

# Life History and Damage by *Systema frontalis* F. (Coleoptera: Chrysomelidae) on *Vaccinium macrocarpon* Ait.

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## Abstract

Pest management of emerging pests can be challenging because very little fundamental knowledge is available to inform management strategies. One such pest, the red-headed flea beetle *Systema frontalis* (Fabricius) (Coleoptera: Chrysomelidae), is increasingly being identified as a pest of concern in cranberries *Vaccinium macrocarpon* Aiton (Ericales: Ericaceae). To improve our understanding of this pest and to develop more targeted management programs, we conducted field and laboratory studies to characterize the development, seasonal emergence patterns, and density-dependent plant injury. We found that significantly more flea beetle eggs hatched when exposed to sustained cold treatment between 0 and 5°C for 15 wk than at warmer temperatures, and for shorter and longer cold-period durations. The adults emerged sporadically over the summer, were patchily distributed, fed on both fruit and foliage, and preferentially fed on new plant growth. Using soil cores, we found eggs and larvae located relatively deep (>30 cm) in the soil. These patterns indicate that *S. frontalis* likely overwinters as eggs, and that targeting the larval stage may be the most effective management approach. Despite the cryptic nature of the larvae, continuing to improve our understanding of this life stage will be critical to optimizing control strategies.

**Key words:** egg diapause, feeding injury, soil depth, larval instars, cranberry flea beetle, red-headed flea beetle

Over the last decade, cranberry (*Vaccinium macrocarpon* Ait.) growers in Wisconsin, USA have expressed concern over the perceived increase in the abundance of red-headed flea beetle *Systema frontalis* (Fabricius) (Coleoptera: Chrysomelidae) in their crops. *Systema frontalis* is a native pest of wild and cultivated plants throughout the Midwestern and Eastern United States (Cuthbert and Reid 1965, Peters and Barton 1969, Jacques 1987, Maltais and Ouellette 2000), and although *S. frontalis* can be a vector of plant diseases (Jiang et al. 1992), it has not been considered a serious pest of interest until recently (Guédot and Perry 2016, Guédot and Lippert 2018, Guédot et al. 2019). As a result, there are few peer-reviewed articles describing its life history (Peters and Barton 1969, Jacques Jr. and Peters 1971). This lack of fundamental knowledge makes it challenging to develop a sustainable integrated pest management (IPM) plan; which rely on a baseline understanding of the ecology and population dynamics of a pest to develop and implement the tools necessary for treatment (Pedigo et al. 1986, Prokopy and Kogan 2009). To help address these gaps, we aimed to describe the developmental timelines, seasonal phenology, spatial distribution, and foliar injury associated with *S. frontalis* in Wisconsin cranberry fields.

*Systema frontalis* adults have been reported on commercial crops in the United States since the late 1800s (Chittenden 1902). Adults

are considered polyphagous and have been observed feeding on a wide range of both wild hosts and commercial crops including alfalfa, blueberry, corn, grape, lettuce, potato, soybean, and various *Brassica* species (Hawley 1922, Storch et al. 1979, Maltais and Ouellette 2000, Lauderdaule 2017). Adults will skeletonize foliage (Lauderdaule 2017) and can also injure buds, flowers, and fruit (Maltais and Ouellette 2000, Jaffe et al. 2019), which may impact yield in subsequent years. While a decrease in yield associated with high population densities has been observed with other species of flea beetles in other crops (Weiss et al. 1991, Knodel 2018), there are no established economic thresholds, or reports of *S. frontalis* outbreaks leading to significant loss in any crops.

Characterizing *Systema frontalis* population dynamics can be challenging because eggs are laid in the soil, and the larvae are soil dwelling and likely root feeders (Hawley 1922, Peters and Barton 1969, Averill and Sylvia 1998, Mahr 2005). Very little is known about the environmental factors that could influence population dynamics. In laboratory experiments *S. frontalis* eggs from a population originating from Iowa in corn crops required an extended cold period of 5°C to hatch (Jacques Jr. and Peters 1971). The percent of eggs eclosed increased from about 50%

after four weeks to nearly 70% after 16 wk, suggesting that embryonic dormancy drives population dynamics in the region and leads to only one generation per year in *S. frontalis*. However, reports from greenhouses and nurseries in more southern regions of the United States have observed multiple generations in a year (Lauderdaule 2017) which indicates that overwintering strategies may be regional and crop specific.

