

Biological Control - Weeds

Does the Presence of the Biological Control Agent, *Hypera opulenta* (Lepidoptera: Erebidæ) on Swallow-Worts Deter Monarch Oviposition?

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Abstract

Invasive black and pale swallow-worts (*Vincetoxicum nigrum* (L.) Moench, and *Vincetoxicum rossicum* Kelopow), which are related to milkweeds, can act as ecological traps for monarch butterflies (*Danaus plexippus* L. (Lepidoptera: Nymphalidae)) as they lay eggs on them that fail to develop. A recently approved biological control agent against swallow-worts, *Hypera opulenta* Christoph, occupies the same feeding guild on swallow-worts as monarch larvae and could be perceived as a competitor to monarchs. We tested how the presence of this defoliating moth on swallow-worts may influence monarch host selection. In a two-year field experiment, we placed pale swallow-wort plants that were either infested with *H. opulenta* or noninfested as well as common milkweed (*Asclepias syriaca* L.), into monarch habitats to assess oviposition rates. In the laboratory, monarchs were either given a choice or not between milkweeds and black swallow-worts with or without *H. opulenta*. While monarchs strongly preferred common milkweed in the field, up to 25% of the eggs we observed were laid on pale swallow-wort, without preference for swallow-wort with (10.7%) or without (14.3%) *H. opulenta*. In laboratory choice and no-choice tests, monarchs did not lay any eggs on black swallow-wort, likely because of the long-term laboratory rearing on common milkweeds. Our results confirm that pale swallow-wort may act as an oviposition sink to monarchs in Michigan as well. Since the biological control program is still in its infancy, the nature of interactions between monarchs and *H. opulenta* may change as the biocontrol agent becomes more widespread.

Key words: ecological trap, oviposition sink, invasive species, weed biocontrol

The arrival of exotic plant species into the habitat of native herbivorous insects can present novel resources (Tong and Shapiro 1989) but may also serve as ecological traps (Casagrande and Dacey 2007). The survival and development of holometabolous insects whose larval stages have limited mobility are dependent on the oviposition decisions of the females since the host plant chosen by the adult will serve as an early food source for the larval stages. Females, however, do not always make optimal oviposition choices and may choose to oviposit on plants that are unsuitable for larval development (Ries and Fagan 2003, Schlaepfer et al. 2005, Casagrande and Dacey 2007, Faldyn et al. 2018). For example, the diamondback moth (*Plutella xylostella* L. (Lepidoptera: Plutellidae)) has been recorded to prefer to lay eggs on *Barbarea vulgaris* W.T. Aiton, a plant on which its larvae cannot develop (Badenes-Perez et al. 2006). The invasion of North America by garlic mustard *Alliaria petiolata*

Bieb. provides another example, as the native West Virginia white butterfly (*Pieris virginiensis* W.H. Edwards (Lepidoptera: Pieridae)) was found to lay more eggs on garlic mustard than on its native mustard host *Cardamine diphylla* (Michx.) A.W. Wood, despite it being toxic for their larvae (Davis and Cipollini 2014). These mistaken oviposition choices have likely contributed to the decline of *P. virginiensis* (Davis and Cipollini 2014). Other similar examples abound in several other Lepidoptera species (Berenbaum 1981, Straatman 1962, Chew 1977).

Monarch butterflies may also be threatened by plant species that can act as ecological traps as the density of their native milkweed host plants decrease due to herbicide use (Thogmartin et al. 2017, Inamine et al. 2016, Pleasants and Oberhauser 2013, Zaya et al. 2017), and as invasive species that are related to milkweeds become more abundant. Two European swallow-wort species,

pale and black swallow-wort (*Vincetoxicum rossicum* (Kleopow) Barbar and *V. nigrum*, respectively), which are members of the Apocynaceae family along with milkweeds, have become invasive in the midwestern and eastern United States and southeastern Canada (DiTommaso et al. 2005). Also called dog strangling vines, swallow-worts can grow in many of the same places as milkweeds, including in disturbed areas along railway lines, highways, and other transportation corridors, in natural areas, as well as in no-till corn and soybean fields and pastures (DiTommaso et al. 2005, Weston et al. 2005, Weed and Casagrande 2010). Therefore, monarchs are often presented with choices between milkweeds and swallow-worts, but the extent to which swallow-worts are used for oviposition is still debated.

