Biological Control of Spotted-Wing Drosophila (Diptera: Drosophilidae)—Current and Pending Tactics

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Abstract

Spotted-wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) is originally from Asia, and in the last decade it has become a global economic pest of small fruits and cherries. Growers have expressed strong interest in biological control and other sustainable tactics to reduce reliance on insecticides. Biological control of spotted-wing drosophila has been studied intensively, with over 75 research publications. Here, we are reporting current information on predators, parasitoids, pathogens (fungi, nematodes, bacteria, endosymbiotic bacteria, and viruses), and competitors of spotted-wing drosophila. When relevant for the natural enemy group, the discussion focuses on the impact each natural enemy has been observed to have in the field, how to optimize control, the efficacy of commercial products available, and options that may be available in the near future. Studies are summarized in tables that can be sorted by species, spotted-wing drosophila life stage targeted, outcomes, lab/field trials, and studies that examined residual activity, dose-dependent responses, or other effects.

Key words: biocontrol, *Drosophila suzukii*, natural enemy, organic, spotted-wing drosophila

Spotted-wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) is a pest of small fruits and cherries. Originally from Asia, spotted-wing drosophila has invaded North and South America and Europe, causing significant economic damage. Spotted-wing drosophila is often controlled by insecticides, which has led to insecticide resistance (Gress and Zalom 2019) and raised concerns about environmental impacts. Growers have increasingly observed secondary pest outbreaks in blueberry, and now apply insecticides more frequently to manage scales and other induced secondary pests (Fig. 1). Consequently, researchers have been developing additional IPM tools including semiochemicals (Cloonan et al. 2018), cultural methods (Rendon and Walton 2019), exclusion (Leach et al. 2016), cold treatment of postharvest fruits (Aly et al. 2017), sterile males (Lanouette et al. 2017), gene drives (Buchman et al. 2018), nonnutritive sugars (Choi et al. 2018), and behavior-modifying compounds developed as organic products (Tait et al. 2018). Biological control is an approach that is expected to reduce long-term management costs of spotted-wing drosophila, and help growers to have more economically and environmentally sustainable farms (Haye et al. 2016, Schetelig et al. 2018).

Naturally occurring or introduced biological control agents have the advantage of being mobile and suppressing spotted-wing drosophila populations in non-crop areas. This sustained suppression can improve area-wide management by reducing spotted-wing drosophila populations that attack various susceptible crops throughout the seasons. While there is ample information and multiple products promoted online for management of spotted-wing drosophila, it is still difficult for growers and homeowners to decide how to incorporate biological control in their spotted-wing drosophila management systems. Thus, this article reviews over 75 publications and provides summary tables on the performance of predators, parasitoids, and pathogens (fungi, nematodes, bacteria, and viruses), and competitors tested against spotted-wing drosophila. As each natural enemy is covered, we address the impact observed in the field (i.e., predation rate), efficacy of commercial products available, and other options that may be available in the future. Summary tables are provided in Excel sheets (Supp Appendix [online only]) for sorting by natural enemy species, whether there was an effect, whether the research was conducted in the field or laboratory, and the type of study (i.e., residual study).

Tables also provide the mode of delivery, source of natural enemy, arena used, and duration of study when relevant.

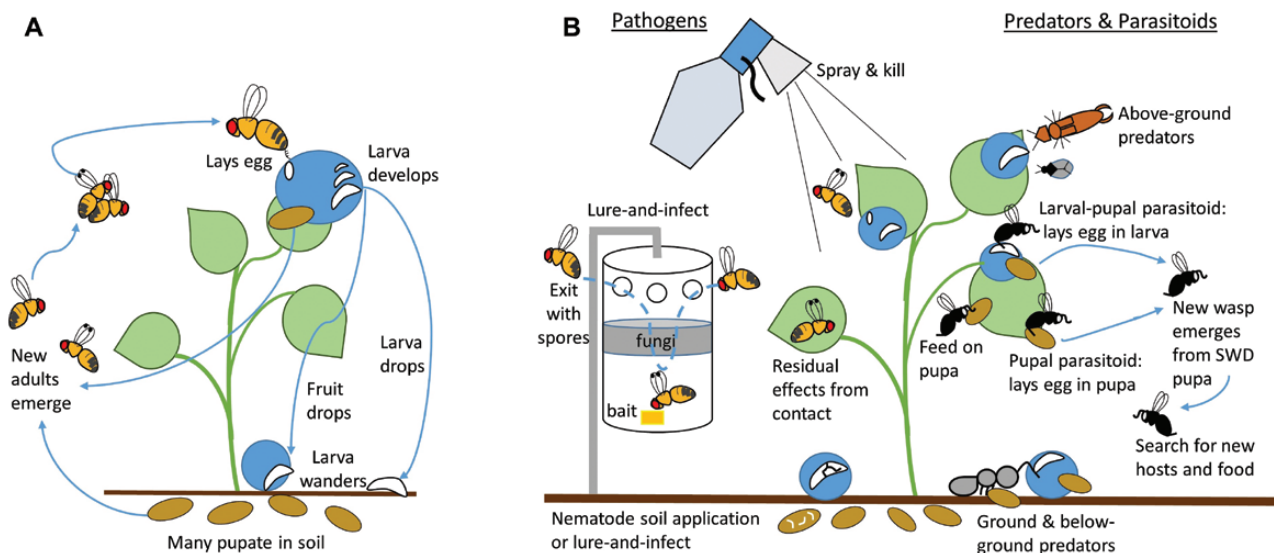## Spotted-Wing Drosophila Life Cycle and Targets for Control

