

Ovipositional preference, fidelity, and fitness of *Drosophila suzukii* in a co-occurring crop and non-crop host system

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Abstract *Drosophila suzukii* (Matsumura) is a devastating pest of soft-skinned fruits including blackberries and raspberries. Management of this pest is focused on preventing infestation in crops, but non-crop hosts may play an important role in enabling *D. suzukii* to persist in the absence of cultivated hosts. *Drosophila suzukii* may also infest fruits of both crop and non-crop hosts concurrently. Our goals were to determine whether (1) *D. suzukii* prefers to oviposit in cultivated blackberry, *Rubus* L. subgenus *rubus* Watson, or American pokeweed, *Phytolacca americana*, a non-crop host commonly found along field edges, (2) *D. suzukii* prefers to oviposit into the same host from which it emerged, and (3) performance differs between *D. suzukii* progeny that develop in blackberries or pokeweed berries. Although the pest was able to infest both hosts at the same rate, we found that *D. suzukii* females emerging from pokeweed preferred to oviposit into blackberries, while females emerging from blackberry had no preference. Progeny that developed in blackberries were more fit than progeny that developed in pokeweed berries based on several measures. In field locations, cultivated blackberries and pokeweed berries only overlapped in availability for a short period of time, and infestation rates were variable

between blackberries and pokeweed berries collected during that period. Nonetheless, these results suggest that non-crop hosts may facilitate the invasion of *D. suzukii* and perpetuate infestation of cultivated hosts under certain circumstances.

Keywords Spotted wing drosophila · Host preference · Fitness · Invasive species

Key message

- *Drosophila suzukii* is an invasive fruit pest with a wide range of crop and non-crop potential hosts.
- We compared several fitness parameters for *D. suzukii* in two known hosts, blackberry (crop) and American pokeweed (non-crop).
- Our data show that *D. suzukii* can use both hosts for reproductive purposes but performs better when using blackberry.
- Because crop hosts are not available year-round, non-crop hosts likely play an important role in the persistence and invasion success of *D. suzukii*.

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Introduction

Invasive species incur great ecological and economic costs worldwide (Bulleri et al. 2008; Haye et al. 2015; Pimentel et al. 2000, 2005; Pyšek and Richardson 2010; Wilcove et al. 1998). These species are often able to exploit available resources (e.g., food, shelter) in a different or more efficient manner than native species, thus enabling success in new regions. For example, *Solenopsis invicta* Buren, the

red imported fire ant, is hugely successful in the southern United States in part due to its ability to quickly colonize disturbed habitats while native ants are slow to recruit to these locations if at all (King and Tschinkel 2006, 2008). The predatory multi-colored Asian lady beetle, *Harmonia axyridis* Pallas, which is arboreal in its home range (Gordon 1985), has expanded its range into agricultural and urban habitats to become pervasive throughout the areas it has invaded, including North America and much of Europe (Brown et al. 2011). Similar to *S. invicta*, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae) exploits an available niche by using fruit resources in the ripe or ripening stages (Mitsui et al. 2006; Poyet et al. 2014), before they are available to other *Drosophila* species, which typically infest overripe or rotting fruits. Like *H. axyridis*, *D. suzukii* has benefitted from a wide range of available hosts in agricultural, natural, and urban habitats in its newly expanded range (Lee et al. 2015; Poyet et al. 2015).

Drosophila suzukii, commonly referred to as the spotted wing drosophila, is a highly invasive insect pest of soft-skinned fruits (Lee et al. 2011a, 2011b; Walsh et al. 2011; Asplen et al. 2015). This pest is now found across North America and Europe, and in South America (Asplen et al. 2015; Calabria et al. 2012; Cini et al. 2012, 2014; Deprá et al. 2014; Hauser 2011; Vilela and Mori 2014; Walsh et al. 2011). Female *D. suzukii* possess a large, heavily sclerotized ovipositor that enables them to oviposit in ripe and ripening fruits (Atallah et al. 2014; Burrack et al. 2013; Lee et al. 2011a; Mitsui et al. 2006; Hauser 2011; Poyet et al. 2014), a resource that is unavailable to other species until overripe or damaged. Unlike native drosophilids, *D. suzukii* are attracted to volatiles associated with leaf odor, fruit-ripening, and fresh fruits (Keesey et al. 2015; Revadi et al. 2015b), enabling this species to locate available resources.

