Review of parasitoids of spotted wing drosophila (SWD, *Drosophila suzukii*) in the UK

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Background to desk study

This review aims to inform fruit growers about recent scientific progress on the use of parasitoids to control spotted wing *drosophila* (SWD). It includes studies funded by AHDB and The Worshipful Company of Fruiterers (WCoF) along with progress on the use of other non-native species which show promise for future biocontrol. To date, six species of Hymenoptera (wasps) have been identified as capable of parasitising SWD in the UK. Detail is given on the niches occupied by these species and their reproductive behaviour so that growers might adapt practices to encourage SWD parasitoids into their farms. We review the latest findings on *Trichopria drosophilae* (Perkins), now commercially available in mainland Europe since 2017 for Integrated Pest Management (IPM) control of SWD. *T. drosophilae* have evolved alongside SWD and as such is better adapted to target SWD compared to generalist parasitoids and should be considered as an additional control measure, should registration be sought and approved in the UK.

Summary of main findings

- In the literature, pupal parasitoids had a higher rate of survival than larval parasitoids. This is likely to be associated with the encapsulation process in which larval SWD can terminate the survival of the parasitoid juvenile.
- Six species of Hymenoptera parasitoid have been found to be actively parasitizing SWD in the Southeast of England.
- Periods of parasitoid activity vary through the season dependent of species.
- Enhancing the environment surround cropping sites can support parasitoid populations y providing alternative hosts and feeding sites.

Grower recommendations

Parasitoids will not completely control SWD in UK fruit crops, but they should form part of an Integrated Pest Management approach. Growers should;

- Prevent chemical sprays from coming into contact with surrounding semi-natural habitats – these can harbour SWD parasitoids.

- Create open wildflower areas and encourage hedgerow species which provide nectar for parasitoids and support both fecundity and longevity in females. When deploying wildflowers:

1. Plant within the crop/field in strips or smaller blocks
2. Use perennial and annual border plantings
3. Plant within hedgerows
4. Establish cover crops
5. Carefully manage flowering weeds
6. Select flowers with an open habit such as the umbellifers and those from the Aster genus

- Consider ways to collect and harvest emerging parasitoids from waste fruit without releasing SWD.

- Employ methods to increase parasitoid populations alongside Integrated Pest Management (IPM) strategies for SWD and other pests.

Introduction

Spotted Wing *Drosophila* (SWD, *Drosophila suzukii* Matsumura) was first detected in the UK in 2012 (Harris and Shaw, 2014) and within two years of detection, they became a problem for soft and stone-fruit production. While much research has focused on IPM strategies to control SWD, little is known about UK native parasitoids that might be contributing to pest control. SWD has a high level of resistance to some larval parasitoid species due to an ability to 'encapsulate' parasitoid eggs, resulting in the death of the parasitoid. Encapsulation is a process in which *Drosophila* haemocytes (cells) bind to the parasitoid egg and cause death by asphyxiation or cellular toxins (Fellowes and Godfray, 2000, Kim-Jo et al., 2019). SWD has a high number of haemocytes compared to other *Drosophila* species, with eight times the amount compared to the common fruit fly (*Drosophila melanogaster*) (Meigen) (Poyet et al., 2013). In addition, the number of haemocytes vary between SWD strains. For example, French strains have four times more haemocytes than strains from the native range in Japan (Poyet et al., 2013). Invasion success in new territories is probably, at least partly, related to this ability to be able to encapsulate parasitoid eggs.

Parasitoid survival and efficacy in suppressing target species is dependent on the ability to complete the lifecycle within the host. Partial or low success rates could lead to parasitoid population crashes if dependent on one host. Due to the high haemocyte load, SWD is not the optimum host for many of the generalist larval parasitoid species, which may not survive through to next generation emergence. SWD is non-native and unlikely to have arrived in the UK along with its specialist parasitoids which have evolved to overcome the encapsulation process which results in the death of larval parasitoids. The process of encapsulation occurs when *Drosophila* is in the larval stage, generally resulting in a higher survival and success rate of parasitoids that target the SWD at a pupae stage (Chabert et al., 2012).

Field surveys in AHDB Project SF/TF 145a (supported by WCoF and Berry Gardens Growers), aimed to identify species of parasitoid wasps laying eggs and successfully emerging from SWD in Southeast England. Surveys were conducted across several commercial fruit crops and semi-natural habitats. This review focuses on the native species that emerged from SWD in the Southeast region of the UK.
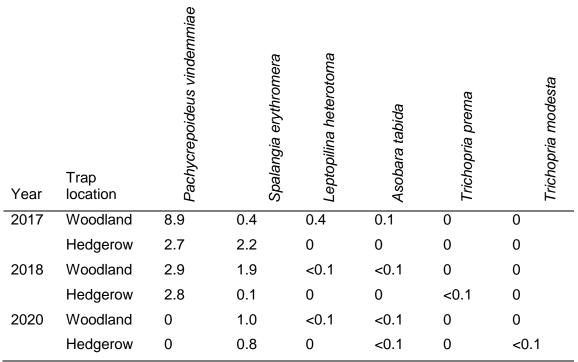
Sentinel traps, containing SWD larvae/pupae infested cornmeal media and fruit, were deployed within the vicinity of commercial crops. Six species of hymenopteran parasitoids were identified (Table 1). Two larval and four pupal parasitoid species were recorded; all six species were generalist parasitoids of *Drosophila*. Roughly 50 Hymenoptera parasitoid species have been identified from *Drosophila* species from several different families (Yi et al., 2020). Those identified in the UK are from four families: Figitidae, Braconidae, Diapriidae and Pteromalidae.
In addition to the species survey, parasitoids that were recovered from the sentinel traps in 2017 were tested for their ability to reproduce in laboratory cultures of SWD, this evaluated their potential efficacy for future biological control options.

