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Population Ecology

Predicting Within- and Between-Year Variation in Activity of the Invasive Spotted Wing Drosophila (Diptera: Drosophilidae) in a Temperate Region

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Abstract

Invasive insect pests can be challenging to manage because their recent arrival provides limited information on which to build predictive population models. The magnitude and timing of activity by the invasive vinegar fly, *Drosophila suzukii*, in crop fields has been unpredictable due to its recent arrival in many new regions of the world and changes in methods for its detection. Using 7 yr of consistent trapping of adults at four blueberry farms in Michigan, United States, we modeled the temporal and environmental factors influencing *D. suzukii* activity. We found that this pest established high levels within 2 yr of being detected, with peak fly activity continuing to increase. Fly activity timing and abundance were predicted by the annual number of days below 0°C, the number of winter and spring days above 10°C, and by the fly activity in the preceding year, providing support for overwintering in our region. We monitored larval infestation for 4 yr at these same sites and found a moderate positive correlation between larvae in fruit and adults in traps. Finally, we developed a generalized additive model to predict *D. suzukii* fly capture throughout the season based on relevant environmental factors and examined the relative timing and magnitude of activity under varying winter and spring temperature conditions. Our results suggest that *D. suzukii* activity is predictable and that environmental conditions can be used in temperate regions to provide regional risk warnings as a component of strategies to manage this invasive insect pest.

Key words: invasive species, establishment, predictive modeling, generalized additive models, GAM

The introduction of invasive pest species has become more common as global trade and commerce have increased (Westphal et al. 2008, Seebens et al. 2017, Meurisse et al. 2018). This presents new challenges, especially to agricultural industries. To manage and assess the risk of these new populations, we need to predict their phenology and population development (Venette et al. 2010). However, this can be challenging when there is limited biological information from the home range where the organism may have not been studied, or from the newly invaded regions where there has been insufficient time to generate this information (Simberloff 2003). Additionally, novel pest species may be monitored with a changing series of approaches as new studies lead to improved techniques, but this can also make it challenging to compare population data among years.

Understanding the temporal and spatial dynamics of a pest is a foundation of integrated pest management (IPM) as it informs decisions about control measures to use and when to use them (Barzman et al. 2015). Prevention is considered the most reliable and least costly control tactic to integrate into a pest management program (Cini et al. 2012, Barzman et al. 2015), but it cannot be effective without background knowledge on the pest. In particular, the phenology of agricultural pests can help growers determine when to apply insecticides or the optimal timing for release of biological control agents, preventing the pest from surpassing economic thresholds. Insect phenology is often predicted using degree-day models (Higley et al. 1986, Manel and Debouzie 1997, Pilkington and Hoddle 2006) or phenology models (Welch et al. 1978, Logan et al. 2006, Nietschke et al. 2007), which rely on understanding the relationships between temperature and pest development.

The rapid international spread of the invasive fruit pest, spotted wing Drosophila (*Drosophila suzukii* Matsumura) (Diptera: Drosophilidae), represents a serious threat to the economic and environmental sustainability of global fruit production (Asplen et al. 2015). This species spread from its native range of East Asia and is now distributed throughout North America, South America, and Europe (Goodhue et al. 2011, Calabria et al. 2012, Deprá et al. 2014, Asplen et al. 2015, Lavagnino et al. 2018). Based on climactic

suitability, potential invasion is also predicted in both Africa and Australia (dos Santos et al. 2017). Females lay eggs in the ripening fruit of many berry and tree fruit crops, creating a risk of infested and unsaleable fruit. After *D. suzukii* is established in a region, adequate control is challenging because of their short generation time and high reproductive capacity (Cini et al. 2014, Asplen et al. 2015, Haye et al. 2016). Current control methods in fruit crops rely heavily on the application of insecticides (Bruck et al. 2011, Van Timmeren and Isaacs 2013, Diepenbrock et al. 2016).

Despite being detected in many fruit production regions for up to 10 yr, the interannual variation in activity of *D. suzukii* in temperate regions is not predictable (Asplen et al. 2015). Degree-day-based models and stage-structured models have been developed for this pest (Wiman et al. 2014, 2016; Pfab et al. 2018), but these have not been widely validated to see how well they predict the interannual variation in pest activity. While these models provide insight into the population potential and structure of *D. suzukii* populations in various regions, we lack an understanding of initial population development after invasion, survival at temperature extremes, and conditions necessary for the development of damaging populations. Moreover, these models rely on development measured in laboratory experiments (Kinjo et al. 2014, Tochen et al. 2014) and have not utilized field detection data from traps or fruit samples. Additionally, data on winter survival and spring populations of *D. suzukii* in regions with cold winter conditions are limited (Dalton et al. 2011, Shearer et al. 2016, Stockton et al. 2018), so there is a need to further evaluate and predict fly activity using field-collected data on adult flies.

Traps have been used to monitor *D. suzukii* across its expanding range, but these traps are variable in design including their size, capture method, and attractant used (e.g., Cha et al. 2012, Landolt et al. 2012, Lee et al. 2012, Burrack et al. 2015). Inconsistent trapping methods compromise our ability to compare fly activity across years, to determine how sex ratio changes over time, or to understand the relationships between larval and adult abundance. Trapping may also be variable throughout a season dependent on competition with other attractants, physiological status of the fly, and trap performance in various environmental conditions (Wong et al. 2018). In Michigan, monitoring for *D. suzukii* was started in spring 2010, and this pest was first detected in September of that year (Isaacs 2011). Beginning in May 2011, year-round monitoring in Michigan began using a consistent trap design and bait: a plastic container baited with a solution of sugar and yeast (described in Van Timmeren and Isaacs 2013). Traps were checked weekly, creating a unique data set that can be used to provide insights into the initial activity of *D. suzukii*, followed by multiple years of collections.