Spotted-wing drosophila eggs are laid under the skin of ripening and ripe fruit, and hatched larvae feed inside the fruit as they develop through three instars. Spotted-wing drosophila larvae are more likely to migrate out of the fruit to pupate when it is crowded (C. S. B. Da Silva, V. M. Walton et al., unpublished data). If the fruit has dropped to the ground, third instar larvae will 'wander' and pupate in the soil (Ballman et al. 2017, Hubner et al. 2017). On hanging fruit, larvae will often drop and pupate in the soil rather than remain in the fruit (Woltz and Lee 2017). A female may lay 20–419 eggs in a lifetime depending on conditions (Hamby et al. 2016). At 22°C (72°F), the egg stage takes 1.4 d, larval stage 6 d, pupal stage 6 d, and a total of 13–14 d to develop from egg to adult (Emiljanowicz et al. 2014, Tochen et al. 2014). The life span of adults in the field is uncertain though both summer and winter-adapted morphs can live up to 30–179 d in the lab when provided food at various temperatures (Shearer et al. 2016, Rendon et al. 2019) and up to 10 wk in small field cages during winter (Stockton et al. 2019). Adults need to mate and feed, additionally females search for suitable food resources to lay eggs. Females do not lay eggs as a newly emerged adult (pre-ovipositional), they first mate and start laying eggs when 1–5 d old under standard lab conditions (Hamby et al. 2016). When crop fruit is not available, wild and ornamental plants bearing fruit (Lee et al. 2015, Kenis et al. 2016) and dropped fruit or pomace have been found to sustain spotted-wing drosophila (Bal et al. 2017).

Figure 2a shows the pest's life cycle and Figure 2b shows the potential targets for biological control. This insect is susceptible to environmental stressors, and its development can be manipulated by changing the temperature and humidity conditions on the soil and in crop canopies (Diepenbrock and Burrack 2016, Rendon and Walton 2019). To our knowledge, there are few predators or parasitoids that target eggs, so this life stage is relatively unaffected. There are multiple parasitoid species that target larvae and pupae, including non-native species being evaluated for potential release. Entomopathogens have the potential to be applied on the foliage and fruit like other pesticides, applied to the soil to target pupae and wandering larvae, or used in a lure-and-infect system such as an autoinoculation trap. In the next sections, we provide detailed descriptions of the current and future potential of these different biological control agents and their impact on spotted-wing drosophila's life stages (Fig. 2).

Fig. 1. Scale outbreaks on stems of blueberry bushes sprayed for spotted-wing drosophila control, photo by B. A. Little.

Fig. 2. Diagram of spotted-wing drosophila life cycle and spatial distribution (a), and potential targets for biological control in the field (b).

Predators

Impact of Predators in the Field

Naturally occurring predators are consuming and removing a substantial portion of spotted-wing drosophila in low-input fields. In field trials where predators forage on infested fruit, spotted-wing drosophila larval infestations decrease by 19–34% in strawberries, and 28–49% in blueberries (Woltz and Lee 2017). When sentinel spotted-wing drosophila pupae were placed on the soil surface, predators removed 80–100% of pupae in blueberry fields in Maine, United States (Ballman et al. 2017). When sentinel pupae were slightly buried, predators removed 61% of pupae in strawberry, 91% in blueberry, and 67% of pupae in blackberry fields in Oregon (Woltz and Lee 2017). Studies with sentinel pupae likely overestimate predation but nonetheless show high activity among ground predators.

