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Timing and order of different insecticide classes drive control of *Drosophila suzukii;* a modeling approach

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Abstract

The spotted-wing drosophila, *Drosophila suzukii* Matsumura, is an invasive pest causing significant damage to soft skinned fruits. Control of *D. suzukii* is critical since there is no tolerance for infested fruit in the market. While most insecticides control one or more *D. suzukii* life-stages (e.g., egg, larvae, and adult), the impact of insecticides that are toxic to immature stages is unclear on the subsequent generation of a field population. Insecticides were applied at field recommended rates on cherries and blueberries in the laboratory to determine immature *D. suzukii* mortality. Spinetoram, cyantraniliprole, malathion, methomyl, spinosad, and phosmet resulted in relatively high mortality of all immature life stages. Zeta-cypermethrin, cyclaniliprole, and fenpropathrin resulted in lower mortality of egg and all larval instars. Malathion was also applied to lowbush blueberries with different fruit sizes (small, medium, and large) in the laboratory and there was no statistical difference in mortality rates depending on fruit sizes. Mortality data from the laboratory experiments were used to parameterize a refined *D. suzukii* population model. The model revealed that the timing and order of different insecticide classes are important to control *D. suzukii* population. Model runs that included early applications of more effective insecticides resulted in high immature mortality and greater reduction of *D. suzukii* populations compared to treatments applied later.

Keywords Spotted-wing drosophila · Blueberry · Cherry · Insecticide application timing · Population modeling · Insecticide

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Key message

- Spinetoram, cyantraniliprole, malathion, methomyl, spinosad, and phosmet provided high mortality for all immature life stages of *D. suzukii* in cherry and blueberry.
- There was no correlation between fruit size and mortality caused by malathion.
- Population modeling with insecticide effects provides new understanding for *D. suzukii* control especially on immature life stages.
- Using high mortality insecticides early in the harvest season decreased *D. suzukii* population more than using low mortality insecticides early.

Introduction

The spotted-wing drosophila, *Drosophila suzukii* Matsumura, (Diptera: Drosophilidae), is an invasive pest that causes crop damage through infestation in several soft skinned fruits e.g., cherry, blueberry, raspberry, and strawberry (Goodhue et al. 2011; Lee et al. 2011). *Drosophila suzukii* is widely distributed through most major fruit production regions worldwide, with infestation reported in Europe, Asia, North America, and South America (Walsh et al. 2011; Wiman et al. 2014; Asplen et al. 2015; Miller et al. 2015). Infestation of susceptible fruit can detrimentally affect market value and local economies (Goodhue et al. 2011; Farnsworth et al. 2017).

Adult females attack ripening and ripe fruit by laying eggs within the outer 1 mm of the fruit surface (Lee et al. 2011), using a serrated ovipositor (Dalton et al. 2011; Lee et al. 2011; Wiman et al. 2014). Larvae feed and burrow into the fruit flesh, rendering the crop unmarketable (Walsh et al. 2011). The egg and larval stages are presumably protected from direct contact with insecticide residues inside the fruit (Hoffmann et al. 2009; Dalton et al. 2011; Mota-Sanchez et al. 2012; Hamby et al. 2016; Plantamp et al. 2016; Andika et al. 2019). Insecticides are currently the most often-used method for *D. suzukii* management, providing protection against fruit infestation (Van Timmeren and Isaacs 2013; Diepenbrock et al. 2016; Fanning et al. 2018). Several insecticide classes including carbamate, diamide, organophosphate, pyrethroid, and spinosyn are used for *D. suzukii* management (Beers et al. 2011; Lee et al. 2011; Van Timmeren et al. 2018), and most management programs recommend the use of insecticides to target the adult life stage through direct and residual contact (Van Timmeren and Isaacs 2013; Cuthbertson et al.

2014; Smirle et al. 2017; Fanning et al. 2018). However, while several studies have demonstrated curative action (e.g., lethality post-infestation), relative toxicity to eggs versus larval instars is not known, as well as the impact of these effects on future *D. suzukii* generations. Limited data are available regarding the effects of insecticides on immature life stages inside susceptible fruit (Wise et al. 2015; Shawer et al. 2018).

Population models could be used to gain a clearer understanding of the relative contributions of various compounds to control different life stages of insects (Wiman et al. 2014, 2016; Langille et al. 2016). Population models allow estimation of the overall impacts by using known insect life table parameters together with weather data to estimate and integrate the effects of different management strategies (Wiman et al. 2014, 2016). Population modeling has been applied to predict population dynamics and life stages of *D. suzukii* (Wiman et al. 2014, 2016; Gutierrez et al. 2016; Dos Santos et al. 2017; de la Vega and Corley 2019). However, up to this point, modeling has not been used to estimate the effect of different insecticide combinations and timing for control of this pest, despite some earlier research showing the importance of timing for insecticide activity against *D. suzukii* (Hamby et al. 2013).

The objectives of the present study were to evaluate the efficacy of different classes of commonly used insecticides on immature life stages of *D. suzukii* in blueberry and cherry fruits, and to use the results from the laboratory trials as mortality parameters in a population model to compare different seasonal spray regimes against *D. suzukii*. The overarching goal was to simulate how the timing and order of insecticide applications affected the predicted *D. suzukii* population size.

Materials and methods

Insecticides

Insecticides used in the present study (Table 1) were those considered effective against *D. suzukii* and used widely in commercial fruit production, including Delgate® WG, Entrust® SC and Lannate® SP (Corteva Agrosicence, Indianapolis, IN), Mustang Maxx® EC and Exirel® SE (FMC Corporation, Philadelphia, PA), Danitol® 2.4 EC (Valent U.S.A. Corporation, Walnut Creek, CA), Harvanta™ 50 SL (Summit Agro USA, Durham, NC), Gowan® Malathion 8F and Imidan® 70 WP (Gowan Company, Yuma, AZ) and Assail® 70 WP (United Phosphorus Inc. King of Prussia, PA).

