J Pest Sci
DOI 10.1007/s10340-016-0756-5

REVIEW

Biotic and abiotic factors impacting development, behavior, phenology, and reproductive biology of *Drosophila suzukii*

Kelly A. Hamby[1] · David E. Bellamy[2] · Joanna C. Chiu[3] · Jana C. Lee[4] · Vaughn M. Walton[5] · Nik G. Wiman[6] · Riki M. York[5] · Antonio Biondi[7]

Received: 30 October 2015 / Revised: 16 March 2016 / Accepted: 21 March 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract Spotted wing drosophila, *Drosophila suzukii*, is a devastating invasive pest of small and stone fruits in the Americas and Europe. To better understand the population dynamics of *D. suzukii*, we reviewed recent work on juvenile development, adult reproduction, and seasonal variation in life history parameters including the abiotic/biotic factors that influence these processes. Juvenile development is optimal at moderately warm temperatures, and larvae exhibit some immunity to parasitism. Adults use visual cues and substrate-borne vibrations for courtship and exhibit a bimodal locomotor activity pattern (except mated females). Under 20–27 °C and various conditions, development from egg to adult can take 10–17 days, females first lay eggs within 1–8 days and their lifetime fecundity varies from <100 to >400. Oviposition is consistently high in raspberry hosts and fruits with lower penetration force, and the presence of *Wolbachia* endosymbionts can lower fertility. *Drosophila suzukii* exhibit seasonal variation with a darker winter morph that is more cold tolerant. Also, *D. suzukii* likely undergo reproductive diapause in the fall, with colder temperatures and shorter day lengths influencing reproduction. To develop viable IPM programs for *D. suzukii,* knowledge of abiotic and biotic conditions that impact *D. suzukii* life history parameters and population dynamics is critical, and gaps in the current knowledge are discussed.

Keywords Invasive species · Chronobiology · Development · Overwintering · Reproduction · Spotted wing drosophila

Communicated by M. Traugott.

Special Issue: Spotted Wing Drosophila.

Electronic supplementary material The online version of this article (doi:10.1007/s10340-016-0756-5) contains supplementary material, which is available to authorized users.

✉ Kelly A. Hamby
kahamby@umd.edu

[1] Department of Entomology, University of Maryland, 4112 Plant Sciences Building, College Park, MD 20742, USA

[2] Agricultural Scientist, Ocean Spray Cranberries, Inc., 1480 State Route 105, Aberdeen, WA 98520, USA

[3] Department of Entomology and Nematology, University of California Davis, One Shields Avenue, Davis, CA 95616, USA

[4] USDA-ARS Horticultural Crops Research Unit, 3420 NW Orchard Avenue, Corvallis, OR 97330, USA

[5] Department of Horticulture, Oregon State University, 4105 Ag and Life Sciences Building, Corvallis, OR 97331, USA

[6] Department of Horticulture, North Willamette Research and Extension Center, Aurora, OR 97002, USA

[7] Department of Agriculture, Food and Environment, University of Catania, Via Santa Sofia, 100, 95123 Catania, Italy

Key message

- We review recent work on the biotic and abiotic factors impacting *Drosophila suzukii* biology and physiology to facilitate the development of integrated pest control strategies.
- Abiotic and biotic conditions affect developmental times from egg to adult, survivorship, longevity, and fecundity; and development can take 10–17 days; preoviposition period is 1–8 days; lifetime fecundity varies from <100 to >400 eggs.

Published online: 09 April 2016

- *D. suzukii* exhibit diel periodicity in courtship, oviposition, and locomotion; larvae exhibit some resistance to parasitism; and *D. suzukii* may exhibit seasonal phenotypes and reproductive diapause.

Introduction

Life history parameters such as reproductive potential and developmental rate determine insect population growth and speed of colonization in agroecosystems (Ferro 1987). Climate, host quality, and other biotic factors such as symbionts and natural enemies can impact insect development, reproduction, and survivorship, ultimately determining whether insect populations can reach densities that are economically damaging (Ferro 1987; Awmack and Leather 2002; Caminade et al. 2012; Kellermann et al. 2012). Approximately 40 % of insect and mite pests of agroecosystems are invasive (Pimentel 1993; Pimentel et al. 2005), and invasive species are often among the most economically damaging pests. Moreover, invasive species have expanded their range, which may be associated with adaptations to newly invaded areas or niche shifts (Monceau et al. 2014; Asplen et al. 2015; Haye et al. 2015). Spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), began a rapid global range expansion in 2008 and has emerged as a devastating invasive pest of small and stone fruits in the Americas and Europe (Walsh et al. 2011; Cini et al. 2014; Deprá et al. 2014). To understand the population dynamics of *D. suzukii* and develop management strategies for areas within the expanded range, it is important to evaluate factors relevant to invaded habitats and populations within the expanded range. Comparing these values with those determined using populations from the native range is also informative.

Here we review recent work on the biotic and abiotic factors that impact the biology, ecology, and physiology of *D. suzukii*. This manuscript focuses on the aspects of these topics that have received recent attention by the research community and by no means is a comprehensive review of the entirety of these topics. Specifically, we review:

- Juvenile development
  - Climate and host constraints
  - Pupation
- Parasitism and immune response
- Reproduction
  - Courtship and diel periodicity in adult activity
  - Oviposition and factors influencing oviposition: ovipositor morphology, climate, host, and *Wolbachia* infections
  - Age-specific reproduction and lifespan
- Adult seasonal biology
  - Overwintering physiology
  - Reproductive diapause

Juvenile development

Drosophila suzukii development is temperature dependent and developmental time decreases with increasing temperature until hotter temperatures induce thermal stress. Laboratory studies of temperature-dependent development vary, with *D. suzukii* developing most rapidly between 26 and 28 °C at constant temperatures and exhibiting highest adult emergence rates between 20 and 26 °C at constant temperatures (Kinjo et al. 2014; Tochen et al. 2014; Asplen et al. 2015). This variation is unsurprising given the different experimental methods used to gather data. A subset of recent egg to adult development data from published experiments that occurred between 20 and 27 °C are presented with their rearing conditions in Table 1. The minimum threshold average daily temperature for development was recently estimated to be 11.6 °C under fluctuating natural conditions (Tonina et al. 2016), and 7.2 °C at constant laboratory conditions (Tochen et al. 2014).

The larval substrate is an experimental parameter that is often varied in development experiments, and larval host nutritional quality impacts *D. suzukii* development time and survivorship (Lee et al. 2011; Bellamy et al. 2013; Burrack et al. 2013; Hardin et al. 2015; Jaramillo et al. 2015; Lee et al. 2015b). *Drosophila suzukii* development on various fruit hosts varies significantly by fruit type (Table 1, Lee et al. 2011; Bellamy et al. 2013; Burrack et al. 2013; Tochen et al. 2014; Lee et al. 2015b). Variety and fruit ripeness impact *D. suzukii* development and success, and *D. suzukii* tends to perform better in no-choice scenarios on the commercial hosts assayed relative to the non-crop and ornamental hosts that have been assayed (Lee et al. 2011, 2015b). Among the commercial hosts that have been evaluated in the laboratory, such as cherries, blackberries, raspberries, and strawberries, *D. suzukii* seems to better develop on raspberries (Lee et al. 2011; Bellamy et al. 2013; Burrack et al. 2013; Tochen et al. 2014). Additionally, diet quality interacts with larval density, affecting development time and adult emergence rates (Tochen et al. 2014; Hardin et al. 2015). The largest differences in development time on different substrates were reported at the highest densities (1.61 days difference between the standard *Drosophila* media and yeast-free media at highest density), and the largest differences in adult emergence were reported at the higher densities (20

Table 1 Rearing conditions and mean egg (or first instar as noted) to adult development time for recently published work rearing *D. suzukii* between 20 and 27 °C

Host substrate	Temp. (°C)	L:D	Humidity (%RH)	Density #*D. suzukii*	Development (days)[a]	Reference
Blackberry agar	24–27	16:8	80	ND	10.2	Bellamy et al. (2013)
Blueberry	25	13:11	ND	10	10.6	Jaramillo et al. (2015)
Blueberry	20.6	16:8	71	≤5	16.3	Tochen et al. (2015)
Blueberry	22	16:8	60–70	≤5	14.0[b]	Tochen et al. (2014)
Blueberry	26	16:8	60–70	≤5	10.9[b]	Tochen et al. (2014)
Blueberry agar	24–27	16:8	80	ND	10.7	Bellamy et al. (2013)
Cherry	22	16:8	60–70	≤5	14.0[b]	Tochen et al. (2014)
Cherry	26	16:8	60–70	≤5	10.8[b]	Tochen et al. (2014)
Cherry agar	24–27	16:8	80	ND	9.7	Bellamy et al. (2013)
Grape agar	24–27	16:8	80	ND	12.1	Bellamy et al. (2013)
Grape	25	16:8	60	ND	16.9	Lin et al. (2014a)
Media	22	15:9	25	1	12.8	Emiljanowicz et al. (2014)
Media	20	12:12	50–65	5	14.9	Hardin et al. (2015)
Media	20	12:12	60	50	16.8[b,d]	Asplen et al. (2015)
Media	20	12:12	60	50	17.1[b,e]	Asplen et al. (2015)
Media	25	13:11	ND	10	11.7	Jaramillo et al. (2015)
Media	25	16:8	60	1	11.3[c]	Kinjo et al. (2014)
Media − molasses	20	12:12	50–65	5	15.6	Hardin et al. (2015)
Media − yeast	20	12:12	50–65	5	15.5	Hardin et al. (2015)
Peach agar	24–27	16:8	80	ND	10.3	Bellamy et al. (2013)
Raspberry	20	12:12	50–65	5	14.7	Hardin et al. (2015)
Raspberry agar	24–27	16:8	80	ND	10.1	Bellamy et al. (2013)
Strawberry agar	24–27	16:8	80	ND	10.9	Bellamy et al. (2013)