Predators Identified

Earwigs, damsel bugs, spiders, ants, and minute pirate bugs (*Orius*) (Hemiptera: Anthocoridae) are known predators in the field. Carabid beetles, crickets, green lacewing larvae, and rove beetles are other likely predators. Predator gut content DNA analyses reveal that 43% of collected earwigs, 16% of damsel bugs, 21% of web-building spiders, and 8% of hunting spiders had fed on spotted-wing drosophila from organic or untreated cherry, blackberry, raspberry fields (Wolf et al. 2018). Video recordings show ants digging up and carrying away pupae in strawberry and blueberry fields (Woltz and Lee 2017). Spiders and ants have been observed to feed on spotted-wing drosophila larvae and pupae among fallen blueberries (Woltz et al. 2015), and *Orius* feed on larvae in field raspberries (Walsh et al. 2011). Carabid beetles, crickets, green lacewing larvae, earwigs, and *Orius* have been found among infested fruits, and they also fed on spotted-wing drosophila in the lab, which suggest that they could be predators in those systems (Arno et al. 2012, Gabarra et al. 2015, Englert and Herz 2016, Ballman et al. 2017). Given that spotted-wing drosophila is a concealed pest during the egg and larval stages, predators targeting immature stages must forage inside fruits. Earwigs, ants, rove beetles, and spiders have been found inside field-infested fruits (Woltz and Lee 2017). Birds or mammals could potentially predate on spotted-wing drosophila. This is supported by the fact that more spotted-wing drosophila pupae were removed from the open field than from cages that excluded birds and mammals (Ballman et al. 2017).

Predators Available Commercially

Currently, the rove beetle *Dalotia coriaria* Kraatz (Coleoptera: Staphylinidae) (also called *Atheta coriaria*), *Orius* bugs, and the predatory mite *Strateolaelaps scimitus* (Wormersley) (Acari: Laelapidae) (also called *Hypoaspis miles*) are available for purchase. The predatory mite has not been observed to feed on exposed spotted-wing drosophila (Cuthbertson et al. 2014) and is not recommended for augmentative release. Lab efficacy trials with the ground predator *D. coriara* varied showing no impact or up to 50% reduction of spotted-wing drosophila in raspberry fruit (Supp Appendix [online only]; Renkema et al. 2015), and greater reductions when combined with *Orius* releases (Renkema and Cuthbertson 2018). *Orius* is a predator found on plants, and positive results with *Orius insidiosus* Say (Hemiptera: Anthocoridae) were obtained in the lab (Renkema and Cuthbertson 2018), but no differences were observed in field trials (Woltz et al. 2015). It would be costly to release predators at high rates. For example, 1,000 *D. coriaria* rove beetles currently cost US$75, costing $750/ha ($304/acre) to release 1 beetle per 1 m³ (Evergreen Growers Supply 2019). Thus, growers may be interested in augmenting these rove beetles by rearing them on dog/fish food and placing 'breeding boxes' in crop areas. Promising results were seen for control of ground-dwelling pests in nursery systems (Bennison et al. 2008), and augmentation box trials for spotted-wing drosophila control warrant future testing.

Aside from augmenting with purchased predators, resident predators can be enhanced through conservation biological control practices. Conservation involves reducing insecticide use or using more selective insecticides, providing shelter and supplemental plant food to attract and encourage predator populations to flourish (Landis et al. 2000). Organic farms may be more amenable to integrating biological control since natural enemies are more evenly distributed throughout organic blueberry fields than conventional fields (Whitehouse et al. 2018). Yet, even organic farms with high spotted-wing drosophila pressure frequently use Organic Materials Review Institute (OMRI)-listed insecticides to minimize infestation risk. The majority of organically approved insecticides are selective for pests with lower risk to beneficial insects, but this is not always the case (Biondi et al. 2012). For instance, spinosad is the most effective and most widely used organic product for spotted-wing drosophila control (Beers et al. 2011, Bruck et al. 2011, Van Timmeren and Isaacs 2013), but is acutely toxic to beneficial insects under greenhouse conditions (Biondi et al. 2013). Recently, we evaluated OMRI-listed products for spotted-wing drosophila on two generalist predators, the green lacewing *Chrysoperla rufilabris* and minute pirate bug *O. insidiosus* (E. Rhodes, R. Isaacs, A. A. Sial et al., unpublished data). Spinosad showed the highest acute toxicity to these predators even when residues were 3 or 7 d old, and *Sabadilla* alkaloids had acute toxicity to minute pirate bugs. These findings emphasize that even in organic systems there are significant challenges to integrating biological control for spotted-wing drosophila.

Parasitoids

Parasitoids play an important role in the regulation of some *Drosophila* populations, with reported levels of parasitism as high as 80–100% (e.g., Janssen et al. 1988, Fleury et al. 2009). A larval-pupal parasitoid is a wasp that lays its egg (oviposits) in spotted-wing drosophila larva, the parasitized larva pupates, and an adult wasp emerges from spotted-wing drosophila pupa (Fig. 2b). A pupal parasitoid will oviposit in and subsequently emerge from spotted-wing drosophila pupa (Fig. 2b).