Casagrande and Dacey (2007) found substantial oviposition on both black and pale swallow-worts in a series of laboratory (up to 21.7%) and field cage experiments (up to 24.5%), with no significant oviposition preference of monarchs between the two swallow-wort species in no-choice tests (11.2% on black vs. 12.6% on pale swallow-wort). In Rhode Island pastures, where both black swallow-wort and common milkweed grew together, 15% of monarch eggs were laid on black swallow-wort (Casagrande and Dacey 2007). Field surveys in New York state also found monarch eggs on both black and pale swallow-worts (Milbrath 2010). However, others showed little (0.5%) (Mattila and Otis 2003) or no oviposition (DiTommaso and Losey 2003) on black and pale swallow-worts in choice and no-choice laboratory experiments. All studies agree, however, that neither swallow-wort species support monarch development as the larvae are not adapted to feed on these plants (Casagrande and Dacey 2007, Mattila and Otis 2003). Thus, swallow-worts may act as an oviposition sink to monarchs (Casagrande and Dacey 2007), which might accelerate their decline (Inamine et al. 2016).

The host plant selection of monarchs is influenced by multiple factors besides food quality, such as the experience of females with different plant species and the risk of larval competition or predation (Jones and Agrawal 2019). Jones and Agrawal (2019) found that when monarchs showed an oviposition preference towards a suboptimal milkweed host *Asclepias incarnata* subspecies *pulchra* (Ehrh. ex Willd.) Woodson, prior oviposition experience on a more suitable milkweed, *A. incarnata* subspecies *incarnata* L. could alter this preference. More importantly, the presence of a monarch larva on the suboptimal host could reverse preference towards that unsuitable plant, likely because monarchs try to avoid cannibalism of their freshly laid eggs and/or larval competition when multiple individuals feed on the same plant (Jones and Agrawal 2019). These results suggest that the presence of another herbivorous larvae on suboptimal host plants, such as swallow-worts, may act as a deterrent to monarch oviposition.

Given that swallow-worts are not native to North America, few indigenous herbivorous insect species were found to feed on them causing only minor damage (Milbrath 2010), and thus native herbivores are unlikely to deter monarch oviposition. However, a classical biological control agent, a defoliating moth *Hypena opulenta* Christoph was approved for field release in 2017 in the U.S. (USDA APHIS 2018). This moth, originating from the native range of pale swallow-wort in Ukraine is a specialist which can feed on both pale and black swallow-wort (Hazlehurst et al 2012). *H. opulenta* larvae feed on the foliage of swallow-worts causing similar defoliation as monarch larvae feeding on milkweeds, therefore, their presence may act as a deterrent for monarch oviposition. To test this hypothesis, we conducted a 2-year field study where naturally occurring monarch butterflies in lower Michigan were presented with common

milkweed and pale swallow-wort plants with and without *H. opulenta*. In addition, we evaluated host choice of laboratory-reared monarchs between common milkweed and black swallow-wort plants which were either free of or attacked by *H. opulenta*.

Materials and Methods

Field Experiments 2019–2020

To assess the preference of monarchs for laying eggs on pale swallow-wort and to test whether the oviposition choices of females would be influenced by the presence of *H. opulenta* on swallow-wort, open field tests were conducted over two years on the south campus of Michigan State University (MSU). Field sites were located in a range of environments including along forest edges, agricultural fields, experimental orchards, and near open fields. At each field site, common milkweed and egg-laying monarchs were present, which was confirmed by checking naturally growing common milkweed plants for monarch eggs. There are no known naturally occurring pale swallow-wort infestations in this area. A small (ca. 10m²) black swallow-wort infestation can be found 7–10 km from the field sites. In 2019, potted plants representing three treatments were placed at six locations on 8 August 2019 (Supp Table S1 [online only]). The treatments were 1) common milkweed (control), 2) noninfested pale swallow-wort, and 3) pale swallow-wort infested with *H. opulenta*. At each location, four potted plants per treatment were arranged in groups, 2–3 m apart, to mimic small patches of milkweed or swallow-wort.