[a] Published mean development time in days for either both sexes mixed or females only, SE are not reported numerically in all publications and therefore are not reported

[b] Females only

[c] Development of 1st instar larvae to adult determined by summation of mean development time from 1st instar larva to pupa and pupa to adult

[d] French population

[e] Spanish population

and 40) between the standard and molasses-free media (Hardin et al. 2015). However, the effect of larval density on development has not been evaluated for most fruit hosts. Like other *Drosophila* species, microbes likely play an important role in host nutritional quality as bacteria and yeasts have been isolated from *D. suzukii* larval frass (Hamby et al. 2012; Chandler et al. 2014). The importance of yeast as a protein source is known for *D. melanogaster* (Good and Tatar 2001; Tu and Tatar 2003), and appears necessary for egg production in lab-reared *D. suzukii* (A. Wallingford, unpublished data). Overall, laboratory egg to adult development time between the relatively optimal temperatures of 20–27 °C varied by about 1 week from the shortest reported time of 9.7 days to longest development time of 17.1 days (Table 1). Currently, little is known about the effect of yeast on larval diet suitability, development time, and survival rate although work in other *Drosophila* indicates that yeasts increase host suitability (Tatum 1939; Becher et al. 2012).

Drosophila suzukii pupariation and pupation often occur partially external or fully external to the larval fruit host (Asplen et al. 2015). Moreover, if pupae are located within the fruit the anterior spiracles of the puparium will often be external to the fruit. Recent work using artificially infested fruit (a high larval *D. suzukii* density was reached by bagging colony flies on fruit clusters in the field) demonstrated that around 90 % of 3rd instar *D. suzukii* may leave the fruit to pupate in the soil (Woltz et al. unpublished). Such wandering behavior is common among 3rd instar *Drosophila* and other brachyceran flies (Sokolowski et al. 1984). Further research investigating variability in pupation site choice in different hosts and climates is necessary because this may be a weak point in the *D. suzukii* life cycle that can be exploited for management. The

periodicity of pupation and eclosion are also important management considerations. While *D. suzukii* pupation and adult eclosion were observed during all 4 h periods evaluated including nocturnal time points, a peak in pupation was seen from 8 a.m. (ZT3.5) [Zeitgeber time (ZT) from the beginning of photophase (ZT0)] to 12 p.m. (ZT7.5) under 16:8 L:D, and adult eclosion was highest in the hours just before and after lights turned on [12 a.m. to 8 a.m. (ZT3.5)] (Lin et al. 2014b).

Parasitism and immune response

Larval and pupal parasitoids of *Drosophila* have been evaluated for *D. suzukii* management (Daane et al. 2016). Pupal parasitoids, including the generalist parasitoids *Pachycrepoideus vindemiae* (Rondani) (Hymenoptera: Pteromalidae) and *Trichopria drosophilae* Perkins (Hymenoptera: Diapriidae), can successfully develop using *D. suzukii* as a host in the U.S. and Italy (Chabert et al. 2012; Rossi Stacconi et al. 2013, 2015; Miller et al. 2015; Mazzetto et al. 2016; Wang et al. 2016a). This widely distributed fruit fly generalist began attacking *D. suzukii* post invasion. It is unclear whether *Drosophila* pupae can mount immune responses or otherwise defend themselves against pupal parasitoids (Kacsoh and Schlenke 2012). *D. suzukii* pupae do not seem to be more resistant to parasitoids than *D. melanogaster* for two pupal parasitoid species (3 strains) that were tested (Kacsoh and Schlenke 2012). Yet, larval parasitoids of *D. suzukii* can be subjected to a strong melanotic encapsulation immune response, and black capsules can be found in the abdomen of wild-caught adults. *Drosophila* hemocytes are an important component of melanotic encapsulation of parasitoid wasp eggs (Carton et al. 2008; Kacsoh and Schlenke 2012). First, plasmatocytes recognize the foreign egg and trigger the differentiation of pro-hemocytes and other circulating plasmatocytes into lamellocytes (Kacsoh and Schlenke 2012). Then, lamellocytes attach to and encapsulate the egg (Carton et al. 2008; Kacsoh and Schlenke 2012). In the final stages of encapsulation, the inner cells release reactive oxygen species and produce an impermeable layer of melanin (Kacsoh and Schlenke 2012). Lamellocytes and crystal cells have been implicated as sources of phenoloxidase-mediated melanogenesis (Carton et al. 2008). The *D. suzukii* larval standing immune defense (constitutive hemocyte production) measured by plasmatocyte, podocyte, and crystal cell numbers is higher than in *D. melanogaster*. Their induced production (12 and 24 h after parasitoid attack) of podocytes and lamellocytes is also elevated (Kacsoh and Schlenke 2012). Indeed, *D. suzukii* larvae are significantly more resistant to wasp parasitism than *D. melanogaster*, encapsulating more parasitoid eggs and successfully eclosing as adult flies more frequently. Of twenty-one larval parasitoids strains (from 12 species) tested against *D. suzukii*, a proportion of eggs from all species were encapsulated, whereas *D. melanogaster* could encapsulate only 8 species (Kacsoh and Schlenke 2012). Melanotic capsules were recently found in the abdomen of wild *D. suzukii* adults captured through vinegar traps in central California (Wang et al. 2016b). The larval parasitoid that most frequently defeated the immune response of *D. suzukii*, *Asobara japonica* Belokobylskij (Hymenoptera: Braconidae), is sympatric with *D. suzukii* in Japan and South Korea (Nomano et al. 2015; Daane et al. 2016). However, other larval parasitoids in the *Ganaspis* and *Leptopilina* genera can successfully complete development on this pest.

Reproduction

Courtship and diel activity

Drosophila courtship may include visual displays, aerial vibrations, substrate-borne vibrations, and short-range sex pheromones. In many species with spotted wings, including *D. suzukii,* courtship behavior includes a visual display that orients the male's wing spots towards the female (Fuyama 1979; Kopp and True 2002; Tomaru and Yamada 2011; Revadi et al. 2015). In addition to melanized spots, recent work suggests that wing interference patterns in transparent wings of *Drosophila* are taxon specific and sexually selected (Shevtsova et al. 2011; Katayama et al. 2014), although the role of wing interference patterns in *D. suzukii* courtship is unknown. Visual and acoustic cues are combined during *D. suzukii* courtship, and male *D. suzukii* produce species-specific substrate-borne vibrations rather than aerial vibrations (Mazzoni et al. 2013). These substrate-borne vibrations are likely transmitted to the substrate directly via the legs because males with amputated wings can still produce the vibrations. Male *D. suzukii* have a repertoire of two different sounds, the first is associated with abdominal quivering and produces a vibration with variable pulse intensity and interpulse interval. Prior to the emission of the second sound, a "toot" or frequency-modulated sound with clear harmonic structure, accelerated abdominal quivering typically occurs (Mazzoni et al. 2013). Most *Drosophila* males produce a close-range pheromone, *cis*-11-octadecenyl acetate (*c*VA), which impacts a variety of sexual and social behaviors. Additionally, species-specific and sex-specific cuticular hydrocarbons (CHC) can act as contact sex pheromones for *Drosophila* (Tomaru and Yamada 2011; Dekker et al. 2015; Revadi et al. 2015). Depending on the species, the pheromone may be female produced or male produced (Tomaru and Yamada 2011). Surprisingly, *D. suzukii* do not produce *c*VA and perfuming males with *c*VA results in reduced mating rates (Dekker et al. 2015); though female

CHCs may impact *D. suzukii* courtship as mating activity increases in the presence of CHCs. Further experiments are necessary to confirm behavioral activity and clarify the role CHCs play in courtship (Revadi et al. 2015).

