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# Monarch butterfly (*Danaus plexippus*) oviposition preference on native milkweeds (*Asclepias*) of the northern Great Plains

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## Abstract

Milkweed (*Asclepias* ssp.) has faced population declines in the Northern Great Plains for several decades due primarily to agricultural conversion. Monarch butterflies (*Danaus plexippus*), which rely on milkweed as the host plant for their larva, have also declined in population throughout the past several decades in North America. Amidst ongoing efforts to protect the monarch butterfly by restoring milkweed populations, the relationship and preferences that monarchs may have for specific milkweed must be better understood. The objective of this study was to investigate monarch oviposition preferences on 18 species of milkweed native to the Northern Great Plains. In a common garden plot, 18 species of milkweed were planted in a randomized block design and assessed throughout the growing season for the presence of monarch eggs and larva. Additional data were collected on plant morphological characteristics to examine whether ovipositing monarchs preferred certain traits over others. The total number of eggs and larva found on plants within each species were used as response variables to determine monarch oviposition preference between species. Monarchs laid the most eggs on *Asclepias incarnata* throughout all three years of data collection, followed by *Asclepias syriaca*, *Asclepias speciosa*, and *Asclepias sullivantii* in 2022 and *A. syriaca*, *A. sullivantii*, and *Asclepias subverticillata* in 2023. Oviposition did not necessarily correlate to larval presence, suggesting higher survival rates on some species than others, such as *A. subverticillata*, which may serve as an ecological trap for monarchs, and *A. sullivantii*, which had a higher ratio of larvae to eggs, suggesting better chances of survival. Our site did not provide ideal conditions for every species of milkweed in this study, so species such as *Asclepias exaltata* may be more appealing to monarchs in different locations.

**KEYWORDS**
coevolution, ecological restoration, habitat, insect behavior, milkweed, monarch butterfly, oviposition

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## INTRODUCTION

Monarch butterflies (*Danaus plexippus*) are a highly charismatic species of butterfly known for their migration from breeding ranges in the United States and Canada to their overwintering site in the Oyamel fir forests of Michoacán, Mexico and southern California (Vidal & Rendón-Salinas, 2014). Despite ongoing monarch conservation efforts, monarch butterflies have faced steep population declines over the past 50 years (Thogmartin et al., 2017). In North America, the smaller western population of monarch butterflies that overwinters at locations throughout southern California is geographically separated from the eastern population, but both populations are experiencing similar population declines (Freedman et al., 2021; Schultz et al., 2017). The eastern population of monarch butterflies reached their second-lowest overwintering population in Mexico during the 2023–2024 winter season, a 59% decrease from the previous year and an overall 80% decrease since 1999 (Rendón-Salinas et al., 2024). The long-term survival of migratory monarch butterflies in North America is dependent on understanding the reasons for the population declines and identifying the most effective and efficient method to bolster monarch butterfly populations (Agrawal, 2017, 2019).

Three main hypotheses of monarch population decline have gained traction over time, each of which has different management implications (Zaya et al., 2017). The first hypothesis is that the loss of overwintering habitat increases mortality rates throughout the winter, so fewer initial butterflies travel north in the spring (Snook, 1993). Monarch butterflies are protected in Mexico, but illegal logging operations have significantly reduced overwintering habitat (Brower et al., 2002; Honey-Rosés, 2009). The second hypothesis is that the loss of available nectar sources due to habitat conversion and fragmentation on the migratory routes reduces the initial number of monarchs that arrive in Mexico to overwinter (Berenbaum, 2015; De Roode et al., 2008; Inamine et al., 2016; Steffy, 2015). The third hypothesis is that the loss of milkweeds, the only host plant of monarch butterflies, reduces population recruitment throughout the summer breeding season for monarchs (Boyle et al., 2019; Pleasants & Oberhauser, 2012; Saunders et al., 2019). None of these hypotheses are mutually exclusive, but improving or creating habitat by planting milkweed for monarchs addresses issues identified by hypotheses 2 and 3 and has gained traction in popular media and governmental initiatives (Roach, 2023; USFWS, 2020; White House, 2015).

