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Research

Behavior

Diurnal Activity of *Drosophila suzukii* (Diptera: Drosophilidae) in Highbush Blueberry and Behavioral Response to Irrigation and Application of Insecticides

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Abstract

Spotted wing Drosophila, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), is an invasive vinegar fly that has become a primary direct pest of berry crops worldwide. We conducted 2 yr of behavioral studies in blueberry plantings to determine how fly activity varied throughout the day. Observations of diurnal activity of adult *D. suzukii* found the greatest activity in the morning hours between 0600 and 0800 hours, when the majority of flies were on the berries. Flies were also active in the evening mainly between 1800 and 2000 hours; however, this trend was more prominent in 2015, which had cooler and more humid evenings. Experiments examining the effect of irrigation on *D. suzukii* behavior showed that flies remained active during and after irrigation. The effect of insecticide treatments alone and in combination with irrigation revealed that treatment with spinosad had limited effects on the number of flies per bush, whereas spinetoram reduced the number flying and on the bushes in some cases. Zeta-cypermethrin caused longer and more consistent reduction in *D. suzukii* flying and on bushes. In all treatments, we observed surviving flies flying near and on treated bushes, indicating that these insecticides do not completely deter fly activity. Irrigation did not influence the effects of zeta-cypermethrin on fly behavior during daily observations up to 3 d after application. Our results highlight that the diurnal patterns of activity of *D. suzukii* on host plants are flexible and are relatively unaffected by irrigation or insecticide applications.

Key words: Spotted wing Drosophila, fruit, IPM, behavior, irrigation

The vinegar fly, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae) commonly referred to as spotted wing Drosophila, is an invasive pest that has spread rapidly across North America since first being detected in California in 2008 (Hauser 2011). It is also spreading globally, with distribution into most of the major fruit-producing regions of the world (Asplen et al. 2015) and new detections being reported recently in Brazil, Poland, Ukraine, and Turkey (Deprá et al. 2014, Łabanowska and Piotrowski 2015, Lavrinienko et al. 2016, Orhan et al. 2016). Through its invasion, *D. suzukii* has become a major challenge to the production of cherries, strawberries, caneberries, and blueberries (Diepenbrock et al. 2016a, Farnsworth et al. 2016, Haye et al. 2016, Mazzi et al. 2017).

In the initial response to invasion by this pest, much of the research focused on insecticide efficacy studies due to their crucial role in protecting fruit from *D. suzukii* (Asplen et al. 2015). Early studies focused on the efficacy of insecticides to control the fly (Bruck et al. 2011, Beers et al. 2011) and exploring ways to optimize insecticide use, including curative control (Wise et al. 2015), effect of rain (Van Timmeren and Isaacs 2013, Gautam et al. 2016), and season-long insecticide programs (Diepenbrock et al. 2016a). Combining insecticides with complementary control tactics has increasingly been explored to either improve the performance or reduce the need for chemical treatments. These include investigations of the use of adjuvants and phagostimulants (Gautam et al. 2016, Knight et al. 2015, Cowles et al. 2015), netting (Leach et al. 2016, Alnajjar et al. 2017), repellents (Wallingford et al. 2016), border sprays (Klick et al. 2016), and cultural control methods (Iglesias and Liburd 2016).

In all aspects of developing management approaches for this pest, understanding where and when the flies are active can inform more targeted approaches (Burrack and Bhattarai 2015). Klick et al. (2015) used protein markers and enzyme-linked immunosorbent assay to track flies to interpret their movement from field margins into adjacent cultivated raspberry plantings. This study and others highlighted that the presence of noncrop hosts in these field margins might be an important source of immigrating flies (Klick et al. 2015, Diepenbrock et al. 2016b, Pelton et al. 2016). Variations in conditions across cultivated fields may also affect the presence of *D. suzukii* flies. Microhabitat conditions within cultivated blackberry canopies can affect the infestation levels (Diepenbrock and Burrack 2016), and humidity levels can also affect fly behavior. Tochen et al. (2016) found that the reproductive potential of *D. suzukii* females increased at higher humidity, and female reproductive success in field cages was higher during the nighttime when temperatures were lower and relative humidity was higher (Evans et al. 2017). There remain many gaps in our understanding of the behavior of adult and larval *D. suzukii*; insights into fly behavior can provide important clues for how best to manage them through chemical and nonchemical means. This approach has proven effective for the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), where knowledge of fly attraction and feeding behavior has resulted in the use of targeted bait sprays to achieve control while reducing negative effects on natural enemies (Vargas et al. 2002).

Fly activity during the day is an important consideration in developing effective management programs. Laboratory experiments using colony-reared *D. suzukii* adults have found bimodal patterns of fly activity, with the highest amount of fly activity occurring in the morning and evening hours (Hamby et al. 2013, Ferguson et al. 2015, Revadi et al. 2015). Also, Evans et al. (2017) found evidence for a bimodal pattern of activity in the field with more flies caught in traps at dawn and dusk periods.

Applications of insecticides may also influence the behavior of insects residing in crop fields. Braga et al. (2011) found certain populations of maize weevils, *Sitophilus zeamais* Motschulsky, exhibited avoidance behavior when exposed to the insecticide fenitrothion. However, studies on this type of repellency behavior are lacking in insect pest species (Guedes et al. 2016). Exposure to insecticides may also result in sublethal effects that can change the behavior of the insect, such as impairment of movement (Tomé et al. 2014), antifeedant behavior (He et al. 2013, Wang et al. 2004), and delay of egg hatching (Nayak et al. 2003). All of these can have a significant effect on the outcome of control programs and may not be reflected in typical insecticide efficacy evaluations (Desneux et al. 2007).