A broad range of both crop and non-crop hosts have been documented within the native and introduced *D. suzukii* range (Lee et al. 2015; Poyet et al. 2015; Walsh et al. 2011). Within crop hosts, *D. suzukii* lays more eggs, develops faster, and has greater survivorship in caneberries (raspberries and blackberries) than in blueberries, strawberries, cherries, or grapes (Bellamy et al. 2013; Burrack et al. 2013; Lee et al. 2011a). *Drosophila suzukii* adults also prefer ripe to unripe crop hosts (Lee et al. 2011a), but can develop in unripe fruits (Walsh et al. 2011). *Drosophila suzukii* adults are present year-round in temperate environments (LMD, *Unpub. data*), and have a wide variety of non-crop hosts available throughout the year (Poyet et al. 2015). It is likely that these non-crop hosts play a vital role in this species' persistence when cultivated hosts are unavailable (Pelton et al. 2016). However, it is currently unknown if *D. suzukii* prefers to oviposit in crop

or non-crop host species or the full extent to which larval performance differs between these hosts (Lee et al. 2015; Poyet et al. 2015). It is also unknown if *D. suzukii* females exhibit host fidelity and prefer to oviposit in the host from which they emerged when an alternative host is present, if they prefer to lay eggs in the best quality host available, or if they have no preference.

To begin to tease apart these relationships, we compared oviposition and progeny performance in two co-occurring hosts, blackberries (*Rubus* L. subspecies *rubus* Watson), a crop frequently devastated by *D. suzukii* (Bolda et al. 2010; Burrack et al. 2013), and American pokeweed (*Phytolacca americana*), a non-crop host and common weedy plant in North America that *D. suzukii* is able to use for development (Kinjo et al. 2013; Lee et al. 2015; Poyet et al. 2015; Van Timmeren and Isaacs 2013). Pokeweed plants are common in areas of non-crop habitat surrounding commercial blackberry fields in North Carolina and fruit concurrently with late-season commercial blackberry varieties. Pokeweed is infested naturally by *D. suzukii* at our field locations (Cleveland County, North Carolina, USA; KASB, *Unpub. data*), and may be an important non-crop host for *D. suzukii* (Kinjo et al. 2013). Recent research has shown that pokeweed is likely a suboptimal host; *D. suzukii* offspring are able to develop in the fruits; however, there is a prolonged development time (23.67 days at 20 °C) and low rate of survival from egg to adult (0.02 %) for flies developing in this host (Poyet et al. 2015). In comparison, development time is much shorter in blackberry (11–12 days at 20 °C) with a higher rate of survival (at least 42 %) (Burrack et al. 2013; Tochen et al. 2014). Using these co-occurring hosts, specific goals of this study were to determine whether (1) *D. suzukii* prefers to oviposit in blackberries or pokeweed berries, (2) *D. suzukii* prefers to oviposit into the same host from which they emerged, and (3) if the performance of *D. suzukii* progeny that develop in blackberries or pokeweed berries differs according to several fitness parameters.

Materials and methods

Source material

Drosophila suzukii were reared from blackberries (cultivar 'Prime-Ark[®] 45') collected in crop fields and pokeweed berries collected from wooded edges adjacent to crop fields in Cleveland County, NC, in September and October 2014 and August 2015. Berries were held at 20 °C in 266 mL plastic containers (up and up brand, Target[®], Raleigh, NC) vented on the bottom with fine mesh fabric (Burrack et al. 2013). A single generation of adults was allowed to emerge within each container and interact with the host from which

they emerged for 1–2 days before they were aspirated into vials with standard *Drosophila* diet (Hardin et al. 2015) and held at room temperature until reproductively mature. Females and males were held together in small groups (10–15 flies) to ensure mating for up to 17 days before they were used in an assay; individual males and females were used only once. Flies were moved to diet vials to reduce mortality and provide adults with a consistent food source prior to assays. Female *D. suzukii* used in assays were between 3 and 14 days old (most were over 5 days old) (Revadi et al. 2015a). To control for potential effects of female age on oviposition, all females used were within 5–8 days of age of each other.