To understand how abiotic conditions affect the first spring detection, fly growth rate during the season, and overall intensity of *D. suzukii* activity in this temperate region with cold winter conditions, we used the 7 yr of data to test the following hypotheses: 1) the fly abundance in the preceding growing season determines the timing and size of the fly abundance in the following year; 2) the first spring detection and early fly activity predict the peak abundance; 3) winter and spring environmental conditions affect the activity of *D. suzukii* during the subsequent summer; and 4) relative abundance of *D. suzukii* between sites is similar within each year. We also used this data set to determine the season-long sex ratio and whether there was correlation between adults in traps and larval infestation in nearby blueberries. Finally, we developed a generalized additive model to predict *D. suzukii* activity based on the parameters mentioned above.

Methods

Trapping

Beginning in May 2011, plastic deli cup traps baited with a mix of sugar, active dry yeast, and tap water (Van Timmeren and Isaacs 2013) were installed at each of four blueberry farms near Fennville in Allegan County, MI. Each site had at least one yeast trap, but in some years had up to three per site. All traps were at least 10 m from each other. Each week the traps were replaced with traps containing freshly made bait and the collected traps were checked for *D. suzukii* adults using the diagnostic characteristics (Hauser 2011). Traps were hung within the blueberry crop at the edge of the field, near a wooded border. Each trap was placed inside the blueberry bush about 1 m from the ground and away from direct sunlight. Weekly checking of traps took place all year long for the duration of the study (2011–2017), except during winter months when traps were not changed during extended cold weather events (air temperature below 4.4°C). These extended weather events usually lasted 2–3 wk during the two coldest months of the year (January and February) and trap checking was timed so that fresh-baited traps were present in fields each time air temperatures rose above 4.4°C. Two of the sites were managed conventionally, with frequent applications of insecticides to control *D. suzukii*. The remaining two sites received minimal management, with infrequent applications of insecticides.

Fruit Infestation

Beginning in 2014, crop infestation data were collected during the harvest season at each of the sites. A minimum of two ripe fruit samples were collected per week at each site, and then assessed for the presence of larvae using a filter salt test (Van Timmeren et al. 2017). Fruit samples were collected on the same day that traps were swapped and collected directly adjacent from the traps. Sample size of each fruit sample varied during the ripening period but at least 4 oz were collected when available.

Weather Data

At all sites, HOBO temperature loggers (64K Pendant data logger, Onset Computer Corporation, Bourne, MA) were deployed to measure air temperature. These loggers were placed inside radiation shields mounted on PVC poles at the same height and placement as the traps at each field. In addition to local ambient temperature, weather data were taken from the nearest weather station at the Trevor Nichols Research Center (MSU Enviroweather) in Fennville, MI. The site farthest from the weather station was 5.7 km away. The weather station provides daily recordings of average ambient temperature, soil temperature, precipitation (except during winter months), relative humidity, and soil moisture.

Statistical Analyses

In the 2 yr following first detection in Michigan (2010 and 2011), *D. suzukii* had low captures in traps relative to subsequent years. These were considered pest establishment years and were omitted from the following analyses. To determine which factors influence the first date of detection in the spring, we used a linear mixed effect model with fixed effects for spring temperatures, winter temperatures, humidity, and the prior year's peak activity level. The dates of first capture had a normal distribution and were mean-centered before analysis. The model parameters were the number of days above 10°C in spring (March–May) and the winter days (November–February) below 0°C. The number of days above 10°C

was selected because this is the temperature at which flight activity is possible for *D. suzukii* (Stockton et al. 2018). The number of days below 0°C was selected because this is a critical threshold for overwintering survival (Stephens et al. 2015, Stockton et al. 2018). Additionally, both of these parameters were variable from year to year, which allowed us to explore their relationships to *D. suzukii* activity and abundance. To incorporate the frequency of winter warm-ups, which may cause *D. suzukii* to become active before spring has arrived, we also included the number of winter days above 10°C.

To determine which factors influence the spring activity, the same factors as above were used in addition to the date of first spring capture. Spring activity was defined using the sum of *D. suzukii* captured beginning on the date of first catch to 4 wk after the date of first catch, then divided by the total number of weeks. The spring activity was log-transformed and a linear mixed effect model was used. To determine which factors affect the peak activity, eight different parameters were included in the model. These include date of first spring capture, spring activity, prior year max activity, the number of days below 0°C, the days above 10°C in spring and winter, the number of days with humidity above 60% RH for the entire year, and the number of days above 28°C for the entire year. Humidity was included in the model because *D. suzukii* is highly susceptible to desiccation (Tochen et al. 2016). Additionally, the number of days above 28°C was included to represent temperature extremes above the ideal range for *D. suzukii* (Kinjo et al. 2014, Tochen et al. 2016, Eben et al. 2017). For all of the above models, each site was nested within year and included as a random factor. For date of first detection, spring activity, and the max abundance models, we selected the best model based on the lowest delta Akaike's information criterion (AICc) value. This was done by comparing the full model to subsequently simpler models with all possible combinations of model factors. We measured the uncertainty of model selection using Akaike's weight, or the probability that the model would be selected as the best fit. Marginal and conditional *R*-squared values for each model were determined using the 'MuMIn' package (Bartoń 2009). A linear mixed effect model was used to evaluate the actual sex ratio compared to an even sex ratio for every month, with site and year as random effects. To evaluate the correlation between adult and larval abundance

by date and at different time points from 2014 to 2017, Pearson's correlation coefficient was used. The variation in management (conventional vs. organic) did not have a large enough sample size and was not analyzed as a fixed effect.