Impact of Parasitoids in Invaded Ranges

In North America and Europe, resident parasitoids have been found by collecting and rearing out from infested fruits or from artificial diet baited with spotted-wing drosophila flies (Supp Appendix [online only]: Parasitoid survey). Two pupal parasitoids, *Pachycrepoideus vindemmiae* (Rondani) (Hymenoptera: Pteromalidae) and *Trichopria drosophilae* (Perkins) (Hymenoptera: Diapriidae) have been commonly collected. Both species have been evaluated for their efficiency, specificity for spotted-wing drosophila, temperature tolerance, and interactions between species. *Pachycrepoideus vindemmiae* seems to have a wider temperature range than *T. drosophilae*, which may explain the current distribution of these species in North America (Wang et al. 2018b). Both species can locate spotted-wing drosophila pupae in fruit or soil, but *T. drosophilae* is more efficient than *P. vindemmiae* under some temperatures (Wang et al. 2018b). However, natural occurring parasitism of spotted-wing drosophila

populations by these two pupal parasitoids is generally below 10% (Supp Appendix [online only]). These parasitoids can attack other fly species, and are speculated to be distracted from spotted-wing drosophila in the field if other *Drosophila* flies are abundant.

During surveys, larval-pupal parasitoids were often found from fruit/diet infested with another *Drosophila* species. However, these parasitoids had less success developing on spotted-wing drosophila in lab conditions (Supp Appendix [online only]: Parasitoid lab trials). Few larval-pupal parasitoids can overcome the defense response of spotted-wing drosophila, in which the parasitoid egg/larva gets encased (encapsulated) with melanized cells. However, if the parasitoids lay eggs on spotted-wing drosophila larvae, they can still reduce the survival of spotted-wing drosophila to adulthood (Kacsoh and Schlenke 2012).

Optimizing Resident Parasitoids

In Italy, *T. drosophilae* is commercially available and has been evaluated for its ability to locate spotted-wing drosophila, disperse and suppress pests when augmentatively released in a netted raspberry field (Rossi Stacconi et al. 2018), and in unmanaged areas surrounding crops to reduce the severity of pest outbreaks (Rossi Stacconi et al. 2019). The parasitoid was able to locate spotted-wing drosophila in traps up to 40 m away from the release site and spotted-wing drosophila emergence was significantly reduced within a radius of 10 m of the release. Thus, sufficient pest suppression might be achieved under repeated release of pupal parasitoids, at least in crops grown within protected systems. A population model predicts that the optimal timing for releasing *T. drosophilae* would be between late spring and early summer when spotted-wing drosophila populations begin to increase (Pfab et al. 2018).

Resident parasitoids are best incorporated by conservation practices as discussed above for predators, since these parasitoids may not be commercially available or are costly. Certain landscape features such as forest cover near crops have been associated with more parasitoids, although the number of *P. vindemmiae* was still low (Haro-Barchin et al. 2018). Water management may enhance mortality caused by *P. vindemmiae*, as water-deprived females fed more on spotted-wing drosophila pupae for water intake in Oregon trials (Da Silva et al. 2019). Selective insecticides should likewise be considered to minimize harm to parasitoids. Direct toxicity tests show that *P. vindemmiae* adults are more susceptible than spotted-wing drosophila to field rates of commonly used pesticides including spinetoram, cyantraniliprole, malathion, methomyl, spinosad, and phosmet (C. S. B. Da Silva, V. M. Walton et al., unpublished data). All of these pesticides caused 100% mortality at 0, 24, and 48 h after application. While this insecticide trial was conducted under worst-case conditions by confining parasitoids in a small area and maximizing exposure, it supports prior research on this species (Rutz and Scott 1990, Ceden et al. 1992, Owens et al. 2015). Not only does excessive insecticide harm biological control agents that directly suppress *D. suzukii*, it can harm other beneficial arthropods that suppress previously unimportant pests such as scales and aphids. The aphid parasitoid, *Aphidius colemani* Viereck (Hympenoptera: Braconidae), may be important in controlling secondary aphid pests in fields. Lab trials show that spinosad, azadirachtin, pyrethrum, *Sabadilla* alkaloids, and a silicone surfactant were toxic to *A. colemani* (E. Rhodes, R. Isaacs, A. A. Sial et al., unpublished data).

Parasitoids With Future Potential

Since spotted-wing drosophila is native to Asia, researchers have traveled to its historical range to search for more effective parasitoids.

Explorations in South Korea, China, and Japan have discovered at least 13 larval-pupal parasitoids associated with spotted-wing drosophila (Supp Appendix [online only]; Fig. 3). In China, parasitism by *Ganaspis brasiliensis* (Ihering) and *Leptopilina japonica japonica* Novković & Kimura (both Hymenoptera: Figitidae) have reached 48 and 42%, respectively (Supp Appendix [online only]). In Japan, parasitism by *G. brasiliensis* was as high as 76% (Girod et al. 2018c), and *Asobara japonica* Belokobylskij (Hymenoptera: Braconidae) was commonly collected from banana traps (Mitsui et al. 2007). The Japanese strain of *G. brasiliensis* is likely specific to attacking spotted-wing drosophila larvae in fresh fruits in the canopy, and rarely attacks spotted-wing drosophila among fallen fruits (Matsuura et al. 2018).