In Wisconsin, adults are first observed in cranberry beds in mid-July and can be caught in sweep nets and sticky cards through October (Jaffe, pers. observation). Adult presence at this time overlaps with cranberry harvest in the region, which may result in increased injury if the populations continues to grow. Even though adults are susceptible to insecticide applications (Guédot and Perry 2016), there are limitations to when chemical control can be applied relative to harvest, particularly in relation to the maximum residue limits tolerated by foreign markets (Polavarapu et al. 2001), and action thresholds have not yet been defined. To begin to address these critical gaps in our baseline understanding of *S. frontalis* it is important to systematically characterize the population dynamics and feeding behavior/risk profile of this pest. In this study, we aimed to 1) assess temperature-dependent egg hatch and larval development in a controlled environment; 2) describe the seasonal phenology of egg, larval, and adult densities in the field via active and passive sampling; and 3) understand density-dependent injury and feeding behavior in both the laboratory and the field.

## Methods

### Sites

In 2017 and 2018, a 25.5 hectare commercial cranberry marsh of mixed cultivars located near Warrens (44.124832834–90.500497998), within the central sands region of Wisconsin, was selected for field studies. In 2018, adult monitoring was conducted at six additional commercial marshes, ranging in size from 30 to 168 hectares of active production, and located within a 10 km radius of the initial marsh. All marshes had reported *S. frontalis* infestations within the past two years.

### Adult Field Collection

Cranberry growers self-reported when *S. frontalis* were found in their marshes. Once marshes with *S. frontalis* populations were identified, adults were collected using sweep nets in cranberry marshes from August through September of 2017 and 2018. Adults were transported from the field to the laboratory in 0.5 m<sup>2</sup> bug dorms (BioQuip, Rancho Dominguez, CA). Once in lab, all adult *S. frontalis* were aspirated from the transport dorms and transferred to bug dorms containing at least three 20 cm tall broccoli plants (*Brassica oleracea* L. var. *italica* Plenck) grown from seed, and planted in 1.9 liters nursery pots with access to filtered water. Cages were maintained at 18–22°C, with ~50% RH and a 16:8 L:D light cycle. *Brassica oleracea* were replaced weekly. All removed plants, soil, pots, and possible *S. frontalis* eggs laid were stored at 5°C, 80–90% RH and a 12:12 L:D light cycle for egg hatch experiments described below.

#### 1) Eliciting egg hatch

##### 1a) Chilling temperature

To determine the effect of chilling temperature on egg hatch, over 1,000 field collected adults were allowed to freely mate and lay eggs for 48 h in 1.9 liters pots planted with organic broccoli. Broccoli plants were germinated from seeds (Seedz, amazon.com). The eggs were retrieved from the potted soil, and placed in polypropylene

soufflé cup (Dixie, Denver, CO) containing 2 g (dry weight) of 1–2 mm soil moist granules (Root Naturally, Denver, CO), 20 ml of filtered water, and a 2 cm<sup>2</sup> piece of Whatman Qualitative Grade 1 filter paper (Fisher Scientific, Worldwide). Five eggs were placed on the filter paper, and the soufflé cup was sealed with Parafilm M (American National Can, Chicago, IL). Ten replicates of each treatment (0–2, 5, 10, and 20°C) were set up in growth chambers maintained between 70 and 90% RH, and on a 12:12 L:D light cycle. The temperature treatment of 0–2°C was selected as the lowest field-relevant temperature that could be consistently maintained in the growth chambers. After 15 wk, the cups were removed from their respective temperature treatments and placed in a growth chamber at 20°C, 75–85% RH, and a 16:8 L:D light cycle. Cups were checked every week for 15 wk for hatched or nonviable eggs. Nonviable or hatched eggs and larvae were removed, and cups were re-covered with Parafilm and placed back in the growth chamber.

##### 1b) Chilling duration

To determine the effect of chilling duration on egg hatch, freshly laid eggs (<24 hr old) were collected from caged adults and placed in soufflé cups following the same protocol as the chilling temperature experiment. Chilling duration treatments involved placing treatment soufflé cups at 5°C for five different durations ( $n = 10$ ): 0, 5, 10, 15, and 20 wk. After the completion of each respective chilling period, the soufflé cups were transferred to a growth chamber (20°C, 75–85% RH, and 16:8 L:D light cycle) and checked weekly for 10 wk following each chilling duration treatment. Cups were checked following the same protocol as the chilling temperature experiment.