For the milkweed control, common milkweed (*Asclepias syriaca* L.) was used that had been grown from seed at Wildtype Native Plant Nursery in Mason, MI in spring 2019. Plants were transplanted into 11 L plastic pots in June 2019 using SUREMIX perlite potting media. For the swallow-wort treatments, pale swallow-wort plants were used that had been collected from an infestation in Holly, MI (N 42°84'62, W 83°41'28) in July 2019 and transplanted to either 7.5- or 19 L plastic pots to accommodate different plant sizes. Milkweed treatments had one or two stems, and swallow-wort treatments had two to four stems per pot. For the experiments, two of the 7.5 L and two of the 19 L pots were used at each site for each swallow-wort treatment. The biological control agent, *H. opulenta*, was reared in the laboratory on black swallow-wort. For the treatment of pale swallow-wort with *H. opulenta*, groups of four plants were infested with eight 3rd to 5th instar *H. opulenta* larvae (two larvae per plant) and 12 adults in 61 cm x 61 cm x 142 cm mesh cages (BioQuip Products, Inc. Rancho Dominguez, CA) for 48 h. After infestation, the adults were removed, and eggs were confirmed to be present on at least one of the plants from each of the cages prior to being set out in the field. Larval feeding by *H. opulenta* left clear feeding marks and frass on the plants. The late instar larvae were not removed from plants upon deployment to the field and were observed occasionally throughout the experiment. Detection can be difficult since larger larvae tend to drop to the ground when the plants are inspected. As eggs hatched, early instar larvae were also seen on the plants during the experiment.

Plants were set out in the field on 9 August and were watered and monitored daily between 4 and 7 pm for monarch eggs until 22 August 2019. The number of eggs found was recorded and then removed from the plants so they would not discourage future monarch oviposition.

In 2020, this field experiment was repeated with some changes to the experimental design. We aimed to increase the visible feeding damage and the number of larvae on the swallow-wort plants compared to 2019 levels by increasing the feeding and oviposition period of *H. opulenta* from 2 d to 15–20 d in 2020. Unfortunately, by the

time the higher level of infestation was achieved, monarch oviposition ceased in the field, and we were unable to test if it would have had greater deterrence. Hence, only common milkweeds and pale swallow-worts without *H. opulenta* were used. The number of field sites was increased from six to fifteen (Supp Table S1 [online only]), and at each field site the number of plants used in each treatment was reduced from four to two. These changes were implemented to increase exposure of the different treatments to monarchs, and to potentially increase the power for statistical analyses.

Potted common milkweed plants that over-wintered outside were reused in 2020. Half of the pale swallow-wort plants were reused and new plants were collected in 2020 to replace the other half. To standardize the age and size of plants, for each treatment at each field site one of the pale swallow-wort plants used was collected in 2020 and the other in 2019. Common milkweed plants and noninfested pale swallow-wort plants were set out to the field on 6 August. The presence of monarch eggs was monitored daily until 14 August 2020. All monarch eggs found were removed.

Laboratory Experiment

To test the affinity of monarchs to lay eggs on black swallow-wort and to assess how the presence of *H. opulenta* on black swallow-wort may influence monarch oviposition, choice and no-choice experiments were conducted in the laboratory in 2019. In the no-choice experiments, 2 female monarchs and 1 male were provided either with one common milkweed plant or with one black swallow-wort plant. For both of these treatments, an additional pea plant (*Pisum sativum* L.) was placed in the cages following the protocols of Casagrande and Dacey (2007) to test for potential egg dumping on a nonrelated plant, which may occur when monarch oviposition choices are limited. In the choice experiments, 2 female monarchs and 1 male were caged with one milkweed and one black swallow-wort plant or with one milkweed and one black swallow-wort infested by *H. opulenta*. Each of the above four treatments was replicated four times with the experimental cages arranged in a completely randomized design.

Plants for the choice tests where black swallow-worts had to be infested by *H. opulenta* were prepared by placing 16 3rd to 5th instar larvae and 12 adults on groups of four plants in a 60 cm x 60 cm x 60 cm domed mesh cage (Bioquip) for 24-h. There were eggs and at least two *H. opulenta* larvae on all black swallow-wort plants used for this treatment. Common milkweed plants were grown from seed in spring 2019 by Wildtype Native Plant Nursery in Mason, MI and potted into 11 L pots. Black swallow-wort plants were collected as rootstock in spring 2018 from an infestation on MSU campus in East Lansing, MI and potted into 1.3 L plastic pots. Potted plants were kept in a greenhouse during the summer months and placed outside for the winter of 2018/2019. Overwintering plants were moved back into the greenhouse in April 2019. Monarch butterflies used for the experiment originated from a colony at MSU that was established using monarch eggs collected in the area in May 2019. Monarchs were reared for two generations on common milkweed prior to the start of the experiment. For the rearing, larvae were fed cut milkweed stems in 42 cm x 33 cm x 17 cm plastic containers (Gordon Food Service, Wyoming, MI) that were placed on bench tops under natural daylight conditions in a laboratory that was kept at ambient temperatures. Pupae were moved to mesh mating cages (Educational Science) (75 cm x 75 cm x 115 cm) and emerging adults were supplied with fruit punch flavored Gatorade via a cotton wick inserted into a 60 ml cup (Gordon Food Service, Wyoming, MI). Adults were approximately 14 d old at the start of experiments.