Of the Asian parasitoids surveyed, three larval-pupal parasitoids, *G. brasiliensis*, *L. j. japonica*, and *A. japonica*, were chosen based on frequent occurrence and imported into quarantine labs for evaluation as classical biological control agents in North America and/or Europe (Daane et al. 2016; Biondi et al. 2017; Girod et al. 2018a,b; Wang et al. 2018a; Giorgini et al. 2019; Wang et al. 2019). All three parasitoids readily attack and develop in spotted-wing drosophila (Supp Appendix [online only]) and prefer to attack young first instar spotted-wing drosophila larvae (Wang et al. 2018a). At 23°C (74°F), *G. brasiliensis* adult females lived 18 d and produced 98 offspring per female when given artificial diet with spotted-wing drosophila larvae, *L. japonica* lived 19 d and produced 107 offspring (Wang et al. 2018a), and *A. japonica* females lived 18 d and produced 117 offspring (A. Biondi, X. Wang, K. M. Daane et al., unpublished data).

Selecting an Asian Parasitoid

Leptopilina j. japonica may outcompete the other two species since its eggs hatched the fastest when spotted-wing drosophila were parasitized by multiple species (Wang et al. 2019). However, *G. brasiliensis* and *A. japonica* can avoid spotted-wing drosophila larvae already parasitized by *L. japonica*, which means that when multiple parasitoid species co-exist (Daane et al. 2016, Giorgini et al. 2019), they likely work synergistically to suppress spotted-wing drosophila. Ideal parasitoids are host-specific, so their introduction will not impact other nontarget species that could be important to an ecosystem. When these parasitoids were screened with other *Drosophila* species, *A. japonica* was considered a generalist, and *L. j. japonica* and certain strains of *G. brasiliensis* were specialized for spotted-wing drosophila and closely related *Drosophila* (Girod et al. 2018a,b; Giorgini et al. 2019; K. M. Daane et al., unpublished data). While the two resident pupal parasitoids, *P. vindemmiae* and *T. drosophilae*, may help suppress spotted-wing drosophila and be manipulated through conservation or augmentative releases, better biological control would likely be achieved through the introduction or augmentation of a specialist Asian parasitoid, such as *G. brasiliensis*. Currently, *G. brasiliensis* is being petitioned for release in North America and Europe. Future studies may include genetic improvement by selecting biological traits among different populations for breeding to improve biological control (Kruitwagen et al. 2018).