Laboratory mortality bioassays

Laboratory experiments included sweet cherry and three blueberry species i.e., northern highbush blueberry, lowbush blueberry, and rabbiteye blueberry (Finn et al. 2014; Stringer et al. 2017). Fruits including cherry, highbush, and rabbiteye blueberries were obtained from local stores for the laboratory mortality assays and lowbush blueberries were obtained from the research field for the fruit size experiment. For laboratory experiments, fruits were washed and dried using paper towels prior to the egg infestation with *D. suzukii*. The bottom portion of fruit was protected from *D. suzukii* egg laying by either wrapping it using parafilm (Parafilm "M" Laboratory Film, Pechiney Plastic Packaging, Chicago, IL) (sweet cherries) or by placing similarly sized fruit within Petri dishes (9 × 1.5 cm) with deionized water (blueberries) to prevent adult flies from accessing the bottom of the fruit. For cherries, the parafilm was used because of the large fruit size that prevented the use of the Petri dish infestation method. Fruit was then placed into Petri dishes (10–11 cherries per dish) allowing *D. suzukii* to oviposit within insect rearing cages (Bugdorm-1, 30 × 30 × 30 cm, MegaView Science Co.,Ltd., Taiwan) for 30–180 min. The fruits were then examined under a stereomicroscope (Leica M165 C coupled with Leica KL 1500 LED external light source) to determine the number of eggs per fruit. Detailed information about the mortality bioassay is provided in supplementary material.

After egg laying, it was possible to classify the fruit containing according to the number of eggs. The infested fruits were kept under laboratory conditions (24.1 ± 0.4 °C, 62 ± 8% R.H., and 14 L:10 D photoperiod) (Hamby et al. 2016). Fruits infested with more than five eggs were discarded from the experiment in order to eliminate larval competition and cannibalism (Da Silva et al. 2019).

The infestation was initiated on different days to allow experimental testing of different life stages including egg (one day), first (three days), second (five days), and third instar (seven days) (Emiljanowicz et al. 2014; Tochen et al. 2014) e.g., fruits were infested seven days prior to the mortality bioassay to be able to obtain third instar larvae. After initial egg laying, the parafilm was removed prior to the insecticide application. Fruit containing the respective life stage were then treated with the particular insecticides using a Potter spray tower (Burkard Manufacturing Co. Ltd., Rickmansworth, England). One or two milliliters (cherry and blueberry, respectively) of insecticide solution were transferred into the spray tower reservoir for each application and the pressure was set to 46.8 or 103.4 kPa, respectively. Insecticides were applied in concentrations equal to the corresponding field application rates, mixed into a 467 L ha^{-1} water diluent (Table 1). Deionized water was used for the control treatment. The spray tower nozzle and delivery system were cleaned using acetone, ethanol, and distilled water three times between each insecticide treatment to mitigate contamination between treatments. After the spray applications, Petri dishes containing the treated fruit were placed in a fume hood for an hour to dry. The laboratory reared insects were used to determine mortality levels of immature life stages for the respective treatments. Fruit containing the respective life stages (egg, first, second, and third instars) were maintained under laboratory conditions (details described below). Sweet cherries were individually placed in a capped vial (Fisher Scientific Company, Hampton, NH) with a piece of filter paper to monitor adult emergence. Blueberries were placed into observation chambers (473 ml plastic deli containers with lids) that had a wire mesh boat hot glued to the bottom (Fabri-Kal Corp., Kalamazoo, MI). Observations were made twice per week

Table 1 Detailed information of the insecticides used in the experiment for control of *Drosophila suzukii* in cherry, and blueberry fruits

Chemical class[a]	Brand name	Active ingredient	Field application rate[b] g AI ha^{-1}	Crop	Manufacturer
Spinosyn	Delegate® WG	Spinetoram	105.08	C, RB	Corteva AgroScience, Indianapolis, IN
	Entrust® SC	Spinosad	94.57	C, RB	
Pyrethroid	Mustang Maxx® EC	Zeta-cypermethrin	25.64	C, HB, RB	FMC Corporation, Philadelphia, PA
	Danitol® 2.4 EC	Fenpropathrin	346.34	RB	Valent U.S.A. Corporation, Walnut Creek, CA
Diamide	Exirel® SE	Cyantraniliprole	146.48	C, RB	FMC Corporation, Philadelphia, PA
	Harvanta™ 50 SL	Cyclaniliprole	52.27	HB	Summit Agro USA, Durham, NC
Organophosphate	Gowan®Malathion 8F	Malathion	175.13 (low)	C,	Gowan Co., Yuma, AZ
	Gowan®Malathion 8F	Malathion	2227.69 (high)	C, RB, LB	
	Imidan® 70 WP	Phosmet	1019.97	HB, RB	
Carbamate	Lannate® SP	Methomyl	1008.77	C, HB, RB	Corteva AgroScience, Indianapolis, IN

C cherry, *HB* highbush blueberry, *RB* rabbiteye blueberry, *LB* lowbush blueberry

[a]https://www.irac-online.org/modes-of-action/

[b]https://www.cdms.net/

until the end of the 14-day observation period and total number of adult flies was recorded.

Modeling parameters

Modeling parameters and equations were previously described in Pfab et al. (2018); however, model parameters were slightly modified for the purpose of the current study. Based on Pfab et al. (2018), the population size was estimated with the insecticide interactions from April to June. Mortality due to insecticide treatments was instantaneously applied to *D. suzukii* populations. Weather data were obtained from the Agrimet weather station in Canby, Oregon (USBR 2017) and only 40 days of the data were included in the model to estimate population development under the given conditions. Temperature was added as a time-dependent environmental factor (e.g., maturation delays, mortality, and fecundity) that determined life stage development rates and the food source was considered unlimited in the model. In addition, fecundities, mortalities, and developmental delays were integrated into the model as environment-dependent factors, using values from Pfab et al. (2018). Mortality effects of insecticide applications were added to the model at seven-day intervals three times in the simulations. The instantaneous mortality was considered in the model for each insecticide application. The respective mortalities for each life stage (e.g., egg and larvae) for insecticides were calculated by determining the mean mortality across all life stages. In addition, reported pupa and adult life stage mortality values were used, irrespective of calculated methodology obtained from the literature (Table 2). For the modeling of D. suzukii populations, we assumed there were no other factors that interacted with D. suzukii development such