For predictive modeling of fly capture, a generalized additive model (GAM) was used to account for the nonlinear relationship between day of year and *D. suzukii* density. GAMs are generalized linear models but with greater flexibility in the predictor variable, allowing the relationship between the independent and dependent variables to be either linear or nonlinear (Wood 2006). We used a negative binomial distribution to account for overdispersion in the count data. The GAM was created using the 'mgcv' package in R (Wood 2003, Wood et al. 2015). As with the models described above, environmental parameters and date were included as smoothing parameters while trap, site, and year were included as random effects. The best model was evaluated using AIC, as described above, and optimized by fixing the number of smoothing knots to prevent overfitting of the model. An interaction term for date and temperature was added to allow for the shape of the *D. suzukii* activity curve to shift based on temperature conditions. For fly activity simulations, warm conditions were calculated using the average maximum temperature using temperature data at each site from 2012 to 2017. Likewise, cold conditions for both winter and spring were calculated using the average minimum temperature at each site from 2012 to 2017. Similarly, the average maximum and minimum abundance in the preceding year was used in the GAM model. All data analyses were conducted using the R program (3.3.3., R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

Results

Overview of Population Trends

In total, 589,932 *D. suzukii* (47.7% female, 52.3% male) were captured across the duration of this study. During the first two full years of monitoring *D. suzukii*, the activity was considerably lower than the subsequent 6 yr (Fig. 1). The activity of *D. suzukii* each year follows predictable trends, with first spring activity usually occurring in late June and the highest fly capture occurring in September or October, before eventually declining rapidly at the onset of winter in late November (Table 1; Fig. 1). The two
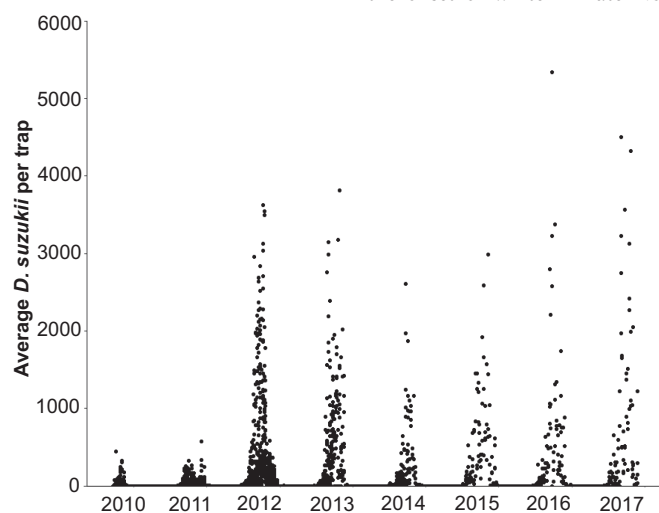

Fig. 1. Average *Drosophila suzukii* captured per trap in each week from 2011 through 2017 across the four monitored blueberry farms. For further analysis, 2010 and 2011 are labeled as 'establishment' years and are not considered for further analyses.

Table 1. Average date of first spring capture of *Drosophila suzukii*, average number of adults on 15 August, the peak capture, and the date when the peak capture was achieved (±SE) across all traps and sites in 2011–2017

Year	Date of first catch ± days	Average adults on 15 Aug. ± SE	Peak capture ± SE	Date of peak capture ± days
2011	15 Aug. ± 7.7	0.5 ± 0.3	128.5 ± 12.9	9 Oct. ± 3.2
2012	17 June ± 3.13	140.7 ± 37.9	1,616 ± 151.4	23 Sept. ± 8.6
2013	3 July ± 6.0	110.9 ± 37.8	1,863.5 ± 187.5	27 Sept. ± 8.8
2014	5 July ± 5.1	38.6 ± 15.2	1,347.8 ± 219.4	24 Sept. ± 3.5
2015	5 July ± 0.0	114.0 ± 24.7	1,602.5 ± 389.5	11 Oct. ± 18.9
2016	22 June ± 2.0	122.5 ± 38.2	3,251.3 ± 873.6	25 Sept. ± 11.4
2017	4 June ± 6.5	236.4 ± 76.0	4,561.5 ± 614.7	22 Sept. ± 11.9

Table 2. Best candidate models explaining date of first spring capture of *Drosophila suzukii* and the null model

Rank	Factors in model	df	ΔAIC	Weight	R^2_m	R^2_c
Null	~1	4	93.4	<0.001	0.0	0.62
1	**Max$t$-1 + days below 0°C + spring days above 10°C + winter days above 10°C**	9	0.0	0.52	0.46	0.55
2	**Max$t$-1 + days below 0°C + spring days above 10°C**	7	1.1	0.30	0.48	0.47
3	Max$_{t\text{-}1}$ + days below 0°C	6	2.1	0.18	0.48	0.48

Max$_{t\text{-}1}$ is defined as the maximum capture in the prior year. Models are ranked according to Akaike's information criterion (AICc). Only models with ΔAIC values of less than 10 are shown. Model weights, marginal (R^2_m) and conditional (R^2_c) R-squared values are also shown. Degrees of freedom (df) for each model is calculated with the number of variance parameters plus the number of fixed effect coefficients.

most recent years of data collection, 2016 and 2017, both had the highest captures of *D. suzukii* compared with prior years. From 2011 to 2017, we detected a weak but significant trend for increasing *D. suzukii* abundance ($R^2 = 0.21$, $P < 0.001$). The date of first spring capture and peak abundance was similar across sites (Table 1), though activity tended to be higher at the sites that were managed less intensively.