The experiment was conducted between 16 and 23 August 2019 by checking all plants daily for monarch eggs. Every day, monarchs

that died were removed and replaced with a living monarch of the same sex. Eggs were counted and removed each morning.

Statistical Analyses

All analyses were conducted in R version 3.6.1 (R Core Team, 2019). Monarch eggs recorded at each site were summed within treatments, and sites where no monarch eggs were recorded were excluded from analyses. To assess whether plant treatment (milkweed, swallow-wort, or swallow-wort with *H. opulenta*) was a significant predictor of monarch oviposition a generalized linear model with a Poisson distribution was used. The full model containing treatment and site as explanatory variables and a null model with only site as a predictor were compared using a likelihood ratio test to assess if plant treatment had a significant effect. Pairwise differences between treatments were assessed with the 'emmeans' package version 1.5.2-1 (Lenth, 2020) and were examined for the 2019 data. Data for 2019 and 2020 were analyzed separately. Data for the laboratory experiment did not undergo statistical tests since all monarch eggs were laid on milkweeds only.

Results

Field Experiments 2019 and 2020

Monarchs laid significantly more eggs on common milkweed than on pale swallow-wort either with or without *H. opulenta* both in 2019 ($F_2 = 8.403$; $P = 0.0002$) and in 2020 ($F_1 = 13.645$; $P = 0.0002$) (Fig. 1). One site was excluded from analyses in 2019 and five sites in 2020 because no monarch eggs were laid on any of the experimental plants. There were no significant differences in the number of eggs laid at the different sites in 2019 or in 2020 (2019: $F_4 = 2.16$, $P = 0.071$, 2020: $F_9 = 1.69$, $P = 0.083$). The models that included plant treatment predicted the data better than without treatment in both years (2019: $P = 3.588\text{e-}05$, 2020: $P = 1.452\text{e-}17$). In total, 21 eggs were laid on milkweeds, 4 on swallow-worts without *H. opulenta* constituting 14.3% of eggs laid, and 3 on swallow-worts with *H. opulenta* making up 10.7% of the total eggs laid across all field sites in 2019 (Fig. 2). There was no difference in the number of eggs laid on swallow-worts without and with *H. opulenta* present (pairwise contrast: $P = 0.925$). In 2020, 42 eggs were laid on common milkweed, one egg on pale swallow-wort without *H. opulenta* (2.3% of all eggs) and no eggs were laid on pale swallow-wort with *H. opulenta* (Fig. 1). The number of eggs laid on pale swallow-wort without *H. opulenta* was significantly lower than on common milkweed (pairwise contrast: $P = 0.0002$).

Laboratory Experiment

A total of 1,315 monarch eggs were laid on common milkweed over the course of this experiment with a daily average of 13.7 per plant. No eggs were laid on any black swallow-wort plants regardless of whether *H. opulenta* was present or not. No eggs were laid on the pea control plants either.

Discussion

Our field experiments showed that monarchs strongly prefer common milkweed over pale swallow-wort, nevertheless they still laid up to 25% of their eggs on swallow-worts. We did not find evidence that the presence of the biological control agent, *H. opulenta* on swallow-worts would deter oviposition by monarch butterflies. Our field experiments utilized monarchs naturally present in the area exhibiting their innate host searching and host acceptance behaviors,