##### 1c) Larval development

To assess the development of *S. frontalis* larvae in the laboratory, eggs that were in soil at 5°C for 30–35 wk were collected, placed in soufflé cups following the previously described protocol and transferred to a growth chamber set to 24°C, 80–90% RH, and a 16:8 L:D light cycle. Beginning seven days after transfer, soufflé cups were checked every 24 h for four consecutive days for newly eclosed larvae. Larvae were transferred to 60 ml nonsterile specimen cups (Karter Scientific, Lake Charles, LA) containing two-week old alfalfa (*Medicago sativa* L.) planted in 2.5 g (d.w.) soil (HP Pro mix; Premier Tech, Quakertown, PA). Two 3 mm holes were drilled into the side of the container to serve as entry points to introduce the newly hatched larvae to the alfalfa roots. Five larvae were delicately introduced to each container using a spatula micro tool (BioQuip, Rancho Dominguez, CA). Fifteen replicates for each duration (7, 14, 21, 28, 35, 42, and 51 d) were set up, and placed in a growth chamber 20°C, 75–85% RH, and 16:8 L:D light cycle. After introduction of the larvae into the container, the holes were covered with Parafilm M, and watered with 10 ml of filtered water from the top. To minimize disturbance to the container, a single larva was collected from each replicate to measure larva length, head capsule width and circumference using a Dino-lite digital microscope (AnMo Electronics; New Taipei City, Taiwan). Eggs and larvae were measured alive, and then placed in a 90% ethanol solution. Eggs and 1-day old larvae were measured without being introduced into soil containers.

#### 2) Seasonal phenology

In 2018, adult abundance was assessed with emergence cages, sweep nets, and clear sticky cards. Egg and larval abundance was assessed with soil cores within and around cranberry beds.

### 2a) Emergence cages

Ten 1-m<sup>2</sup> emergence cages were constructed out of 38 mm PVC pipe and 0.02 cm mesh fiberglass charcoal screening (Phifer Better View, Tuscaloosa, AL). The fiberglass screening was buried 15.25 cm deep into the soil along each side of the emergence cage using a landscaping edger. A yellow sticky card (15.25 cm × 30.5 cm; Olson, Medina, OH) was hung 12 cm from the top of each cage, and replaced weekly. Cages were placed in randomly selected beds ( $n = 5$ ) at one cranberry marsh. Within each bed, two cages were placed orthogonally to the edge of the bed: one cage at 1 m from the edge and the other 10 m from the edge. Previous work suggests that most *S. frontalis* emerge from the bed versus the surrounding dikes (Bosak et al. 2013), thus we focused our sampling to address distribution within the beds. Cages were placed in the field from 10 July to 18 September 2018.

### 2b) Sweep netting

To assess the seasonal phenology and abundance of adult *S. frontalis* populations surrounding the beds, sweep netting, pitfall traps, and clear sticky cards were deployed across six cranberry marshes near Warrens, Wisconsin. Pitfall traps and sticky cards were not successful in trapping any *S. frontalis* and are not reported here. One hundred sweeps were completed across a 10 m<sup>2</sup> area in two locations, each week for 10 wk. One location ('Dike') was placed on the dikes that separate the cranberry beds, and the other ('Wild') was located within an unmanaged portion of land within 10 m of a cranberry bed. Each area was delineated and no mowing or direct pesticide application was completed for the duration of the sampling period. No sweeping was done within the beds due to growers concern over walking on the cranberry plants at fruit set. Sweeping was completed at the marshes weekly from 4 June to 13 August 2018.

### 2c) Egg and larval abundance

In 2018, twenty 30.5 cm × 6.35 cm soil cores were collected weekly using a custom soil corer from 14 May through 25 September 2018 and then again on 15 November 2018. Beds selected for coring each week were randomized following the same selection parameters used for the emergence cage placements. One 30.5 cm deep soil core was collected from both 1 m and 10 m from the bed edge in ten randomly selected beds. Immediately after collecting, each soil core was divided into 0–15.25 cm and 15.25–30.5 cm from the surface and stored in plastic bags. Soil cores were stored at 5°C until soil was sifted through 4.76, 2, and 1 mm sieves to count the number of eggs and larvae in each sample under magnification. Eggs were identified based on morphology, they are pale yellow, <1 mm in length, and oval-shaped (Jacques Jr. and Peters 1971, Jaffe et al. 2019), and were compared to lab collected reference material. Larvae collected from the soil were identified by a diagnostic fleshy projection on the last abdominal segment (i.e., urogomphi).

### 3) Feeding injury

Two experiments, one in the field and one in the laboratory, were conducted to assess the effect of *S. frontalis* adult density on feeding injury on cranberry plants.