Organic blackberries used in bioassays were purchased at a local grocery store (2014: Sunbelle, Los Reyes, Mexico; 2015: Driscoll's, Watsonville, CA, USA). Pokeweed berries used in assays were collected from wild plants in Cleveland and Wake Counties, NC. Clusters of green pokeweed berries were covered using small drawstring bags made from No-see-um mesh (Denver Fabrics, Denver, Colorado, USA) to prevent infestation. Clusters were collected once berries were ripe and returned to the laboratory in floral water picks (Koyal Wholesale, Fullerton, CA) filled with 10 mL of water.

No-choice assays

A series of no-choice assays were conducted with flies that had emerged from either blackberries or pokeweed berries to determine the rate at which *D. suzukii* will oviposit into blackberries and pokeweed and if greater numbers of eggs are laid in either host when an alternative host is not present. In no-choice assays, groups of five male and five female *D. suzukii* that had emerged from either blackberry or pokeweed were exposed to ca. 15 g of fruit (2 blackberries or 31–55 pokeweed berries) for 4 h. Fruit mass was held constant to mitigate effects of fruit size on oviposition (Burrack et al. 2013). The host from which the adult flies emerged is referred to as the *natal host* hereafter, while the host in which eggs were laid and progeny developed is referred to as the *oviposition host*. A total of 24 no-choice assays were conducted, including six replicates of each natal host/oviposition host combination.

Choice assays

A series of choice assays were conducted with flies that had emerged from either blackberries or pokeweed berries to determine if *D. suzukii* prefers to lay eggs in their natal host when an alternative host is present. In choice assays, groups of five male and five female flies with either blackberry or pokeweed as their natal host were exposed to 15 g of blackberries and 15 g of pokeweed berries

simultaneously for 4 h. A total of 16 choice assays were conducted, including eight replicates with flies that emerged from each natal host.

Assays were conducted in 0.30 m² fine mesh collapsible cages (Bioquip Products, Rancho Dominguez, CA) at room temperature on three dates in 2014 (October 24 and 30, November 13) and two dates in 2015 (September 14 and 16). Berries were removed after 4 h of exposure to *D. suzukii*, and the number of eggs laid was counted using a stereomicroscope. Berries were then held in 266 mL plastic containers at 20 °C for 7 days, after which visible pupae were removed daily and placed into a 60 mm Petri dish with a moistened paper towel square (Burrack et al. 2013). Petri dishes with pupae were held at room temperature until all adults emerged or pupae were determined to be dead. Larval development time (days from egg to pupa), the proportion of eggs that survived to the adult stage, and the sex ratio of emerged adults were calculated. In 2015, individual pupae were weighed using a precision analytical balance (Sartorius Ultra Microbalance MSA2.7SOTRDM) to determine if pupae that emerged from the two hosts differed in mass. A total of 262 pupae were weighed across all treatments, 161 from assays with blackberry natal hosts and blackberry oviposition hosts, 56 with blackberry natal hosts and pokeweed oviposition hosts, 41 with pokeweed natal hosts and blackberry oviposition hosts, and 4 with pokeweed natal hosts and pokeweed oviposition hosts.

Field infestation patterns

To determine natural field infestation patterns in blackberries and pokeweed berries, we collected fruit samples weekly from June 17 to October 22, 2014 at two commercial blackberry farms in Cleveland County, NC, where wooded edges ran along the length of crop fields. Blackberry samples consisted of 40 ripe berries and were collected at sampling points within crop fields that were located approximately 30 m away from each other and 30 m away from the wooded edge. Pokeweed samples consisted of approximately 50 berries per sampling point and were collected from plants located along the wooded edge. For both hosts, samples were collected whenever ripe berries were available; therefore, sample sizes varied according to fruit availability and were smaller at the beginning and end of each host's fruiting period. Samples were collected, weighed in the laboratory, and stored in 266-mL plastic containers (up and up brand; Target®, Raleigh, NC) vented on the bottom with fine mesh fabric. Fruit samples were held at 20 °C and dissected within 14 days of collection, on average. During dissections, pupae were placed into 60-mm Petri dishes with moistened paper towel squares and were held at room temperature

until adults emerged or pupae were determined to be dead. Total infestation, a measure of the number of *D. suzukii* able to infest and survive to at least the third instar, was calculated for each sample by adding the number of *D. suzukii* adults, dead pupae, and dead third instars present (smaller dead larvae were difficult to detect and may have been missed during the dissection process). For each sample, total infestation was then divided by the weight of the sample to determine *D. suzukii* per gram of fruit.