With widespread grassland conversions to corn (*Zea mays*) and soy (*Glycine max*), monarch breeding habitat in the midwestern region of the United States is particularly imperiled (Conant et al., 2018; Plourde et al., 2013; Wright & Wimberly, 2013). The increased use of pesticides has been implicated in monarch population decline, but evidence suggests that habitat conversion has been impacting eastern monarch butterfly populations since the 1950s, before their widespread use (Boyle et al., 2019; Pleasants, 2017). Like much of the Midwest, eastern South Dakota consists of predominantly agricultural land where milkweed was once much more abundant on the landscape (Pleasants & Oberhauser, 2012). From 1999 to 2012, the midwestern region of North America experienced a 71% decline in monarch support capacity or the ability to provide forage for monarch larvae (Pleasants & Oberhauser, 2012).

Determining which species of milkweed monarch butterflies prefer to oviposit on will aid efforts to support the eastern population of monarch butterflies. Nineteen species of milkweed occur in the northern Great Plains region of the United States (South Dakota, North Dakota, and Minnesota; Table 1). Some of these species have a low tolerance to disturbance and are found primarily in remnant prairies (*Asclepias amplexicaulis*, *Asclepias purpurascens*, Biota of North America Program [BONAP] Plants Database, http://bonap.net/Napa/TaxonMaps/Genus/County/Asclepias), and others are highly disturbance tolerant (*Asclepias syriaca, Asclepias incarnata*). Additionally, some species require more moisture than others, such as *Asclepias exaltata*, whereas others can be found in southwestern climates including Arizona and New Mexico and require less precipitation to thrive (*Asclepias arenaria*, *Asclepias latifolia*; BONAP Plants Database, http://bonap.net/Napa/TaxonMaps/Genus/County/Asclepias). Among these 19 species, there is height variation from less than half a meter to nearly two meters tall, floral color variation, and adapted habitat preference variation in soil, precipitation, and sun conditions (Baker & Potter, 2018; Borders & Lee-Mäder, 2015; Woodson, 1954). The different milkweed species also possess a wide range of other morphological and chemical characteristics, including trichome density, number of stems, cardenolide content, and growth pattern, all of which can influence monarch oviposition and larval survival (Agrawal & Fishbein, 2008; Agrawal et al., 2008; Cohen & Brower, 1982; Jones & Agrawal, 2019; Zalucki & Kitching, 1982).

Plant chemical characteristics that influence monarch preference have been quantified in a subset of our milkweed species. Specifically, cardenolide concentration, which is the cardiac glycoside that monarch caterpillars have adapted to sequester, has been measured (Agrawal et al., 2008, 2012; Brower et al., 1967; Cohen & Brower, 1982). Because plant defensive chemicals can be produced at higher rates due to factors such as herbivory or at lower rates due to factors such as lack of available

**TABLE 1** All the species identified as native to the northern Great Plains and whether they have been studied for monarch butterfly use.

| | | In SD, ND, or MN | | | Peer-review data on monarch preference | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **Abbreviation** | **USDA** | **BONAP** | **Herbaria** | **A** | **B** | **C** | **D** | **E** | **F** | **G** |
| *Asclepias amplexicaulis* | AAMP | x | x | | | | | | | | |
| *Asclepias arenaria* | AARE | x | | x | | | | | | | |
| *Asclepias engelmanniana* | AENG | | | x | | | | | | | |
| *Asclepias exaltata* | AEXA | x | x | x | x | | | x | | | |
| *Asclepias hirtella* | AHIR | x | | x | x | | | x | | | |
| *Asclepias incarnata* | AINC | x | x | x | x | x | x | x | x | x | x |
| *Asclepias lanuginosa* | ALAN | x | x | x | | | | | | | |
| *Asclepias latifolia* | ALAT | | x | x | | x | | | | | |
| *Asclepias ovalifolia* | AOVA | x | x | x | | | | | | | |
| *Asclepias pumila* | APUM | x | x | x | | | | | | | |
| *Asclepias purpurascens* | APUR | x | x | x | | | | | | | |
| *Asclepias speciosa* | ASPE | x | x | x | x | x | | x | x | | x |
| *Asclepias stenophylla* | ASTE | x | x | x | | | | | | | |
| *Asclepias subverticillata* | ASUB | | | x | | | | | | | |
| *Asclepias sullivantii* | ASUL | x | x | x | x | | | x | | | x |
| *Asclepias syriaca* | ASYR | x | x | x | x | x | x | x | x | | x |
| *Asclepias tuberosa* | ATUB | x | x | x | x | x | x | x | | | x |
| *Asclepias verticillata* | AVER | x | x | x | x | x | x | x | | | x |
| *Asclepias viridiflora* | AVIR | x | x | x | | | | | | | x |