Mating, locomotor, and oviposition activity vary with time of day. Diurnal mating activity was quantified as the number of mating couples, and counted during 3 h intervals under a 12 h photoperiod at constant 23 ± 2 °C (Revadi et al. 2015). Significantly more couples mated within the first 30 min after lights on, and the first interval from 6 a.m. (Zeitgeber time (ZT) 0) to 9 a.m. (ZT3) exhibited the highest mating activity compared to the other 3 h periods (Fig. 1b, Revadi et al. 2015). Nocturnal courtship activity was not measured in this study. Lin et al. (2014b) evaluated copulation rhythms every 4 h for 48 h under a 16:8 L:D cycle at 25 ± 1 °C. Mating couples were recorded at every time point (including time points that were nocturnal), with peak copulation occurring on the second day during the 8 a.m. (ZT3.5) to 12 p.m. (ZT7.5) interval. This copulation peak occurred later in the light cycle (after ZT3) when compared to the previous study, perhaps due to the extended daylight period. *Drosophila* locomotor activity assays were performed using the *Drosophila* Activity Monitoring System using either virgin females or males (Hamby et al. 2013). Under simulated summer conditions with 14:10 L:D photoperiod and 22.2/12.2 °C max/min temperature, peak activity of both male and female flies occurred during the lights-on period, with a bimodal activity pattern where maximum activity occurs near dawn and dusk (Hamby et al. 2013, Fig. 1a). However, a unimodal peak in activity was exhibited during the period of peak temperature under simulated winter conditions with 11:13 L:D and 16.7/6.8 °C max/min temperature (Hamby et al. 2013). A recent study showed a similar bimodal activity pattern with a quiescent afternoon (siesta) period for males and virgin females, whereas mated females were more active overall and active during the siesta period (Ferguson et al. 2015). Feeding activity is higher during the daylight hours under 16:8 L:D cycle and constant 25 ± 1 °C, with slightly more feeding in the morning relative to the afternoon (Lin et al. 2014b). Previous unpublished work by York et al. evaluated circadian oviposition patterns when *D. suzukii* were reared on *Drosophila* diet under a 12:12 L:D photoperiod 21.4/9.0 °C max/min temperature [peaking at 6 p.m. (ZT11)] with gradually ramping light intensity [peaking at 4 p.m. (ZT9)]. Oviposition started at 11 a.m. (ZT4) increasing to a maximum rate of 11 eggs/female/hour at 5 p.m. (ZT10) and ceasing at 2 a.m. (ZT19) (York et al. unpublished, Fig. 1c). This oviposition peak occurred 1 h prior to lights off. Previous work under a 16:8 L:D cycle observed a peak in oviposition from 8:00 p.m. (ZT15.5) to 12:00 p.m. (ZT19.5), a period that was mostly nocturnal [lights off at 8:30 p.m. (ZT16)] (Lin et al. 2014b). Overall, peaks in locomotor activity at 14:10 L:D align relatively well with peaks in mating activity and oviposition under 12:12 L:D and warmer temperatures (Fig. 1). Other factors impacting oviposition are discussed in the following section.

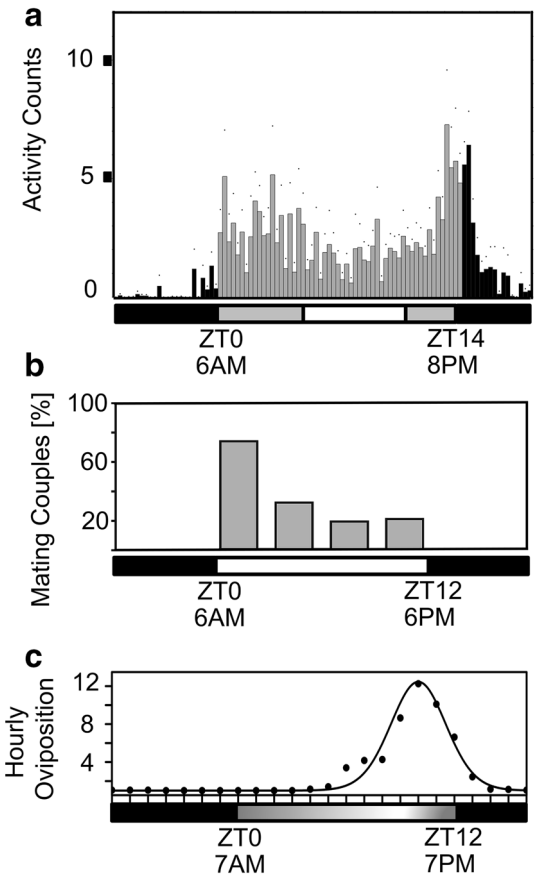

Fig. 1 Zeitgeber time (ZT), natural time, and light intensity are shown on the *X*-axis. Light intensity is indicated by *gray* and *white shading* where appropriate within the *horizontal bars* beneath the graph. **a** Female *D. suzukii* circadian locomotor activity monitored using the *Drosophila* activity monitoring system. *Black bars* lights off; *dark gray bars* dim light (1 bank of lights); *white bar* bright light (2 banks of lights). The temperature range was 12.2–22.2 °C with the peak temperature of 22.2 °C occurring between 2 p.m. (ZT8) and 3:30 p.m. (ZT9.5). Modified from Hamby et al. (2013). **b** Diurnal mating activity of *D. suzukii* during the first 30 min of each three-hour time interval. Nocturnal mating activity was not measured. *Black bars* = lights off, *white bar* = lights on. Temperature was a constant 23.0 ± 2.0 °C. Modified from Revadi et al. (2015). **c** *Black bars* lights off, *shaded bar* gradually ramping light intensity. Peak light intensity occurred at 4 p.m. (ZT9). The temperature range was 9.0–21.4 °C with the peak temperature of 21.4 °C occurring at 6 p.m. (ZT11). York et al. in the Supplemental Materials

Oviposition and factors influencing oviposition

Drosophila suzukii females can be characterized by the of the oviscape valve (bilateral pair of ovipositor plates), which has enabled their utilization of fresh fruit hosts

(Hauser 2011; Atallah et al. 2014). Mechanistically, insect oviscape valves can move back and forth on one another in a sawing motion that provides a functional basis for piercing fruit tissue (Austin and Browing 1981). The oviscape valves of *D. suzukii* are larger in area than most other *Drosophila* and have thick, heavily pigmented bristles near the distal tip of the valve, the region that comes into contact with fruit (Atallah et al. 2014). In comparison to *D. subpulchrella* Takamori and Watabe, *D. suzukii* have more modified bristles on the lateral side of the oviscape valve as well as more streamlined "sharp" shape as measured by the length-to-width ratio (Atallah et al. 2014). As a female lays her eggs, the oviscape valves ratchet against one another and the posteriorly oriented denticles (ovipositor scales) on the inside of the valve (part of the eversible membrane) act as a "linear ratchet" and produce unidirectional movement of the egg along the ovipositor (Austin and Browing 1981, Fig. 2a–d, g–j). As the eversible membrane fully expands, the now upright denticles may anchor the ovipositor at an optimal depth for egg deposition as the egg passes through and is released (see Fig. 2e–f, k–l). While *D. suzukii*'s ovipositor allows for oviposition in fresh fruit hosts, the physical limitations likely impact oviposition preferences on fruit hosts.

Oviposition preference has been correlated with ripeness and varies significantly between fruit hosts, with pH, total soluble solids (or Brix°), skin penetration force, firmness of flesh, and indumenta (fuzz) (Lee et al. 2011; Burrack et al. 2013; Stewart et al. 2014; Lee et al. 2015a, b; Ioriatti et al. 2015). Fruit susceptibility can be lowered to a limited degree using compounds such as foliar-sprayed calcium silicate on blueberry fruit, which increases the penetration force needed to pierce the epidermis (Lee et al. 2015a). More eggs are laid on fruit without indumenta or where previous damage to fruit allows flies to bypass the indumenta, and on fruit with lower skin penetration force, higher pH, and higher total soluble solids (Burrack et al. 2013; Stewart et al. 2014; Lee et al. 2015a). In laboratory no-choice assays, more eggs were laid in raspberries compared to blackberries, blueberries, and strawberries (Burrack et al. 2013). Raspberries tend to be among the most preferred fruit hosts in laboratory choice tests (Lee et al. 2011; Bellamy et al. 2013), and are infested at a greater rate than blackberries in the field (Burrack et al. 2013). Indeed, raspberries are among the fruit hosts with

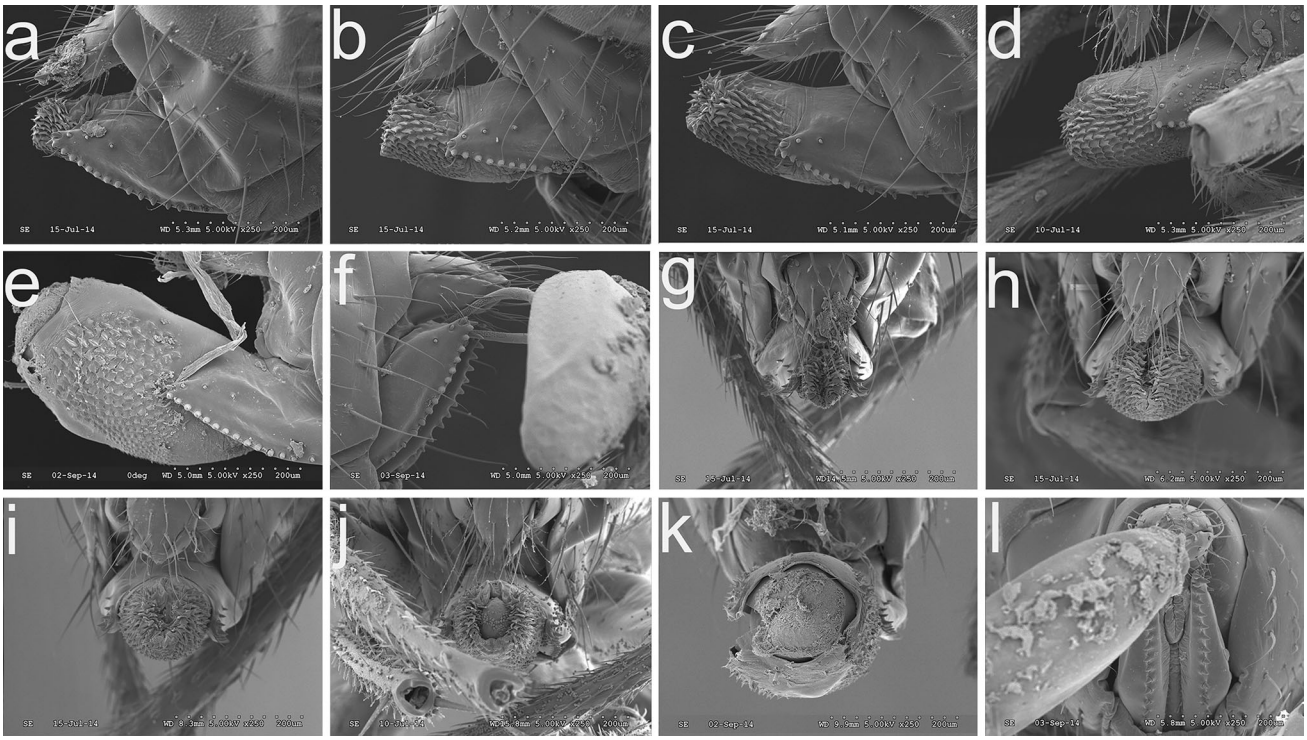

Fig. 2 *Drosophila suzukii* scanning electron microscope (SEM) oviposition image sequence by Dennis Margosan (see Supplemental Materials). Lateral view (*a*) and posterior view (*g*) of the oviscape valves that cut into ripe fruit and push eggs through the ovipositor in a sawing action. Lateral view (*b–d*) and posterior view (*h–j*) of the posteriorly oriented denticles on the eversible membrane of the ovipositor expanding and pushing the egg unidirectionally between the oviscape valves as egg deposition begins. Lateral view (*e*) and posterior view (*k*) of fully expanded membrane where upright denticles anchor the ovipositor at an optimal depth for egg deposition. Lateral view (*f*) and posterior view (*l*) of oviscape valves as they are withdrawn and the egg is released