This review summarises:

1. The biology and ecology of the six species identified in AHDB Project SF/TF 145a

2. The latest research findings on *Trichopria drosophilae* (Perkins); a commercially produced parasitoid for augmented release in Europe, but not authorised for release in the UK

3. Practical management options that growers can implement on farm to enhance the environment to promote SWD parasitoids

4. The progress of non-native parasitoids in newly introduced territories and their impact on SWD in the field

5. Future research directions.

Table 1. Parasitoid species recorded in Southeast England and mean emergence per SWD sentinel trap (unknown numbers of SWD pupae and larvae) in semi-natural habitats in 2017, 2018 and 2020.

Year	Trap location	*Pachycrepoideus vindemmiae*	*Spalangia erythromera*	*Leptopilina heterotoma*	*Asobara tabida*	*Trichopria prema*	*Trichopria modesta*
2017	Woodland	8.9	0.4	0.4	0.1	0	0
	Hedgerow	2.7	2.2	0	0	0	0
2018	Woodland	2.9	1.9	<0.1	<0.1	0	0
	Hedgerow	2.8	0.1	0	0	<0.1	0
2020	Woodland	0	1.0	<0.1	<0.1	0	0
	Hedgerow	0	0.8	0	<0.1	0	<0.1

Parasitoid wasps (Hymenoptera) able to develop in SWD in the UK

Larval parasitoids

Leptopilina heterotoma

Leptopilina heterotoma Thomson (Hymenoptera: Figitidae) (Figure 1) is a generalist parasitoid of *Drosophila,* native to Europe and other Palearctic regions (Lue et al., 2016). It was first recorded as *Pseudeucoila bochei* (Schilthuizen et al., 1998) and several other classifications later on (Lue et al., 2016). It is sexually dimorphic: males have longer antennae than females (Lue et al., 2016). Females oviposit in *Drosophila* larvae typically less than 48 hours old. In SWD, this is 1st - 2nd instar larvae. Females mate once in their lifetime (Van Den Assem, 1968). A mated female *L. heterotoma* produce male and female offspring, while unfertilized females exclusively produce female offspring. Once eggs are laid, *L. heterotoma* adults emerge after 10-14 days (Bakker et al., 1967). *Leptopilina* sp. females are gravid with mature eggs at eclosion (the point at which the adult emerges from the pupal case) (Flanders, 1950)). Young females have a potential fecundity of 349.3 ± 3.3 eggs (n = 100) and an adult lifespan of ~25 days (Van Den Assem, 1968). Unlike many parasitoid species, where only the juvenile stage can take in lipids from the host, *L. heterotoma* can replenish lipids from fructose as an adult (Visser et al., 2012).

Figure 1. *Leptopilina heterotoma* adult from SWD sentinel fruit baited traps. Credit: NIAB EMR

L. heterotoma females generally lay one egg per host. However, dissected host larvae often contain more than one egg when the ratio of hosts to parasitoids decrease, reducing resource availability (Bakker et al., 1967). The total number of eggs laid by a female also reduces, as the number of available hosts decrease (Bakker et al., 1967).

L. heterotoma can cause high mortality in SWD larvae in laboratory trials, resulting in low SWD survival through to adult emergence (Knoll et al., 2017). However, *L. heterotoma* survival was also low. This is because whilst the parasitoid presence results in lower SWD survival, there is low to no survival of the parasitoid offspring due to the high haemocyte load of SWD (Poyet et al., 2013). In research by Girod et al. (2018), surprisingly, although egg survival was low (only one parasitoid adult emerging from roughly 900 SWD larvae), attraction of *L. heterotoma* to SWD was high with over 70% of female parasitoids laying eggs in SWD larvae in no-choice laboratory bioassays. In AHDB Project SF/TF 145a, *L. heterotoma* emerged from sentinel traps deployed in woodlands from the end of August to beginning of September in 2020 and was found in low numbers in the three years surveyed (Table 1). When *L. heterotoma* adults were recovered from the field and exposed to SWD cultures, there was a low emergence rate with only one offspring emerging per 10 adults applied (SF 145a) (Table 2).

Table 2. Total numbers of parasitoid offspring that emerged from inoculated *D. suzukii* laboratory cultures in 2017.

Culture I.D.	Species	No. of adult parasitoids applied	No. of emerged offspring after 6 weeks incubation	No. offspring per adult
T14	*L. heterotoma*	10	1	0.1
F9	*A. tabida*	3 (♀ only)	0	0.0
T72	*S. erythromera*	11	3	0.3
T8	*S. erythromera*	10	5	0.5
T30	*S. erythromera*	12	2	0.2
T29	*S. erythromera*	13	1	0.1
T16	*P. vindemmiae*	25	80	3.2
T22	*P. vindemmiae*	10	45	4.5
T20	*P. vindemmiae*	14	41	2.9
T15	*P. vindemmiae*	8	11	1.4
T41	*P. vindemmiae*	9	67	7.4
T38	*P. vindemmiae*	16	47	2.9

Asobara tabida

Asobara tabida (Nees) (Hymenoptera: Braconidae) (Figure 2), a solitary parasitoid of *Drosophila* larvae, occurs throughout Europe, in different ecological niches depending on region and availability of resources. Adult *A. tabida* populations in North-Western Europe feed on tree sap whereas in Southern Europe they feed on fermenting fruit (Janssen, 1989). Populations of *A. tabida* thrive in Southern areas due to the increase in host availability with *Drosophila* feeding on fermenting fruits. *Drosophila melanogaster* Meigen and *Drosophila obscura* Fallén, are primary hosts for *A. tabida* in Southern European regions (Kraaijeveld and Godfray, 1999, Kraaijeveld and Van Alphen, 1995).