Abbreviations: BONAP, Biota of North America Program; USDA, United States Department of Agriculture.
*Source*: A, Pocius et al. (2017); B, Baker and Potter (2018); C, Pocius, Debinski, et al., (2018); D, Pocius, Pleasants, et al., (2018); E, Ladner and Altizer (2005); F, Jones and Agrawal (2019); G, Lukens et al. (2020).

resources, different species of milkweed may be more preferential to ovipositing monarchs at different times of year or in different locations (Agrawal et al., 2022; Hahn et al., 2019; Rasmann & Agrawal, 2011; Woods et al., 2012). Other research suggests that monarch oviposition preference can be influenced by pest presence and that strategically mowing milkweed to support the growth of fresh, new leaves can increase monarch oviposition by providing more appealing foliage and decreasing competition with other milkweed herbivores (Fischer et al., 2015; Haan & Landis, 2019; Jones & Agrawal, 2019). Additionally, the role of milkweed morphological factors in monarch oviposition is unclear. For example, some studies report that monarchs preferentially oviposit on longer stems and others report that stem length or plant height does not play a significant role in monarch oviposition (Cohen & Brower, 1982; Pocius, Debinski, et al., 2018).

Only 12 species of milkweed have previously been studied for monarch oviposition preference: *A. exaltata, Asclepias fascicularis, Asclepias hirtella, A. incarnata, A. latifolia*, *Asclepias speciosa, Asclepias sullivantii, A. syriaca, Asclepias tuberosa, Asclepias verticillata, Asclepias viridis*, and *Cynanchum laeve* (Baker & Potter, 2018; Gustafsson et al., 2015; Pocius, Debinski, et al., 2018; Pocius, Pleasants, et al., 2018). Of these 12 species, only 8 have been studied in an outdoor setting, which may reflect monarch oviposition and larval success differently than laboratory experiments (Baker & Potter, 2018). Among these select species, *A. incarnata* and *A. syriaca* have been documented as the most preferred by ovipositing monarchs (Baker & Potter, 2018; Pocius, Pleasants, et al., 2018), but *A. syriaca* is significantly more common than *A. incarnata* on the landscape (Zaya et al., 2017). As a result, *A. syriaca* is hypothesized to be the most important milkweed species for ovipositing monarchs across the midwest (Zaya et al., 2017). People seeking to create monarch habitat may be hesitant to plant *A. syriaca* due to its history as a noxious weed, capacity to grow up to two meters tall, and tendency to produce shoots in undesired locations (Baker & Potter, 2018; South Dakota Weeds, 2009). Further research of monarch oviposition on a wider range of

milkweed species may provide alternatives to milkweeds that have a negative public perception for being difficult to manage in garden settings.

This experiment is designed to perform a head-to-head comparison of monarch oviposition preference among native milkweed species in the Northern Great Plains region of the United States. To investigate how different factors may influence monarch oviposition preferences, all species of milkweeds were planted in a common garden plot in a randomized block design, and data were collected on egg presence, larval presence, and milkweed morphological characteristics (stem length, number of stems, and leaf shape) throughout three years.

## MATERIALS AND METHODS

Using data from the BONAP (http://bonap.net/Napa/TaxonMaps/Genus/County/Asclepias), the United States Department of Agriculture (USDA), and Herbaria collections, we identified 19 species of milkweed that occur in Minnesota, North Dakota, and South Dakota (Table 1, Figure 1). These species have varying morphologies, native ranges, and habitat preferences. Seeds of all species were obtained commercially, except *A. amplexicaulis*, *Asclepias engelmanniana*, *Asclepias ovalifolia*, *Asclepias pumila*, and *Asclepias viridiflora*, which were collected by volunteers. BONAP North American Plant Atlas does not distinguish between *A. hirtella* and *A. longifolia*, but *A. hirtella* seeds for this study were obtained commercially. Due to the study site's location in eastern South Dakota, we limited our species list to the surrounding states (North Dakota and Minnesota). Eighteen species were used in this study because *Asclepias lanuginosa* is rare, and we were unable to obtain sufficient viable seeds for this experiment.