Table 2 Fecundity and female lifespan of *D. suzukii* under various conditions based on recent work

Oviposition substrate	Colony source[a]	Age of males (days)[b]	Temp. (°C)	L:D	Humidity (%RH)	Fecundity[c]	Age of first egg laying (days)	Female lifespan (days)[d]	Reference
Banana media	B	ND	21	ND	ND	230	<2 days	Apprx. 60[d]	Chabert et al. (2013)
Blueberry	A	3–14	22	16:8	70	148.4 ± 19.1 (4 weeks)	3.7 ± 0.3	ND	Lee, supplemental
Blueberry	B	Mixed	20.6	16:8	20, 33, 71, 82, 94[e]	0.0 ± 0.0–84.8 ± 11.2[e]	1–7[e]	1.5 ± 0.3–27.5 ± 3.4[e]	Tochen et al. (2015)
Blueberry	B	Mixed	14, 18, 22, 26, 28[e]	16:8	60–70	6.6 ± 2.1–19.8 ± 7.9[e]	1–15[e]	11.7 ± 0.4–17.0 ± 2.1[e]	Tochen et al. (2014)
Cherry	B	Mixed	14, 18, 22, 26, 28[e]	16:8	60–70	12 ± 0.5–141 ± 20.3[e]	1–20[e]	10.5 ± 4.2–27.3 ± 3.9[e]	Tochen et al. (2014)
Grape	A	3–14	22	16:8	70	85.2 ± 10.9 (4 weeks)	5.2 ± 0.3	ND	Lee, supplemental
Grape	B	0–1[b]	25	16:8	60	68.0 ± 3.0	3.0 ± 0.2	26.2 ± 0.8	Lin et al. (2014a)
Grape agar	B	0[b]	25	16:8	60	~26 ± 1.0 (1 day)	ND	ND	Kinjo et al. (2014)
Media	B	3–14	22	16:8	70	418.5 ± 100.6	7.8 ± 1.6	86.6 ± 10.0	Lee, supplemental
Media	B	ND	22	15:9	25	635.6[c]	ND	~114	Emiljanowicz et al. (2014)
Media	B	Mixed	25	13:11	ND	~41, ~60 (1st week[c]) ~167 ± 9 (2nd week)	~4.1 ± 0.2	ND	Jaramillo et al. (2015)

[a] Colony source: *A* first generation raised on diet from wild parents, *B* flies from stock colony

[b] Age of males during initial placement with females for mating, expressed in days; females tested after 4 days of mate exposure in Kinjo et al. (2014); pairs remained together for their lifespan in Lin et al. (2014a)

[c] Fecundity is over lifetime unless otherwise noted; ~indicates estimates from bar graphs; and fecundity is ~41 for females that reared on blueberry as larvae, and ~60 for those reared on media as larvae for Jaramillo et al. (2015); fecundity is represented by an estimate of the gross fecundity rate for Emiljanowicz et al. (2014)

[d] Mean female lifespan unless otherwise noted; ~indicates maximum lifespan estimates derived from graphs using the age where last where daily oviposition value was reported; *D. suzukii* longevity was reported as comparable to *D. melanogaster* which live ~60 days on average at 19 °C in Chabert et al. (2013)

[e] Reported values were temperature dependent (Tochen et al. 2014) or humidity dependent (Tochen et al. 2015)

the lowest skin penetration force, 8.53 ± 0.31 cN as measured by Burrack et al. (2013), and between 5.5 and 20.2 cN for ripe fruit as measured by Sexton et al. (1997). Host not only affects female oviposition preference, but also laboratory evaluated fertility and fecundity.

Fertility and fecundity have been measured in multiple experiments, with lifetime fecundity varying from less than 100 to greater than 400 eggs (Table 2). Temperature, humidity, and host were found to influence *D. suzukii* reproductive output. Fecundity on cherry and blueberry fruit at various constant temperatures and 60–70 % RH was evaluated. More eggs were laid at 18 and 22 °C and significantly higher oviposition was observed on cherries across all temperatures (Tochen et al. 2014). While the aforementioned study observed no oviposition at 30 °C, *D. suzukii* were found to lay significantly more eggs in grape juice agar at 25 °C compared to 28, 31, and 33 °C when exposed for a 24 h oviposition period and were able to produce eggs at the higher temperatures (Kinjo et al. 2014). When mating couples were exposed to temperature treatments for 4 days prior to oviposition at 25 °C, the number of eggs laid decreased significantly as temperature increased (Kinjo et al. 2014). Fertility declined as temperature increased for both experiments; however, the effect of temperature during mating resulted in more extreme changes in fertility with no fertile egg production when mating occurred for 4 days at 31 °C prior to oviposition at 25 °C (Kinjo et al. 2014). When *D. suzukii* were exposed to fluctuating temperatures during mating with 8–12 h periods of high temperatures (31 or 33 °C) interspersed with moderate temperatures (25 °C), fecundity and fertility were significantly reduced compared to a constant moderate temperature of 25 °C (Kinjo et al. 2014). Humidity also impacts *D. suzukii* egg production. Flies reared on blueberries at constant temperature (22 °C) laid more eggs at higher humidity, with peak lifetime egg production of 84.8 ± 11.2 eggs at 94 % RH (Tochen et al. 2015). While infection status of the α-Proteobacteria *Wolbachia* was not tested among the females assayed for fecundity, its presence can reduce *Drosophila* reproduction (Hamm et al. 2014).

Drosophila species exhibit complex interactions with *Wolbachia* that influence their fitness and reproduction. *Wolbachia* are maternally transmitted endosymbionts that often exhibit imperfect transmission. Therefore, *Wolbachia* are expected to confer fitness benefits to the host or manipulate host reproduction to achieve a stable infection frequency in wild populations (Hamm et al. 2014). A species-specific *Wolbachia* *w*Suz was recently separated from *w*Ri, a *Wolbachia* strain that is prevalent in *Drosophila simulans* Sturtevant (Siozios et al. 2013; Hamm et al. 2014). The geographic distribution and infection frequencies of *w*Suz in wild populations suggest that the infection is maintained stably; however, previously described mechanisms for reproductive manipulation (e.g., cytoplasmic incompatibility) are not present in the *w*Suz infection of *D. suzukii* (Hamm et al. 2014). *Drosophlia suzukii* fecundity was evaluated for various crosses between *Wolbachia* infected and uninfected *D. suzukii,* and *Wolbachia* infected females produced fewer offspring than uninfected females (Hamm et al. 2014). There was no significant difference in fertility among the crosses from a California population, with mean hatch rate ranging from 0.538 ± 0.07 to 0.596 ± 0.03. However, a New York population exhibited significantly higher fertility (0.51 ± 0.06) when uninfected females were crossed with infected males. The hatch rate of the other New York treatments ranged from 0.30 ± 0.06 to 0.38 ± 0.04. Currently, no fitness benefits have been discovered for *w*Suz; though, mutualistic effects may explain *Wolbachia* prevalence (Hamm et al. 2014). Further research is necessary to explain the mechanism for maintenance of *w*Suz infections in *D. suzukii* (Hamm et al. 2014).

