the adaptive significance of ovoviviparity is still not well understood. It may benefit the population by shortening the developmental time or larval life thereby reducing the exposure of the vulnerable immature stage to natural enemies, or facilitating accessibility to breeding substrates (Meier et al. 1999). The current observations do demonstrate facultative ovoviviparity in *D. suzukii*, but the ecological mechanisms and in the degree to which it occurs is unclear and deserve further specific investigations.

In conclusion, the more favorable California climate and seasonal availability of fruits (Table 3), such as citrus and ornamental fruits, could enable *D. suzukii* to remain active and reproducing through the winter. Non-crop habitats may contribute to increasing or decreasing pest density in cultivated crops. An understanding of *D. suzukii* seasonal use of host plants and potential dispersal patterns would be of aid in the timing of and need for pest treatments, and may allow for implementation of alternative management strategies such as crop 'border-sprays,' mass trapping or bait sprays, or possible targeting for future release of biological control agents to reduce the source populations in the environment. Management strategies to reduce *D. suzukii* populations in cherries may also include lessening the source potential of certain crops and uncultivated habitats, or manipulating the spatial arrangements of source and sink habitats.

Author contribution

KD and XW conceived and designed this research. All authors had a role in data collection. XW, TS, KD, and AB analyzed data and wrote the manuscript, which was then reviewed and edited by all authors.

Acknowledgments We thank John Hutchins, Racheal Muradian, Gülay Kaçar, Sean Tomajan, Paris Marler, James Feng, and Laura Wolf (University of California, Berkeley) for laboratory assistance, numerous growers for using their orchards, and two reviewers for critical comments. Thomas Stewart was supported by a Graduate Scholarship from California State University, Fresno. Antonio Biondi received funding from the People Program (Marie Curie Actions) of the European Union's Seventh Framework Program FP7/2007-2013/ under REA Grant Agreement 318246 and from the Italian Ministry of Education, University and Research (PRIN Project GEISCA 2010CXXHJE_004, and SIR Project ENTOBIONANO, RBSI14I02A). Funding was provided by the California Cherry Board, USDA APHIS (Farm Bill, Fund 14-8130-0463), and the National Institute of Food and Agriculture, USDA Specialty Crops Research Initiative under Agreement No. 2015-51181-24252.

Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

Human and animal rights statement All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors. Informed consent was obtained from all individual participants included in the study.

References

Abraham J, Zhang A, Angeli S, Abubeker S, Michel C, Feng Y, Rodriguez-Saona C (2015) Behavioral and antennal responses of *Drosophila suzukii* (Diptera: Drosophilidae) to volatiles from fruit extracts. Environ Entomol 44:356–367

Asplen M, Anfora G, Biondi A, Choi D-S, Chu D, Daane KM, Gilbert P, Gutierrez AP, Hoelmer KA, Hutchison W, Isaacs RA, Jiang Z, Karpati Z, Kimura M, Pascual M, Phillips C, Plantamp C, Ponti L, Vetek G, Vogt H, Walton VM, Yu Y (2015) Invasion biology of spotted wing drosophila (*Drosophila suzukii*): a global perspective and future priorities. J Pest Sci 681:469–494

Atallah J, Teixeira L, Salazar R, Zaragoza G, Kopp A (2014) The making of a pest: the evolution of a fruit-penetrating ovipositor in *Drosophila suzukii* and related species. Proc R Soc Biol Sci B 281:2013–2840

Beers EH, Van Steenwyk RA, Shearer PW, Coates WW, Grant JA (2011) Developing *Drosophila suzukii* management programs for sweet cherry in the western United States. Pest Manag Sci 67:1386–1395

Bellamy DE, Sisterson MS, Walse SS (2013) Quantifying host potentials: indexing postharvest fresh fruits for spotted wing drosophila, *Drosophila suzukii*. PLoS One 8:e61227

Briem F, Eben A, Gross J, Voght H (2016) An invader supported by a parasite: mistletoe berries as a host for food and reproduction of spotted wing drosophila in early spring. J Pest Sci. doi:10.1007/s10340-016-0739-6

Bruck DJ, Bolda M, Tanigoshi L, Klick J, Kleiber J, DeFrancesco J, Gerdeman B, Spitler H (2011) Laboratory and field comparisons of insecticides to reduce infestation of *Drosophila suzukii* in berry crops. Pest Manag Sci 67:1375–1385

Burrack HJ, Asplen M, Bahder L, Collins J, Drummond FA, Guedot C, Isaacs R, Johnson D, Blanton A, Lee JC, Loeb G, Rodriguez-Saona C, van Timmeren S, Walsh D, McPhie DR (2015) Multistate comparison of attractants for monitoring *Drosophila suzukii* (Diptera: Drosophilidae) in blueberries and caneberries. Environ Entomol 44:704–712