Figure 2. *Asobara tabida* adult from SWD sentinel fruit baited traps. Credit: NIAB EMR

Longevity of *A. tabida* varies depending on resource abundance; between 5 and 12 days without food and 10 and 63 days with food (Ellers, 1996). There is also a negative linear relationship between the number of eggs produced and life span where each egg produced, decreases lifespan by an equal amount. Females that laid an average of 250 eggs lived 7.8 days and females that laid 197 eggs lived 8.5 days which was a significant result (Ellers et al., 2000a). *A. tabida* females can feed on fermenting fruits and decaying plant materials to replenish fat reserves (Eijs et al., 1998). However, this does not counteract the trade-off between egg production and lifespan reduction (Ellers et al., 2000b, Ellers et al., 2000a).

In the field, only 7.3% of *A. tabida* lay their full egg potential (<140 eggs) (Ellers et al., 1998). After egg laying, offspring emerge after 26-29 days (Van Alphen and Nell, 1982). Mature *A. tabida* females normally lay one egg per host, but young females may initially lay more than one (Van Alphen and Nell, 1982). Mature females can also lay eggs in pre-parasitised hosts if unparasitised hosts are unavailable (Van Alphen and Nell, 1982). This is called superparasitism (where a host is attacked by more than one parasitoid) and occurs when a high parasitoid to host ratio is present in the field (Van Alphen and Nell, 1982). *A. tabida* can discriminate between parasitised and unparasitised hosts but cannot discriminate between hosts with different numbers of eggs. Thus, *A. tabida* will first distribute its eggs among the hosts, until all (or nearly all) contain one egg.

In laboratory trials, Knoll et al. (2017) found that *A. tabida* was unable to reproduce in SWD, with eggs failing to survive through to adult emergence. In addition, Knoll et al. (2017) found there was no significant reduction in SWD emergence when offered to *A. tabida* as a host.

In contrast, results from AHDB Project SF/TF 145a demonstrated *A. tabida* actively utilising SWD in the field with individuals emerging from sentinel traps baited with immature SWD. Although emergence of *A. tabida* was low (two individuals in 2020), there was a reduction in SWD emergence in the parasitoid exposed sentinel fruit, compared to those in which *A. tabida* were excluded. It is likely that actual rates of parasitism in the field are underestimated. *A. tabida* emerged from sentinel traps deployed in both woodlands and hedgerows. *A. tabida* activity occurred in early summer (June 2017) in the AHDB project. In laboratory-based bioassays (Project SF/TF 145a) where parasitoids were taken from the sentinel traps and exposed to SWD cultures, *A. tabida* were not able to survive, but this is likely due to the low initial number introduced (only three females) (Table 2).

Pupal parasitoids

Trichopria prema and *Trichopria modesta*

There is no literature suggesting that *Trichopria prema* and *Trichopria modesta* (Hymenoptera: Diapriidae) parasitise SWD in the field. Findings from AHDB Project SF/TF 145a are the first record of this occurring. In addition, there is very little literature on their behaviour and biology. *T. modesta* is a generalist parasitoid of *Drosophila* spp. found in Western Europe and is native to Britain. It is found locally in England as far north as Lancashire. In the laboratory *T. modesta* is reported to be less adapted to parasitise SWD than other *Drosophila* species, this due to a longer developmental time than other parasitoid species (Trivellone et al., 2020).

T. prema, a North-west European species, is solitary and was first described in 1980 (Notton, 2014). *T. modesta* is more likely to emerge from sentinel traps (baited with; *D. hydei, D. immigrans, D. melanogaster, and D. subobscura*) placed closer to the ground, than those placed higher in the canopy (Trivellone et al., 2020).

In our study (Project SF/TF 145a) both species were recorded from hedgerows. Two individual *T. modesta* emerged in 2020 from traps deployed between 1st and 21st September. Two *T. prema* emerged from sentinel traps deployed in June, in hedgerows.

Spalangia erythromera

Spalangia erythromera (Forster) (Hymenoptera: Pteromalidae) is a solitary parasitoid of many Hymenoptera and Diptera species in Palearctic regions and is common in Western Europe (Boucek, 1963, Graham, 1969, Gibson, 2009) (Figure 3). It is associated with habitats with a high density of grassy vegetation (Boucek, 1963). *S. erythromera* is mostly a parasitoid of house flies (*Musca domestica* L.) (Hall and Fischer, 1988), but is also known to parasitise species in several other common fly families in Europe, including the Anthomyiidae, Lance flies (Lonchaeidae), scuttle flies (Phoridae) and blow flies (Sepsidae) (Gibson, 2009). *S. erythromera* have slightly yellow tarsi (lower legs) with thick antennae (Gibson, 2009). Adult females live for 11-17 days at high temperatures (27°C) and lay between four (Carton et al., 1986) and 15 eggs per day (Wolf et al., 2020a). *S. erythromera* is parthenogenetic, with unfertilised eggs emerging as females and fertilised eggs emerging as male or female (Wolf et al., 2020a). This *Drosophila* pupal parasitoid is thermo-dynamic, with the size of emerging adults decreasing with increasing temperatures (Le Lann et al., 2014). This is generally considered to be a cooler climatic species which is more adapted to milder conditions and hence thrives at lower temperatures (Le Lann et al., 2011).