Age-specific reproduction and lifespan

Age-specific reproduction values have been measured in multiple experiments with considerable variation in reported time to first egg laying from around 1 day to 7.8 days (Table 2). Female *D. suzukii* have been reported to lay their first egg about 4 days after emergence when larvae were reared on blueberries or *Drosophila* media at 25 °C and 13:11 L:D (Jaramillo et al. 2015). While there was no significant difference in time to the first egg laid between these larval diets, there was a significant difference in the number of eggs laid in the first 7 days, with more eggs laid by the flies that were raised on *Drosophila* media (Jaramillo et al. 2015). One potential source of variation between these studies could be the age of the male flies provided as mates for the females. Revadi et al. (2015) found that 100 % of freshly emerged females produced offspring 2.5 days after emergence when mated with 4-day-old males *Drosophila* media at 23 °C and 12:12 L:D, whereas only 43 % of females placed with freshly emerged males produced offspring. Indeed, it was not until 3.5 days post emergence that 100 % of the freshly emerged pairs produced offspring (Revadi et al. 2015). Another source of variation is potential selection pressure on laboratory colonies. Previously unpublished data compared a laboratory colony that had been cultured for around 3 months to a first generation colony (Lee, see Supplemental Materials). This study observed the mean age of first egg laying to be between 3.7 and 7.8 days, with the longest time to oviposition and greatest daily oviposition in the 3-month-old laboratory colony with *Drosophila* media as a substrate (Table 2). The laboratory colony may have been selected

for delayed reproduction because newly emerged adults were gathered for some time and then given fresh media for reproduction; therefore, the initial eggs laid on the media that the adults emerged from were discarded. The age of females at the time of peak reproduction varies between experiments and with access to males (Emiljanowicz et al. 2014; Asplen et al. 2015; Lee Supplemental Materials), and although egg production does eventually decline with age, *D. suzukii* females lay eggs for very close to the entirety of their lifespan (Emiljanowicz et al. 2014; Asplen et al. 2015). Additionally, the demographic growth parameters estimated for *D. suzukii* are related with the environmental conditions and the feeding substrate (Tables 1, 2). For instance, the *D. suzukii* intrinsic rate of natural increase on cherries vary from 0.02 to 0.22 at unfavorable and optimal temperatures, respectively; while at 22 °C it was estimated to be 0.22, 0.17, and 0.18 when using cherries, blueberries, and cornmeal–yeast media, respectively (Emiljanowicz et al. 2014; Tochen et al. 2014).

Adult lifespan of *D. suzukii* varies with temperature, humidity, oviposition substrate, and adult food resources. Total lifespan from egg to adult mortality was 86.1 ± 4.25 days with a maximum value of 153.7 days (male) when reared on *Drosophila* media at 22 °C, 25 % RH, and 15:9 (L:D) (Emiljanowicz et al. 2014). Tochen et al. (2014) reported significant differences in female survival rates between cherry and blueberry fruit as juvenile and adult hosts at 60–70 % RH, with higher survivorship on cherry when controlling for temperature. Adult female longevity was longer at the lower temperatures of 14, 18, 22 °C at 40.7, 44.2, and 14.9 days, respectively when reared on cherries and 34.3, 28.3, 13.8 days, respectively than when reared on blueberries (Tochen et al. 2014). Nevertheless, at 22 °C on blueberries under varying humidity, *D. suzukii* adults survived significantly longer with increasing humidity, with highest longevity of 27.5 ± 3.4 (females) and 20.3 ± 3.8 (males) days at 94 % RH (Tochen et al. 2015). Egg laying and longevity can be standardized over physiological time as both these parameters are strongly impacted by physiological age (Wiman et al. 2016).

Adult access to food resources affects *Drosophila* egg production and longevity (Min et al. 2006; Kaçar et al. 2016). *Drosophila suzukii* adults emerge with limited glycogen and sugar reserves, energetic reserves that are utilized for maintenance and mobility (Tochen et al. 2016). When provided access to sugar sources, freshly emerged *D. suzukii* quickly increase their carbohydrate reserves, and providing adult *D. suzukii* with cherry or blueberry blossoms extends their survivorship in the laboratory (Tochen et al. 2016). Adult *D. suzukii* may also use microbes, such as yeast and bacteria as suitable dietary resources (Hamby et al. 2012; Chandler et al. 2014). Early season adult food sources may play an important role in enabling overwintering adults to maintain themselves when fruit hosts are limited (Tochen et al. 2016). The impacts of season on adult population dynamics and physiology are described in the following section.

Adult seasonal biology

Seasonal monitoring of adult *D. suzukii* populations with baited traps has been performed in many regions worldwide (Burrack et al. 2012; Lee et al. 2013; Asplen et al. 2015). Captures typically begin at low levels in the spring, building until a strong decline as soon as daily temperature means increase above 30 °C in the hottest part of the summer season (Wiman et al. 2014). This is subsequently followed by another increase as soon as temperatures drop below 30 °C (Dalton et al. 2011; Harris et al. 2014; Wiman et al. 2014; Mazzetto et al. 2015; Wang et al. 2016b). This summer decline is not seen in production regions where temperatures do not reach these high thresholds. In central California, higher fly numbers were captured in non-crop habitats late in the growing season (Wang et al. 2016b), highlighting the importance of area-wide *D. suzukii* control programs. Traps placed in evergreen shrubs and trees captured between 20 and 120 flies weekly from November through the end of January while mean minimum monthly temperatures ranged from 0 to 6 °C (Harris et al. 2014). In some capture locations, temperatures reached −5 °C preceding weekly trap captures of ca. 20 *D. suzukii*; however, in other locations, trap captures ceased after temperature lows of −2 °C (Dalton et al. 2011). At the moment, it is unclear whether *D. suzukii* adults overwinter in refugia under leaf litter and snow, or by migrating to more sheltered (structures or woods) habitats (Dalton et al. 2011; Harris et al. 2014). It is also possible that they migrate longer distances to more favorable climates, although specific studies are still lacking.

Many temperate *Drosophila* species diapause or migrate seasonally, allowing them to endure or avoid unfavorable conditions (Kimura and Beppu 1993; Schmidt et al. 2005; Salminen et al. 2015). Evidence suggests that *D. suzukii* progressively migrate to higher elevations over the summer both in their native range and in Europe (Mitsui et al. 2010; Tonina et al. 2016). Adult *Drosophila* are considered to be chill susceptible and *Drosophila* have been used as models for investigating acclimation responses to various climatic stressors. In *D. melanogaster*, cold shock resistance increases with latitude, as does the incidence of reproductive diapause, although non-diapausing genotypes are also found at northern latitudes (Tatar et al. 2001; Schmidt et al. 2005; Schmidt and Paaby 2008). Without acclimation, *D. suzukii* desiccation tolerance, measured as the time

to death following exposure to RH <5 % at 20 °C, was 17–19 h, and the critical thermal minimum where flies entered chill coma (lost the ability to move any body part) was between 3 and 4 °C (Kellermann et al. 2012). Various experiments have evaluated the impact of short- to medium-term acclimation of adult *D. suzukii* to cold temperatures. Dalton et al. (2011) acclimated adult laboratory flies to 10 from 22 °C by lowering the temperature 2.5 °C every 2 days (12 days total cold acclimation) prior to performing thermal tolerance experiments. These acclimated flies were then exposed to constant 1, 3, 5, 7, and 10 °C at 8:16 (L:D) for 6 weeks and then photoperiod was changed to 12:12 (L:D) and flies were held for another 6 weeks. Within 8 days these adult flies reached 75 % mortality for 1 and 3 °C, and survived for up to 66 days at 10 °C (Dalton et al. 2011). Wallingford et al. (2016) evaluated chill coma recovery after 24 h exposure to −1 °C among un-acclimated, cold-hardened (held at 10 °C for 24 h), and cold-acclimated (light entrained to 12:12 L:D and held at 10 °C for 7 days) *D. suzukii*. Cold-hardened and cold-acclimated females survived significantly better than un-acclimated females, and cold-acclimated females recovered significantly faster than either the cold-hardened or un-acclimated females (Wallingford et al. 2016). Jakobs et al. (2015) subjected *D. suzukii* to acclimation treatments of rapid cold hardening (chilling at 0 °C for 1 h), a constant temperature acclimation (5 days at 6 °C), and a fluctuating acclimation [2 weeks total of 1 week at 9/21 °C (min/max) for 12:12 L:D and a second week at 5.5/19 °C (min/max) 11.5:12.5 (L:D)]. *Drosophila suzukii* exhibited improved survival after acute cold exposure (1 h at ca. −7 °C) and chill coma recovery time relative to control flies after the longer fluctuating and constant acclimation treatments. However, no difference was observed in rapid cold hardening. This study concluded that *D. suzukii* may lack a capacity for rapid cold hardening or that treatment conditions were not sufficient to induce rapid cold hardening in *D. suzukii*. However, cold tolerance as measured by chill coma recovery and survival of short-term acute cold treatments (1–24 h at −1 to −7 °C) is improved by short- to medium-term acclimation treatments (Jakobs et al. 2015; Wallingford et al. 2016). Jakobs et al. (2015) concluded that *D. suzukii* must overwinter in sheltered habitats or exhibit seasonal cold hardening to survive the winter climate in Ontario.

Drosophila suzukii exhibit seasonal phenotypic plasticity that may confer seasonal cold hardening (Stephens et al. 2015; Shearer et al. 2016). The mean wing length and darkness of pigmentation of field-captured *D. suzukii* increases as summer progresses to winter, and this winter morph phenotype can be induced with short day length and cooler temperatures (12:12 L:D and 10 °C) (Shearer et al. 2016). The winter morph phenotype can be observed from October through December (when evaluated bimonthly from 14 August to 11 December, 2012 in Hood River, OR) (Shearer et al. 2016, Fig. 3a), and is accompanied by differences in global gene expression (Shearer et al. 2016). Indeed, when comparing a control laboratory fly reared at 16:8 L:D and 20 °C, hereafter referred to as the summer morph phenotype, to winter morph flies, gene expression differences are observed in both the head and the body. These were assayed independently to increase the resolution of the gene expression analysis, given that they contain tissues that play different roles in hormone regulation and