#### 3a) Field: foliage and fruit

A cranberry bed ('Stevens' variety) was randomly selected to assess adult feeding injury associated with different densities. Ten replicates of 5–10 fruiting uprights, containing 3–10 berries were isolated using 20 × 30.5 cm reinforced organza drawstring bags (Supp Fig. 1 [online only]). Uprights were inspected for any signs

of injured fruit (i.e., chew marks) or leaves (e.g., defoliation, webbing, chew marks) and only 100% intact, uninjured, uprights were included in the experiment. Cotton balls were placed at the opening of the bag surrounding the stems to secure the stem. A drawstring was cinched around the cotton and the bag sealed around the stem with duct tape. Since there are no formal economic thresholds for *S. frontalis*, we chose densities that reflect the recommended nominal action threshold of 15 beetles per 25 sweeps (Armstrong 2010). Ten replicates of three different adult *S. frontalis* densities (0, 5, and 20 beetles) were established on 7 August 2018. Adult beetles of unknown age or sex were collected with a sweep net from the same marsh, and then briefly anesthetized using dry ice. The beetles were then transferred, at the appropriate density, into each organza bag. After seven days, the experiment was terminated by cutting the base of the uprights below the bag, placing the entire bags containing the uprights and beetles in a portable cooler and returning bags to the laboratory. All samples were processed the same day to determine the total number and percent of uprights, leaves, and fruit showing diagnostic flea beetle injuries, as well as the relative distance of the injury from the tip of upright (0–2 cm; 2–4 cm; 4 cm +) and beetle mortality.

#### 3b) Lab: foliage only

Experimental cages were constructed from 1,000 ml plastic deli cups (Fabri-Kal; Kalamazoo, MI). A 5-cm diameter hole was cut out of the lid and 0.02 cm mesh fiberglass charcoal screening (Phifer Better View, Tuscaloosa, AL) was attached over the hole. Each cage contained three field-collected, cranberry uprights ('Stevens' variety), with foliage extending down the stem at least 12 cm from the apical end, and with all fruit and flowers removed. A single cotton ball saturated with filtered water was added to each cage. Cages were maintained in a growth chamber at 20°C, 75–85% RH, and a 16:8 L:D light cycle. Ten replicates of three field-collected adult *S. frontalis* densities (1, 5, or 10 beetles) were maintained for 7 d. After seven days, the same injury protocol assessment as in the field experiment was conducted.

### 4) Statistical analyses

All analyses were conducted using JMP PRO 11 (SAS Institute, Inc., 2007).

- 4a) *Egg chilling temperature and duration*: A  $\chi^2$  analysis was used to discern any effect of temperature or duration on latency to egg hatch. Following a significant result, a Wilcoxon posthoc test was used to distinguish specific effects of the different treatments for each experiment on latency to hatch ( $P < 0.05$ ).
- 4b) *Larval development*: An ANOVA was used to compare larval characteristics as a function of age class. Tukey HSD posthoc analyses were used to distinguish specific relationships following significant ANOVA tests ( $P < 0.05$ ).
- 4c) *Emergence cages*: No statistical analyses were completed comparing distance from dike due to low emergence rates (less than 2 adults/per cage/per week).
- 4d) *Sweep netting*: *Systema frontalis* were only caught at 17 out of 120 replicates, and thus replicates were only included in analysis if at least one beetle was collected at one of the sampling locations on each marsh at each date. Beetle abundance was  $\log_{10}(x + 1)$  transformed to better meet the assumptions of normality. A paired *t*-test was used to determine whether there was significant difference in the number of beetles collected on the dike versus the wild for each collection type.
- 4e) *Egg and larval abundance*: An ANOVA was used to measure the effect of distance from edge, soil depth, and date on the

number of eggs and larvae collected, and the ratio of eggs to larvae.

- 4f) *Feeding injury*: An ANOVA was used to measure the effect of adult density on the amount of leaves injured, the location of injury, and the percent of fruit injured (*Field assessment only*). Percent of leaves and fruit injured was transformed using an arcsine transformation to meet the assumptions of normality.

## Results

### 1) Eliciting egg hatch

Eggs were oblong in shape, and  $0.77 \pm 0.03$  (mean  $\pm$  SE) mm in length, with color ranges from yellow to creamy white.

- 1a) *Egg chilling temperature*: There was an effect of temperature on percent of eggs hatched ( $\chi^2_3 = 16.9$ ,  $P < 0.001$ ) with significantly more eggs hatching after exposure to 0–2°C and 5°C than 10°C or 20°C (Wilcoxon  $P < 0.05$ ; Fig. 1).
- 1b) *Egg chilling duration*: The duration eggs spent at 5°C had a significant effect on the percent of eggs hatching ( $\chi^2_4 = 11.5$ ,  $P < 0.05$ ), with significantly more eggs hatching after 15 wk at 5°C than 0, 5, and 10 wk (Wilcoxon,  $P < 0.05$ ; Fig. 2).
- 1c) *Larval development*: Following the 15 wk chilling treatment at 5°C and transfer to 20°C, eggs began to eclose after 11 d. There was a significant effect of measurement day on larval length ( $F_{5,55} = 147$ ,  $P < 0.0001$ ), head capsule width ( $F_{5,55} = 45.9$ ,  $P < 0.0001$ ), and head capsule circumference ( $F_{5,55} = 109$ ,  $P < 0.0001$ ). In general, these morphological features differentiated across three age classes: 1 and 7 d, 14 and 21 d, and 28 and 34 d (Table 1). There was high mortality after 42 d and only three larvae were observed to pupate by 51 d.