as predators, parasitoids, extreme climate, etc. We also assumed no immigration or emigration from and to the surrounding landscape. All simulations were started with one individual with unlimited food resources. Half of the fecundity value found for females were used to average out the reproductive output of male and female flies. *Drosophila suzukii* life table parameters on cherry and blueberry were used for population estimation (Tochen et al. 2014; Wiman et al. 2014, 2016; Pfab et al. 2018; Guedes et al. 2020) together with the mortality factors associated with each of *D. suzukii* life stage generated from this study (egg and larvae) and the literature (pupae and adult) (Bruck et al. 2011; Van Timmeren and Isaacs 2013; Wise et al. 2015; CCRR 2018; Shawer et al. 2018). Insecticides were categorized into three toxicity ratings e.g., low, medium, or high mortality in the six classes of insecticides used for this study for simplicity (Table 2). Individual mortality values of each respective life stage were used to parameterize the population model (Table 2). The percent mortality for larvae was calculated by considering first, second, and third larval instars as a single composite stage. This was accomplished by taking the arithmetic average of all three larval stage mortalities (Table 2, Supplementary Material). Three applications of cyclaniliprole (low mortality), malathion (medium mortality), and phosmet (high mortality) were applied consecutively and/or interchangeably with seven-day intervals starting from the second week of May (8th, 15th, 22nd) when fruit typically first become infested. A total of five scenarios were created. The first illustrated a no-intervention scenario and four additional programs using three applications of varying toxicity and order: (1) low, low, low; (2) high, high, high; (3) low, medium, high; and (4) high, medium, low.

Table 2 Mortality rates (% control) of *Drosophila suzukii* based on efficacy of commonly used insecticides against adult and immature life stages

Insecticide	Egg	Larvae	Pupa	Adult	Average mortality of all stages
Gowan® Malathion 8F (malathion)	85.1	72.4	98.0[d]	90.0[a,d]	86.4
Mustang Maxx ®EC (zeta-cypermethrin)	52.2	59.5	99.2[b,d]	99.7[a,d]	77.7
Entrust® SC (spinosad)	82.8	75.9	99.7[d]	94.8[a,c,d]	88.3
Delegate® WF (spinetoram)	84.4	81.1	99.2[a,b,d]	95.0[a,c,d]	89.9
Lannate® SP (methomyl)	84.3	77.0	100[d]	99.0[a,d]	90.1
Exirel® SE (cyantraniliprole)	72.8	69.2	95.0[c]	95.0[c]	83.0
Danitol® 2.4 EC (fenpropathrin)	63.0	66.5	95.0[b]	95.0[a,b]	79.9
Imidan® 70 WP (phosmet)	91.1	91.5	99.5[b,c,d]	99.0[c,d]	95.3
Harvanta™ 50 SL (cyclaniliprole)	67.3	71.8	70[e]	70.0[e]	69.8

[a]Bruck et al. (2011)

[b]Wise et al. (2015)

[c]Shawer et al. (2018)

[d]Van Timmeren and Isaacs (2013)

[e]CCRR (2018)

Statistical analysis

To determine the effects of insecticides on different *D. suzukii* immature life stages, a generalized linear model was fitted on the number of eggs and larvae that failed to survive. For data on sweet cherry, highbush blueberry, rabbiteye blueberry, and lowbush blueberry, binomial logistic regression was conducted with the number of eggs as the binomial totals. For data on lowbush blueberry, Poisson loglinear regression was conducted, with the number of fruits as the offset. Over-dispersion was allowed in both types of models. A quasi-likelihood F-test was performed to assess the overall difference between the insecticide treatments, which was followed by a post hoc pairwise comparisons of the treatments based upon Tukey HSD (Honest Significance Difference). Figures were generated using "ggplot2" package (Wickham 2016) on R studio (R version 3.6.1) (R Development Core Team 2018). The α value was set to 0.05 to determine the statistically significant difference among the treatments. Wolfram Mathematica (Wolfram Research 2019) software was used for the simulations and the coded algorithms are available upon request (Supplementary Material).

Results

Immature laboratory mortality bioassays

Sweet cherry

There was a significant effect of the tested insecticide treatments on mortality of *D. suzukii* across the four life stages ($F_{4,434} = 24.64$, $P < 0.01$ for eggs, $F_{4,414} = 20.44$, $P < 0.01$ for first instars, $F_{4,434} = 4.62$, $P < 0.01$ for second instar, $F_{4,336} = 3.54$, $P < 0.01$ for third instar) (Fig. 1). Cyantraniliprole was found to be the most effective across the life stages and was significantly more effective than untreated control for eggs ($P < 0.01$), first instars ($P < 0.01$), second instars ($P < 0.01$), and third instars ($P < 0.01$). Spinetoram was significantly more effective in killing eggs ($P < 0.001$), first instars ($P < 0.01$), and second instars ($P = 0.04$), but not third instars ($P = 0.28$). No effect was found with zeta-cypermethrin and malathion low in all life stages.

Malathion high, methomyl, and spinosad, were found to provide significantly different mortality in each life stage ($F_{3,375} = 9.75$ for eggs, $F_{3,368} = 20.44$ for first instars, $F_{4,367} = 4.62$ for second instar, $F_{4,351} = 3.54$, for third instar, $P < 0.01$ for all life stages) (Fig. 1). Malathion high, methomyl, and spinosad yielded significantly or borderline higher mortality in each life stage compared to untreated control. Specifically, malathion high, methomyl, and spinosad provided more than 70% mortality on *D. suzukii* eggs (compared with untreated control, $P < 0.01$). In addition, the mortality