Rain events and irrigation are common in blueberry production, and they may also play an important role in insect pest behavior. Overhead irrigation sprinklers or microsprinklers are common for blueberries and can be used to irrigate when water demand is high and to cool the bushes in warm regions, respectively. Regular rain and irrigation events can wash insecticide residues off, making pest control more challenging to achieve. Hulbert et al. (2012) found increased feeding by Japanese beetle, *Popillia japonica* Newman, on blueberry foliage exposed to simulated rainfall. Other studies have found decreased efficacy of insecticides against *D. suzukii* after rainfall and simulated rainfall (Van Timmeren and Isaacs 2013, Gautam et al. 2016).

Research on chemical control of *D. suzukii* to date has focused primarily on preventing infestation. However, more research focusing on how applications of insecticides and the associated residues affect fly behavior can allow more effective control. Likewise, there is little understanding of how fly activity may change during or after rain events. They might remain active and continue to lay eggs, particularly with washed off insecticide residues (Van Timmeren and Isaacs 2013), or they may reduce activity and wait for the fruit and foliage to dry. In this study, we aimed to determine 1) how *D. suzukii* activity varies throughout the day, 2) how insecticide treatments on bushes affect their activity, 3) the effect of irrigation on *D. suzukii* activity, and 4) how irrigation after an application of insecticides affects *D. suzukii* activity.

Materials and Methods

General Methods

All experiments were done in a mature highbush blueberry planting at the Trevor Nichols Research Center in Fennville, Michigan. All rows within this planting contained 12 bushes spaced 1.2 m apart, with black weed fabric under the bushes, and maintained with a 0.8-m herbicide strip on either side of the row. Bushes used in experiments were either 'Jersey' or 'Bluecrop' variety depending on the location of a specific experiment. Bluecrop bushes were an average of 1.3-m high with a crown width of 1.3 m, whereas Jersey bushes were an average of 1.2-m high with a crown width of 1.1 m. Bushes received no insecticide sprays except in experiments where their application was an independent variable. All insecticides in the experiments were applied using an FMC 1029 airblast sprayer calibrated to deliver 468 liters of water per hectare.

To count flies in the field, two observers walked slowly along opposite sides of a focal blueberry row, counting and recording the number of *D. suzukii* adults seen within the bushes. *D. suzukii* individuals were identified by the wing spot on each wing (males) or by abdomen shape and color (females) with flies that could not be positively identified as *D. suzukii* being recorded as undetermined. The location of each observed fly was recorded at the time the fly was first seen, either flying within the bush canopy or stationary on leaves or fruit on the bush. To verify the accuracy of field identifications, vacuum sampling (2820GA model, BioQuip Products, Rancho Domiquez, CA) of bushes was regularly conducted in both years. Flies caught in vacuum samples were 93% *D. suzukii* in 2015 experiments and 100% *D. suzukii* in 2016 experiments. Temperature, relative humidity, and wind speed were recorded immediately before each fly observation event using a handheld Kestrel weather meter (Model 4500, Nielsen-Kellerman Co., Boothwyn, PA). During some observations, later in the season, a few treatment rows had little to no fruit on the bushes, so data from these replicates were excluded from the data analysis to avoid lack of fruit affecting the results.

Experiment 1: Diurnal Activity

Observations to compare *D. suzukii* activity during different times of the day were conducted in 2015 (12 August to 3 September) and again in 2016 (3 August to 8 August). These periods represent the time when the population of *D. suzukii* in Michigan is increasing rapidly. Growers are commonly applying insecticide for the control of *D. suzukii*, harvesting fruit and irrigating at this time also, thus making the period representative in terms of the host crop and the phenology of *D. suzukii*. Surveys for adult flies were conducted on Jersey bushes and took place during 0600–0800, 1200–1400, 1500–1700, and 1800–2000 hours on the same days. Observations of fly activity were on a single 15 m row over a 15-min period. Burrack and Bhattarai (2015) showed that adult *D. suzukii* did not infest fruit or get captured in baited traps after sunset or before sunrise, so observations for this study focused after 0600 hours and before 2000 hours. Observations were conducted on days with no rain, wind speeds under 10 km per hour, and where daytime high temperatures were at least 23°C. In total, there were 6 d of observations in 2015, and four in 2016.

Experiment 2: Response to Irrigation

To test the effect of rain on *D. suzukii* activity, an overhead irrigation system was used as a proxy for rainfall. Four one-row plots were set up in each of two sections of Bluecrop bushes with one section receiving overhead irrigation and the other receiving no irrigation. Observations of fly behavior took place during the morning period (0600–0800 hours), using previously described methods with two observers counting flies for 2.5 min each on five-bush sections within each plot. Irrigated plots were treated with water on two consecutive mornings (28 August 2016 and 29 August 2016), and fly behavior was observed during the irrigation event in both the irrigated and nonirrigated plots. Plots were irrigated throughout the time it took to conduct fly observations in all plots. Observations on 29 August 2016 were also conducted immediately before and after the irrigation event.

Experiment 3: Insecticide Applications and Activity

Three experiments were conducted in 2016 to assess the effect of select insecticides on fly activity on blueberry bushes. This experiment tested one organic, one reduced-risk, and one conventional insecticide namely spinosad (Entrust 22.5SC, 94.6 g AI ha^{-1}, Dow AgroSciences LLC, Indianapolis, IN), spinetoram (Delegate WG, 105.1 g AI ha^{-1}, Dow AgroSciences LLC), and zeta-cypermethrin (Mustang Maxx 0.8EC, 26.9 g AI ha^{-1}, FMC Corp., Philadelphia, PA), respectively. Three separate experiments were set up, each comparing one insecticide and an untreated control. The zeta-cypermethrin experiment took place on Jersey bushes, and the spinetoram and spinosad experiments took place on Bluecrop bushes. All three experiments used four half-row (7.5-m long) replicate plots. Behavioral observations in each plot were conducted during the early morning period (0600–0800 hours), using methods similar to those used in diurnal activity observations with flies counted on bushes by two observers for 2.5 min in a five-bush section of each plot. Insecticides were applied to plots approximately once a week from late July to late August. In the first run of observations, fly activity assessments took place 1 d after treatment (DAT) (26 August 2016), and for the second run of observations these assessments were conducted at 1 DAT (30 August 2016) and 3 DAT (1 September 2016). Additional 3 DAT observations were unable to be completed due to numerous rain events washing off insecticide residue.