### Preparation and planting

Plants were started in a greenhouse in early spring. Seeds of each species were planted in RayLeach Cone-tainers in potting media (Pro-Mix Bx). Greenhouse conditions were maintained between 10 and 24°C, with ambient lighting. Pots were watered for 5 min twice a day to maintain surface moisture until the seeds germinated. After germination, the pots received 10 min of fertigation once per day until they were planted in the field. Fertigation was 67 ppm N. Throughout the spring in 2022 and 2023, all species with available seeds were grown in the greenhouse to replace plants that did not survive the previous planting or winter.

In 2021, nine species were planted in a common garden plot at the South Dakota State University (SDSU) campus in Brookings, SD: *A. arenaria*, *A. hirtella, A. incarnata, A. speciosa, Asclepias stenophylla, A. sullivantii, A. syriaca, A. tuberosa*, and *A. verticillata*. In 2022, the remaining species were planted. This area was previously under conventional row crop management and was re-dedicated for specialty crop research. The soil is Barnes clay loam with a 0%–2% slope. The area is well-drained prime farmland and is assigned a land capability class of 1 without irrigation (Soil Survey Staff, 2020). The elevation is 494 m, the mean air temperature range is 4–8°C, and the mean annual precipitation range is 48–74 cm (Soil Survey Staff, 2020). Seedlings were planted in the field in mid-May. Milkweed was planted in a randomized block design with six replicate blocks. Each block consisted of eleven 3 m × 3 m plots, and each plot contained nine individual milkweed plants of a single species. Species were randomly assigned to plots. Landscape fabric was used for weed control.

### Data collection

During the growing season, data on the milkweed plants and monarch eggs and larva were recorded. We adapted our data collection methods to account for morphological differences among milkweed species. Some species were uniform in their growth patterns, whereas others were not, such as *A. pumila*, which sometimes grew multiple branches from individual stems and other times produced individual stems with no branches. To measure the relative size of each plant, we counted the number of stems, measured the length of the longest stem, and measured the plant width (the farthest distance from one stem to another on an individual plant). To best approximate size, the maximum stem length and plant width measurement were used to represent stem length and plant width in data analysis. Each species was also categorized by general leaf shape: wide (e.g., *A. syriaca,* $n = 9$), medium (e.g., *A. incarnata,* $n = 4$), and narrow (e.g., *A. verticillata,* $n = 5$). See Table 2 for leaf shape designations and measurements across species each year. Reproductive potential was recorded as the number of flowering umbels. During the assessments, data on plant condition were also collected, and dead plants were removed from data collection unless they were replanted or regrew.

Egg and larval presence were quantified using methods from the Monarch Larva Monitoring Project from the Monarch Joint Venture (https://mlmp.org/). Monarch eggs and larvae were counted on each plant two to three times a week, every week after the milkweeds were planted to the end of the season when no




**FIGURE 1** Images of the different species of milkweed included in this study in an alphabetical order. Photo credit: G. Damiano.

**TABLE 2** Means comparisons for maximum stem length, maximum plant width, number of stems, number of blooming umbels, and leaf shape for 2021, 2022, and 2023.