Fly Capture Initiation and Peak

First spring capture date

In 2013–2015, first spring capture dates occurred in early July, whereas 2016 and 2017 had first capture 1–3 wk earlier (Table 1). First spring capture date was best predicted using values from the maximum population in the prior year, the number of days below 0°C, and the number of days in spring and winter that were above 10°C (Table 2). The number of days below 0°C, winter days above 10°C, and spring days above 10°C were significantly correlated to the first spring capture ($R^2 = 0.66$, $P < 0.001$; $R^2 = 0.37$, $P = 0.005$; $R^2 = 0.43$, $P < 0.001$, respectively), whereas the prior max abundance was not significantly correlated ($R^2 = 0.06$, $P = 0.7$). The number of days with spring humidity above 60% RH was not included in any of the candidate models.

Spring activity

The spring activity was best predicted by including the date of first spring catch, the prior max activity, and the number of spring days above 10°C (Table 3). The number of days above 10°C in winter was also an important factor. As the date of first catch became later, the spring activity increased ($R^2 = 0.32$, $P = 0.02$) (Fig. 2). While the prior max activity was a significant factor, it was not significantly correlated with spring activity ($R^2 = 0.03$, $P = 0.86$). The number of days above 60% RH during spring and the number of days below 0°C were not included in any of the candidate models.

Estimating peak capture

The peak capture was best predicted using the full model, which included all variables (Table 4). While the best model incorporated

all factors, only the first capture date, spring activity, and number of days below 0°C were significantly correlated with the subsequent peak capture ($R^2 = 0.27$, $P = 0.04$; $R^2 = 0.35$, $P = 0.007$; $R^2 = 0.39$, $P = 0.003$, respectively).

Season-Long Sex Ratio

More males were observed at high population levels (Fig. 3A) and more females were observed in the early and late season (Fig. 3B). However, there was no statistical difference between the actual sex ratio and an even sex ratio across each month ($F_{1,11} = 4.79$, $P = 0.05$). The best predictors for sex ratio were the average fly density and the time of year (Table 5).

Correlating Adult and Larval Abundance

Adult and larval *D. suzukii* abundance were positively correlated by date ($R^2 = 0.42$, $P < 0.001$), and the relationship was even stronger when the data were restricted to events with fewer than 2,000 flies captured per trap ($R^2 = 0.58$, $P < 0.001$) (Fig. 4). When the fly capture was not restricted to below 2,000, the correlation was similar when larval populations were compared with adults captured in traps 1 wk before ($R^2 = 0.43$, $P < 0.001$) or 2 wk before ($R^2 = 0.43$, $P < 0.001$). The correlation was also similar when comparing larval populations with adults captured in traps 1 wk later ($R^2 = 0.37$, $P < 0.001$) or 2 wk later ($R^2 = 0.39$, $P < 0.001$). The correlation between adult and larval populations was found to be significant in July ($R^2 = 0.47$, $P < 0.001$) and August ($R^2 = 0.47$, $P < 0.001$), but not in September ($R^2 = 0.21$, $P = 0.05$). These trends were also the same when adult capture was restricted to below 2,000.

Predicting Fly Capture

The greatest initial growth and subsequent peak activity of *D. suzukii* was achieved during years where winter and spring conditions were warm and the preceding peak capture was high (Fig. 5; Table 6). By contrast, the lowest spring growth and subsequent peak capture were achieved under the opposite conditions. The predicted date of first catch ranged from 13 June to 25 June. The date of first catch was similar when the prior peak capture was either low or high if all other parameters

Table 3. Best candidate models explaining spring activity, which is defined as the sum of *Drosophila suzukii* flies caught in monitoring traps divided by the first four weeks of activity

Rank	Factors in model	df	ΔAIC	Weight	R^2_m	R^2_c
Null	~1	4	43.0	<0.001	0.0	0.40
1	**Date of first catch + max*t*-1 + spring days above 10°C**	7	0.0	0.81	0.36	0.87
2	Date of first catch + max$_{t-1}$ + spring days above 10°C + winter days above 10°C	8	4.5	0.09	0.35	0.87
3	Date of first catch + max$_{t-1}$	6	4.7	0.08	0.38	0.88
4	Date of first catch + max$_{t-1}$ + winter days above 10°C	7	8.4	0.01	0.36	0.88
5	Date of first catch + max$_{t-1}$ + days below 0°C	7	8.8	0.01	0.37	0.89