### 2) Seasonal phenology

- 2a) *Emergence cages*: The first *S. frontalis* adult emerged on July 24, and the last adult emerged within the cages on 11 September 2018 (Supp Fig. 2 [online only]). The average number of adults that emerged per cage over the season was

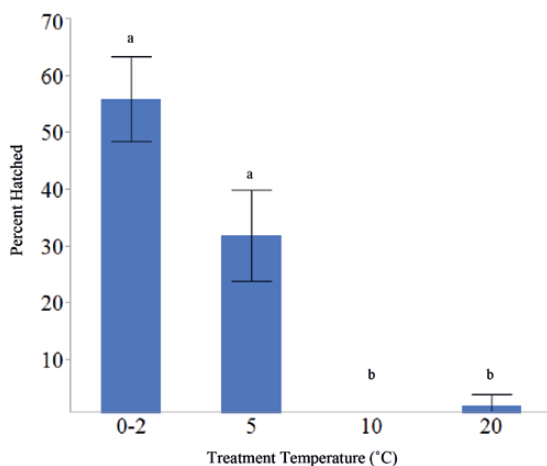


Fig. 1. Average percent of eggs hatched ( $\pm$ SE) at 15 wk at 20°C after exposure to 0–2, 5, 10, 20°C for 15 wk. Treatment temperatures not connected by the same letter are significantly different from each other (Tukey HSD;  $P < 0.05$ ).

$0.14 \pm 0.05$  (mean  $\pm$  SE) at 1 m from the edge and  $0.18 \pm 0.05$  at 10 m from the edge.

- 2b) *Sweep netting*: The first *S. frontalis* adults were caught on July 9. Adults were caught every week up until sampling was stopped on August 13. Although there was a trend for more *S. frontalis* to be trapped on the un-mowed dikes (mean  $\pm$  SE;  $2.54 \pm 1.01$ ) than in the wild areas ( $0.92 \pm 0.33$ ), there was no significant difference between these areas ( $t_{12} = 1.45$ ,  $P = 0.09$ ; Supp Fig. 3 [online only]).

- 2c) *Egg and larvae abundance*: Overall, there were approximately twice the number of eggs found at 10 m (mean  $\pm$  SE;  $7.35 \pm 5.46$ ) than at 1 m ( $3.55 \pm 1.40$ ) from the dike, although this difference was not significant ( $t_{82} = 0.38$ ,  $P = 0.65$ ). Eggs generally occurred in clumps within the beds, when one egg was found often several more were found as well (Supp Fig. 4 [online only]). When considering only soil samples that contained eggs, and lumping all distances together, there were significantly more eggs found at the 15–30 cm depth ( $9.57 \pm 5.55$ ) than at 0–15 cm ( $0.98 \pm 0.52$ ;  $t_{82} = 1.76$ ,  $P < 0.05$ ). Very few larvae were collected (16 total) within the soil samples. The first sample containing larvae was collected on June 19 and larvae continued to be found in soil into early August (Fig. 3).

### 3) Feeding injury

- 3a) *Field: foliage and fruit*: Including *S. frontalis* density (treatment), location of injury on the upright (location), and their interaction as explanatory effects on percent foliage injury, there was an overall significant effect of these factors on percent of leaves injured ( $F_{8,89} = 40.4$ ;  $P < 0.0001$ ; Table 2). There was a significant positive relationship between *S. frontalis* density and percentage of leaves injured ( $F_{\text{density}} = 118$ ;  $P < 0.0001$ ), location of the injury ( $F_{\text{location}} = 26.4$ ;  $P < 0.0001$ ), and their interaction ( $F_{\text{density} \times \text{location}} = 8.61$ ,  $P < 0.0001$ ). A Tukey HSD showed that beetles preferentially feed on leaves closer to the apical end than the base of the uprights, and that the more beetles in the container the higher the proportion of injured leaves (Table 2). As beetle density increased, so did the percent of leaves injured farther away from the tip of the up-