of first instars was found to be similar to the egg life stage with these insecticides. The mortality of first instars was above 60% for all three of these insecticides (compared with untreated control, $P < 0.01$ for all three insecticides). A similar pattern of mortality was found in second instars of *D. suzukii* with the insecticides tested. All three insecticides caused above 60% mortality and they were significantly higher (over 60% mortality) compared to the untreated control ($P < 0.01$ for spinosad, $P < 0.01$ for methomyl, $P < 0.01$ for malathion high). Spinosad and methomyl caused significantly higher mortality compared to the untreated control ($P < 0.01$ for both insecticides), and malathion high was borderline significantly higher than the untreated control on third instar life stage ($P = 0.05$).
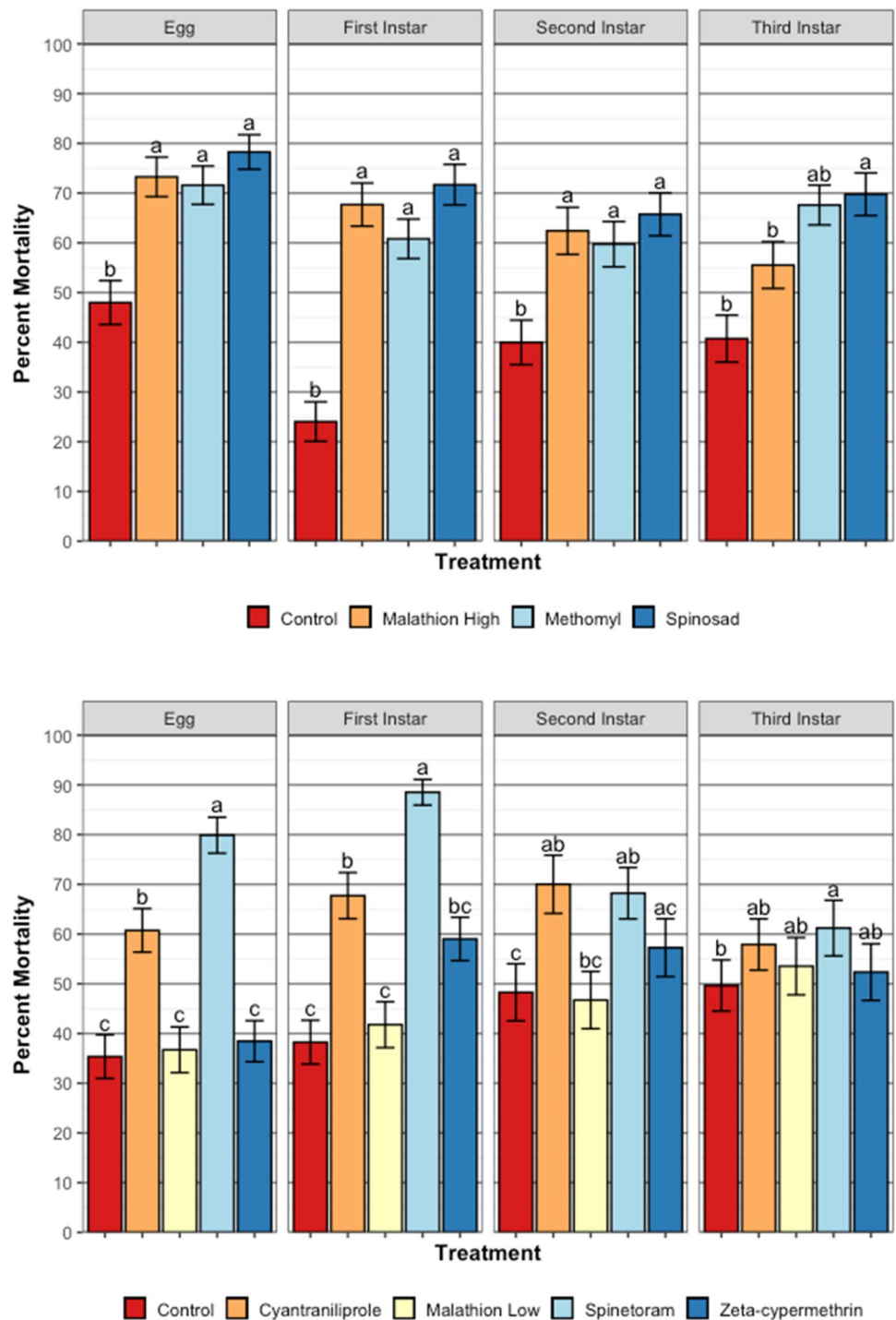
Highbush blueberry

The insecticide treatments tested for *D. suzukii* immature life stages caused increased rates of mortality in all immature life stages (Fig. 2, $F_{4,36} = 59.7$ for egg, $F_{4,36} = 53.4$ for first instar, $F_{4,35} = 37.4$ for second instar, $F_{4,36} = 26.6$ for third instar, $P < 0.01$ for all four stages). Methomyl and phosmet caused the highest mortality on eggs, over 95% mortality compared to the untreated control ($\sim$30% mortality). In addition, zeta-cypermethrin and cyclaniliprole caused approximately 65% mortality on eggs, which was still significantly higher than the untreated control ($P < 0.01$ for both). Furthermore, cyclaniliprole, methomyl, and phosmet caused high mortality (more than 90%) and zeta-cypermethrin caused 70% mortality on first instar larvae, while the untreated control had a significantly lower mortality rate ($\sim$55%, $P < 0.01$ compared to each of the four insecticides). The same results were seen for the second instar larval stage as in the first instar larval stage ($P < 0.01$ for cyclaniliprole, methomyl and phosmet, $P = 0.02$ for zeta-cypermethrin). For the second instars, methomyl, phosmet caused more than 95% mortality followed by zeta-cypermethrin (75%) and cyclaniliprole (60%) compared to the untreated control. Additionally, the mortality effects of insecticides on the third instar were statistically different from the untreated control ($P < 0.01$ for all four insecticides). However, the pattern was slightly different than other life stages. Phosmet (90%) caused the highest mortality followed by methomyl (85%), cyclaniliprole (60%), and zeta-cypermethrin (55%) compared to untreated control.