Fungi

Fungi in the Field

An outbreak of *Entomophora muscae* was recorded on spotted-wing drosophila during cool and wet conditions in June 2017 in Mississippi, United States (Dara et al. 2017). Sporulating adult
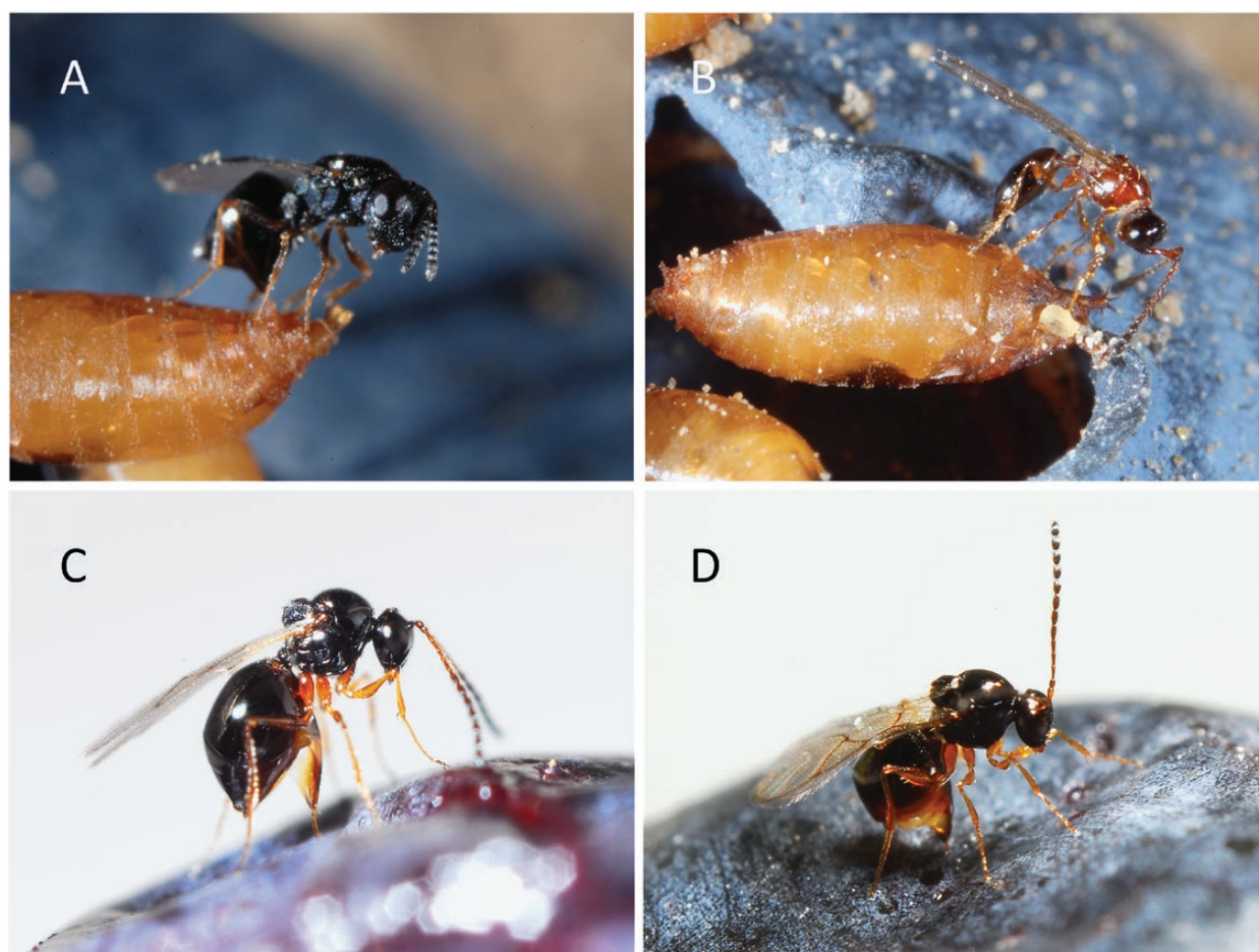
Fig. 3. Four of the major *D. suzukii* parasitoids are shown attacking spotted-wing drosophila on blueberry, including two cosmopolitan pupal parasitoids (A) *Pachycrepoideus vindemmiae* and (B) *Trichopria drosophilae* and two Asian larval parasitoids (C) *Ganaspis brasiliensis* and (D) *Leptopilina japonica japonica*, photos by K. M. Daane.

Table 1. Trials with commercial fungal products, see Supp Appendix (online only) for studies

Fungal strain	Kill adults by direct/close contact	Lower development treat infested fruit	Residual effect[a]	Lower reproduction
Beauveria bassiana ATCC74040, Naturalis	3 of 3 trials sig. mortality	1/2	1/2	0/1
Beauveria bassiana GHA, Botanigard	5/6	1/1	3/4	3/4
Isaria fumosorosea Apopka97	2/3	–	0/3	0/3, more eggs w/ fungi
Isaria fumosorosea FE9901, No-fly	3/4	–	–	–
Metarhizium brunneum (=*anisopliae*) F52, Met52	8/8	–	0/1	1/2
Verticillium lecanii Ve6, Mycotal	0/2	–	0/1	0/1, more eggs w/ fungi

[a]Residual impact tested by spraying fruit or foliage and then allowing adults access to them in arenas.

spotted-wing drosophila with white/gray powdery fluff were dead or immobilized on fig plants. Subsequent lab exposure tests showed ~25% of spotted-wing drosophila adults die when exposed to sporulating house fly cadavers (Becher et al. 2017). This fungus is difficult to culture unlike commercial fungal pathogens. It thrives on a living host but grows very slowly on media, and will unlikely be developed as a biopesticide. Nevertheless, this fungal pathogen can suppress spotted-wing drosophila populations in fields when present.

Fungal Products

Six commercial fungal products tested in multiple studies have shown promise. Outcomes vary from no effect to inducing high mortality (Table 1), so it is important to check how the product

was applied, the life stage targeted, and the design of the test arenas (Supp Appendix [online only]). Most studies examined adult mortality when adults were either directly sprayed, put in small treated vials/dishes, or put in close proximity to a 'conidia carpet'. Many fungal products kill adults in this manner. However, for fungal products to be effective in the field, several aspects should be considered: residual activity, spore degradation, and impact on spotted-wing drosophila inside fruit and its fecundity. First, not all adult flies will come into immediate contact with the product. Flies will likely encounter residues on leaves and fruit, and be exposed to lower doses or aged spores. Two *Beauveria bassiana* products showed evidence of residual effects when flies could forage on treated fruit or foliage. *Metarhizium brunneum* F52 consistently killed adults in eight trials (Table 1), but had little impact when adults were enclosed with sprayed leaves (Woltz et al. 2015). Second, fungal sprays in the field will be less concentrated and subject to quicker degradation. One field trial with *B. bassiana* did not show any impacts, and spores were mostly nonviable after a day (Alnajjar et al. 2017). Third, fruits that are already infested will get sprayed and the fate of the internal developing spotted-wing drosophila is of interest. Two *B. bassiana* strains lowered the number of developing spotted-wing drosophila when infested fruit were dipped in solution. Fourth, spotted-wing drosophila takes several days to die from fungal infection, and it would be ideal if infection prevented females from laying eggs before they died. Fungal products sometimes lowered fecundity, and other times treated flies laid more eggs than untreated flies (Cahenzli et al. 2018). While not explicitly tested, the age of the female may affect susceptibility. Lower egg maturation was observed when newly emerged females were exposed (Alnajjar et al. 2017), but females exposed at 3–4 or 10–14 d old did not lay fewer eggs before they died (Woltz et al. 2015).