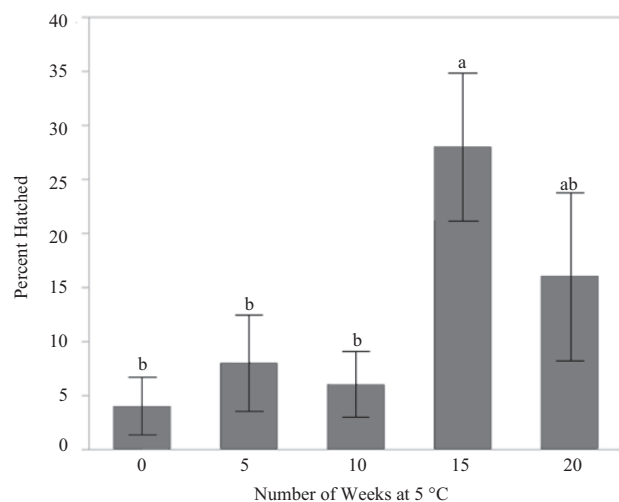
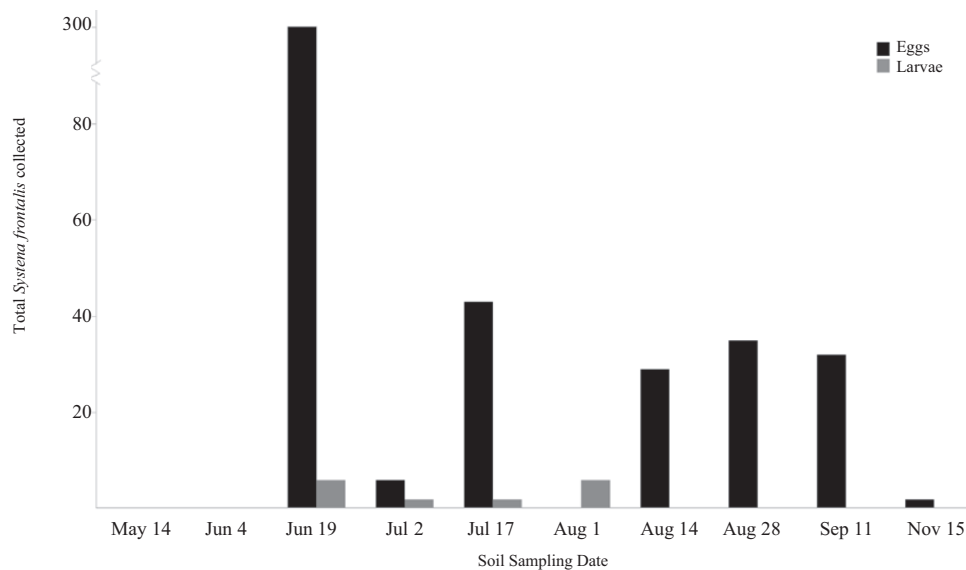


Fig. 2. Average percent of eggs hatched ( $\pm$ SE) for various cold treatment durations after at least 10 wk at 20°C. Cold treatments not connected by the same letter are significantly different from each other (Tukey HSD;  $P < 0.05$ ).

**Table 1.** Average length, capsule width and circumference ( $\pm$ SE) of *Systema frontalis* larvae at various ages.

Age (d)	<i>n</i>	Length (mm)	Capsule width (mm)	Capsule circumference (mm)
1	15	1.67 $\pm$ 0.05 <sup>d</sup>	0.27 $\pm$ 0.01 <sup>d</sup>	0.79 $\pm$ 0.03 <sup>c</sup>
7	15	3.69 $\pm$ 0.13 <sup>c</sup>	0.27 $\pm$ 0.01 <sup>d</sup>	0.81 $\pm$ 0.03 <sup>c</sup>
14	10	5.39 $\pm$ 0.20 <sup>b</sup>	0.39 $\pm$ 0.02 <sup>c</sup>	1.21 $\pm$ 0.04 <sup>b</sup>
21	8	6.25 $\pm$ 0.47 <sup>b</sup>	0.45 $\pm$ 0.02 <sup>bc</sup>	1.47 $\pm$ 0.04 <sup>a</sup>
28	8	8.56 $\pm$ 0.28 <sup>a</sup>	0.49 $\pm$ 0.02 <sup>ab</sup>	1.63 $\pm$ 0.04 <sup>a</sup>
35	5	9.59 $\pm$ 0.72 <sup>a</sup>	0.55 $\pm$ 0.02 <sup>a</sup>	1.54 $\pm$ 0.05 <sup>a</sup>

Metrics within a column not connected by the same letter are significantly different from each other (Tukey HSD;  $P < 0.05$ ).

**Fig. 3.** Total number of *Systema frontalis* eggs and larvae collected over time in soil cores collected in commercial cranberry beds.

right (Table 2). *Systema frontalis* actively fed on cranberries, as there was a significant effect of the presence of adults on the percent of cranberries injured ( $F_{2,29} = 5.75$ ;  $P < 0.01$ ), but there was no significant difference in the percent of cranberries injured between the 5 beetles ( $14.3 \pm 5.8\%$ ) and 20 beetles ( $22.2 \pm 7.9\%$ ) densities ( $F_{1,18} = 0.72$ ;  $P = 0.41$ ).