Rabbiteye blueberry

The insecticide treatments caused significantly different mortality rates for all life stages ($F_{7,92} = 36.4$ for eggs, $F_{7,101} = 31.4$ for first instars, $F_{7,102} = 41.0$ for second instar, $F_{7,112} = 13.6$ for third instar, $P < 0.01$ for all stages). Cyantraniliprole, malathion, phosmet, spinetoram, and spinosad
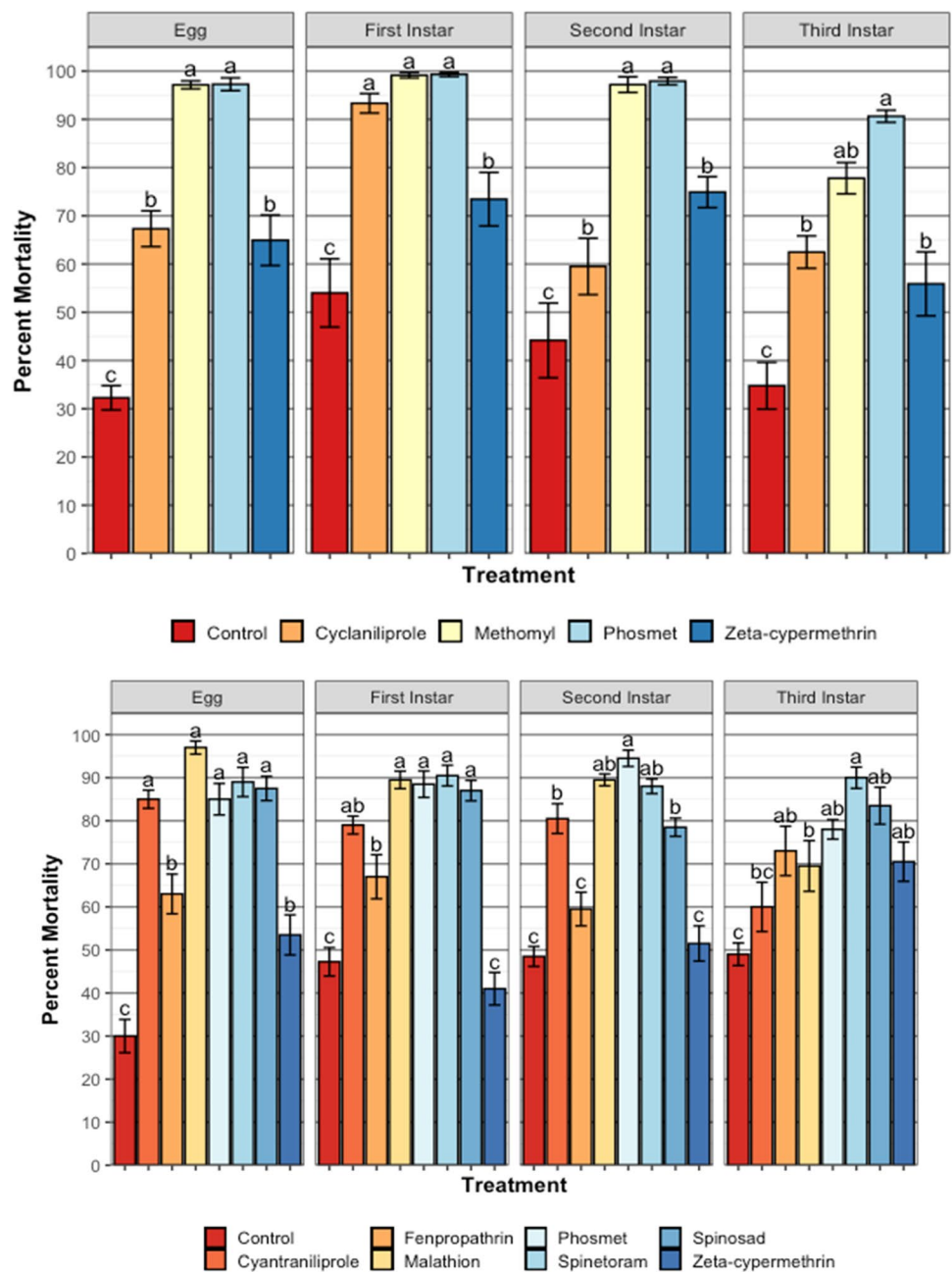
Fig. 1 Percent mean (± SE) mortality of *D. suzukii* in response to insecticides applied to sweet cherries containing different immature life stages in a laboratory experiment. Different letters indicate significant differences between treatments within a life stage ($P < 0.05$)

caused higher mortality ($P < 0.01$ compared with untreated control for all five treatments), while fenpropathrin and zeta-cypermethrin caused a medium level of mortality on the egg stage of *D. suzukii* ($P < 0.01$ and $P < 0.01$ compared with untreated control, respectively) (Fig. 2). Similar mortality rates were observed on first instars as with the eggs, with the exception of zeta-cypermethrin, where mortality was not statistically different than that of the untreated control.

Insecticides including cyantraniliprole, malathion, phosmet, spinetoram, and spinosad were found to be associated with significantly higher mortality rates (~ 80% mortality), while fenpropathrin and zeta-cypermethrin mortality rates were not statistically significant compared to untreated control for the second instar stage ($P < 0.01$ for all five insecticides). Cyantraniliprole caused 60% mortality on the third instar stage; however, this was not significantly different from

Fig. 2 Percent mean (±SE)
mortality of *D. suzukii* in
response to insecticides applied
to different immature life stages
in the laboratory on highbush
blueberry (top) and rabbiteye
blueberry (bottom). Different
letters indicate significant differ-
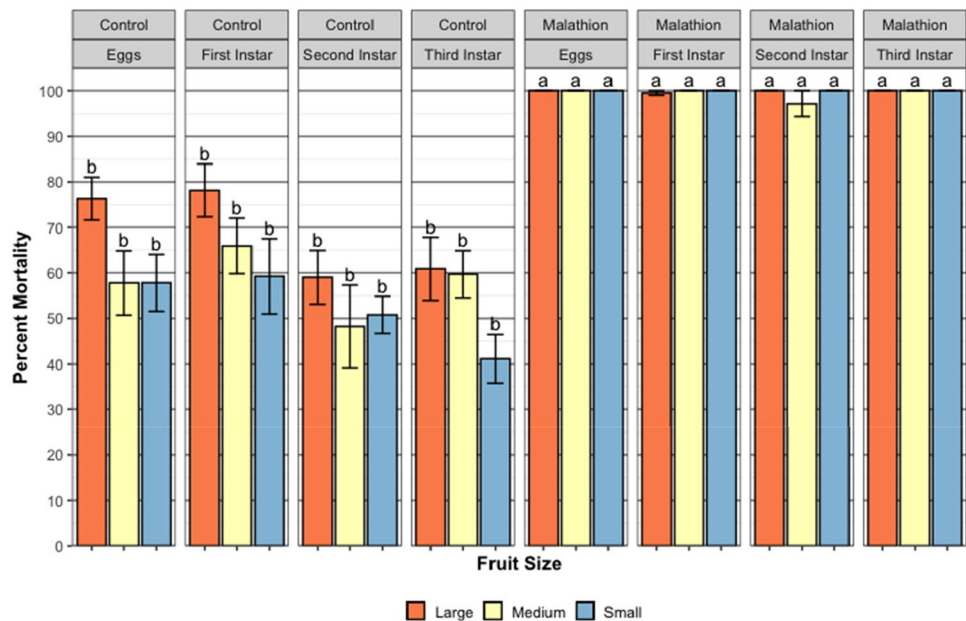ences between treatments within
a life stage ($P < 0.05$)

the untreated control. All other insecticides (fenpropathrin,
malathion, phosmet, spinetoram, spinosad, and zeta-cyper-
methrin) caused significantly higher mortality compared to
the untreated control (all $P < 0.01$) on the third instar stage.