Fruit samples were collected from three blackberry fields at the two commercial farms, although the number of samples collected per field varied as follows. Three blackberry samples were collected weekly from two separate fields at the first farm, one with cultivar ‘Ouachita’ blackberries (Clark and Moore 2005) and the other with cultivar ‘Navaho’ blackberries (Moore and Clark 1989); pokeweed samples were collected weekly from two plants located along the wooded edge near each field when available. At the second farm, four blackberry samples were collected weekly from a mixed planting with both ‘Ouachita’ and ‘Navaho’ cultivars present; pokeweed samples were collected weekly from three plants located along the wooded edge when available. Both ‘Ouachita’ and ‘Navaho’ bear fruit during the summer months and are commonly grown in the southeastern United States.

Blackberry fields in western North Carolina are actively managed to prevent *D. suzukii* infestation, while no management actions are performed on potential nearby non-crop hosts (Anonymous growers, *pers. comm.*). Insecticide applications targeting *D. suzukii* began in early June, when ripe blackberries were first present. Thereafter, broad spectrum insecticides were applied in rotation weekly until ripe berries were no longer available.

Statistical analysis

Oviposition (number of eggs laid in no-choice assays or proportion of eggs laid in each host in choice assays), larval development time, pupal mass, and survival were analyzed using mixed-model ANOVA (SAS PROC MIXED, v. 9.4) with natal and oviposition hosts as fixed effects and replicate as a random variable when appropriate. Means were separated using Tukey’s honest significant difference (HSD). A Chi-square comparison of the sex ratio of progeny that survived to the adult stage was performed using GraphpadQuickCalcs.

Mean *D. suzukii* infestation rates in blackberries and pokeweed berries collected in the field were compared during weeks when ripe berries of both hosts were present using mixed-model ANOVA with host and sample date as fixed effects (SAS PROC MIXED, v. 9.4).

Results

Oviposition

Drosophila suzukii laid eggs in both blackberries and pokeweed berries at the same rate. There was no difference in the number of eggs laid in no-choice assays due to natal host or oviposition host ($F_{1,11} = 2.08$, $p = 0.18$; $F_{1,11} = 0.26$, $p = 0.62$, respectively). The mean number of eggs laid per assay ranged from 11.33 to 29.75.

In choice assays, females that emerged from pokeweed laid a greater proportion of eggs in blackberries than in pokeweed berries ($F_{1,28} = 14.68$, $p < 0.01$), while those with blackberry as a natal host laid a similar proportion of eggs in both oviposition hosts ($F_{1,28} = 0.31$, $p = 0.58$) (Fig. 1).

Development

Drosophila suzukii progeny that developed in blackberries fared better than those that developed in pokeweed berries based on several fitness measures (Table 1). Larvae that developed in blackberries developed faster than those in pokeweed berries, regardless of natal host, in both no-choice and choice assays. Overall, larvae that developed in blackberries pupated approximately 4 days earlier than those in pokeweed berries (blackberry: 8.79 ± 0.33 days; pokeweed: 12.27 ± 0.49 ; $F_{1,36} = 34.02$, $p < 0.01$; data combined across choice and no-choice tests). Additionally, progeny that developed in blackberries were almost twice as heavy at the pupal stage than those that developed in pokeweed berries (blackberry: 1.96 ± 0.06 mg; pokeweed: 1.04 ± 0.08 mg; $F_{1,65} = 82.22$, $p < 0.01$; data combined across choice and no-choice tests).