3b) *Lab: foliage only*: The model that included beetle density, location of injury, and their interaction as explanatory variable showed an overall significant effect of the factors on percent of leaves injured ( $F_{8,81} = 33.8$ ;  $P < 0.0001$ ). Within this model, there was a significant relationship between *S. frontalis* density and percentage of leaves injured ( $F_{\text{density}} = 120$ ;  $P < 0.0001$ ), as well as a significant difference in the location of the injury ( $F_{\text{location}} = 5.21$ ;  $P < 0.01$ ), but no interaction effect ( $F_{\text{density} \times \text{location}} = 1.52$ ;  $P = 0.21$ ). Significantly more leaves were injured in the presence of 10 beetles ( $70.0 \pm 3.7\%$ ), than 5 beetles ( $32.0 \pm 3.7\%$ ), than 1 beetle ( $6.93 \pm 0.1\%$ ;  $P < 0.05$ ; Table 3). There was a significantly higher percentage of leaves injured 0–2 cm from the apical end ( $44.5 \pm 5.8\%$ ) than at >4 cm ( $27.1 \pm 4.8\%$ ) but not between either of these distances and 2–4 cm ( $37.2 \pm 6.0\%$ ; Tukey HSD;  $P < 0.05$ ; Table 3).

## Discussion

*Systema frontalis* eggs were found in the soil in mid-June through mid-July, August through September, and into November. Despite

a small percentage of eggs hatching with no chilling temperature (4%), significantly more eggs hatched (22%) after a chilling period of at least 15 wk. After the chilling period, the first eggs hatched within 11 d of experiencing 20°C. Using larval head capsule width as the primary metric (Castañeda-Vildózola et al. 2016, and references therein), there were four larval stages by 51 d of development, and each instar stage lasted between 7 and 14 d. Since few larvae pupated by 51 d, we were unable to definitively determine the number of larval instars. Larvae were found in the soil beginning in mid-June and continued to be collected into early August. Both larvae and eggs were found to be as deep as 15–30 cm, and were patchily distributed within and between cranberry beds. Adults were first observed in mid-July and were trapped through mid-September. Adults injured leaves and fruit, and preferred newer vegetative growth closer to the apical end (0–2 cm from tip) of cranberry uprights.

This study revealed several key biological insights that could be leveraged to inform more effective management practices. In Wisconsin, *S. frontalis* eggs had a significantly higher hatch rate after an extended exposure to cold, indicating an ability to overwinter and an adaptation to survive and thrive in cold temperatures. Dormancy is an important adaptation, especially in cold climate regions such as the U.S. Upper Midwest, because it allows an organism to synchronize its life-cycle with favorable abiotic conditions and access to key resources (Danks 2002). The physiological aspects of embryonic dormancy, and in insect diapause in general, are complex (Hand et al. 2016, Spurgeon and Suh 2017), but appear to be important for *S. frontalis*. Adaptive responses by insects, such as the apparent embryonic dormancy reported here,

**Table 2.** Percent of leaves injured ( $\pm$ SE) by distance from apical end of upright and adult *Systema frontalis* density (0, 5, and 20) in the field

Adult density	Distance from apical end	Percent of leaves injured ( $\pm$ SE)
20	0–2	20.1 $\pm$ 3.5 <sup>a</sup>
20	2–4	10.0 $\pm$ 1.5 <sup>b</sup>
20	4+	3.6 $\pm$ 1.0 <sup>c</sup>
5	0–2	6.0 $\pm$ 4.0 <sup>bc</sup>
5	2–4	2.5 $\pm$ 1.0 <sup>cd</sup>
5	4+	1.0 $\pm$ 1.0 <sup>dc</sup>
0	0–2	0 <sup>e</sup>
0	2–4	0 <sup>e</sup>
0	4+	0 <sup>e</sup>

Percentages not connected by the same letter are significantly different from each other (Tukey HSD;  $P < 0.05$ ).

**Table 3.** Percent of leaves injured ( $\pm$ SE) by distance from apical end of upright and adult *Systema frontalis* density (1, 5, and 10) in the laboratory

Adult density	Distance from apical end	Percent of leaves injured ( $\pm$ SE)
10	0–2	78.6 $\pm$ 5.1 <sup>a</sup>
10	2–4	78.1 $\pm$ 4.4 <sup>a</sup>
10	4+	53.1 $\pm$ 6.1 <sup>b</sup>
5	0–2	41.3 $\pm$ 7.6 <sup>bc</sup>
5	2–4	27.5 $\pm$ 5.1 <sup>cd</sup>
5	4+	27.1 $\pm$ 6.7 <sup>cd</sup>
1	0–2	13.1 $\pm$ 3.0 <sup>de</sup>
1	2–4	6.02 $\pm$ 1.1 <sup>de</sup>
1	4+	1.19 $\pm$ 0.5 <sup>e</sup>