Figure 3. *Spalangia erythromera* adult from SWD sentinel fruit baited traps. Credit: NIAB EMR

It is infrequently found in Switzerland field surveys as a parasitoid of *D. melanogaster* (Wolf et al., 2020a). As a parasitoid of SWD, its survival has been poor in laboratory bioassays, and it did not reduce SWD survival. In contrast, within the UK, it was identified emerging from SWD in all three years of the AHDB SF/TF 145a project survey, in both woodland and hedgerow habitats from May through to October, peaking in July. When exposed to laboratory cultures of SWD, next generation emergence was relatively low in comparison to *P. vindemmiae* but was more successful than *A. tabida* and *L. heterotoma* (Table 2).

Pachycrepoideus vindemmiae

Pachycrepoideus vindemmiae (Rondani) (Hymenoptera: Pteromalidae) (Figure 4) is a generalist *Drosophila* pupal parasitoid in Europe (Bakker et al., 1967). It has a wide host range (Crandell, 1939) and is idiobiont in behaviour (the act of oviposition kills the host and the parasitoid offspring develops in the host cadaver) (Askew, 1986). It is recorded in over 60 countries around the world, found parasitising over 60 Diptera species, including tephritid fruit flies. The parasitoid has been evaluated mainly for the control of stable (*Stomoxys calcitrans* L.) and house flies (*M. domestica*) (Meyer et al., 1990) and was introduced as an augmentative biocontrol into several countries to supress Mediterranean fruit fly (*Ceratitis capitata* Wiedemann) (Ovruski et al., 2000).

Figure 4. *Pachycrepoideus vindemmiae* adults from SWD sentinel fruit baited traps. Credit: NIAB EMR

P. vindemmiae is also a hyperparasitoid (uses parasitoids as a host, whilst within another insect host) of the pupae of several larval parasitoids of *Drosophila* (Bakker et al., 1967, Van Alphen and Thunnissen, 1982). As a hyperparasitoid, *P. vindemmiae* can oviposit in *A. tabida* and *L. heterotoma* inside *Drosophila* larvae (Van Alphen and Nell, 1982, Van Alphen and Thunnissen, 1982).

P. vindemmiae can locate SWD pupae in dropped fruit and the soil (Wolf et al., 2020a). Female *P. vindemmiae* produce a small number of eggs and have a relatively low fecundity (roughly 120 progeny per female compared to 350 of *L. heterotoma*) (Phillips, 1993, Podoler, 1981, Wang and Messing, 2004), a characteristic typical of ectoparasitic idiobionts (Godfray, 1994, Quicke, 1997). Unlike typical ectoparasitoids that attach eggs to the outside surface of hosts, *P. vindemmiae* attacks fly pupae enclosed within a protective case. Within a young puparium, the fly pupa is not fully formed and separated from the puparium shell. Under such circumstances, the hosts are attacked during the late larval or prepupal stage, and the pupal parasitoid places its egg into the host haemolymph because there is no space between the pupal body and puparium shell. When the *P. vindemmiae* attacks old puparia, in which the fly pupae have separated from the puparia, it lays eggs in the space between the pupa and puparium shell (Dresner, 1953, Nøstvik, 1954). Female *P. vindemmiae* inject toxic venom at the time of oviposition, which has a paralytic action on its primary host, and on competitors of other species. Host age affects *P. vindemmiae* offspring survival; younger hosts being less than optimum (Vinson, 1990) and offspring in young puparia often die because the unformed host pupa degrades quickly and the parasitoid egg or larva becomes trapped inside the dead host tissues (Wang and Messing, 2004).

P. vindemmiae adult lifespan is 18-23 days post emergence and fecundity peaks at 2 days post emergence (Rueda and Axtell, 1987). *P. vindemmiae* generally lays one egg per host, however super-parasitism is not uncommon. *P. vindemmiae* hold 12–14 mature eggs and can lay up to 10 eggs within 12 hours (Phillips, 1993). New eggs are matured continuously, with older eggs aborted and resorbed (Edwards, 1954, King and Richards, 1968). Due to the relatively long-life span and a gradual maturation of eggs, female *P. vindemmiae* feed on the tissue and haemolymph the host.

P. vindemmiae offspring developmental time and size varies according to the size of the host species, with smaller hosts producing smaller adult *P. vindemmiae* (Wang and Messing, 2004). Developmental time can range from 21 days in Drosophila to 24 days from *C. capitata* (Wang and Messing, 2004).

In AHDB Project SF/TF 145a in Southeast England, *P. vindemmiae* were the most abundant and widely recovered parasitoid from sentinel trapped SWD, from both agricultural and semi-natural habitats between June and October. Trivellone et al. (2020) found significantly more *P. vindemmiae* in traps deployed in cropping areas compared to wild areas and where traps were higher in the canopy. Results from our studies and other researchers (Knoll et al., 2017, Wang et al., 2016a) show *P. vindemmiae* has a high parasitism rate of SWD in both laboratory and field trials. In our laboratory trials, *P. vindemmiae* had the highest next

generation emergence compared to other species when exposed to SWD cultures for four days, with an average of four offspring per adult (Table 2).