Experiment 4: Effect of Insecticide Applications and Irrigation

To examine the effect of irrigation following an application of insecticides on *D. suzukii* activity, eight one-row plots were set up in each of two Bluecrop sections, one irrigated and one nonirrigated. Four of the rows in each section received a zeta-cypermethrin application (Mustang Maxx 0.8EC, 26.9 g AI ha^{-1}) in the afternoon of 30 August 2016, while the other four rows in each section remained untreated. Fly observations took place the following morning (1 DAT) on both the irrigated and nonirrigated plots immediately before, during, and after a 27-min irrigation event. Observations were also conducted on the following two mornings (2 and 3 DAT, 1 and 2 d after rain event).

A separate irrigation event was conducted after the 3 DAT behavioral observation to investigate how the density of the bush canopy affects the volume of water penetrating to the base of bushes during irrigation. Plot irrigation lasted for 27 min, and 453 ml plastic deli cups (Gordon Food Service, Wyoming, MI; cup opening surface area: 95.03 cm^2) were placed on the ground either directly under the bush canopy or in the middle of the grassy row middle. In each 12-bush plot, a cup was placed under the bushes between bushes 3 and 4, 6 and 7, and 10 and 11, and an additional three cups in the adjacent row middle. At the end of the irrigation event, the amount of water collected in each cup was measured.

Experiment 5: Irrigation Duration and Insecticide Applications

An experiment was conducted to investigate the effect of irrigation duration on *D. suzukii* activity and egg laying behavior following an insecticide application. Half-row plots of Jersey blueberries received either a zeta-cypermethrin (Mustang Maxx 0.8EC, 26.9 g AI ha^{-1}) application or were left unsprayed and subsequently received either 15 min of irrigation, 1 h of irrigation, or no irrigation. Each treatment was replicated four times for a total of 24 plots. Insecticide applications were done on the morning of 6 September 2016, and irrigation was applied in the afternoon of the same day. Fly observations (two observers counting flies on five bushes for 2.5 min) were conducted the following morning (1 DAT) and again at 2, 3, and 8 DAT. Semi-field bioassays, using the methods described in Van Timmeren and Isaacs (2013), examined the effect of irrigation on insecticide residues at 1 and 2 DAT. Five ripe berries and blueberry shoots containing 10 leaves were collected and placed in water picks in a 0.95-liter clear plastic container. A small portion of fly diet and a 4-cm long piece of moist dental wicking were placed in the cup to reduce fly mortality. Six male and six female *D. suzukii* adults from a laboratory colony were added to the containers, and adult mortality assessed 24 h later. Seven days after the start of the bioassays, the fruit was removed and assessed for offspring of *D. suzukii* using a filter salt test (Van Timmeren et al. 2017). Field collected fruit was submerged in a strong salt solution (55.5 g/l) in a 45-ml plastic deli cup. Samples were allowed to soak for 1 h, after which the liquid was passed through a coarse sieve (4 mm) to remove large plant material and further sifted through a reusable coffee filter (Medelco 4-Cup Universal Coffee Filter, Medelco Incorporated, Bridgeport, CT) to trap the larvae. A stereomicroscope (Olympus SZX10, Olympus America, Inc., Center Valley, PA) was used to count the number of *Drosophila* larvae and pupae, with larvae being classified into small, medium, and large size categories. These are equivalent to first, second, and third instar larvae (Van Timmeren et al. 2017).

Statistical Analysis

All statistical analyses were performed using Systat 13 (Systat Software, Inc., Chicago, IL). Data were tested for normality using a Shapiro-Wilk test for normality and tested for homogeneity of variances using a Levene's test. Non-normal data were $\log(X+1)$ transformed to achieve normality; data that did not meet the assumptions of normality after transformation were subsequently analyzed using nonparametric tests.

For diurnal activity observations conducted in Experiment 1, the total number of flies per observation data in 2015 and 2016 did not meet the assumptions of normality and were analyzed using a Kruskal–Wallis test followed by a Conover–Inman test for post hoc comparisons. Temperature and relative humidity data in 2015 were analyzed using analysis of variance (ANOVA) and Tukey's honest significant difference (HSD) test for means separation; 2016 temperature and relative humidity data were not normal and were analyzed using Kruskal–Wallis tests followed by Conover–Inman tests for post hoc comparisons. A Mann–Whitney *U*-test was used for between year comparisons within each time category for the number of flies, temperature, and relative humidity.

In response to irrigation experiment, data from both observation dates met the assumption of normally distributed data. Two-sample *t* tests compared the total number of flies flying, on bushes and total flies (those flying plus those on bushes) in irrigation and no irrigation plots. The percentage of flies on berries was arcsine transformed before comparison between treatments using two-sample *t* tests.

For the experiment investigating the effect of insecticide applications on fly activity, observation data collected at 1 DAT and 3 DAT were $\log(X+1)$ transformed where appropriate before analysis. Comparisons between insecticide treatments for the number of flies flying and on bushes in all experiments, on all dates, were made using two-sample *t* tests. Where significant, dependent variable interactions were present, comparisons were made using two-way ANOVA.

In the experiment looking at the effect of insecticide applications and irrigation, data from observations conducted at 1, 2, and 3 DAT were analyzed using a Kruskal–Wallis test followed by a Conover–Inman test for post hoc comparisons. Analysis of the number of flies, flying versus on bushes were conducted using Mann–Whitney *U*-tests. In the test of bush canopy on water deposition in cups, insecticide treatment did not have a significant effect on the amount of water in the cups, so the amount of water per cup data was analyzed with a two-sample *t* test.