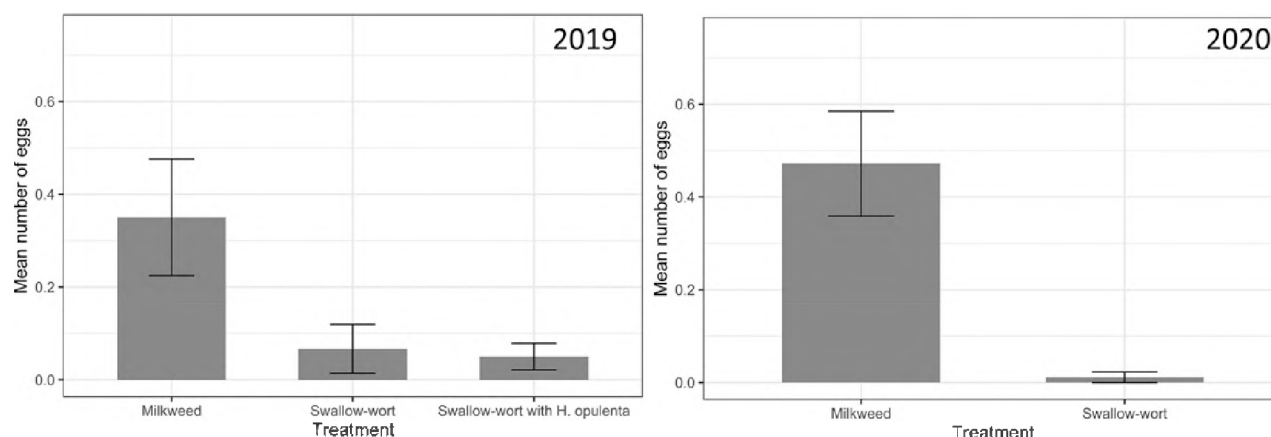


Fig. 1. Mean number of monarch butterfly eggs laid at each site daily over the course of the experiment (nonmodel mean \pm SE) in 2019 (left) and in 2020 (right) on experimental common milkweed plants and on pale swallow-worts that were either infested or not with *H. opulenta*.

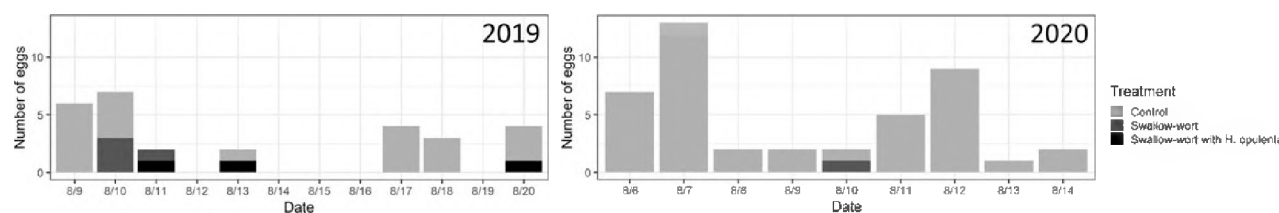


Fig. 2. Number of eggs laid daily by monarch butterflies on common milkweed (control), pale swallow-wort and pale swallow-wort plants infested with the biocontrol agent *H. opulenta* in 2019 (left) and 2020 (right) in an open field experiment. Egg counts for each day represent sums across all field sites. Note, the treatment of "swallow-wort with *H. opulenta*" were not applied in 2020.

and thus provide a realistic assessment of their oviposition choices. In 2019, monarchs laid 14.3% of their eggs on pale swallow-wort plants that were free of heterospecific herbivores and a similar portion, 10.7% of eggs on pale swallow-worts with *H. opulenta* feeding and larvae present. These results suggest that the presence of the foreign *H. opulenta* that monarchs have not previously encountered may not elicit the same response as the presence of a conspecific larva, which was found to dissuade monarch oviposition on swamp milkweeds (Jones and Agrawal 2019). However, it should be noted that a subtle effect *H. opulenta* may have had on monarch oviposition would have been difficult to detect given that the number of monarch eggs laid on pale swallow-wort plants without *H. opulenta* was relatively low.

Interspecific competition is known to be important in shaping species interactions among phytophagous insects (Kaplan and Denno 2007, Denno et al. 1995), and the likelihood of competition deterring oviposition has been well documented in a range of insects, particularly in Lepidopterans (Schoonhoven 1990, Vasconcellos-Neto and Monterio 1993, Honda 1995, Hilker and Meiners 2008, Jones and Agrawal 2019). For example, the confused tiger wing butterfly, *Mechanitis lysimnia* (Fabricius, 1793) (Lepidoptera: Nymphalidae) will adjust the number of eggs laid based on plant size and the presence of conspecifics to avoid intraspecific competition (Vasconcellos-Neto and Monterio 1993). The presence of conspecific or heterospecific larvae may also act as a deterrent by leaving feeding marks and frass on the plants (Ditrick et al. 1983, Mitchell and Heath 1985, Renwick and Radke 1980, Hilker and Klein 1989, Nufio and Papaj 2001). In our experiment, the swallow-wort plants were infested by both *H. opulenta* larvae and egg-laying adults, and thus had visible feeding marks and both early and later instar larvae ($n < 5$) when they were presented to monarchs in the field. Despite

these cues indicating the presence of a possible competitor monarchs still laid similar numbers of eggs on these plants than on nonattacked swallow-wort plants.