Comparison of life history traits

Table 3 displays the primary features of the four main parasitoid species identified in the Southeast of England in AHDB Project SF/TF 145a. Information on *T. prema* and *T. modesta* has not been included due to the lack of information on these species.

Table 3. Main biological features of UK SWD parasitoids. Information gathered from references discussed in the above text and SF 145a.

Family, Species	Host stage	Ave lifespan (days)	Emergence time (days)	Oviposition rate (egg/hours)	Active in the field	Population growth in culture?
Pteromalidae						
Pachycrepoideus vindemmiae	Pupa	18-23	21-24	0.83	June-October	Yes
Spalangia erythromera	Pupa	7-18	29-40	0.17	May-October	No
Figitidae						
Leptopilina heterotoma	Larva	≈25	10-14	0.21	August-September	No
Braconidae						
Asobara tabida	Larva	10-63	26-29	0.19	June	No

Trichopria drosophilae; a commercially produced generalist parasitoid

Trichopria drosophilae (Perkins) (Hymenoptera: Diapriidae) is a parasitoid of Drosophila pupae associated with fruit. In addition, it has a preference for SWD over other common *drosophila* species in the field (Wolf et al., 2020a), which is thought to be due to the larger pupal size.

The use of *T. drosophilae* is not currently approved in the UK, and, to date, it has not been identified as a native species. If identified in the field, the approval process for use as augmented biological control would be simplified in comparison to the use of a non-native species.

T. drosophilae is globally distributed and found naturally in SWD's native range and invaded areas. This is an endoparasite and idiobiont (oviposition kills the host and the parasitoid offspring develops in the host cadaver) (Yi et al., 2020). The eggs of unmated females emerge as males, while eggs of fertilised females, emerge as female. The development time of juvenile males is ~2 days, quicker than that of juvenile females with males emerging ~18 days post egg laying and females ~20 days post egg laying (at 23°C) (Wang 2016). A single egg is laid per host (Quicke, 1997) and females can lay up to 50 eggs within 24 hours, with a typical daily average of 39 (Wolf et al., 2020a). The optimum temperature range for *T. drosophilae* is 15-30°C (Yi et al., 2020) and it can also survive at 4°C, again making it suitable for use in the UK. *T. drosophilae* has a high rate of parasitism with 3 females able to parasitise 75 out of 100 pupae in laboratory trials (Rossi Stacconi et al., 2015).

In laboratory bioassays, *T. drosophilae* is more successful than *P. vindemmiae* at supressing SWD populations (Wang et al., 2016b, Yi et al., 2020), with a higher parasitism rate than other species (Chen et al., 2018). In laboratory and semi-field bioassays by Wolf et al. (2020a) *T. drosophilae* preferred SWD over two native *Drosophila* species (*Drosophila melanogaster* and *Drosophila subobscura* Collin), even though the parasitoid cultures had originally been maintained on *D. melanogaster*. In subsequent semi-field trials, significantly more *T. drosophilae* emerged from SWD pupae than was placed on the substrate (total 574) rather than in the foliage (total 34), indicating this parasitoids' preference for hosts on the ground (Wolf et al., 2020a). This is not unexpected, as SWD pupation often occurs in dropped fruit or substrate and so *T. drosophilae* is more likely to be active in this area. In addition, *T. drosophilae* can distinguish between fruit containing SWD and fruit that does not and so will actively search for inoculated fruit (Wolf et al., 2020b).

Semi-field trials by Rossi Stacconi et al. (2018) recovered no *T. drosophilae* from fruit collected within the crop. In fruit that had been dropped from the crop, 8-14 days prior to collection, there was significantly higher *T. drosophilae* emergence than from fruit that had dropped 0-7 days prior to collection. In addition, significantly fewer SWD emerged from the old dropped fruit in comparison to the control, which was not exposed to parasitoids. This indicates that *T. drosophilae* may require a longer period to locate inoculated fruit. SWD oviposition in ripening fruits causes the degrading of the fruit through larval feeding, and if frequent picking is not carried out, it will result in the fruit dropping to the ground. The development of SWD from egg to pupa takes between 8-14 days at 14-18°C (Tochen et al., 2014) indicating that fruit on the crop and recently dropped fruit would contain larvae. As *T. drosophilae* parasitise SWD pupa, it is therefore understandable that *T. drosophilae* was only found emerging from older, dropped fruit, as these would contain SWD pupae.

In field trials, where 1,000 *T. drosophilae* adults were released into various crops, individuals were recovered in sentinel traps up to 40 metres away from the release site (Rossi Stacconi et al., 2018). At these sites, no *T. drosophilae* emerged from sentinel traps deployed prior to the release date, indicating that the individuals recovered were released within the bioassay. Significantly more *T. drosophilae* were recovered at 10 metres and SWD emergence was significantly reduced at this distance. It is promising for future biological control that the parasitoid is capable of dispersing into the crop across such a distance.

In laboratory-based no-choice tests *T. drosophilae* produced significantly more offspring on SWD than on *D. immigrans,* although the offspring size was larger on *D. immigrans* (Boycheva Woltering et al. (2019). In a three-way choice bioassay, where *T. drosophilae* was offered SWD, *D. melanogaster* and *D. immigrans,* significantly more *T. drosophilae* offspring emerged from SWD (average 25) than *D. melanogaster* (average 5) or *D. immigrans* (average 7). In addition, there was a higher ratio of female offspring from SWD compared to the other two species (Boycheva Woltering et al., 2019).