For the irrigation duration and insecticide residues experiment, counts of flies per plot were analyzed using factorial ANOVA followed by Tukey HSD for mean separation. For the semi-field bioassays, adult percent mortality data and the number of larvae per bioassay container were arcsine transformed and analyzed using two-way ANOVA and Tukey's HSD for means separation.

Results

Experiment 1: Diurnal Activity

In 2015, there was a bimodal pattern of fly activity, with significantly more flies present on bushes in the 0600–0800 and 1800–2000 hours than in the two mid-day periods (Fig. 1; $H = 16.35$; df = 3, 20; $P = 0.001$). In 2016, the highest level of activity recorded was in the 0600–0800 hours, the second highest at the 1800–2000 hours, and lowest activity during the two mid-day periods (Fig. 1; $H = 11.72$; df = 3, 12; $P = 0.008$). There were more flies observed in 2015 than 2016, a trend that was significant for the 1800–2000 hours ($U = 24$; df = 1, 8; $P = 0.011$).

In both years, temperature readings were lowest (Fig. 2; 2015: $F = 7.62$; df = 3, 20; $P = 0.001$; 2016: $H = 12.20$; df = 3, 12; $P = 0.007$) and relative humidity readings were highest (2015: $F = 4.71$; df = 3, 20; $P = 0.01$; RH 2016: $H = 8.99$; df = 3, 12; $P = 0.029$) during the 0600–0800 hours. Temperatures were higher in 2016 than during 2015 at the 1500–1700 and 1800–2000 hours. Relative humidity readings in 2016 were similar to 2015 for the 0600–0800 and 1200–1400 hours but were significantly lower in 2016 at the latter two periods (Fig. 2).

Experiment 2: Response to Irrigation

During the first irrigation event on 28 August 2016, flies were present in both irrigation and no irrigation plots; however, there were significantly fewer flies observed in plots that received irrigation (Table 1).

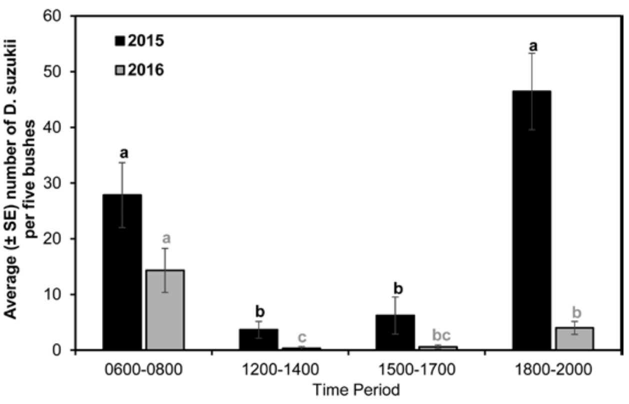

Fig. 1. Average total number of *Drosophila suzukii* adults found on blueberry bushes during 15-min visual observations conducted during four diurnal periods in 2015 and 2016. Values are presented ± SE, an alpha value of 0.05 was used, and different letters indicate significant differences within each year.

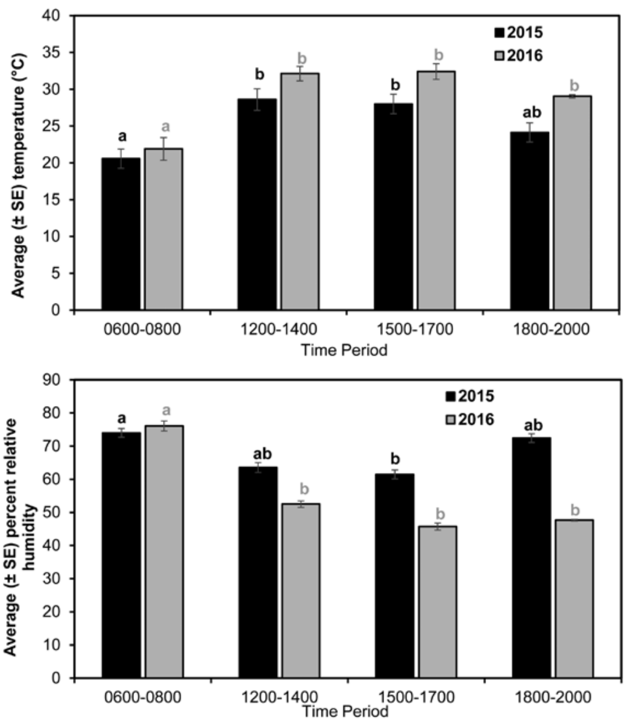

Fig. 2. Average air temperature (top) and relative humidity (bottom) when fly observations were conducted in a mature blueberry field in 2015 and 2016. Values are presented ± SE, and an alpha value of 0.05 was used. Letters indicate significant differences within each year.

Similar patterns were observed for flies flying or on the bushes in both treatments, with more flies observed flying than on bushes in both the irrigation ($t = 3.15$; df = 1, 6; $P = 0.02$) and no irrigation ($t = 5.23$; df = 1, 6; $P = 0.002$) treatment plots. Of the flies that were on the bushes, most were observed on berries (86.1 ± 4.4%) rather than on the leaves, and irrigation did not affect this distribution ($t = -0.53$; df = 1, 6; $P = 0.63$). In the second observation on 29 August 2016, there were no significant differences in the number of flies present in the two irrigation treatments (Table 1). This was the case for the total number of flies as well as flies that were flying and on bushes. There were no significant differences between the number of flies, flying and on bushes before irrigation ($F = 1.51$; df = 1, 12; $P = 0.24$), but during and after irrigation fewer flies were observed on the bushes (during irrigation: $F = 11.57$; df = 1, 12; $P = 0.005$; post irrigation: $F = 12.17$; df = 1, 12; $P = 0.004$), with no significant interaction for either time period (during irrigation: $F = 1.08$; df = 1,12; $P = 0.32$; post irrigation: $F = 0.66$; df = 1, 12; $P = 0.43$). The majority of flies on the bushes were observed on berries (pre-irrigation: 89.3 ± 2.9%, during irrigation: 95.0 ± 0.3%, post irrigation: 90.0 ± 5.4%). The percentage of flies on the bushes that were present on berries was not significantly affected by irrigation treatment, a result that was consistent for the three phases of the experiment ($t \leq 0.38$; df = 1, 6; $P > 0.73$).