Progeny survival and sex ratio

Across all trials and treatments, adults that developed in blackberries laid more eggs than those that had pokeweed as a natal host ($F_{1,43} = 4.50$, $p = 0.04$), and more adult flies emerged from the oviposition host blackberry ($n = 637$) than pokeweed ($n = 37$). A greater proportion of eggs laid in blackberries survived to the adult stage as compared to those laid in pokeweed berries (Table 1). Differences in survival were influenced by both the natal host ($F_{1,38} = 4.43$, $p = 0.04$) and the oviposition host ($F_{1,38} = 54.81$, $p < 0.01$), with the oviposition host explaining more variability than the natal host. There was also a significant interaction between natal and oviposition host ($F_{1,38} = 8.82$, $p = 0.01$), with the oviposition host still explaining the majority of the variation.

Fig. 1 Proportion of eggs laid in each oviposition host in choice assays. Females that emerged from pokeweed laid a greater proportion of eggs in blackberry than in pokeweed ($F_{1,28} = 14.68, p = 0.0007$), while those with blackberry as natal host laid a similar proportion of eggs in each oviposition host ($F_{1,28} = 0.31, p = 0.582$)

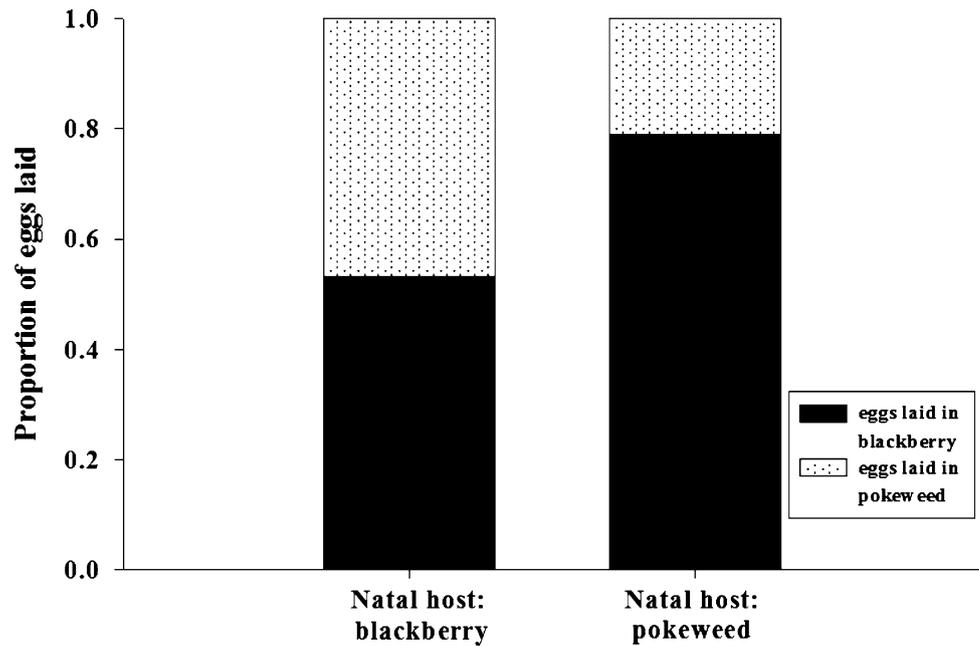


Table 1 Mean performance of *D. suzukii* progeny in laboratory no-choice and choice assays

Assay	Natal host	Oviposition host	Larval development time \pm SEM (days)	Pupal mass \pm SEM (mg)	Proportion surviving to adult \pm SEM	
No-choice	Blackberry	Blackberry	8.70 \pm 0.51a	2.00 \pm 0.06a	0.44 \pm 0.07b	
		Pokeweed	13.34 \pm 0.51a	1.17 \pm 0.07b	0.17 \pm 0.07c	
	Pokeweed	Blackberry	8.39 \pm 0.73a	1.06 \pm 0.25b	0.79 \pm 0.09a	
		Pokeweed	11.88 \pm 0.89a	0.88 \pm 0.18b	0.05 \pm 0.10c	
			<i>F</i>	0.72	4.44	7.49
			<i>df</i>	1,13	1,28	1,13
			<i>p</i>	0.41	0.04	0.02
Choice	Blackberry	Blackberry	8.84 \pm 0.57a	1.78 \pm 0.06b	0.43 \pm 0.08a	
		Pokeweed	13.24 \pm 0.69a	1.26 \pm 0.07c	0.05 \pm 0.09a	
	Pokeweed	Blackberry	9.65 \pm 0.81a	2.04 \pm 0.09a	0.85 \pm 0.12a	
		Pokeweed	10.00 \pm 1.81a	0.87 \pm 0.16d	0.00 \pm 0.00a	
			<i>F</i>	3.46	10.51	2.40
			<i>df</i>	1,19	1,33	1,19
			<i>p</i>	0.08	<0.01	0.14