As *T. drosophilae* is a parasitoid of fruit-associated *Drosophila*, it should also utilise other common *Drosophila* species found in crop habitats. While this could be perceived as detrimental by increasing alternative host availability, it may be beneficial. Chen et al. (2018) evaluated the variation in characteristics and life parameters of *T. drosophilae* when reared on *D. melanogaster* and *D. hydei* Sturtevant. *T. drosophilae* offspring reared on *D. hydei* were significantly larger, had a higher female:male ratio, females

produced more mature eggs and overall had a longer life span (23 days v 10 days). This indicated that SWD parasitism could benefit from having species like *D. hydei* in the local vicinity. It would be beneficial to know what other common *Drosophila* species could enhance *T. drosophilae* populations in UK habitats.

Enhancing farmland habitats to encourage SWD parasitoids

Growing practices and environments could be modified to promote parasitoids if a better understanding of SWD parasitoid resource requirements were known. To date, there is little information on the basic ecology on UK native SWD parasitoids, especially *T. prema. T. modesta* and *S. erythromera*. Further study is needed to understand how these species could be enhanced in and around commercial crops. For the more common and cosmopolitan species, *P. vindemmiae, L. heterotoma* and *A. tabida,* there is some data, but this is limited. Because of the commercialisation of *T. drosophilae*, more information is available on its association and impact on SWD, with a better understanding of how environmental and growing practices can be modified to promote this species. Although there will be species-specific requirements, it is likely that some attributes which support one species are appropriate for another.

The parasitoids of SWD identified in the UK are known to inhabit different niches, some being more common within agricultural land and others in semi-wild habitats (Table 3). In research by Knoll et al. (2017) in Switzerland, significantly more *P. vindemmiae* emerged from sentinel traps deployed in commercial cropping locations in comparison to semi-natural locations. This is expected, as the *Drosophila* species it parasitises are common in cropping areas, due to an association with decomposing fruit. However, the detection of this species appears to be greatly dependent on crop management practices as *P. vindemmiae* is highly sensitive to plant protection products (PPP). Chemical Plant Protection Products (cPPPs), in particular spinosad, are frequently used to target SWD (Schlesener et al., 2019), which is likely to reduce the presence of parasitoids in some conventional growing systems. This is supported by results from Rossi Stacconi et al. (2013), who recovered *P. vindemmiae* from traps deployed in vineyards which utilised mating disruption instead of cPPP for other key pests. Figure 5 lists the cPPPs used to control SWD in the UK and their known impacts on three species of commercial braconid (the same family as *A. tabida*) parasitic wasps (*Aphidius ervi*, *Aphidoletes aphidimyza* and *Aphidius colemani*), which are introduced for aphid control. While the effects of cPPP have not been tested directly on SWD parasitoids in the UK, we could infer that the impacts would be similar to *Aphidus*, an aphid parasitoid.

Side effects		acetamiprid		cyantraniliprole (cyazypyr)	lambda-cyhalothrin	FLIPPER potassium salts of fatty acids (organic)	spinosad		spirotetramat
		SP	DR	SP	SP	SP	SP	DR	SP
Aphidius colemani	adult	3	1	1	4	1	1	1	1
	larva	1	1	1			1	1	1
	mummy				4	2			
	persistence				8 - 12 w				0 w
Aphidius ervi	adult	4	1	1	4		3	1	2
	larva			1			3	3	1
	mummy	1	1		4				
	persistence	> 2 w			8 - 12 w				
Aphidoletes aphidimyza	adult	3	1		4		1	1	1
	larva	4	1		4		1	1	1
	persistence				8 - 12 w				

Natural enemies

1 = harmless or only slightly harmful < 25% reduction

2 = moderately harmful 25 - 50% reduction

3 = harmful 50 - 75% reduction

4 = very harmful > 75% reduction

= effect/persistence unknown

Persistence

d = days, w = weeks

Figure 5. Chemical plant protection products (cPPP) commonly used to control SWD in UK commercial crops and their impacts on commercial parasitoids. SP-sprayed product. DR- drench product. Sourced from https://sideeffects.koppert.com/ 11/08/2021

Higher numbers of *L. heterotoma, A. tabida*, and *T. drosophilae* are present in semi-wild habitats in Switzerland (Knoll et al., 2017). These habitats included hedgerows and woodlands on the edges of commercial crops rather than in the crops themselves. This is likely to be due to the diversity of plant communities and availability of other hosts, along with overwintering habitats and shelters required for season long survival, all of which were found to have a positive impact on parasitoid populations (Gillespie et al., 2016). In the UK, parasitoids were more abundant in sentinel traps deployed in woodlands compared to other habitat types which included wild, semi-wild and urban locations (Table 4) (SF/TF 145a). Habitat surveys conducted by Fraser et al. (2008) in the UK, found significant correlations between parasitoid assemblages and ground cover, species richness, plant density, plant height and plant architecture diversity in a 20metre radius around monitoring traps. Within this research, increased diversity of plant heights was concluded to be the most reliable predictor of parasitoid diversity, although only for specific taxa.

Table 4. Total number of parasitoid species that emerged from sentinel traps in Southeast England in different habitats from June-September 2017, number of field sentinel traps deployed and total number of parasitoids per trap location, including individuals and percentage of emerged parasitoids of each species out of all emerged parasitoids.