Experiment 3: Effects of Insecticide Application on Fly Activity

There were no significant differences between the treatments on the day after spinosad application during the first run of this experiment (Table 2). However, during the second run, fewer flies were observed in the spinosad-treated plots than the untreated plots on the DAT. The reduced number of flies was true for the total number of flies and number of flies on bushes but not for flying flies.

Table 1. Average total number of *Drosophila suzukii* flies counted in and around five-bush highbush blueberry plots during morning observations

Treatment	28 August			29 August								
	During irrigation			Before irrigation			During irrigation			After irrigation		
	Flying	On bushes	Total	Flying	On bushes	Total	Flying	On bushes	Total	Flying	On bushes	Total
No irrigation	22.8 ± 1.6	13.3 ± 0.9	36.0 ± 1.1	23.0 ± 7.1	20.3 ± 4.3	43.3 ± 8.0	32.0 ± 4.6	19.8 ± 1.0	51.8 ± 4.5	20.3 ± 3.9	10.8 ± 0.3	31.0 ± 4.1
Irrigation	18.8 ± 2.3	10.0 ± 1.6	28.8 ± 2.3	34.3 ± 3.5	24.3 ± 5.2	58.5 ± 8.0	39.3 ± 8.8	16.3 ± 2.8	55.5 ± 8.5	31.0 ± 4.7	15.8 ± 3.6	46.8 ± 7.6
$t_{(1,6)}$	−1.43	−1.81	−2.87	1.42	0.60	1.35	0.73	−1.18	0.39	1.76	1.38	1.83
P-value	0.21	0.14	**0.042**	0.22	0.57	0.23	0.50	0.31	0.71	0.13	0.26	0.13

Bushes received irrigation or no irrigation. Observations were conducted during the irrigation event on 28 August and before, during, and after the irrigation event on 29 August 2016. Significant *P*-values are bold.

Table 2. Average total number of *Drosophila suzukii* flies observed in and around five-bush blueberry plots during observations on mornings after application of insecticides to bushes

Treatment	First run			Second run					
	1 DAT			1 DAT			3 DAT		
	Flying	On bushes	Total	Flying	On bushes	Total	Flying	On bushes	Total
Untreated	16.0 ± 1.5 a	16.3 ± 2.3 a	32.3 ± 3.8 a	16.7 ± 3.7 a	18.3 ± 2.7 a	35.0 ± 1.0 a	9.7 ± 4.7	11.7 ± 1.5	21.3 ± 4.9
Spinosad	18.0 ± 5.5 a	19.0 ± 4.4 a	37.0 ± 9.6 a	11.0 ± 2.3 a	7.3 ± 0.7 b	18.3 ± 2.9 b	8.7 ± 0.3	6.0 ± 2.6	14.7 ± 2.3
$t_{(1,4)}$	0.35	0.54	0.45	−1.31	−4.0	−5.42	0.80	−1.88	−1.23
P	0.76	0.62	0.69	0.26	0.047	**0.02**	0.50	0.13	0.31
Untreated	21.5 ± 3.9 a	15.8 ± 5.2 a	37.3 ± 6.7 a	40.0 ± 8.2 a	37.5 ± 5.2 a	77.5 ± 3.8 a	67.8 ± 10.7 a	14.3 ± 2.2 a	81.5 ± 12.2 a
Spinetoram	9.8 ± 2.1 b	6.3 ± 0.5 a	15.8 ± 2.1 b	28.7 ± 9.8 a	13.3 ± 6.6 b	41.7 ± 13.3 a	64.3 ± 16.0 a	7.0 ± 2.5 a	71.3 ± 18.5 a
$t_{(1,5)}$	−3.25	−1.80	−3.27	−0.89	−2.92	−2.583	−0.19	−2.18	−0.048
P	**0.033**	0.17	**0.036**	0.41	**0.033**	0.11	0.86	0.081	0.65
Untreated	11.3 ± 2.1 a	7.5 ± 3.8 a	18.8 ± 5.3 a	9.3 ± 2.1 a	21.8 ± 2.2 a	31.0 ± 3.0 a	7.0 ± 2.4 a	44.8 ± 5.3 a	57.8 ± 12.5 a
Zeta-cypermethrin	3.3 ± 0.3 b	1.0 ± 0.7 b	4.3 ± 0.9 b	5.8 ± 0.8 a	6.5 ± 3.9 b	12.3 ± 4.3 b	5.3 ± 1.3 a	20.8 ± 4.6 b	26.0 ± 4.6 b
$t_{(1,6)}$	−5.15	−2.78	−4.25	−1.57	−3.38	−3.59	−0.20	−3.31	−2.64
P	**0.009**	**0.032**	**0.005**	0.20	**0.015**	**0.011**	0.85	**0.016**	**0.039**

Observations were conducted at 1 and 3 d after treatment (DAT). Means are presented ± SE and values followed by the same letter within each insecticide treatment in a column are not significantly different ($\alpha = 0.05$). Significant *P*-values are in bold.