Values within a column followed by the same letter are not statistically different ($\alpha = 0.05$, Tukey's HSD)

The sex ratio of progeny differed between the two hosts (Table 2). More females than males emerged from blackberries across all trials and treatments. Conversely, roughly equal numbers of females and males emerged from pokeweed berries, indicating that neither sex had greater development success in this host.

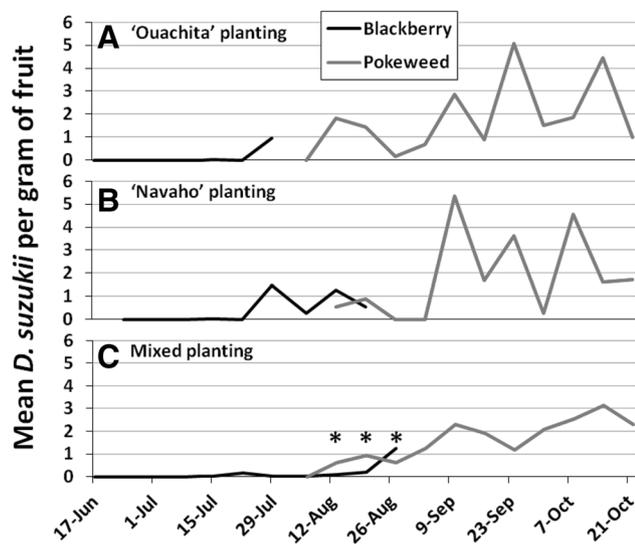
Field infestation patterns

Ripe blackberries were present from mid-June until late August, and ripe pokeweed berries were present starting in

August through the end of October. At the first farm, ripe 'Ouachita' blackberries were collected from June 17 to August 29, 2014. Because pokeweed berries growing adjacent to this field were not ripe until August 6, the fruiting periods of the two hosts did not overlap (Fig. 2a). Ripe 'Navaho' blackberries were collected in a separate field at the same farm from June 24 to August 20, 2014. Ripe pokeweed berries were present starting on August 13, and ripe blackberries and pokeweed berries were available concurrently for two weeks (Fig. 2b). The 'Ouachita' and 'Navaho' fields at the first farm are located over 500 m

Table 2 Sex ratio of *D. suzukii* progeny that developed to the adult stage in blackberries or pokeweed berries (oviposition host) in no-choice and choice assays

Natal host	Oviposition host	Male <i>D. suzukii</i>	Female <i>D. suzukii</i>	χ^2	df	<i>p</i>
Blackberry	Blackberry	154	192	5.50	1	0.02*
	Pokeweed	18	16	0.12	1	0.73
Pokeweed	Blackberry	110	181	17.32	1	<0.01*
	Pokeweed	2	1	0.33	1	0.56
	Total	284	396	18.45	1	<0.01*

* Indicates significance at $p \leq 0.05$ **Fig. 2** Mean *D. suzukii* infestation rates per gram of fruit in blackberry and pokeweed samples collected weekly in ‘Ouachita’ (a) and ‘Navaho’ (b) fields and a mixed planting of the two cultivars (c) on two commercial blackberry farms in Cleveland County, North Carolina, in 2014. Asterisk denotes a significant difference in infestation rates during certain weeks at $p \leq 0.05$

apart and are separated by a wooded area, and are therefore considered to be independent. At the second farm, ripe blackberries in a mixed ‘Ouachita’ and ‘Navaho’ planting were collected from June 17 to August 27, while the first pokeweed berries did not ripen until August 8. The fruiting periods of the two hosts overlapped for 4 weeks during August (Fig. 2c).