Carriere Y, Goodell PB, Ellers-Kirk C, Larocque G, Dutilleul P, Naranjo SE, Ellsworth PC (2012) Effects of local and landscape factors on population dynamics of a cotton pest. PLoS One 7:e39862

Chabert S, Allemand R, Poyet M, Eslin P, Gibert P (2012) Ability of European parasitoids (Hymenoptera) to control a new invasive Asiatic pest, *Drosophila suzukii*. Biol Control 63:40–47

Cini A, Anfora G, Escudero-Colomar LA, Grassi A, Santosuosso U, Seljak G, Papini A (2014) Tracking the invasion of the alien fruit pest *Drosophila suzukii* in Europe. J Pest Sci 87:559–566

Daane KM, Wang XG, Biondi A, Miller BE, Miller JC, Riedl H, Shearer PW, Guerrieri E, Giorgini M, Buffington M, van Achterberg K, Song Y, Kang T, Yi H, Jung C, Lee DW, Chung BK, Hoelmer KA, Walton VA (2016) First exploration of parasitoids of *Drosophila suzukii* in South Korea as potential classical biological agents. J Pest Sci. doi:10.1007/s10340-016-0740-0

Deprá M, Poppe JL, Schmitz HJ, De Toni DC, Valente VLS (2014) The first records of the invasive pest *Drosophila suzukii* in the South American continent. J Pest Sci 87:379–383

Harris DW, Hamby KA, Wilson HE, Zalom FG (2014) Seasonal monitoring of *Drosophila suzukii* (Diptera: Drosophilidae) in a mixed fruit production system. J Asia Pac Entomol 17:857–864

Haye T, Girod P, Cuthberstson AGS, Wang XG, Daane KM, Hoelmer K, Baroffio C, Zhang J, Desneux N (2016) Current SWD IPM tactics and their practical implementation in fruit crops across different regions around the world. J Pest Sci. doi:10.1007/s10340-016-0737-8

Hertlein MB (1986) Seasonal development of *Leptopilina boulardi* (Hymenoptera: Eucolidae) and its hosts. *Drosophila melanogaster* and *Drosophila simulans* (Diptera: Drosophilidae) in California. Environ Entomol 15:859–866

Ioriatti C, Walton V, Dalton D, Anfora G, Grassi A, Maistri S, Mazzoni V (2015) *Drosophila suzukii* (Diptera: Drosophilidae) and its potential impact to wine grapes during harvest in two cool climate wine grape production regions. J Econ Entomol 108:1148–1155

JMP®, Version 11, 2013, SAS Insititute Inc., Cary, NC

Kaçar G, Wang XG, Stewart TJ, Daane KM (2016) Overwintering survival of *Drosophila suzukii* (Diptera: Drosophilidae) and the effect of food on adult survival in California's San Joaquin Valley. Environ Entomol. doi:10.1093/ee/nvv182

Kacsoh BZ, Schlenke TA (2012) High hemocyte load is associated with increased resistance against parasitoids in *Drosophila suzukii*, a relative of *D. melanogaster*. PLoS One 7:e34721

Keesey IW, Knaden M, Hansson BS (2015) Olfactory specialization in *Drosophila suzukii* supports an ecological shift in host preference from rotten to fresh fruit. J Chem Ecol 41:121–128

Kinjo H, Kunimi Y, Nakai M (2014) Effects of temperature on the reproduction and development of *Drosophila suzukii* (Diptera: Drosophilidae). Appl Entomol Zool 49:297–304

Klick J, Yang WQ, Walton VM, Dalton DT, Hagler JR, Dreves AJ, Lee JC, Bruck DJ (2016) Distribution and activity of *Drosophila suzukii* in cultivated raspberry and surrounding vegetation. J Appl Entomol 140:37–46

Lee JC, Burrack HJ, Barrantes LD, Beers EH, Dreves AJ, Hamby KA, Haviland DR, Isaacs R, Richardson TA, Shearer PW, Stanley CA, Walsh DB, Walton VM, Zalom FG, Bruck DJ (2012) Evaluation of monitoring traps for *Drosophila suzukii* (Diptera: Drosophilidae) in North America. J Econ Entomol 105:1350–1357

Lee JC, Dreves AJ, Cave AM, Kawai S, Isaacs R, Miller JC, van Timmeren S, Bruck DJ (2015) Infestation of wild and ornamental noncrop fruits by *Drosophila suzukii* (Diptera: Drosophilidae). Ann Entomol Soc Am 108:117–129