There were no significant differences between the number of flying and flies on bushes for either of the 1 DAT runs (t < 1.6; df = 1, 4; P > 0.24), and the majority (77–100%) of flies on bushes were on the berries. At 3 DAT, there was no significant effect of spinosad on observed fly abundance, and no significant differences in whether flies were flying or on the bush (t < 1.0; df = 1, 4; P > 0.43). Flies that were on the bushes were found mostly on berries in the untreated plots (70.3 ± 4.9%) and found on both berries and leaves in the spinosad-treated plots (50.0 ± 28.9%).

When spinetoram was applied, flies were observed in all plots on all sampling dates (Table 2), with lower numbers in spinetoram-treated plots than untreated plots 1 DAT. However, this trend was significant only for 1 DAT on the first run. Flies were more often observed flying than on the bushes, but this trend was not significant on either of the 1 DAT observation dates (t < 1.66; df = 1, 6; P > 0.18). In the second run of this trial, there was a 65% reduction in the number of flies on the bushes in the spinetoram-treated plots. Of the flies that were on the bushes, over 85% were on the berries rather than leaves. By 3 DAT, there were no significant differences between insecticide treatments for either flying or flies on the bushes (Table 2). However, there were more flies flying around bushes than on the bushes, a trend that was significant on untreated bushes (t = 4.90; df = 1, 6; P = 0.013) but not on spinetoram-treated bushes (t = 3.55; df = 1, 4; P = 0.066). As with the 1 DAT observations, the majority of flies that were on the bushes were on berries (untreated; 92.4 ± 3.4%, spinetoram; 63.3 ± 23.3%).

There was a consistent reduction in the number of flies observed in plots treated with zeta-cypermethrin compared to the paired untreated plots on all of the observations conducted 1 or 3 DAT (Table 2). At 1 DAT on the first run, there were more flies observed flying around bushes than on bushes, a trend that was significant for zeta-cypermethrin–treated bushes, (t = 4.77; df = 1, 6; P = 0.015) but not on untreated bushes (t = 2.27; df = 4.42; P = 0.079). For 1 DAT on the second run, there were significantly more flies on bushes than flying around the bushes for untreated bushes (t = −4.10; df = 1, 6; P = 0.006), but there were no significant differences for zeta-cypermethrin–treated bushes (t = −0.19; df = 1, 6; P = 0.86).

On the first 1 DAT observation date, about half of the flies on both untreated and zeta-cypermethrin bushes were found on berries (untreated: 48.4% ± 16.5; zeta-cypermethrin: 50.0% ± 50). On the second run, flies observed on the bushes in the untreated plots were more likely to be found on berries (93.8% ± 2.8; F = 10.07; df = 1, 12; P = 0.008), while there was no such trend present in the zeta-cypermethrin plots (48.1% ± 23.1). At 3 DAT, there were significantly fewer flies flying than on the bushes (untreated: t = −6.45; df = 1, 6; P = 0.002; zeta-cypermethrin: t = −3.26; df = 1, 6; P = 0.039); of those flies that were on the bushes, the vast majority were on berries rather than on the leaves (untreated: 94.9 ± 2.4%, zeta-cypermethrin: 86.5 ± 3.7%).

Experiment 4: Effect of Insecticide Application and Irrigation

Bush canopy significantly reduced water deposition in cups; with less water deposited under the blueberry bushes compared to cups placed on the ground in row middles (Bush: 6.03 ± 1.04 ml water; Ground: 12.85 ± 1.37 ml water; t = −3.97; df = 1, 14; P = 0.002).

At 1 DAT, significantly fewer flies were in plots treated with zeta-cypermethrin than untreated plots (Fig. 3). This result was consistently found before, during, and after the irrigation event on that day; it was noticeable for flies counted as both flying and on the bushes (H > 8.69; df = 3, 11; P < 0.034). The same trend was found the day

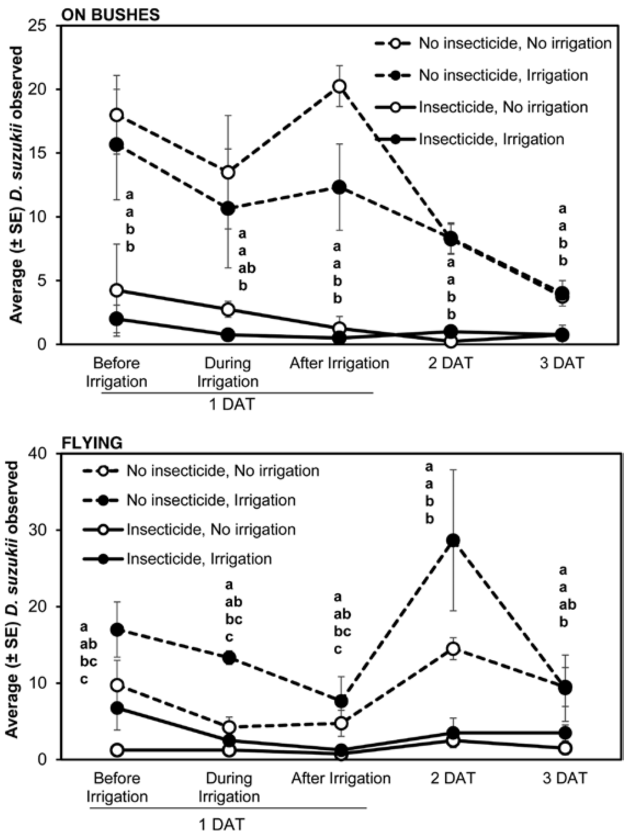

Fig. 3. Effect of overhead irrigation and previous insecticide (zeta-cypermethrin) application on the number of *Drosophila suzukii* flies observed on blueberry bushes (top) or flying near the bushes (bottom). Letters indicate significant differences between treatments within each assessment period.

after the irrigation event (2 DAT) and the following day (3 DAT). There were no indications that the irrigation significantly reduced flies present in either the zeta-cypermethrin plots or the untreated plots (Fig. 3), and as in most previous experiments, the majority of flies that were on the bushes were on berries (88.0 ± 8.4%). There were no significant differences between the number of flies flying and on the bushes for any treatment either before or during the irrigation event. However, there were significantly more flies on the bushes in the no insecticide, no irrigation treatment after the irrigation event at 1 DAT (U = 0; df = 1, 6; P = 0.019). At 2 DAT, there were significantly more flies flying than on the bushes in all treatments except the insecticide, no irrigation treatment (U ≥ 9; df = 1, 6; P < 0.05). At 3 DAT, there were no significant differences between the number of flies, flying than on the bushes except for the insecticide, irrigation treatment where there were significantly more flies flying than on the bushes (U = 14.5; df = 1, 6; P = 0.046).