Infestation in blackberries and pokeweed berries exhibited some general patterns over the course of the sampling period. Infestation rates per gram of fruit in blackberries were generally low until the end of the fruiting period, when the number of ripe berries present in the field dropped and the remaining berries were heavily infested (Fig. 2a, c). An exception to this pattern occurred in the ‘Navaho’ field at the first farm, where two peaks of infestation were observed in late July and mid-August (Fig. 2b). In general, infestation rates per gram of fruit varied more in pokeweed berries than in blackberries over

the sampling period, most noticeably at the first farm where rates increased and decreased from week to week starting in September (Fig. 2a, b). Despite this variability in infestation rates per gram of fruit, infestation rates in individual pokeweed berries remained below one *D. suzukii* per berry on average.

During weeks when ripe blackberries and pokeweed berries were both available in particular fields, infestation rates per gram of fruit sometimes varied between the two hosts. Infestation rates in blackberries and pokeweed berries were not significantly different on either August 13 or 20 in the ‘Navaho’ field at the first farm (Fig. 2b). However, the fruiting periods of the two hosts overlapped for a longer period of time in the mixed planting and ripe berries were collected from both hosts on four dates in 2014, including August 6, 13, 20, and 27 (Fig. 2c). There was a significant interaction between date and host ($F_{3,13} = 8.59$, $p = 0.0021$), where infestation rates in the two hosts were not different on August 6, were higher in pokeweed berries than in blackberries on August 13 and 20, but higher in blackberries than in pokeweed berries on August 27. All field infestation data were collected on commercially managed farms which are intensively managed for *D. suzukii* with weekly insecticide applications and frequent harvest, therefore the observed infestation rates in blackberries are much lower than they would be if fields were not actively managed for *D. suzukii*.

Discussion

Drosophila suzukii has a broad host range (Lee et al. 2015; Poyet et al. 2015), but the degree of progeny success likely varies by host. In our experiments, *D. suzukii* laid eggs in both blackberries and pokeweed berries at the same rate when they had no other option, although survivorship differed between hosts. However, when given a choice, female *D. suzukii* that had emerged from pokeweed preferred to lay eggs in blackberries over pokeweed (Fig. 1). This suggests a hierarchy in oviposition host choice, where females will lay eggs into either available host, but prefer to lay eggs in a high-quality host such as blackberry after

developing on a suboptimal host. Field observations from another system suggest that pokeweed may even be a preferred oviposition host for *D. suzukii* under some conditions. For example, in Michigan, pokeweed berries collected in 2011 along the wooded edge of vineyards were heavily infested with *D. suzukii* (Lee et al. 2015), while riverbank grape berries (*Vitis riparia*) collected at the same time and location were uninfested (Van Timmeren and Isaacs 2014). It is likely that suboptimal oviposition hosts are used more often by *D. suzukii* in the absence of a higher quality host option.

Host fidelity is common in insects, and several studies have shown that prior experience can influence the future behaviors of insects (Papaj and Prokopy 1989). Within *Drosophila* species, field released *D. melanogaster* were found to return to traps baited with the same fruit pulp in which they had developed (Hoffman and O'Donnell 1992). Progeny were also found to be attracted to the natal host of their parents. However, the apparent lack of host fidelity for an invasive species, such as *D. suzukii*, may aid in its ability to persist in a wide variety of habitats.

In the absence of host fidelity, habitat fidelity may play an important role in the attraction and orientation of *D. suzukii* to a location where optimal hosts are available (Hoffman and O'Donnell 1992). Many *Drosophila* species are attracted to odors of their natal host (Hoffmann 1985) suggesting that these flies rely on olfactory cues to locate preferred hosts. In a recent study, *D. suzukii* responded to odors from both mulberry and figs, two potential hosts, but lacked fidelity to their natal host (Yu et al. 2013). It may be that specific odors attract *D. suzukii* to the general location of hosts, but once in the presence of hosts, they either lose this cue or are overwhelmed by cues in close proximity to one another. Similarly, *D. suzukii* is attracted to strawberry leaf odors (Keeseey et al. 2015), further supporting the idea that this species may use long-range host odors to locate a habitat with available hosts.