Max$_{t-1}$ is defined as the maximum capture in the prior year. Models are ranked according to Akaike's information criterion (AICc). Only models with ΔAIC values of less than 10 are shown. Model weights, marginal (R^2_m) and conditional (R^2_c) R-squared values are also shown. Degrees of freedom (df) for each model is calculated with the number of variance parameters plus the number of fixed effect coefficients.
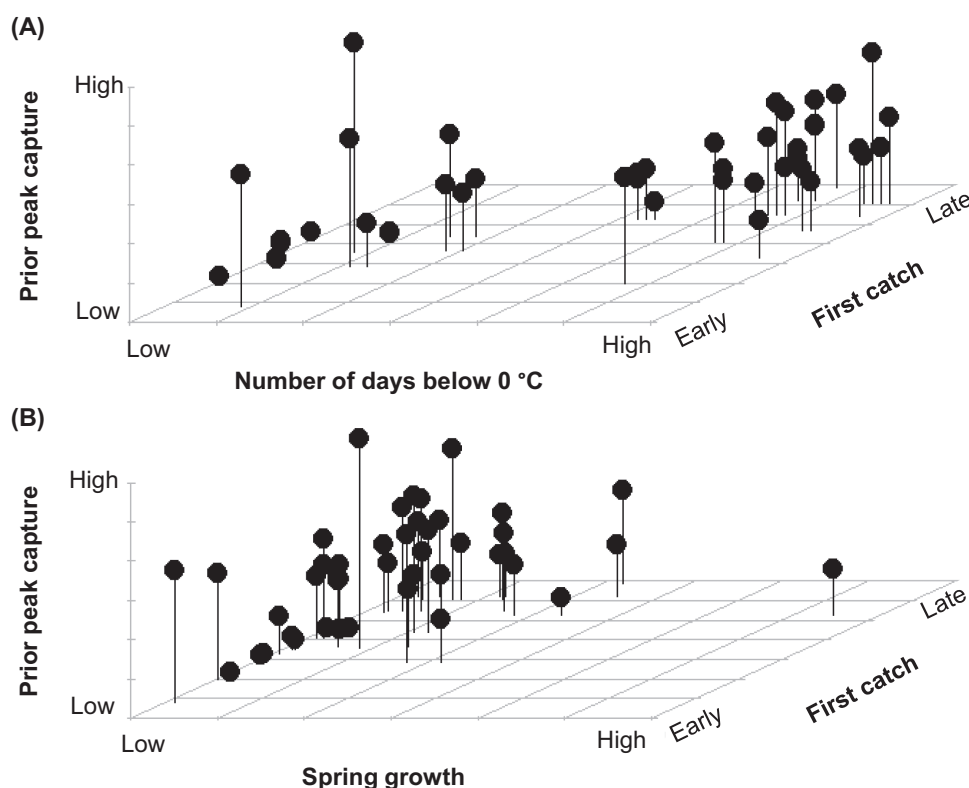
Fig. 2. The relationship between the first capture date of *Drosophila suzukii* and the maximum activity in the prior year and either (A) the number of days below 0°C from each trap within a site and year or (B) the spring activity.

Table 4. Best candidate models explaining maximum activity of *Drosophila suzukii*

Rank	Factors in model	df	ΔAIC	Weight	R^2_m	R^2_c
Null	~1	4	267.5	<0.001	0.0	0.82
1	**First catch + max*t*-1 + spring slope + days below 0°C + spring days above 10°C + winter days above 10°C + days with humidity above 60% + days above 28°C + date of first catch * spring slope**	14	0.0	0.98	0.60	0.85
2	First catch + max$_{t-1}$ + spring slope + days below 0°C + spring days above 10°C + winter days above 10°C + days with humidity above 60% + date of first catch * spring slope	13	7.8	0.02	0.60	0.85

Max$_{t-1}$ is defined as the maximum population in the prior year. Models are ranked according to Akaike's information criterion (AICc). Only models with ΔAIC values of less than 10 are shown. Model weights, marginal (R^2_m) and conditional (R^2_c) R-squared values are also shown. Degrees of freedom (df) for each model is calculated with the number of variance parameters plus the number of fixed effect coefficients.

were held constant; however, a low prior peak resulted in a reduced predicted capture on 15 August and a lower subsequent peak capture (Table 6). The predicted date of the peak activity was almost 2 wk later when the winter was cold, compared to warm winter conditions.

Discussion

Over 7 yr of monitoring *D. suzukii* capture in a region with warm summers and very cold winters, we have tracked the establishment of this invasive pest and found predictable trends in its annual phenology.
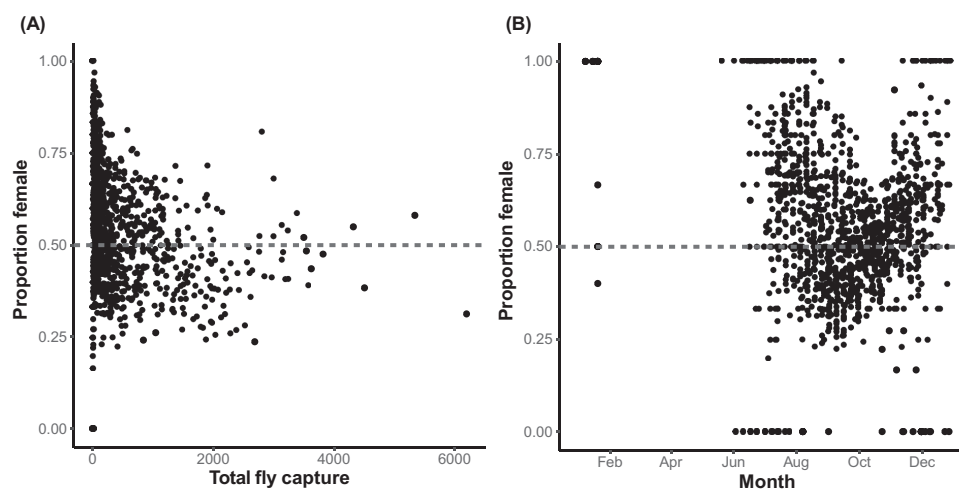
Fig. 3. Proportion of the *Drosophila suzukii* population captured that is female as (A) captures increase and (B) through time from all sites in 2012–2017. The dotted line indicates an even sex ratio.