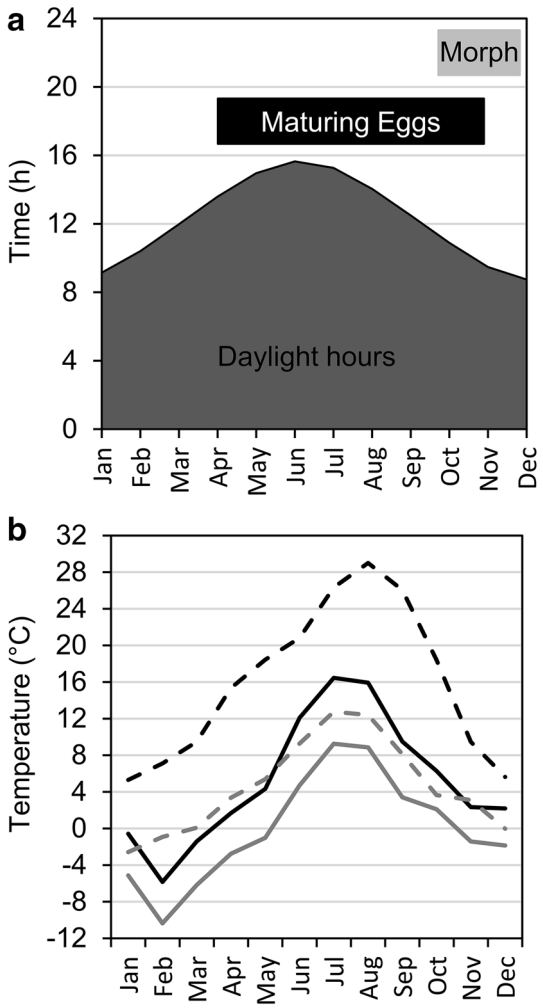

Fig. 3 *Drosophila suzukii* seasonal reproductive status and phenotype (summarized from Zerulla et al. 2015 and Shearer et al. 2016). **a** Monthly mean hours of daylight (*daylight hours*) in Hood River, OR, USA; period (*morph*) in the fall when *D. suzukii* winter phenotype (morph) can be collected in Hood River, OR, USA (October–December); and period (*maturing eggs*) when *D. suzukii* females carry mature or maturing eggs in South Tyrol, Italy (April–November). **b** Monthly mean min (*dark gray*) and max (*black*) temperatures for 2012 Hood River, OR, USA (*dashed lines*) and 2013 Paganella, Italy (*solid lines*). See Supplemental Materials for methods used to summarize data

metabolism, e.g., the brain and fat body. Moreover, a higher number of genes are differentially expressed and the degree of differential expression (fold change) is more extreme in the body as compared to the head. Gene expression differences indicate that *D. suzukii* winter morphs may exhibit altered metabolism compared to summer morphs, with significant up-regulation of genes involved in cellular respiration and metabolism. Genes that are involved in morphogenesis, development, pigmentation, chitin biosynthesis, and cuticular protein synthesis were also up-regulated, which is consistent with the larger darker phenotype and may be associated with enhanced desiccation resistance and cold tolerance (Shearer et al. 2016). Indeed, winter morph adult flies are the most cold-tolerant *D. suzukii* life stage (Dalton et al. 2011; Stephens et al. 2015; Shearer et al. 2016). Adult winter morph *D. suzukii* exhibit a significantly colder lower lethal temperature (Stephens et al. 2015), and live significantly longer at constant 1 °C than summer morphs (Shearer et al. 2016). *Drosophila suzukii* winter morphs may exhibit a reproductive diapause because genes involved in DNA replication, female meiosis, and egg production were highly down-regulated (Shearer et al. 2016).

Assays of seasonal reproductive status and laboratory induction of reproductive diapause indicate that *D. suzukii* may undergo a facultative reproductive diapause (Zerulla et al. 2015; Wallingford et al. 2016). Zerulla et al. (2015) evaluated the reproductive status of field-captured flies via dissection of ovarioles from August 2012 to September 2013 at one location in the Adige Valley, South Tyrol, Italy. Immature ovarioles were common at the beginning of winter and females with maturing eggs could be captured until the end of November, with the first spring maturing eggs found in April 2013 (Fig. 3a). In 2014, the first spring mature eggs were found in mid-March (Zerulla et al. 2015). In northern regions of the USA, female flies captured in adult traps were dissected and mature eggs counted from July to December in 2012 (Benton Co., OR, USA) and 2013 (Ontario Co., NY, USA) (Wallingford et al. 2016). Significantly fewer mature eggs were observed in the fall/winter compared to the summer, with mature eggs present from July–October in Oregon and July–November in New York (Wallingford et al. 2016). Whereas, in warmer areas, such as central California, the majority of field-captured females contained mature eggs starting in April. Moreover, about 3 % of these females contained at least one live larva suggesting facultative ovoviviparity (Wang et al. 2016b). The impact of photoperiod and temperature on *D. suzukii* reproduction were evaluated in laboratory experiments (Wallingford et al. 2016). Less than 2 eggs/female were produced at 10 °C; therefore, no effect of photoperiod was observable under those conditions. Significantly fewer mature eggs were produced under most short day lengths with less than 14 h of light at 15 °C, and 12:12 L:D entrained females produce significantly fewer mature eggs compared to control females (experienced the same temperature as the experimental flies and constant darkness during the experimental period but were entrained to long day length 16:8 L:D prior to the experiment) at 15 and 20 °C. Females held at 10 °C 12:12 L:D begin to produce more mature eggs than their controls after 7 weeks of exposure, and produced similar numbers of eggs as their controls when returned to summer conditions (after 7 weeks of exposure). This suggests that diapause is spontaneously terminated during the winter and females remain quiescent until favorable conditions occur.

Concluding remarks

Globally, research groups continue to develop *D. suzukii* management tactics moving towards viable integrated pest management (IPM) programs in affected crops (Haye et al. 2016). A recent review provided research directions to improve *D. suzukii* IPM programs, highlighting a need for improved population modeling (Wiman et al. 2016), understanding of the role of non-crop host plants, and *D. suzukii* movement at various geographic scales (Asplen et al. 2015). Our ability to address these questions is hindered by our knowledge of *D. suzukii* biology, physiology, and ecology; and additional research in these areas is crucial. We present current knowledge of *D. suzukii* biology and physiology, specifically focusing upon juvenile and adult development, reproduction, and seasonal impacts on physiology.

Drosophila suzukii development and reproduction is affected by host type, host quality, temperature, humidity, and biotic factors such as symbionts and parasitoids. However, information is currently lacking, including the role of microorganisms and their impact on larval survival and adult reproduction. Other species of *Drosophila* exhibit complex interactions with various symbiotic microorganisms including bacteria, hyphal fungi, and yeasts. Such interactions are underutilized for pest management, and their potential for use against *D. suzukii* is described elsewhere in this issue (Hamby and Becher 2016). Although *D. suzukii* clearly exhibit strong immune responses in the face of parasitism, biological control agents from its native range will likely play a role in managing *D. suzukii* in its expanded range. Differences in experimental design and intrinsic variables, such as *Wolbachia* and population genetics, contribute to the variability in the *D. suzukii* life history parameters that have been measured, complicating interpretations of life history traits across experiments. Moreover, these differences suggest that more work is necessary to better understand the impact

of these variables on the life history parameters to effectively exploit them for pest management. Accurate population modeling requires additional measurement of life history parameters across the breadth of environmental conditions experienced by natural populations (Wiman et al. 2014; Asplen et al. 2015). Such modeling can provide critical decision support for pest management such as improving the timing of management action and forecasting *D. suzukii* populations. Additional work is needed to determine the effects of season and climate on *D. suzukii* populations, particularly at upper and lower extremes of temperature and humidity. Winter temperature determines the range of many insect species (Stahl et al. 2006; Caminade et al. 2012), and mortality due to climate can regulate the size of insect populations (Ferro 1987). Indeed, low winter temperature can cause high mortality in overwintering populations of insects in temperate climates effectively reducing the number of colonizers in the following spring (Ferro 1987). Therefore, *D. suzukii* overwintering including: critical temperatures and photoperiods for inducing reproductive diapause and seasonal cold hardening, biology at temperatures <10 °C, and the potential for seasonal migrations are important areas of future *D. suzukii* biology and physiology research.

Here we summarize the most recent knowledge of the biotic and abiotic factors impacting the biology, ecology, and physiology of *D. suzukii*. We focused on aspects of these topics that have received research attention, which are by no means comprehensive. Several fields of study remain poorly understood including behavioral, physiological, and genetic adaptations to environmental extremes and interactions between mutualistic and parasitic organisms. We believe that increased research focus will be given to these and other aspects of *D. suzukii*'s life history that are outside the scope of this manuscript.

Author contribution statement

KAH, VMW, and AB organized the review based on contributions from all authors. DB, JCC, JCL, VMW, RMY contributed original data, which were analyzed by JCC, JCL, and NGW. KAH drafted the manuscript. All authors contributed to the writing of the manuscript and approved the final manuscript.

Acknowledgments We thank Adam Cave, Christina Fieland, and Amanda Lake, USDA-ARS Corvalis, OR, and Daniel Dalton, Oregon State University, for assistance and rearing of *D. suzukii* used in assays. We thank Nathalie Steinhauer, University of Maryland, for translating Chabert et al. (2013). We thank Dennis Margosan, USDA-ARS Parlier, CA, for his SEM images. Funding was provided by the USDA SCRI Grant 2010-51181-21167, and USDA CRIS 5358-22000-037-00D. Antonio Biondi received funding from the People Programme (Marie Curie Actions) of the European Union's Seventh Framework Programme 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).