Percentages not connected by the same letter are significantly different from each other (Tukey HSD;  $P < 0.05$ ).

are important attributes that can facilitate the expansion and survival of insects into new habitats (Tauber et al. 1986, Hopper 1999, Diniz et al. 2017, Kellermann and van Heerwaarden 2019, Lehmann et al. 2020). Interestingly, some *S. frontalis* eggs hatched without exposure to any chilling period, which is consistent with the multivoltine patterns observed in warmer climates and greenhouses (Lauderdaule 2017). The adaptive responses that may dictate *S. frontalis* expansion across different regional and agricultural practices demonstrates the need for more work to understand the plasticity associated with overwintering strategies in this species.

Describing larval development continues to be a challenge for *S. frontalis* (Peters and Barton 1969, Jacques Jr. and Peters 1971, Maltais and Ouellette 2000). While this study was able to identify the necessary conditions to elicit egg hatch and successfully develop a protocol to rear larvae through thirty days, most larvae failed to pupate. The inability to rear a significant number of adults could be indicative of a limitation in the containers used for rearing. The small chambers selected to rear the larvae were effective for identifying early instar individuals in the soil matrix, but were also subject to mold and fluctuations in soil moisture. Since the length of larval development can be influenced by external stressors (Esperk et al. 2007, Zanetti et al. 2016), survivability may be improved by transferring larvae weekly to larger chambers containing newly planted material. Despite these continued challenges associated with

laboratory rearing, characterizing the pupal stage and determining the number of development days in each stage are the critical steps in building a degree day model and subsequent targeted IPM programs.

Adult *S. frontalis* fed on fruit and preferred new cranberry growth over older foliage, as indicated by preferential feeding near the apical end of the cranberry vine. A preference for younger foliage suggests that *S. frontalis* might be adapted to overcome the defensive properties associated with younger leaves to exploit the nutritional value that is generally considered higher in younger leaves (Cates 1980, Price 1991, Blüthgen and Metzner 2007, Moreira et al. 2016). However, these preferential feeding patterns are more characteristic of monophagous and oligliophagous herbivores than of polyphagous species (Cates 1980, Andow and Imura 1994) such as *S. frontalis*. An additional consideration is that cranberry breeding efforts to improve yield and quality of the fruit has also been linked to an increased susceptibility to phytophagous insect pests (Rodriguez-Saona et al. 2011). The emergence of *S. frontalis* as a pest of concern in cranberry may be a result of this insect becoming increasingly specialized to feed on cranberry plants (Andow and Imura 1994), selective breeding programs leading to reduced plant defenses (Rodriguez-Saona et al. 2011), and agricultural practices (Dutcher 2007). While these questions were outside the scope of this study, future work should look to measure the physiological characteristics associated with preferred foliage and to assess potential differences in varietal susceptibility.

The field sampling efforts did not elucidate any clear trends in the location and abundance of adults within cranberry beds, but did confirm a low abundance of adults immediately outside of the beds. These results present an interesting dichotomy, although *S. frontalis* are considered phytophagous species, it appears that most adults are found in the cranberry beds. Furthermore, agricultural practices to protect vines from freezing temperatures (Supp Fig. 5 [online only]) via ice sheets could also have the unintended consequence of protecting eggs laid within the bed. Although it remains unknown whether the presence of adults in a specific area is associated with increased oviposition in that area, developing an effective management plan will likely require understanding inter-seasonal spatial distribution of adults (i.e., do adult ‘hot spots’ in cranberry beds in one year correlate with egg and adult ‘hot spots’ in the following year?), and how on- and off-farm factors that influence population dynamics. Despite the somewhat cryptic nature of soil-dwelling eggs and larvae, these developmental stages may represent the best opportunity to effectively manage this pest. A recent study showed that the application of native nematodes to the soil in cranberry beds was associated with a lower emergence of adult *S. frontalis* (Foye and Steffan 2019). However, the virulence of soil treatments can vary by developmental stage (Kurtz et al. 2009), and thus timing applications with the most susceptible life stages are critical to effective management (Smits 1996, Georgis et al. 2006). Future studies, focusing on soil-based control techniques, should consider the efficacy across all soil-based-developmental stages, and connect the potential abiotic factors influencing these stages to deliver more targeted control applications.

## Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

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## Conflict of Interest

The authors report no conflict of interest.

## Author Contributions

BDJ and CG: conceived research; BDJ and SR: conducted experiments; BDJ and SR: conducted statistical analyses; BDJ and CG: wrote the manuscript; BDJ and CG: secured funding. All authors read and approved the manuscript.

## Data Availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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