Experiment 5: Irrigation Duration Effects on Insecticides

As above, fewer flies were observed in the zeta-cypermethrin–treated plots after irrigation (Table 3), but we found no significant differences among the irrigation durations on any of the observation dates. The number of flies flying or on bushes were also similar between the treatments on the individual observation dates. As observed previously, most flies that were on the bushes were on berries (1 DAT: 90.5 ± 9.5%, 2 DAT: 88.6 ± 12.9%, 3 DAT: 79.1 ± 12.2%, 8 DAT: 95.2 ± 3.2%).

Table 3. Average total number of *Drosophila suzukii* flies counted in five-bush blueberry plots during morning observations

		DAT				All dates		
		1	2	3	8	Flying	On bushes	Total flies
No Irrigation	Untreated	4.3 ± 1.4 a	6.5 ± 2.6 a	14.5 ± 2.4 a	14.5 ± 2.4 a	10.3 ± 0.6 a	25.8 ± 3.4 a	36.0 ± 3.3 a
	Zeta-cypermethrin	4.0 ± 1.5 a	2.8 ± 1.1 b	5.5 ± 1.6 b	5.5 ± 1.6 a	6.3 ± 1.1 b	15.0 ± 2.8 b	21.3 ± 2.5 b
15 min irrigation	Untreated	4.5 ± 1.0 a	6.3 ± 1.3 a	8.8 ± 1.8 a	8.8 ± 1.8 a	7.0 ± 0.4 a	23.5 ± 7.0 a	30.5 ± 6.6 a
	Zeta-cypermethrin	2.5 ± 0.6 a	5.3 ± 2.0 b	6.8 ± 1.7 b	6.8 ± 1.7 a	6.3 ± 0.8 b	19.5 ± 4.1 b	25.8 ± 4.5 b
1 h irrigation	Untreated	9.0 ± 3.9 a	7.5 ± 1.2 a	8.0 ± 0.9 a	8.0 ± 0.9 a	14.5 ± 3.9 a	27.8 ± 1.8 a	42.3 ± 5.6 a
	Zeta-cypermethrin	4.0 ± 1.3 a	2.5 ± 1.6 b	5.5 ± 1.0 b	5.5 ± 1.0 a	8.3 ± 2.3 b	14.5 ± 2.5 b	22.8 ± 4.6 b
	$F_{(2,18)}$	2.4	5.4	11.4	3.2	4.9	8.3	11.4
	P	0.14	**0.032**	**0.003**	0.092	**0.039**	**0.01**	**0.003**

Bushes received either a zeta-cypermethrin spray or were left untreated. That same afternoon bushes were either irrigated with overhead irrigation for 15 min, 1 h, or received no irrigation. Observations were conducted at 1, 2, 3, and 8 d after treatment (DAT). Means are presented ± SE and values followed by the same letter within a column are not significantly different (α = 0.05).

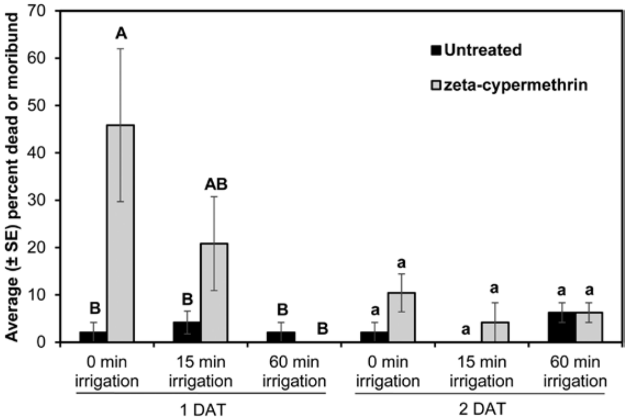

Fig. 4. Average percent of adult *Drosophila suzukii* that were dead or moribund after 24 h in semi-field bioassay containers. Flies were exposed to 10 blueberry leaves and 5 berries that were either treated with zeta-cypermethrin or left untreated. In addition, foliage and fruit were exposed to either 15 min of irrigation, 1 h of irrigation, or no irrigation. Bioassays were conducted at 1 and 2 d after treatment (DAT). Letters indicate significant differences between treatments within each assessment period.

Adults of *D. suzukii* exposed to shoots from the different irrigation treatments in the laboratory, at 1 DAT, there was significantly higher adult mortality in the no irrigation zeta-cypermethrin treatment than any of the treatments (Fig. 4). However, by 2 DAT, adult mortality in all treatments was low with no significant differences among any of the treatments. There were no significant differences in the number of larvae found in the bioassay containers ($F = 0.81$; df = 2, 18; $P = 0.38$).