Fungi With Future Potential

Recent research has explored autoinoculation devices, where spotted-wing drosophila adults are attracted to a trap by its food/odor, enter it, are dusted with spores, and leave carrying spores (Cossentine et al. 2016a, Yousef et al. 2018). Both studies have shown that inoculated flies can cross-infect the opposite sex in confined arenas. This 'lure-and-infect' strategy has advantages in that far less inoculum is needed than costly broadcast sprays (Shah and Pell 2003). Fungal spores could be better protected from UV degradation, cold weather, and rain runoff. Devices could be placed in surrounding wild fruit borders where spotted-wing drosophila populations have survived, and where there are few spray options for non-crop areas. While most fungal strains kill over several days, a noncommercial strain from Spain killed 50% of infected adults in 7 h, and lowered production of the next generation of spotted-wing drosophila by 85% (Yousef et al. 2018). Further work is need to develop such tools, such as optimizing spore viability and delivery to transient flies, and confirming transmission between flies in the field.

Nematodes

Current information about nematodes for spotted-wing drosophila control is from laboratory trials, and natural infestation reports are currently lacking. Nematodes need a moist environment to survive and move to find a host, and they are typically applied as soil drenches and sometimes as foliar sprays if coupled with a surfactant (Labaude and Griffin 2018). The infective juvenile (IJ) is the only mobile stage. Since IJs do not feed, they have limited energy to find a host, and nematode quality will reduce with time (Labaude and Griffin 2018). Spotted-wing drosophila trials with nematodes often test larvae in diet or fruit since they would normally be concealed in the field. All species tested have shown a positive outcome

in reducing spotted-wing drosophila counts or successful penetration: *Heterorhabditis bacteriophora* in 10/16 trials, *Steinernema carpocapsae* in 13/17, *S. feltiae* in 16/18, *S. kraussei* in 2/3, and unspecified *Steinernema* from a hazelnut orchard in 2/2 (Supp Appendix [online only]).

Some variation in results may be due to dose, as applying more nematodes increased the percent of infected larvae (Hübner et al. 2017), and trials with low doses were unsuccessful (Woltz et al. 2015). Sometimes, infection of spotted-wing drosophila larvae was more successful than similar trials with spotted-wing drosophila pupae possibly because nematodes have difficulty penetrating pupae (Garriga et al. 2017, Hübner et al. 2017). Notably, *S. carpocapsae* and *S. feltiae* penetrated blueberry fruit placed in treated sand (Hübner et al. 2017), and produced 388 and 330 IJs per spotted-wing drosophila larva, respectively (Garriga et al. 2017). The high cost of nematode drenches would likely limit this biological control strategy for small areas. A lure-and-infect strategy of attracting the pest to a source of nematodes is being tested in other systems (Labaude and Griffin 2018), and should be considered for infecting wandering spotted-wing drosophila larvae before they pupate.

Bacteria

Current information about bacterial pathogens for spotted-wing drosophila control is from laboratory trials, and natural infestation reports are lacking. Spraying adults with commercial *Bacillus thuringiensis* var. *kurstakii* strain SA-11 or *B. thuringiensis* var. *israeliensis* preparations killed 48–85% of adults in lab trials, but placing adults directly on dried residue was not lethal (Cahenzli et al. 2018). In another trial, three commercial products of *B. thuringiensis* var. *israelensis* at high doses did not cause significant mortality among spotted-wing drosophila larvae and adults, nor reduce their reproductive output (Biganski et al. 2018). Further screening of other *B. thuringiensis* serovars from bacterial collections identified 5 out of 22 serovars that killed 75–100% first instar larvae; first instar were more susceptible than later instars (Cossentine et al. 2016b). One serovar was found to kill adults, but it produced a toxin harmful to vertebrates that would preclude its use in IPM. Field trials with bacterial pathogens are needed before recommendation.