Lowbush blueberry

Different fruit sizes, small, medium, and large, were evalu-
ated to determine difference in malathion mortality as well
as mortality in the untreated control group in association
with fruit size across life stages (Fig. 3). First, comparing
insecticide treatment with untreated control, application

of malathion resulted in significantly higher mortality for
all *D. suzukii* life stages and fruit sizes ($P < 0.01$ for all
comparisons), ranging from 95–100% in almost all cases
(Fig. 3). Mortality of eggs, first instars, second instar, and
third instar were not statistically different among fruit sizes
in the malathion treatment. Malathion provided high mor-
tality of all life stages in each fruit size with no statistical
difference among the sizes. Second, to assess how mortal-
ity differs between the fruit sizes for the untreated control,
we analyzed the data on each fruit size separately using a
binomial logistic model. There was no statistical difference
among the fruit sizes in each life stage (Fig. 3). In addition,

Fig. 3 Percent mean (± SE) mortality of *D. suzukii* in response to insecticides applied to different life stages (egg, first instar, second instar, and third instar life stages) in a laboratory experiment on lowbush blueberries. Different letters indicate significant differences between treatments within a life stage ($P < 0.05$). Fruits are categorized based on the sizes; small (0.21 g), medium (0.33 g), and large (0.55 g)

to determine how mortality differs among immature life stages for the untreated control and how this difference may vary depending on the size of the fruit, we evaluated a binomial logistic model incorporating both fruit size and life stage as explanatory variables as well as their interaction. The life stages including eggs, first, second, and third instars were found to have significantly different mortality rates in the untreated control group ($F_{3,114} = 4.53$, $P < 0.01$). Fruit size was found to be positively associated with mortality rate in the untreated control ($F_{2,114} = 7.51$, $P < 0.01$). Specifically, mortality of all life stages was found to be around 60–80% in larger fruit, which was higher than small and medium size fruits in the untreated control ($P < 0.01$, $P < 0.01$, respectively), while the latter two were not significantly different ($P = 0.34$). Life stage and fruit size did not interact significantly in association with mortality in the untreated control ($F_{6,108} = 0.529$, $P = 0.79$), indicating that the effect of fruit size on mortality is consistent across life stages.

Model parameters and assigned mortality rates for all life stages of *D. suzukii*
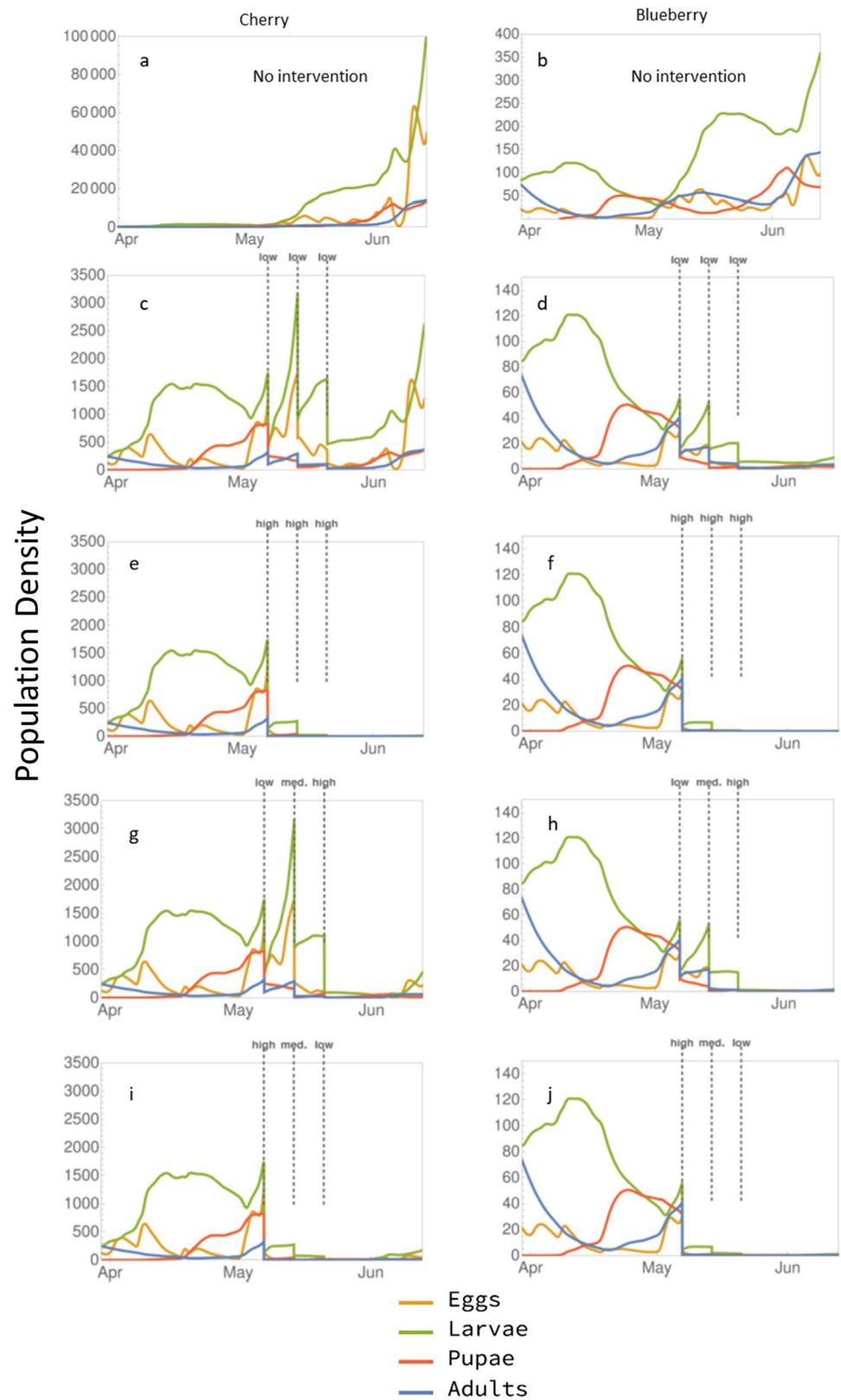
Model estimates of population densities reached lower abundance of eggs, pupae, and adults during the harvest period depending on the modeled host crop (Fig. 4a, c, e, g, i (cherry) and Fig. 4b, d, f, h, j (blueberry)). The estimates showed that untreated populations increased starting in early April through late June (Fig 4a and b).