References

Asplen MK, Anfora G, Biondi A, Choi D-S, Chu D et al (2015) Invasion biology of spotted wing Drosophila (*Drosophila suzukii*): a global perspective and future priorities. J Pest Sci 88:469–494. doi:10.1007/s10340-015-0681-z

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 B 281:20132840. doi:10.1098/rspb.2013.2840

Austin AD, Browing TO (1981) A mechanism for movement of eggs along insect ovipositors. Int J Insect Morphol 10:93–108. doi:10.1016/S0020-7322(81)80015-3

Awmack CS, Leather SR (2002) Host plant quality and fecundity in herbivorous insects. Annu Rev Entomol 47:817–844. doi:10.1146/annurev.ento.47.091201.145300

Becher PG, Flick G, Rozpędowska E, Schmidt A, Hagman A, Lebreton S, Larsson MC, Hansson BS, Piškur J, Witzgall P, Bengtsson M (2012) Yeast, not fruit volatiles mediate *Drosophila melanogaster* attraction, oviposition and development. Funct Ecol 26:822–828

Bellamy DE, Sisterson MS, Walse SS (2013) Quantifying host potentials: indexing postharvest fresh fruits for spotted wing drosophila, *Drosophila suzukii*. PLoS One 8:e61227. doi:10.1371/journal.pone.0061227

Burrack HJ, Smith J, Powell J, Pfeiffer DG, Koeher G, Laforest J (2012) Using volunteer-based networks to track *Drosophila suzukii* (Diptera: Drosophilidae) an invasive pest of fruit crops. J Integr Pest Manag 3:B1–B5. doi:10.1603/IPM12012

Burrack HJ, Fernandez GE, Spivey T, Kraus DA (2013) Variation in selection and utilization of host crops in the field and laboratory by *Drosophila suzukii* Matsumara (Diptera: Drosophilidae), and invasive frugivore. Pest Manag Sci 69:1173–1180. doi:10.1002/ps.3489

Caminade C, Medlock JM, Ducheyne E, McIntyre KM, Leach S, Baylis M, Morse AP (2012) Suitability of European climate for the Asian tiger mosquito *Aedes albopictus*; recent trends and future scenarios. J R Soc Interface 9:2708–2717. doi:10.1098/rsif.2012.0138

Carton Y, Poirie M, Nappi AJ (2008) Insect immune resistance to parasitoids. Insect Sci 15:67–87. doi:10.1111/j.1744-7917.2008.00188.x

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. doi:10.1016/j.biocontrol.2012.05.005

Chabert S, Allemand R, Pyet M, Ris N, Gibert P (2013) *Drosophila suzukii*, versune lute biologique contre ce ravageur des fruits rouges. Phytoma 660:34–38

Chandler JA, James PM, Jospin G, Lang JM (2014) The bacterial communities of *Drosophila suzukii* collected from undamaged cherries. PeerJ 2:e474. doi:10.7717/peerj.474

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 JC, Miller B, Miller JC, Reidl H, Shearer PW, Guerrieri E, Giorgini M, Buffington M,

van Achterberg K, Song Y, Kang T, Yi H, Jung C, Lee DW, Chung B-K, Hoelmer KA, Walton VM (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

Dalton DT, Walton VM, Shearer PW, Walsh DB, Caprile J, Isaacs R (2011) Laboratory survival of *Drosophila suzukii* under simulated winter conditions of the Pacific Northwest and seasonal field trapping in five primary regions of small and stone fruit production in the United States. Pest Manag Sci 67:1368–1374. doi:10.1002/ps.2280

Dekker T, Revadi S, Mansourian S, Tamasamy S, Lebreton S, Becher PG, Angeli S, Rota-Stabelli O, Anfora G (2015) Loss of *Drosophila* pheromone reverses its role in sexual communication in *Drosophila suzukii*. Proc R Soc B 282:20142018. doi:10.1098/rspb.2014.3018

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

Emiljanowicz LM, Ryan GD, Langille A, Newman J (2014) Development, reproductive output and population growth of the fruit fly pest *Drosophila suzukii* (Diptera: Drosophilidae) on artificial diet. J Econ Entomol 107:1392–1398. doi:10.1603/EC13504

Ferguson CTJ, O'Neill TL, Audsley N, Isaac RE (2015) The sexual dimorphic behavior of adult *Drosophila suzukii*: elevated female locomotor activity and loss of siesta is a post-mating response. J Exp Biol. doi:10.1242/jeb.125468

Ferro DN (1987) Insect pest outbreaks in agroecosystems. In: Barbosa P, Schultz JC (eds) Insect outbreaks. Academic Press Inc, San Diego, pp 195–212

Fuyama Y (1979) A visual stimulus in the courtship of *Drosophila suzukii*. Experientia 35:1327–1328

Good T, Tatar M (2001) Age-specific mortality and reproduction response to adult dietary restriction in *Drosophila melanogaster*. J Insect Physiol 47:1467–11473

Hamby KA, Becher PG (2016) Current knowledge of interactions between *Drosophila suzukii* and microbes, and their potential utility for pest management. J Pest Sci (submitted)

Hamby KA, Hernández A, Boundy-Mills K, Zalom FG (2012) Yeast associations of spotted wing drosophila (*Drosophila suzukii*, Diptera: Drosophilidae) in cherries and raspberries. Appl Environ Microb 78:4869–4873. doi:10.1128/AEM.00841-12

Hamby KA, Kwok RS, Zalom FG, Chiu JC (2013) Integrating circadian activity and gene expression profiles to predict chronotoxicity of *Drosophila suzukii* response to insecticides. PLoS One 8:e68472. doi:10.1371/journal.pone.0068472

Hamm CA, Begun DJ, Vo A, Smith CCR, Saelao P, Shaver AO, Jaenike J, Turelli M (2014) *Wolbachia* do not live by reproductive manipulation alone: infection polymorphism in *Drosophila suzukii* and *D. subpulchrella*. Mol Ecol 23:4871–4885. doi:10.1111/mec.12901

Hardin JA, Kraus DA, Burrack HJ (2015) Diet quality mitigates intraspecific larval competition in *Drosophila suzukii*. Entomol Exp Appl 56:59–65. doi:10.1111/eea.12311

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. doi:10.1016/j.aspen.2014.08.006

Hauser M (2011) A historic account of the invasion of *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) in the continental United States, with remarks on their identification. Pest Manag Sci 67:1352–1357. doi:10.1002/ps.2265

Haye T, Gariepy T, Hoelmer K, Rossi JP, Streito JC, Tassus X, Desneux N (2015) Range expansion of the invasive brown marmorated stinkbug, *Halyomorpha halys*: an increasing threat to field, fruit and vegetable crops worldwide. J Pest Sci 88:665–673. doi:10.1007/s10340-015-0670-2

Haye T, Girod P, Cuthbertson AGS, Wang XG, Daane KM, Hoelmer KA, Baroffio C, Zhang JP, 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

Ioriatti C, Walton VM, Dalton DT, 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

Jakobs R, Gariepy TD, Sinclair BJ (2015) Adult plasticity of cold tolerance in a continental-temperate population of *Drosophila suzukii*. J Insect Physiol 79:1–9. doi:10.1016/j.jinsphys.2015.05.003

Jaramillo SL, Mehlferber E, Moore PJ (2015) Life-history trade-offs under different larval diets in *Drosophila suzukii* (Diptera: Drosophilidae). Physiol Entomol 40:2–9. doi:10.1111/phen.12082

Kaçar G, Wang X, 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. doi:10.1371/journal.pone.0034721

Katayama N, Abbott JK, Kjærandsen J, Takahashi Y, Svensson EI (2014) Sexual selection on wing interference patterns in *Drosophila melanogaster*. PNAS 111:15144–15148. doi:10.1073/pnas.1407595111

Kellermann V, Loeschcke V, Hoffmann AA, Kristensen TN, Fløjgaard C, David JR, Svenning JC, Overgaard J (2012) Phylogenetic constraints in key functional traits behind species' climate niches: patterns of desiccation and cold resistance across 95 *Drosophila* species. Evolution 66:3377–3389. doi:10.1111/j.1558-5646.2012.01685.x

Kimura MT, Beppu K (1993) Climatic adaptations in the *Drosophila immigrans* group: seasonal migration and thermal tolerance. Ecol Entomol 18:141–149. doi:10.1111/j.1365-2311.1993.tb01195.x

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. doi:10.1007/s13355-014-0249-z

Kopp A, True JR (2002) Evolution of male sexual characters in the oriental *Drosophila melanogaster* species group. Evol Dev 4:278–291. doi:10.1046/j.1525-142X.2002.02017.x

Lee JC, Bruck DJ, Curry H, Edwards D, Haviland DR, Van Steenwyk RA, Yorgey BM (2011) The susceptibility of small fruits and cherries to the spotted-wing drosophila, *Drosophila suzukii*. Pest Mang Sci 67:1358–1367. doi:10.1002/ps.2225

Lee JC, Dalton DT, Swoboda-Bhattarai KA, Bruck DJ, Burrack HJ, Strik BC, Woltz JM, Walton VM (2015a) Characterization and manipulation of fruit susceptibility to *Drosophila suzukii*. J Pest Sci. doi:10.1007/s10340-015-0692-9

Lee JC, Dreves AJ, Cave AM, Kawai S, Isaacs R, Miller JC, Van Timmeren S, Bruck DJ (2015b) Infestation of wild and ornamental noncrop fruits by *Drosophila suzukii* (Diptera: Drosophilidae). Ann Entomol Soc Am 108:117–129. doi:10.1093/aesa/sau014

Lee JC, Shearer PW, Barrantes LD, Beers EH, Burrack HJ, Dalton DT, Dreves AJ, Gut LJ, Hamby KA, Haviland DR, Isaacs R, Nielsen AL, Richardson T, Rodriguez-Saona CR, Stanley CA, Walsh DB, Walton VM, Yee WL, Zalom FG, Bruck DJ (2013)