The ability to locate optimal hosts can have impacts on population fitness (Liu and Trumble 2007). Based on our data, pokeweed is a suboptimal host compared to blackberry based on several fitness measures. Larvae that developed in pokeweed berries took longer to pupate and developed into smaller pupae than larvae that developed in blackberries. Pupal mass has been shown to be a proxy for female fecundity in other dipterans (Armbruster and Hutchison 2002; Steinwascher 1982). However, some females still laid eggs in pokeweed, a less suitable host, even in the presence of blackberries, both in the field and in choice assays. It is possible that, at close range, *D. suzukii* are not able to discern hosts from one another based on odor cues, or that other factors including fruit firmness, color, or shape (Burrack et al. 2013; Kinjo et al. 2013; Poyet et al. 2014), have a strong influence on the direct interaction of *D. suzukii* laying eggs into hosts.

The sex ratio of surviving progeny also differed between the two hosts and may have implications for invasiveness. In the laboratory, more females emerged from blackberries, while similar numbers of males and females emerged from pokeweed berries. It is possible that males, which are generally smaller than females, are able to survive in less suitable substrates like pokeweed because they need to consume fewer resources to reach their critical weight for pupation. While sex ratio is not a fitness parameter, per se, it has important implications for how quickly a population grows, as female replacement rate can directly influence population growth. Thus, in a location where optimal hosts (e.g., blackberry) are abundant, populations of *D. suzukii* grow quickly, while in locations with suboptimal hosts (e.g., pokeweed), local populations are unlikely to build as quickly, but are likely to persist until optimal hosts are once again abundant. Because flies that emerged from pokeweed preferred to lay eggs in blackberries in choice assays, it is plausible that there could be spillover from pokeweed plants located along field edges into crop fields. However, these two hosts only overlapped in availability for a short period of time in August. Infestation rates were variable in blackberries and pokeweed berries during this period (Fig. 2), likely due to differences in host availability and variability in weather patterns during the late summer season. More likely, female flies that infested pokeweed berries in this study may have developed in blackberries and moved out of the field into adjacent wooded edges where they encountered pokeweed plants. *Drosophila suzukii* does move between crop fields and wooded edges in this system (KASB, Unpub. data), although the purpose of such movement has yet to be determined.

Drosophila suzukii that emerge from pokeweed may pose more risk to late-season crops including fall strawberries and primocane-fruiting blackberry cultivars such as 'Prime-Ark[®] 45' (Clark and Perkins-Veazie 2011) that bear fruit in the fall until the first hard freeze, much like pokeweed. Additionally, it is unclear if other non-crop hosts that fruit earlier in the season along wooded edges, such as wild brambles and black cherries, both of which were infested with *D. suzukii* earlier in 2014 in the same fields (KASB, Unpub. data), pose more risk to crop hosts. However, based on our results, it is likely that *D. suzukii* would not show host specificity for wild brambles, black cherries, or other suboptimal non-crop hosts and may preferentially infest blackberries or other suitable fruit crops that are better quality oviposition hosts than their natal host. If so, the management of non-crop hosts should be included in farm-scale IPM programs. Management actions may include local removal of non-crop hosts (Prokopy 2003), which is impractical for plants like pokeweed that are dispersed widely by seed predators (Orrock et al. 2006), or the use of these hosts for targeted

management action including bait sprays (Prokopy et al. 2003) or mass trapping (Cohen and Yuval 2000; Lee et al. 2011b; Wu et al. 2007) to reduce pest pressure.

Drosophila suzukii is able to use a wide variety of food and oviposition resources (Lee et al. 2015; Poyet et al. 2014; Stewart et al. 2014). Further research into the role(s) of these resources in the population maintenance and growth of this species is needed to understand the ecology of this organism. By gaining a better understanding of its life history, pest management practitioners can exploit this information to control the spread of this destructive invasive pest.

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Author contributions LMD and KASB conceived and designed research. LMD and KASB conducted experiments and analyzed data. HJB supplied laboratory materials and support staff. LMD and KASB wrote the manuscript with advice from HJB. All authors read and approved the manuscript.

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Compliance with ethical standards

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

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