Habitats	*P. vindemmiae*	*S. erytrhomera*	*L. heterotoma*	*A. tabida*	Total emergence	Total traps deployed in area
Wild						
Woodland centre	374	16	15	5	410	42
Woodland edge	56	8	0	4	68	19
Hedgerow (mixed species)	108	89	0	0	197	40
Hedgerow brambles	4	0	0	0	4	6
Semi-wild						
Wild Cherry Orchard	95	3	0	0	98	38
Elderberry (edge of raspberry crop)	32	0	0	0	32	1
Commercial						
Strawberry	143	77	0	0	220	22
Raspberry	193	11	0	0	204	30
Vineyard	86	0	0	0	86	20
Urban						
Packhouse yard	39	0	0	0	39	3

Some of the parasitoids discussed in previous sections are unable to replenish fat reserves as an adult, so flying long distances uses a large amount of energy (Cockbain, 1961; Mason, Johnson and Woodring, 1989). In some species, the use of energy reserves in flying reduces longevity and reproductive rates (Ellers, 1996). There is also a trade-off between reproduction and adult survival, with those females laying more eggs having a shorter life span than those which lay fewer (Ellers, 1996). For *A. tabida,* once reserves have begun to be used for reproduction, it cannot then be absorbed for adult survival (Ellers and Van Alphen, 1997). In addition, in mark-release-recapture bioassays, *A. tabida* were found to only travel up to 20metres from a release site, with larger females recaptured further away (Ellers et al., 1998). For these reasons, parasitoids would benefit from having reduced distances to travel from their emergence sites and hosts which would reduce fitness trade-off between travel and reproduction for future generations. In addition, *L. heterotoma* can replenish lipid reserves as adults (Visser et al., 2012) and would benefit from fructose availability.

To enhance the environment for parasitoids, growers could establish semi-wild, mixed habitats in surrounding locations, which would also promote many other beneficial organisms such as pollinators and predators. Numbers of parasitoids in apple and pear orchards decrease as distance from semi-wild hosts increases (Miliczky and Horton, 2005) and so fragments of semi-wild hosts could be established within

crops to maintain corridors to support parasitoids (Tscharntke et al., 2002). In laboratory trials in Germany, *T. drosophilae* female survival increased four-fold when provisioned with buckwheat (*Fagopyrum esculentum* Moench) and sweet alyssum (*Lobularia maritima* L. (Desv.)) flowers, compared to females not offered floral resources (Herz et al., 2021). Average offspring was also positively influenced with buckwheat and alyssum provisions, resulting in females producing 69 and 61 offspring per female compared to 27 in the untreated control. These results highlight the direct value of floral resources on SWD parasitoids which would support parasitism rates in the field.

Hygiene practices in the crop which have been successful at reducing SWD re-inoculation, may have a negative impact on pupal parasitoids such as *P. vindemmiae.* No *T. drosophilae* (also a pupal parasitoid) emerged from healthy fruit picked from the crop (Rossi Stacconi et al., 2018). *T. drosophilae* emerged from fruit which had dropped to the ground 8-14 days post collection. Clearing these fruits away will also remove parasitoids from the cropping area. It may be possible to collect emerging parasitoids from waste fruit to reintroduce into the crop and wild SWD hosts could be left unmanaged to boost parasitoid numbers. Wild fruit is a source of SWD, but also *T. drosophilae* (Wolf et al. (2020b). Wolf et al. (2020b) also found a significant reduction in SWD emergence from common wild species when exposed to parasitoids. SWD emergence was reduced by 78% in mistletoe (*Viscum album* L. subsp. *album* (Santalaceae)), 67% in snowy mespilus 'Edelweiss' (*Amelanchier ovalis* Medik. (Rosaceae)) and 80% in Oregon grape or holly-leaved berberry (*Mahonia aquifolium* (Pursh) Nutt. (Berberidaceae)). However, it is noteworthy that some of these hosts are also likely to support SWD populations. Hosts such as black nightshade (*Solanum nigrum* L.) have low natural SWD emergence (Kenis et al., 2016), although reproduction was observed in no-choice laboratory bioassays (Arnó et al., 2016). Several fruit hosts have also been identified in which SWD will oviposit, but from which no emergence occurs (Poyet et al., 2015).

Further studies on the interaction of SWD, parasitoids and their wild hosts would be useful to direct habitat management. For example, it is possible that termination of the SWD juvenile prior to adult emergence is also detrimental to parasitoids. Once wild hosts have been confirmed for their ability to host Drosophila and their parasitoids, these species could replace the SWD-promoting hosts such as wild blackberry (*Rubus* sp.) and elderberry (*Sambucus nigra* L.) in surrounding crops.

Augmented releases of non-native parasitoids

From the limited published research on augmented releases of *T. drosophilae*, results are positive, but more studies are needed on optimising release points, timing, and rates. Methods and approaches differ between published studies and so direct comparisons between them are not possible.

The first research to be published on augmented releases of *T. drosophilae* was by Rossi Stacconi et al. (2018). In this study, 1,000 adult *T. drosophilae* were released weekly for five weeks in a range of soft and stone fruit crops across Italy. Sentinel traps were deployed at various distances from the release site to ascertain the distance the parasitoids dispersed. *T. drosophilae* were recovered from SWD inoculated fruit up to 40metres from the release location, the maximum distance assessed. They also reported a significant reduction in the number of SWD that emerged from fruit collected <10 metres from the release site in all but one of the eight treated semi-field trial sites. Finally, in plots where all waste fruit was gathered from the crop and covered with a fine mesh to allow emerging parasitoids to transfer back into the crop, there was a significant reduction in SWD emergence from fruit which had dropped from the crop 8-14 days post collection. This effect was seen four weeks post *T. drosophilae* release. In crops where waste fruit was completely removed, a significant reduction in SWD from old dropped fruit was only seen in comparison to the control after 7 weeks post *T. drosophilae* release. These treatments were compared to control plots where no *T. drosophilae* were released.