Table 5. Best candidate models predicting sex ratio of *Drosophila suzukii*, defined in the model as proportion of the adults in each trap that are female

Rank	Factors in model	df	ΔAIC	Weight	R^2_m	R^2_c
Null	~1	3	140.8	<0.001	0.0	0.02
1	**Average *D. suzukii* + date**	12	0.0	0.58	0.28	0.32
2	**Average *D. suzukii* + date * temperature**	13	0.7	0.42	0.21	0.24

Models are ranked according to Akaike's information criterion (AICc). Only models with ΔAIC values of less than 10 are shown. Model weights, marginal (R^2_m) and conditional (R^2_c) *R*-squared values are also shown. Degrees of freedom (df) for each model is calculated with the number of variance parameters plus the number of fixed effect coefficients.
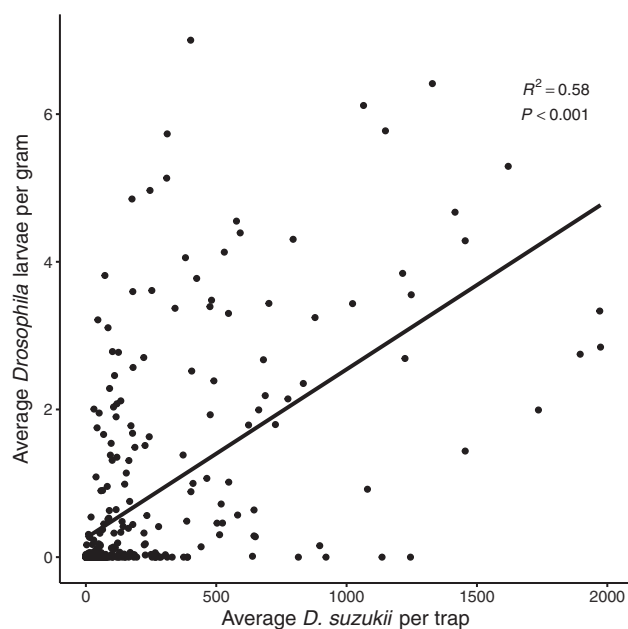

Fig. 4. Correlation of the average number of adult *Drosophila suzukii* per trap and larval infestation per gram of blueberries for each week during harvest. Adult counts shown exclude values where the average trap capture was greater than 2,000 adults. *R²* and *P*-value indicated Pearson's correlation coefficient.

During the first two initial establishment years in Michigan the captures in traps were low, followed by rapid growth into the third year and a steady increase in peak activity thereafter. This increase in activity is often seen among other invasive insects, such as *Halyomorpha halys*, which was present in the United States for several years before reaching damaging activity levels (Leskey et al. 2012). The time until invasive organisms become detected and then reach economic pest status is likely different depending on life-table parameters, and a combination of generational buildup, spatial establishment, detectability, and environmental conditions (Mack et al. 2000, Smith and Knapp 2001, Van Kleunen et al. 2010).