For all simulations, the mortality events (insecticide interventions) recorded for each insecticide were simulated with seven-day intervals starting on the second week of May. After the first mortality event, simulating the application

of low efficacy insecticides with cherry as a host crop, the population decreased from 1500 to 500. Within one week, the populations rapidly increased to 3000 larval individuals. The second and last mortality events reduced the population to 1000 and 500 individuals, respectively. Simulated population levels increased after the last event, especially for egg and larval stages in cherry (Fig. 4c). For blueberry, the consecutive mortality events decreased the population density gradually and the last application resulted in a population of almost zero (Fig. 4d). Similar simulation parameters were applied for the high mortality insecticide for cherry (Fig. 4e) and blueberry (Fig. 4f). Here, simulated population levels for all life stages gradually decreased and reached almost zero after the second application for both crops.

Additional simulations were added to compare typical growers' practices by altering/rotating insecticides for subsequent mortality events. Growers usually alternate insecticides on a weekly schedule to manage resistance development, while maintaining control. The order of the insecticide was set to provide increasing mortality with each spray. The first simulation, which included mortalities similar to those found for insecticides showing low efficacy reduced the hypothetical populations to 500 individuals from 1500, however, the populations increased to 3000 larval individuals after the first application. The second mortality event, of medium efficacy, resulted in decreased populations to ~ 1000 larval individuals. The last mortality event, of high efficacy insecticide, reduced the population levels down to almost zero for cherry (Fig. 4g). A similar trend was observed for blueberry; however, after the low mortality insecticide application, population levels did not increase to the levels found for the cherry simulations. The second

Fig. 4 *Drosophila suzukii* population levels for each life-stage from the beginning of April until the end of June. Insecticides were applied with 7 days intervals. Weather data were obtained from Oregon throughout the season. No intervention such as insecticides or biological control for **a** cherry and **b** blueberry. Insecticide causes low mortality on all life stages in **c** cherry and **d** blueberry. Insecticide causes high mortality on all life stages in **e** cherry and **f** blueberry. Insecticides cause low, medium, and high mortality on all life stages in **g** cherry and **h** blueberry. Insecticides cause high, medium, and low mortality on all life stages in **i** cherry and **j** blueberry. Note that the *y*-axis is scaled differently for the plots with and without intervention. Intervention days are May 8th, May 15th, and May 22nd

application with medium mortality insecticide reduced the population levels down to 20 individuals and the last high mortality event decreased the population levels close to zero for blueberry (Fig. 4h).

In the final simulation, the order of the mortality events was changed from high to low mortality over time. For this sequence of events, simulated population levels displayed similar trends for both crops. After the series of the applications from the first to the last, the simulated population levels displayed a drastic decrease close to zero for both cherry (Fig. 4i) and blueberry (Fig. 4j).

Discussion

The present study brings together an understanding of life-stage variation in sensitivity to insecticides with population modeling of D. suzukii to understand how different insecticide programs can affect populations of this pest in crops. Understanding how immature life-stages respond is important because during summer months, the majority of this pest's population is inside the fruit as eggs or larvae. The mortality caused by commercially used insecticides was evaluated on the immature life stages of D. suzukii on cherry and blueberry in the laboratory. Previous studies have shown that certain insecticides including malathion, methomyl, phosmet, spinetoram, and zeta-cypermethrin are effective for control of the immature stages of D. suzukii (Van Timmeren and Isaacs 2013; Wise et al. 2015). However, the implication of insecticide effects to population levels remained unknown until now. In addition to population modeling, Emiljanowicz et al. (2014) suggested the overall stable age-distribution in a population of D. suzukii on artificial diet consists of 25% eggs, 51% larvae, 16% pupae, and 8% adults. In the field the stable life-stage distribution of D. suzukii is approximated as 30% eggs, 50% larvae, 10% pupae, and 10% adults in the field (Wiman et al. 2014). Population structure suggests that the majority of the population is in the larval stage, followed by eggs throughout most of the growing season. Population modeling can be useful to estimate the most optimal time to control pest populations (Wiman et al. 2016). For this reason, we used mortality parameters generated in laboratory conditions in this study to model different scenarios and to provide insights into optimal control practices for D. suzukii pest populations.

Fruit size had no significant impact on the efficacy of malathion. However, the results from the fruit size study showed decreasing survival with increasing fruit size in untreated berries, in contrast to the results of Da Silva et al. (2019). Lowbush blueberry fruit is significantly smaller compared to fruit trialed by Da Silva et al. (2019), possibly resulting in these diverging findings. Fruit size can be affected by soil moisture and water uptake (Seymour et al. 2004) thus, larger

fruits may consist of dilute nutrient content such as sugars, anthocyanins, and vitamins. Therefore, larger fruits may not be the optimal food source for larval consumption in order to develop and survive at an optimal rate. The second hypothesis is related to potential gas exchange, which is known to be low across blueberry fruit skin (Dadzie et al. 1993; Beaudry 1999). Small fruit has a higher surface area per unit volume ratio, which results in elevated oxygen diffusion per unit fruit volume and higher gas exchange capacity (e.g., high O_2 concentrations compared to low CO_2 concentrations) within the fruit compared to larger blueberries, which might enhance survival of larvae in small blueberries.