Our results corroborate findings from Rhode Island, where depending on the year of survey, 0–15.4% of monarch eggs were found on black swallow-wort in field sites where both common milkweed and black swallow-worts grew in mixed stands (Casagrande and Dacey 2007). Both in our potted plant study in Michigan and in the field surveys in Rhode Island, monarchs showed a clear preference for common milkweed, yet in some years still laid a nontrivial portion of their eggs on black or pale swallow-worts, especially at sites where common milkweed densities were relatively low and black swallow-wort densities were high (Casagrande and Dacey 2007). At our study sites in East Lansing in Michigan, the reverse was true, with swallow-worts being rare and common milkweeds being more common in the area where the experiments took place. Despite the higher availability of common milkweed relative to black swallow-worts, monarchs still laid a total of 25% of their eggs between the two swallow-wort treatments in 2019 and 2.3% of their eggs in 2020 on swallow-worts. Annual variation in monarch egg counts on swallow-worts is expected as there can be natural variation in monarch densities (Casagrande and Dacey 2007).

It is possible that our experiment underestimated the proportion of monarch eggs that may be laid on pale swallow-worts. The experiment took place late in the season, in August, when both swallow-worts and naturally growing milkweed plants in the area begin to senesce. Our potted common milkweeds were younger, and thus likely attracted higher rates of monarch oviposition compared to the naturally growing older common milkweeds (Haan and Landis 2019). In addition, the pale swallow-wort plants used

were field-collected and were close to setting seed which may have made them less desirable for oviposition. This could have inflated the number of monarch eggs found on our experimental milkweed plants and skewed the proportion of eggs found on swallow-worts.

Monarchs laid all their eggs on common milkweed and none on black swallow-wort in our choice and no-choice laboratory experiments regardless of whether *H. opulenta* was present or not. These results align well with those of DiTommaso and Losey (2003) who also did not find oviposition on black or pale swallow-worts in cage choice test, while Mattila and Otis (2003) found minimal (0.5%) egg laying of monarchs on pale swallow-wort in a choice test. In contrast, monarchs were shown to lay 20.3% of their eggs in a no-choice and 21.7% in a choice laboratory experiment on black swallow-wort, and 11.2% in a no-choice and 7.9% in a choice experiment on pale swallow-wort (Casagrande and Dacey 2007). The reason for this discrepancy likely lies in the source of monarchs used in the different experiments. Casagrande and Dacey (2007) pointed out that experiments that used wild-caught monarchs found oviposition and those where monarchs were reared in the laboratory did not find oviposition on swallow-worts, and that the source of populations of monarchs might also play a role. Monarchs can alter their oviposition choices based on experience, and prior exposure to an alternative host can increase the likelihood of accepting this host for oviposition in the future (Jones and Agrawal 2019). The monarchs we used had been reared in the laboratory for multiple generations on common milkweed, without exposure to alternate host or nonhost plants, which could account for why they did not lay any eggs on black swallow-wort. It seems clear now from all the above experiments that the source of monarchs can change the outcome of tests and that only field-collected individuals should be used in future studies evaluating their oviposition choices.

Our results provide additional evidence that swallow-worts may serve as oviposition sinks for monarchs (Casagrande and Dacey 2007). In addition, we found that the presence of a potential competitor in the form of the foliage feeder biological control agent *H. opulenta* may not be enough to deter monarchs from laying eggs on this non-host plant. However, additional, larger-scale studies are needed to confirm the role *H. opulenta* may play in the long-term on monarch oviposition. Biological control of swallow-worts is still in the early stages in North America, with *H. opulenta* establishment confirmed only at a few locations in Canada (Bourchier et al. 2019, Livingstone et al. 2020). As *H. opulenta* populations expand geographically and grow in density with increasing feeding damage and exposure to monarchs the interactions between these species may change over time.

Supplementary Data

Supplementary material is available at *Environmental Entomology* online.

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