Discussion

Observations of *D. suzukii* flies in blueberry fields support evidence from other regions, of a bimodal pattern of fly activity during the dawn and dusk periods (Hamby et al. 2013, Ferguson et al. 2015, Revadi et al. 2015, Evans et al. 2017). This study extends our understanding by showing inter-annual variation in those patterns. A shift away from evening activity in 2016 when conditions were hotter and drier, might suggest that flies are reacting to specific environmental conditions rather than daylight cues. However, more observation dates over additional years would be needed to draw more definitive conclusions. High temperatures limit survival and development of *D. suzukii* (Tochen et al. 2014), and low humidity also decreases survival of this pest in blueberry fields (Tochen et al. 2016), and our results indicate that flies are shifting the timing of their activity to avoid these less optimal environmental conditions. Our results highlight that *D. suzukii* activity is reduced during the hottest and driest parts of the day, thus avoiding adverse environmental conditions. Further, *D. suzukii* can also shift their activity in response to stressful conditions.

Blueberry plants require significant water inputs to maximize growth and yield (Holzapfel et al. 2004, Bryla and Strik 2007). Water is provided through irrigation or rainfall; because the timing and amount of rainfall is not reliable in most regions, commercial blueberry fields usually have irrigation installed. Increasingly drip irrigation is used at the base of the bushes due to greater efficiency (Bryla et al. 2011), but many fields also have overhead irrigation systems to cool and water the plants, also providing an option for frost protection. There is limited information on how irrigation affects crop pests, but studies suggest that it can be used to manipulate pest abundance through altered plant vigor (Daane and Williams 2003). While some flies, such as mosquitoes, have behaviors initiated by rainfall (Day et al. 1990), we know little about how crop pests respond directly to rain or irrigation exposure. We observed limited changes in the behavior of *D. suzukii* when exposed to overhead irrigation. There was some reduction in flies in irrigated plots during the first irrigation event, but the data indicated no significant differences during the second event. Additionally, the changes in fly abundance were relatively small suggesting limited benefit for reducing infestation. On both dates, numerous *D. suzukii* flies were observed flying in irrigated plots, on foliage, or fruit, and we did not find support for the prediction that their activity would stop during irrigation or rain. The bushes used in these trials were mature and contained plentiful shoots and foliage that provided protection from the irrigation and so flies could avoid droplets. It is still unknown whether flies respond differently to rain and irrigation; this deserves further investigation.

The continued activity of adult flies observed around and on blueberry bushes treated with spinosad and spinetoram indicates that crop protection can be achieved by behavioral effects of these insecticides in addition to their direct toxic effects (Desneux et al. 2007). Three days after application, flies remained active in all treated rows with no evidence that the application of these insecticides were changing fly behavior. However, both are effective against *D. suzukii* under laboratory and field conditions (Van Timmeren and Isaacs 2013), suggesting disruption of egg-laying or post-infestation activity mechanisms to reduce infestation (Wise et al. 2015, Nansen et al. 2016). This contrasting pattern of reduced fly activity in and around blueberry bushes treated with zeta-cypermethrin indicates that this insecticide causes a greater and more long-lasting reduction in the activity of flies, flying around and present on the bushes. However, even in this case, there were still some flies present, both flying and on bushes, in the treated rows, highlighting the need for treatments that can prevent egg-laying and larval development. These results may also help explain why infestation by *D. suzukii* is greater at crop field borders as observed by Iglesias and Liburd (2016), as flies in a large field are likely to having increased mortility, due to topical application of insecticides followed by immigration from adjacent habitats. This pattern has resulted in strategies to manage this pest through border applications, similar to other fruit pests (Chouinard et al. 1992, Blaauw et al. 2015). Because the flies can quickly regain activity around treated bushes, good coverage of fruit with insecticide sprays is essential for pest control success in blueberry (VanEe et al. 2000). Furthermore, these results highlight the importance of maintaining regular spray intervals to achieve control of *D. suzukii*, especially in rainy regions. With the rapid resurgence of fly activity in treated areas, there is a greater chance that flies will start to infest fruit as soon as residues decline.

Previous studies on how irrigation influences control of *D. suzukii* have found that insecticide performance is compromised by rain or irrigation (Van Timmeren and Isaacs 2013, Gautam et al. 2016), but those studies measured efficacy in containers with adult flies exposed to treated foliage and fruit in small containers. In our open-field setting, irrigation applied to zeta-cypermethrin–treated bushes did not affect the abundance of flies, even though longer irrigation events caused significantly greater survival of adult *D. suzukii* in the bioassay containers. These contrasting results suggest that insecticide applications may kill most flies in the treated areas, followed by reinvasion of flies over time or that flies are simply avoiding treated bushes in the first place. The relationship between avoidance and reinvasion cannot be definitively determined from this study but would be a fruitful topic to explore in future studies. The results highlight the importance of local fly movement both within a field and between the field and border areas (Cini et al. 2012, Klick et al. 2016), and the current developing research on marking and recapturing flies is expected to illuminate the extent of this local movement among habitats further. Harvesting of ripe and ripening fruit was not regularly conducted in the experimental plots, and thus bushes had numerous dropped fruit, most of which were infested with later instar larvae (S. Van Timmeren, unpublished data). These ground fruit could serve as constant sources of reinfection even if insecticides are applied, highlighting the importance of clean sanitation within fields and the need to minimize sources of reinfection (Leach et al. 2017). However, the effect of removal or burial of downed fruit on the activity of flies both alone or in combination with insecticides have not yet being quantified.

Direct in-field observations of adult *D. suzukii* in this study revealed the timings and locations where the flies are active and how that activity can be affected by biotic and abiotic factors. Focusing future research efforts during these periods of activity will yield greater insight into the responses of *D. suzukii* to other management approaches and will help focus observations to evaluate the success of these management approaches. A key limitation of this study is the number of days on which observations were made, which were restricted mainly by weather and the intensity of labor required to make the observations. Future observations at more sites over a longer span of time would allow for a more in-depth examination of the interplay of multiple environmental factors affecting *D. suzukii* behavior on host plants. Further studies are needed to determine the location of this pest when it is not actively foraging on or around host plants, to provide additional opportunities for targeted control of the adult flies before their infestation of susceptible fruit.

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