In addition to pathogenic bacteria, endosymbiotic bacteria such as *Wolbachia* can affect spotted-wing drosophila reproduction positively or negatively. One study found that *Wolbachia*-infected females produced more offspring than uninfected females (Mazzetto et al. 2015), while another study found lowered reproduction with *Wolbachia* infection (Hamm et al. 2014). The *Wolbachia* variant *wSuz* was found in 7–58% of individuals sampled from North American and European populations (Hamm et al. 2014, Cattel et al. 2016a). Unfortunately, *wSuz* does not cause the desired population reductions with 'cytoplasmic incompatibility', where an infected male mates with an uninfected female and no offspring are produced. The *Wolbachia* variants *wTei* and *wHa* cause cytoplasmic incompatibility, and cage trials have been promising (Cattel et al. 2018). This approach combined with sterile insect release has been suggested for spotted-wing drosophila control (Nikolouli et al. 2017). Releases of *Wolbachia*-infected spotted-wing drosophila need to be carefully planned to only include males since a mating between infected males and infected females will produce offspring.

Viruses

Viral infections, as determined by DNA tests, are clearly present among spotted-wing drosophila in the field. Drosophila A virus

(DAV) and La Jolla virus (LJV) were found among moribund larvae from cherry fields in Germany (Carrau et al. 2018). Spotted-wing drosophila adults collected from Japan, France, and United Kingdom contained viral-like DNA sequence of 18 novel viruses, and 18 other viruses found in other *Drosophila* (Medd et al. 2018). Viral exposure can be lethal as injection of DAV, LJV, Drosophila C virus, Cricket paralysis virus, and Flock house virus into the thorax (midsection) of adult flies resulted in 100% mortality by 17–19 d (Lee and Vilcinskas 2017, Carrau et al. 2018). More studies are needed to determine whether viruses can be delivered and spread among spotted-wing drosophila in the field, and which viruses to target in different locations. Viral lethality will depend on the spotted-wing drosophila population; if spotted-wing drosophila contain symbiotic *Wolbachia* bacterium, they are more resistant to certain viruses (Cattel et al. 2016b). Spotted-wing drosophila from Canada, United States, Italy, and Germany were found to have the sensitive *pastrel* gene which makes them susceptible to viruses (Lee and Vilcinskas 2017).

Competitors

A competitor that is not harmful can be used to suppress an economically damaging pest. *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) is a nuisance fly often attacking damaged, dropped, or overripe fruit, as it has a higher ethanol tolerance than spotted-wing drosophila (Gao et al. 2018). *Drosophila melanogaster* is a superior competitor to spotted-wing drosophila under various lab conditions: when both species are introduced simultaneously to diet or fruit, when spotted-wing drosophila lays eggs on media already laden with *D. melanogaster* eggs and larvae, and when *D. melanogaster* lays eggs on media already laden with spotted-wing drosophila eggs and larvae (Dancau et al. 2017, Shaw et al. 2018). Moreover, *D. melanogaster* reduced spotted-wing drosophila presence in test cages, whereas the parasitoid *P. vindemmiae* did not, suggesting that competitive mechanisms can be more effective than expected (Dancau et al. 2017). *Drosophila melanogaster* is not expected to have an impact on harvested fruit since spotted-wing drosophila has a serrated ovipositor and can puncture and oviposit in intact fruit (Atallah et al. 2014), whereas *D. melanogaster* cannot. Yet, during late season, spotted-wing drosophila can use fallen and damaged fruit when fresh fruit is not available (Stemberger 2016). Competition from *D. melanogaster* for these resources can potentially reduce spotted-wing drosophila populations that would otherwise overwinter, and follow-up studies are needed in the field to demonstrate this.

Conclusion

In conclusion, resident predators and parasitoids can suppress spotted-wing drosophila, and should be conserved in crop fields and adjacent wild habitat. Notably, biological and chemical management techniques are not always compatible; insecticides can disrupt natural enemies through lethal and sublethal means (Desneux et al. 2007, Roubos et al. 2014, Damos et al. 2015). When incorporating predators or parasitoids, growers must consider potential nontarget impacts of their spotted-wing drosophila control programs and adjust as needed to minimize negative impacts on beneficial insects. Augmentative releases with predators and parasitoids are still under development, may be suitable for non-crop or protected areas, and future work might consider the compatibility of parasitoid releases in areas with high natural predation. Once release permits are approved, we expect that the imported specialist Asian parasitoid(s) will be important for suppressing spotted-wing drosophila in the

overall landscape. Of the entomopathogens, some fungi, nematodes, bacteria, and viruses have shown promise in small test arenas or by direct injection, but require larger scale field testing. Given the costs of applying entomopathogens, future work should develop lure-and-infect strategies where pests are drawn in and less product is needed to achieve suppression. Lastly, competition from *D. melanogaster* for dropped fruit should be investigated in the field to determine whether it can suppress late-season spotted-wing drosophila populations when ripe fruit are not available.

Supplementary Data

Supplementary data are available at *Journal of Integrated Pest Management* online.

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