Markow TA, Beall S, Matzkin LM (2009) Egg size, embryonic development time and ovoviviparity in *Drosophila* species. J Evol Biol 22:430–434

Mazzetto F, Pansa MG, Ingegno BL, Tavella L, Alma A (2015) Monitoring of the exotic fly *Drosophila suzukii* in stone, pome

and soft fruit orchards in NW Italy. J Asia Pac Entomol 18:321–329
Mazzi D, Dorn S (2012) Movement of insect pests in agricultural landscapes. Ann Appl Biol 160:97–113
Meier R, Kotrba M, Ferrar P (1999) Ovoviviparity and viviparity in the Diptera. Biol Rev 74:199–258
Mitsui H, Beppu K, Kimura MT (2010) Seasonal life cycles and resource uses of flower- and fruit-feeding drosophilid flies (Diptera: Drosophilidae) in central Japan. Entomol Sci 13:60–67
Murphy KA, West JD, Kwok RS, Chiu JC (2016) Accelerating research on spotted wing drosophila management using genomic technologies. J Pest Sci. doi:10.1007/s10340-016-0741-z
Pelton E, Gratton C, Isaacs R, Van Timmeren S, Blanton A, Guédot C (2016) Earlier activity of *Drosophila suzukii* in high woodland landscapes but relative abundance is unaffected. J Pest Sci. doi:10.1007/s10340-016-0733-z
Poyet M, Eslin P, Heraude M, Le Roux V, Prévost G, Gibert P, Chabrerie O (2014) Invasive host for invasive pest: when the Asiatic cherry fly (*Drosophila suzukii*) meets the American black cherry (*Prunus serotina*) in Europe. Agric For Entomol 16:251–259
Steffan SA, Lee JC, Singleton ME, Vilaire A, Walsh DB, Lavine LS, Patten K (2013) Susceptibility of cranberries to *Drosophila suzukii* (Diptera: Drosophilidae). J Econ Entomol 106:2424–2427
Stewart TJ, Wang XG, Molinar A, Daane KM (2014) Factors limiting peach as a potential host for *Drosophila suzukii* (Diptera: Drosophilidae). J Econ Entomol 107:1771–1779
Tochen S, Dalton DT, Wiman N, Hamm C, Shearer PW, Walton VM (2014) Temperature-related development and population parameters for *Drosophila suzukii* (Diptera: Drosophilidae) on cherry and blueberry. Environ Entomol 43:501–510
Van Timmeren S, Isaacs R (2013) Control of spotted wing drosophila, *Drosophila suzukii*, by specific insecticides and by conventional and organic crop protection programs. Crop Prot 4:126–133
Walsh DB, Bolda MP, Goodhue RE, Dreves AJ, Lee JC, Bruck DJ, Walton VM, O'Neal SD, Zalom FG (2011) *Drosophila suzukii* (Diptera: Drosophilidae): invasive pest of ripening soft fruit expanding its geographic range and damage potential. J Integr Pest Manag 2:G1–G7
Wang XG, Johnson MW, Daane KM, Nadel H (2009) High summer temperatures affect the survival and reproduction of olive fruit fly (Diptera: Tephritidae). Environ Entomol 38:1496–1504
Wang XG, Kaçar G, Biondi A, Daane KM (2016) Foraging efficiency and outcomes of interactions of two pupal parasitoids attacking spotted wing drosophila. Biol Control 96:64–71
Wiman NG, Walton VM, Dalton DT, Anfora G, Burrack HJ, Chiu JC, Daane KM, Grassi A, Miller B, Tochen S, Wang XG, Ioriatti C (2014) Integrating temperature-dependent life table data into a matrix projection model for *Drosophila suzukii* population estimation. PLoS One 9:e106909
Yee WL, Chapman PS (2008) Seasonal amounts of nutrients in Western cherry fruit fly (Diptera: Tephritidae) and their relation to nutrient availability on cherry plant surfaces. Environ Entomol 37:1086–1098
Yu D, Zalom FG, Hamby KA (2013) Host status and fruit odor response of *Drosophila suzukii* (Diptera: Drosophilidae) to figs and mulberries. J Econ Entomol 106:1932–1937
Zappalà L, Campolo O, Grande SB, Saraceno F, Biondi A, Siscaro G, Palmeri V (2012) Dispersal of *Aphytis melinus* (Hymenoptera: Aphelinidae) after augmentative releases in citrus orchards. Eur J Entomol 109:561–568
Zerulla FN, Schmidt S, Streitberger M, Zebitz CPW, Zelger R (2015) On the overwintering ability of *Drosophila suzukii* in South Tyrol. J Berry Res 5:41–48