Trap designs for monitoring Drosophila suzukii (Diptera: Drosophilidae). Environ Entomol 42:1348–1355

Lin Q-C, Zhai Y-F, Zhang A-S, Men X-Y, Zhang X-Y, Zalom FG, Zhou C-G, Yu Y (2014a) Comparative developmental times and laboratory life tables for *Drosophlia suzukii* and *Drosophila melanogaster* (Diptera: Drosophilidae). Fla Entomol 97:1434–1442. doi:10.1653/024.097.0418

Lin Q-C, Zhai Y-F, Zhou C-G, Li L-L, Zhuang Q-Y, Zhang X-Y, Zalom FG, Yu Y (2014b) Behavioral rhythms of *Drosophila suzukii* and *Drosophila melanogaster*. Fla Entomol 97:1424–1433. doi:10.1653/024.097.0417

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

Mazzetto F, Marchetti E, Sacco D, Francati S, Jucker C, Lupi D, Tavella L (2016) Drosophila parasitoids in northern Italy and their potential to attack the exotic pest *Drosophila suzukii*. J Pest Sci. doi:10.1007/s10340-016-0746-7

Mazzoni V, Anfora G, Virant-Doberlet M (2013) Substrate vibrations during courtship in three *Drosophila* species. PLoS One 8:e80708. doi:10.1371/journal.pone.0080708

Miller B, Anfora G, Buffington M, Daane KM, Dalton DT, Hoelmer KM, Rossi Stacconi MV, Grassi A, Ioriatti C, Loni A, Miller JC, Ouantar M, Wang X, Wiman NG, Walton VM (2015) Seasonal occurrence of resident parasitoids associated with *Drosophila suzukii* in two small fruit production regions of Italy and the USA. B Insectol 68:255–263

Min K-J, Hogan MF, Tatar M, O'Brien DM (2006) Resource allocation to reproduction and soma in *Drosophila*: a stable isotope analysis of carbon from dietary sugar. J Insect Physiol 52:763–770. doi:10.1016/j.jinsphys.2006.04.004

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

Monceau K, Bonnard O, Thiéry D (2014) *Vespa velutina*: a new invasive predator of honeybees in Europe. J Pest Sci 87:1–16. doi:10.1007/s10340-013-0537-3

Nomano FY, Mitsui H, Kimura MT (2015) Capacity of Japanese *Asobara* species (Hymenoptera; Braconidae) to parasitize a fruit pest *Drosophila suzukii* (Diptera; Drosophilidae). J Appl Entomol 139:105–113

Pimentel D (1993) Habitat factors in new pest invasions. In: Kim KC, McPheron BA (eds) Evolution of insect pests—patterns of variation. Wiley, New York, pp 165–181

Pimentel D, Zuniga R, Morrisonn D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52:273–288. doi:10.1016/j.ecolecon.2004.10.002

Revadi S, Lebreton S, Witzgall P, Anfora G, Dekker T, Becher PG (2015) Sexual behavior of *Drosophila suzukii*. Insects 6:183–196. doi:10.3390/insects6010183

Rossi Stacconi MV, Grassi A, Dalton DT, Miller B, Ouantar M, Loni A, Ioriatti C, Walton VM, Anfora G (2013) First field records of *Pachycrepoideus vindemiae* as a parasitoid of *Drosophila suzukii* in European and Oregon small fruit production areas. Entomologia 1:11–16. doi:10.4081/entomologia.2013.e3

Rossi Stacconi MV, Buffington M, Daane KM, Dalton DT, Grassi A, Kaçar G, Miller B, Miller JC, Baser N, Ioriatti C, Walton VM, Wiman NG, Wang X, Anfora G (2015) Host stage preference, efficacy and fecundity of parasitoids attacking *Drosophila suzukii* in newly invaded areas. Biol Control 84:28–35. doi:10.1016/j.biocontrol.2015.02.003

Salminen TS, Vesala L, Laiho A, Merisalo M, Hoikkala A, Kankare M (2015) seasonal gene expression kinetics between diapause phases in *Drosophila virilis* group species and overwintering differences between diapausing and non-diapausing females. Sci Rep 5:11197. doi:10.1038/srep11197

Schmidt PS, Paaby AB (2008) Reproductive diapause and life-history clines in North American populations of *Drosophila melanogaster*. Evolution 62:1204–1215. doi:10.1111/j.1558-5646.2008.00351.x

Schmidt PS, Matzkin LM, Ippolito M, Eanes WF (2005) Geographic variation in diapause incidence, life history traits, and climatic adaptation in *Drosophila melanogaster*. Evolution 59:1721–1732. doi:10.1111/j.0014-3820.2005.tb01821.x

Sexton R, Palmer JM, Whyte NA, Littlejohns S (1997) Cellulase, fruit softening, and abscission in red raspberry *Rubus ideaeus* L. cv Glen Clova. Ann Bot 80:371–376. doi:10.1006/anbo.1997.0465

Shearer PW, West JD, Walton VM, Brown PH, Svetec N, Chiu JC (2016) Seasonal cues induce phenotypic plasticity of *Drosophila suzukii* to enhance winter survival. BMC Ecol 16:11. doi:10.1186/s12898-016-0070-3

Shevtsova E, Hansson C, Janzen DH, Kjærandsen J (2011) Stable structural color patterns displayed on transparent insect wings. PNAS 108:668–673. doi:10.1073/pnas.1017393108

Siozios S, Cestaro A, Kaur R, Pertot I, Rota-Stabelli O, Anfora G (2013) Draft genome sequence of the *Wolbachia* endosymbiont of *Drosophila suzukii*. Genome Announc 1:e00032-13. doi:10.1128/genomeA.00032-13

Sokolowski MB, Kent C, Wong J (1984) *Drosophila* larval foraging behaviour: developmental stages. Anim Behav 32:645–651

Stahl K, Moore RD, McKendry IG (2006) Climatology of winter cold spells in relation to mountain pine beetle mortality in British Columbia, Canada. Clim Res 32:13–23. doi:10.3354/cr032013

Stephens AR, Asplen MK, Hutchinson WD, Venette RC (2015) Cold hardiness of winter-acclimated *Drosophila suzukii* (Diptera: Drosophilidae) adults. Environ Entomol 44:1619–1626. doi:10.1093/ee/nvv134

Stewart TJ, Wang X-G, Molinar A, Daane KM (2014) Factors limiting peach as a potential host for *Drosophila suzukii* (Diptera: Drosophilidae). J Econ Entomol 107:1771–1779. doi:10.1603/EC14197

Tatar M, Chien S, Priest NK (2001) Negligible senescence during reproductive dormancy in *Drosophila melanogaster*. Am Nat 158:248–258. doi:10.1086/321320

Tatum EL (1939) Nutritional requirements of Drosophila melanogaster. Proc Natl Acad Sci USA 25:490–497

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. doi:10.1603/EN13200

Tochen S, Walton VM, Lee JC (2016) Impact of floral feeding on adult *Drosophila suzukii* survival and nutrient status. J Pest Sci (in press)

Tochen S, Woltz JM, Dalton DT, Lee JC, Wiman NG, Walton VM (2015) Humidity affects populations of *Drosophila suzukii* (Diptera: Drosophilidae) in blueberry. J Appl Entomol. doi:10.1111/jen.12247

Tomaru M, Yamada H (2011) Courtship of *Drosophila*, with a special interest in courtship songs. Low Temp Sci 69:61–85

Tonina L, Mori N, Giomi F, Battisti A (2016) Development of *Drosophila suzukii* at low temperatures in mountain areas. J Pest Sci. doi:10.1007/s10340-016-0730-2

Tu MP, Tatar M (2003) Juvenile diet restriction and the aging and reproduction of adult *Drosophila melanogaster*. Aging Cell 2:327–333

Wallingford AK, Lee JC, Loeb GM (2016) The influence of temperature and photoperiod on the reproductive diapause and cold tolerance of spotted-wing drosophila, *Drosophila suzukii* (Matsumura). Entomol Exp Appl in press

Walsh DB, Bolda MP, Goodhue RE, Dreves AJ, Lee J, 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. doi:10.1603/IPM10010

Wang XG, Kaçar G, Biondi A, Daane KM (2016a) Foraging efficiency and outcomes of interactions of two pupal parasitoids attacking the invasive spotted wing drosophila. Biol Control 96:64–71. doi:10.1016/j.biocontrol.2016.02.004

Wang XG, Stewart TG, Biondi A, Chavez BM, Ingels C, Caprile JA, Grant J, Walton VM, Daane KM (2016b) Population dynamics and ecology of *Drosophila suzukii* in Central California. J Pest Sci. doi:10.1007/s10340-016-0747-6

Wiman NG, Walton VM, Dalton DT, Anfora G, Burrack HJ, Chiu JC, Daane KM, Grassi A, Miller B, Tochen S, Wang X, Ioriatti C (2014) Integrating temperature-dependent life table data into a matrix projection model for *Drosophila suzukii* population estimation. PLoS One 9:3106909. doi:10.1371/journal.pone.0106909

Wiman NG, Dalton DT, Anfora G, Biondi A, Chiu JC, Daane KM, Gerdeman B, Gottardello A, Hamby KA, Isaacs R, Grassi A, Ioriatti C, Lee JC, Miller B, Rossi Stacconi V, Shearer PW, Tanigoshi L, Wang X, and Walton VM (2016) *Drosophila suzukii* population response to the environment and management strategies. J Pest Sci. doi:10.1007/s10340-016-0757-4

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. doi:10.3233/JBR-150089