Similar mortality rates were obtained with the respective insecticides regardless of the two tested fruit species (Wise et al. 2015; Shawer et al. 2018). The average mortality of all life stages showed that phosmet, spinosad, spinetoram, and methomyl provided a high level of mortality (90–96.6%); malathion, cyantraniliprole, fenpropathrin, acetamiprid, and zeta-cypermethrin provided a medium level of mortality (85.5–86.3%), and cyclaniliprole provided a lower level of mortality (70%) for immature stages of D. suzukii (Table 2). Because different colonies were used from different parts of the United States and with different fruits for this study, the consistent results suggest that the findings are robust across different crops and regions.

The laboratory generated mortality data were used as additional input parameters in the D. suzukii population model. Model outputs provided insights into how insecticide application timings might be used to optimize efficacy against D. suzukii. Frequent insecticide spray application is the key to protect susceptible crops because of the high economical value and the severe economic risk of detecting D. suzukii in fruit. However, D. suzukii is a challenging pest to control due to the short duration of its life cycle along with high egg laying capacity (Cini et al. 2012). Knowing the insecticide efficacy on different life stages of D. suzukii can help with selection of optimal insecticide application order and planning. The clearer knowledge gained of the mortality potential of insecticides could help growers and/or IPM (Integrated Pest Management) practitioners to choose the appropriate insecticide class to keep the population under control with less pressure on resistance development. The model does not include immigration or competition, and thus describes approximate exponential growth when a stable age distribution is reached. This implies that the specific order of insecticide application does not influence the final population densities. The modeling output does, however, suggest that high efficacy insecticides applied earlier during the season will result in improved D. suzukii population suppression over the course of the ripening period. This demonstrates that the order of insecticide applications is crucial for managing D. suzukii population densities as fruit begin to ripen. Data from the present work suggests

that crop type can have an impact on overall seasonal insecticide application strategy. In cherry, *D. suzukii* populations have a much higher potential for population increase compared to blueberry because of favorable life cycle parameters e.g., a three to eightfold higher fecundity, higher juvenile survival (Tochen et al. 2014) and preference for egg laying in cherry (Bellamy et al. 2013). In the model, different sets of parameters are used for cherry and blueberry (Supplementary Material, Fig. 2 and Fig. 3), which is reflected in lower overall population densities as well as a higher impact of insecticides on blueberries compared to cherries (Fig. 4). The modeling data suggest that starting with an insecticide that causes the high mortality would put more pressure on the population in the beginning of the season both in cherry and blueberry. The optimal scenario for cherry production would be with three insecticide applications that have high-high-high mortality rates (Fig. 4e) and other scenarios such as low-med-high (Fig. 4g) and high-med-low (Fig. 4i) applications indicated a slight population increase, which result in potential infestation. Such scenarios would not be acceptable for cherry growers during the harvest period. Based on our modeling simulations, the optimal insecticide regime for *D. suzukii* in cherry production would be applying high mortality insecticides in the first and second application and finishing with the application sequence with a medium or low mortality insecticide (data not shown). On the other hand, scenarios for blueberry were found to be slightly different. Since *D. suzukii* prefers cherry over blueberry (Bellamy et al. 2013) and has a tendency to have higher fecundity on cherry (Tochen et al. 2014), population densities in the two crop types result in different levels. Based on the model output, the three insecticide application scenarios such as high-high-high (Fig. 4f), low-med-high (Fig. 4h), and high-med-low (Fig. 4j) could be sufficient to control *D. suzukii* in blueberry production and result in low population levels at the end of the season. It is important to emphasize that the pressure in the beginning of the season could actually change the fate of the population later in the season. Eliminating more individuals in the beginning of the season provides fewer individuals in the crop later on, which could potentially be controlled with low and medium mortality insecticides. Furthermore, it is important to mention that the model is a simple representation of a field scenario, however, in certain cases growers apply more than 5-8 application per season depending on the environmental factors and infestation level (Van Timmeren and Isaacs 2013). In the case of high infestation, three application per season might not be enough to control D. suzukii damage, which there might be a need for frequent and consecutive applications. In addition, certain compounds may have label restriction regarding number of applications per season, thus consecutive application should be done based on the label instruction of the formulations.

We acknowledge that the model used in the present study was not empirically validated, but ongoing research aims to address this lack of knowledge in commercial fruit crops. The outcome of similar insecticide application protocols in actual field conditions might differ, but this study provides a guide for future validations by highlighting important factors to consider. Ecological factors including fly movement, predators, parasitoids, and other insects that might influence *D. suzukii* population were excluded from the current model. However, such factors should be considered in future studies to incorporate (factors affecting abundance e.g., fly movement and other mortality factors) into a more holistic assessment of the population dynamics of *D. suzukii* (Pfab et al. 2018). The current modeling study does not consider adverse effects of insecticides on populations of beneficial organisms. This can directly affect pollinators and natural enemies of *D. suzukii*, such as parasitoid wasps. Parasitoids are thought to be a main reason why *D. suzukii* is less of a problem to farmers in its region of origin in Asia (Asplen et al. 2015). Beyond that insecticide applications are known to lead to adverse effects resulting in secondary pest outbreaks. For example, mite outbreaks can happen when intense pesticide applications were made during the preceding year (Szczepaniec et al. 2011). Alternative control methods of *D. suzukii* include netting of plants (Stockton et al. 2020), planting less susceptible fruit varieties (Little et al. 2017) and the release of local or imported parasitoids (Gonzalez-Cabrera et al. 2020). These control methods can be implemented alone or integrated with insecticide applications. Models similar to the model presented here could be used to investigate the long-term costs and benefits of different control strategies. In addition, behavioral responses which might be exhibited by *D. suzukii* against insecticides (e.g., repellency) were not included in the current population model. We acknowledge the importance of adult life stages of *D. suzukii*, but emphasize the need for greater attention focused on the role of immature stage control in management of *D. suzukii*. We believe that the present study contributes to a clearer knowledge of the impacts of insecticides on overall *D. suzukii* populations, and to a better understanding of how the sequence of insecticide applications and crop type impacts the level of control of *D. suzukii.*

Compliance with ethical standards

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