In following trials, releases of *T. drosophilae* were made to target SWD early in the growing season when SWD population pressure is low (Rossi Stacconi et al., 2019). Trials were done in Italian commercial and unmanaged cherry orchards, with releases of *T. drosophilae* made between March and April with average daily temperatures of 11-15°C. The first parasitoid release was seven days after the first fecund SWD females (females able to lay eggs) were observed in the field. Releases of *T. drosophilae* were made for seven weeks with between 10,000 and 40,000 individual parasitoids dispensed weekly. By the end of the release period, a total of 200,000 individual *T. drosophilae* had been dispensed. The efficacy of this trial was assessed by the number of eggs laid in cherry fruit collected from the cherry trees, in comparison to orchards that had no parasitoid releases and from other host plants neighbouring the cherry trees. In commercial cherry, a 2.4% reduction of SWD damage in fruit was found in the *T. drosophilae* treated areas compared to untreated. In unmanaged cherries, for which no plant protection products were used to target SWD, a reduction in the number of damaged fruit was identified in the *T. drosophilae* treated areas (12.4% damaged) compared to untreated (24.5% damaged). In the unmanaged cherry plots, a 34% reduction in SWD pupal survival was seen in the *T. drosophilae* treated areas compared to untreated. Parasitoids were more abundant in areas not treated by cPPPs, which is in agreement with previous findings. This indicates that augmented parasitoid releases may be beneficial in unsprayed, wild areas where unmanaged crops are located. The parasitoid population could be maintained in these untreated areas allowing *T. drosophilae* to disperse up to 40metres into the crop (Rossi Stacconi et al., 2018).

The final publication reports on augmented release of *T. drosophilae* in raspberry within Mexico, where year-round fruit production is common. In these field trials, the sites were treated with the grower standard IPM strategies and either treated with a single release of 450 *T. drosophilae* or a single release of 450 *T. drosophilae* and 150 *Leptopilina boulardi* Barbotin, Carton & Kelner-Pillault and compared to an untreated control. The impact these treatments had on SWD was assessed by the number of adults in liquid baited monitoring traps (containing vinegar) and the number of adults in fruit monitoring traps (containing raspberries). A 50% and 55% total reduction in adult trap catches was found in the single species and combined species release sites, respectively, in comparison to untreated areas. There is no indication how this reduction in adult SWD affected fruit damage in the crop.

A few studies have investigated the impact that parasitoid releases have on SWD in crops and, to date, no investigations have looked at the impact on native non-target species. Daane et al. (2021) evaluated the potential host species range for three Asian origin parasitoids which could be deployed for future augmented control. As these are from the SWD's native range, they are likely to be adapted to overcome the encapsulation process previously described. In laboratory trials, 24 species of *Drosophila* were evaluated for their ability to host the larval parasitoids: *Asobara japonica* Belokobylskij, *Leptopilina japonica* Novković and Kimura, and *Ganaspis brasiliensis* (Ihering). All three parasitoids were successful at completing their life cycle on SWD. As for non-target species, *A. japonica* followed by *L. japonica* had the widest possible host range utilising 18 and 10 out of the 24 species offered, respectively. *G. brasiliensis* had the smallest range, only emerging from 3 other species. A broad host range may be desirable as there are more frequent hosts available for parasitoid populations to expand.

To date, there have been no augmented releases of parasitoids to target SWD in the UK. The use of native parasitoids for augmented release negates restrictions associated with the release of non-native species (Rossi Stacconi et al., 2017). So far, the most reliable parasitoid species for augmented release in the UK would be *P. vindemmiae* and *S. erythromera* (AHDB Project SF/TF 145a). Although *T. drosophilae* is more effective at reducing SWD populations in comparison to the other tested species, the regulatory restrictions result in barriers to this process. *P. vindemmiae* and *S. erythromera* are both active in the UK from May to October (Figure 6) which is the primary harvesting period of soft- and stone-fruit. Their cold tolerance makes

them suitable for the mild conditions in late spring and autumn. In addition, they could be reared on non-SWD hosts or selected for optimisation through rearing on SWD. Combined, these species have accounted for 98% of parasitoids that emerged from the 3-year AHDB Project SF/TF 145a, with both species found in woodland and hedgerow traps. In addition, both species completed development to adulthood in laboratory cultures of *D. suzukii*, demonstrating the ability for mass rearing of these species for augmented release.

⧆ Pachycrepoideus vindemmiae ☐ Spalangia erythromera ▦ Asobara tabida ■ Leptopilina heterotoma ▥ Trichopria prema

Figure 6. Total emergence of parasitoid species each month from SWD sentinel traps deployed in Southeast England in 2018.

Future research

Future work should focus on;

- Laboratory studies of parasitoids to understand lifecycle parameters of the key SWD parasitoids in the UK.

- Modelling the phenology of parasitoids with SWD seasonal life cycle and generations in combination with the SWD model from SF/TF 145a.

- Studies on the interaction of parasitoids with other UK drosophila and more accurate estimations of SWD mortality, including population growth of parasitoids in the field.

- Habitat management to optimise UK native SWD parasitoids including laboratory studies of flora that enhance the fecundity of female parasitoids.

- Estimation of the distance parasitoids move into different cropping systems from floral margins, woodlands, and hedgerows.

- Harvesting and releasing parasitoids from waste fruit.

Acknowledgements

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