The annual trends in *D. suzukii* activity observed in this study in a northern temperate region also suggest that this pest is not receptive to traps during the winter. Overwintering flies may be less attracted to yeast-sugar traps due to their physiological status or nutrient needs (Rendon et al. 2018, Wong et al. 2018). Spring activity begins with low abundance, indicating that winter temperatures are likely a major bottleneck period for this pest. Klesener et al. (2018) found very similar patterns of *D. suzukii* development in southern Brazil, where there was no winter activity followed by rapid expansion in the early summer. Thistlewood et al. (2018) studied *D. suzukii* in British Columbia and also found that winter temperatures significantly influence *D. suzukii* activity, with colder winter temperatures suppressing this pests' summer activity. Stockton et al. (2018) showed decreasing survival of *D. suzukii* with an increasing number of days at 0°C. Indeed, we found that the number of days below 0°C was an important predictor of both first
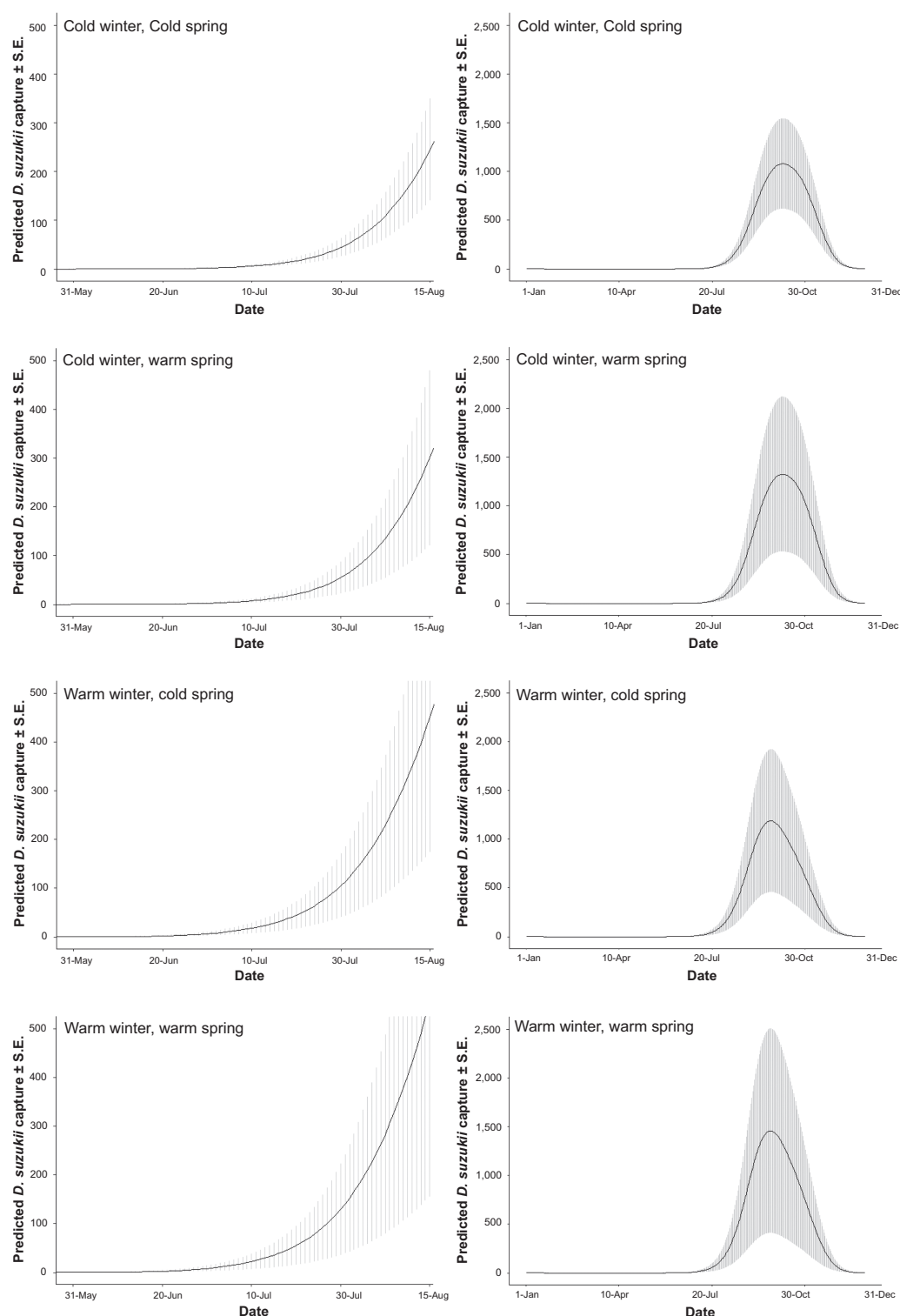
Fig. 5. Generalized additive model (GAM) showing seasonal change in predicted captures of *Drosophila suzukii* from 30 May to 15 August when summer fruit crops may be susceptible to infestation (left), and the year-long populations (right) for combinations of cold and warm spring and winter periods.

spring detection and peak capture in our region. This warrants future research to understand the resources needed for *D. suzukii* to successfully overwinter and the mechanisms underlying this adaptation to survival in colder climates (e.g., Ohtsu et al. 1993). This also suggests that overwintering conditions will have utility in predicting *D. suzukii* severity before the fruit become susceptible during the

late spring and summer, potentially reducing the need for early insecticide applications.

The number of spring days above 10°C was also an important predictor of first capture date, though the number of days below 0°C had a stronger correlation to these spring captures. This adds further support to the hypothesis that adult flies overwinter in our region

Table 6. Predicted average date of first spring capture (± days) of *Drosophila suzukii*, average number of adults on 15 August, mean peak capture, and the date when the peak capture was achieved when the prior peak capture (*N*) was high or low, and when winter and spring temperatures were either cold or warm

Prior peak (*N*)	Winter	Spring	Predicted date of first catch	Predicted number on 15 August	Predicted mean peak capture	Predicted date of peak capture
Low	Cold	Cold	25 June	191.2 ± 97.2	978.0 ± 500.0	2 Oct.
Low	Cold	Warm	23 June	234.4 ± 162.7	1,199.2 ± 835.2	2 Oct.
Low	Warm	Cold	14 June	362.4 ± 245.1	1,076.1 ± 728.6	19 Sept.
Low	Warm	Warm	13 June	444.4 ± 356.5	1,319.5 ± 1,059.4	19 Sept.
High	Cold	Cold	24 June	195.3 ± 83.3	1,078.8 ± 463.9	3 Oct.
High	Cold	Warm	22 June	239.5 ± 143.2	1,322.6 ± 794.1	3 Oct.
High	Warm	Cold	15 June	375.1 ± 231.1	1,187.1 ± 732.4	20 Sept.
High	Warm	Warm	13 June	459.9 ± 330.9	1,445.6 ± 1,048.1	20 Sept.

rather than migrating from warmer regions as has been proposed in its native range (Mitsui et al. 2010, Stockton et al. 2018, Tait et al. 2018). Additionally, we found the peak capture of *D. suzukii* in the prior year to be a significant predictor of first spring detection; however, these two factors were less strongly correlated than the temperature conditions. There was a trend for increasing *D. suzukii* catches in traps from 2011 through 2017, and we expect that this trend is driving the significance of the activity in the previous year in the model, since first capture date also became progressively earlier across these years. Interestingly, first spring detection date was negatively correlated with spring activity, where a later catch resulted in faster spring activity. The spring activity was also positively correlated with spring temperatures, reflecting temperature-related life stage succession in this species (Kinjo et al. 2014, Tochen et al. 2014).

We found that humidity was not a significant predictor of *D. suzukii* abundance, despite this species being highly sensitive to desiccation and low humidity conditions (Tochen et al. 2016). These findings were also not consistent with those of Thistlewood et al. (2018), where low humidity conditions were negatively correlated with high *D. suzukii* populations, though this could also be associated with movement of cold winter air. However, our study was conducted in the more humid Great Lakes region of the United States where days below 60% RH were rare, and we expect that low humidity is a much less important limiting factor for this species in our region. The suitable humidity may also explain why peak capture in our region is so much greater than those observed in the more arid regions of the Pacific Northwest (Thistlewood et al. 2018).

The size of the peak capture of *D. suzukii* in each year was strongly influenced by all factors included in the model, indicating that the beginning spring activity is not the only critical piece of information when estimating potential activity and abundance. While not investigated here, management actions can significantly influence peak activity of *D. suzukii* (Diepenbrock et al. 2016). For later ripening crops such as blueberry and raspberry, the timing and severity of the peak activity is unlikely to change based on first capture alone, and we suggest that management actions as part of an IPM system (i.e., Van Timmeren and Isaacs 2013, Diepenbrock et al. 2016, Leach et al. 2017) will remain critical for prevention of fruit infestation by this invasive pest. Intensity of management was not formally evaluated in this study because each of the farms used different levels and types of management for *D. suzukii* and other pests. Despite this, similar timing of first catch and peak capture were observed among sites (Table 1). Further research should focus on how management decisions can modify the activity curve and potential carrying capacity of the local population of *D. suzukii*, similar to Wiman et al. (2016). Additionally, activity of *D. suzukii* can be compared to the baseline data presented

here after the release of biological control agents (Daane et al. 2016, Wang et al. 2018) or implementation of the sterile insect technique (Nikolouli et al. 2018), which may reduce the carrying capacity and have influence on the surviving population through the winter.

The sex ratio for *D. suzukii* was found to be even throughout the majority of the year, except in the early season, where the first catch was dominated by females. When the fly activity was high, sex ratio tended to be skewed toward males. This matches reports from Europe and Canada by Rossi-Stacconi et al. (2016) and Thistlewood et al. (2018), respectively. These data suggest that females may be more successful at overwintering. Supporting this, Wallingford et al. (2016) found that a higher percentage of females survived chilling compared to males. The correlation between adult and larval abundance of *D. suzukii*, while significant, was not very strong, but it does align with previous reports from monitoring programs for this pest (Burrack et al. 2015). When larval abundance was compared to adult captures 1 and 2 wk before or after, the correlation remained similar. Additionally, there was no significant correlation between adult and larval abundance from samples in September, and the correlation was higher when adult capture was limited to 2,000. This indicates that generations are overlapped, especially during the high activity periods, making it difficult to determine the number of generations for this species. High infestation in fruit can be present when low numbers of adults are captured in traps and vice versa (Fig. 4), and this is likely highly dependent on resource availability and management strategies on individual farms. Additionally, this correlation may be reflective of trap efficiency, which may not be capturing a consistent percentage of the *D. suzukii* activity due to changing environmental conditions (Cha et al. 2012, Lee et al. 2012) or competition with other attractants (Rice et al. 2016). Fly captures may also be related to the developmental and physiological status of the flies, as Swoboda-Bhattarai et al. (2017) found that female *D. suzukii* were more likely to be captured on fruit than fermenting-based traps when they have mature eggs. In addition, Wong et al. (2018) found that starved and virgin flies were more likely to be trapped compared to mated and fed flies in lab experiments.

Using the GAM developed in this study, we were able to explore the combined influence of winter and spring conditions on predicted *D. suzukii* capture. Warm winter and spring conditions elicited the fastest growth and highest activity levels, particularly when the prior peak activity was also high. When spring and winter temperatures differed, there were intermediate amounts of *D. suzukii*. Peak activity and growth were predicted to be the lowest when the insects were exposed to both cold winter and spring temperatures (Fig. 5). While colder conditions influence the peak

activity, exponential growth which would cause damaging levels to crops if left unmanaged, is still predicted. To simulate these predictions, we used the minimum or maximum temperature conditions and previous year activity values, representing *D. suzukii* activity under extreme conditions. Utilization of the GAM to predict distributions of populations has been used elsewhere, including modeling the spatial and temporal variation of butterfly populations as a result of climate change (Hodgson et al. 2011). While Leslie matrix modeling has been developed for *D. suzukii* (Wiman et al. 2014, 2016), these models are likely to be highly sensitive to the geographic and environmental factors related to these sites. With the GAM approach, we can predict phenology with real-time adult capture data and flexible temperature parameters with nonlinear relationships to the insects' activity. Our modeling is based on activity of *D. suzukii* trapped in blueberries in a particular region of Michigan. However, given that the observations of *D. suzukii* activity are very similar to those from southern Brazil (Klesener et al. 2018) and the Okanagan-Columbia Basin (Thistlewood et al. 2018), we expect that our modeling results can be extrapolated to other temperate regions and crops.

There are high levels of uncertainty in the current GAM, especially as projected *D. suzukii* activity increases (Fig. 5). Data collected from more sites and in years with differing temperature parameters would help reduce the variation in estimates for future models. However, here we have demonstrated that predictive modeling can provide a general estimate of fly intensity and trends based on winter and spring temperature data, which can help growers determine the level of approaching risk from this pest and identify critical periods for taking management actions to reduce pressure. This will be particularly valuable for growers who produce crops that ripen when *D. suzukii* transitions from low activity to exponential growth, such as June-bearing strawberries, cherries, and blueberries.

Acknowledgments

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