| | Mean max. stem length (cm) | | | Mean max. plant width (cm) | | Mean no. stems | | | Mean no. blooming umbels | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 2021 | 2022 | 2023 | 2022 | 2023 | 2021 | 2022 | 2023 | 2021 | 2022 | 2023 | Leaf shape |
| AAMP | NA | 9.77 I | 12.04 H | 4.62 F | 9.29 H | NA | 1.15 | 1.30 | NA | 0 | 0 | W |
| AARE | 20.89 D | 26.50 D | 27.52 D | 37.63 D | 21.27 EF | 1.13 | 20.8 | 1.99 | 0 | 3.00 | 0.21 | W |
| AENG | NA | 19.57 E | 25.00 D | 10.83 EF | 19.75 FG | NA | 1.20 | 2.11 | NA | 0 | 0.79 | N |
| AEXA | NA | 14.13 G | 25.48 DE | 10.88 EF | 16.72 FGH | NA | 1.16 | 1.56 | NA | 1.75 | 0.31 | W |
| AHIR | 13.34 E | 17.73 EF | 12.41 H | 14.97 EF | 11.13 H | 1.04 | 1.25 | 1.44 | 0 | 1.59 | 0.01 | M |
| AINC | 90.55 A | 49.55 B | 87.49 A | 82.01 B | 67.09 A | 1.11 | 5.57 | 6.50 | 0.07 | 13.4 | 20.59 | M |
| ALAT | NA | 16.00 FG | 14.35 FGH | 15.10 EF | 17.60 FGH | NA | 1.05 | 2.60 | NA | 1.8 | 0.02 | W |
| AOVA | NA | 14.63 FG | 24.64 DEF | 11.03 EF | 22.88 DEF | NA | 1.12 | 3.14 | NA | 0 | 0.27 | W |
| APUM | NA | 14.14 G | 13.70 H | 17.96 E | 30.54 D | NA | 2.54 | 27.45 | NA | 6.47 | 7.86 | N |
| APUR | NA | 10.45 HI | 15.63 GH | 7.73 EF | 13.15 GH | NA | 1.02 | 1.23 | NA | 0 | 0.03 | W |
| ASPE | 55.64 B | 54.74 A | 62.25 B | 118.05 A | 49.36 B | 1.31 | 5.85 | 3.50 | 0 | 8.00 | 0.70 | W |
| ASTE | 18.10 DE | 25.76 D | 22.24 DEFG | 35.66 D | 20.44 EFG | 1.22 | 2.54 | 1.90 | 0 | 4.93 | 0.45 | N |
| ASUB | NA | 28.35 D | 16.58 EFGH | 32.96 D | 16.85 FGH | NA | 5.81 | 5.84 | NA | 10.61 | 0.49 | N |
| ASUL | 17.30 DE | 32.32 C | 53.37 C | 32.26 D | 41.05 C | 1.01 | 1.71 | 3.25 | 0 | 1.83 | 0.52 | W |
| ASYR | 57.39 B | 46.35 B | 82.91 A | 81.29 B | 70.29 A | 1.12 | 5.33 | 4.14 | 0 | 8.95 | 1.64 | W |
| ATUB | 40.91 C | 26.15 D | 24.11 DEFG | 63.97 C | 29.23 DE | 1.15 | 6.85 | 5.19 | 0.22 | 20.89 | 2.29 | M |
| AVER | 40.11 C | 33.96 C | 28.77 D | 80.16 B | 29.15 D | 1.60 | 18.08 | 17.39 | O | 17.51 | 6.79 | N |
| AVIR | NA | 13.84 GH | 16.96 EFGH | 6.55 F | 13.13 GH | NA | 1.23 | 1.42 | NA | 0 | 0.03 | M |

*Note*: Leaf shape designations: W, wide; M, medium; N, narrow. Measurements in the same column with the same letter are not significantly different from one another. "NA" indicates that measurements were not taken that year because the species was not present in the study. Plant width was not measured in 2021. See Table 1 for explanations of species abbreviations.

eggs were recorded for seven consecutive days, indicating that oviposition had ceased. The instar, or period between molts, was also recorded for each monarch larva found. Every leaf, stem, and flower was searched for monarch eggs and larvae on each plant every three days for the growing season.

## Data analysis

Because monarch butterflies typically lay only one egg per plant and larval survival rates are low, eggs and larvae are infrequent, resulting in many zeros in the data set. Appropriately, a zero-inflated Poisson (ZIP) regression was used to analyze egg and larval presence. Response variables include total monarch abundance by life stage (egg, larva). Explanatory variables include milkweed species, aspects of plant morphology (number of flowering heads, number of stems, stem length, leaf type), and date. Date was treated as a continuous predictor. Means were compared for egg and larval counts and morphological measurements between species using a one-way ANOVA. Because 2021 only contained nine species of milkweed, data were analyzed separately for all three years of study. Data were analyzed in JMP Pro 17 (JMP, version 17, SAS Institute, Cary, North Carolina, USA). Since monarch larvae take approximately two weeks to pupate, a single larva in this study could be counted four to six times. An egg, which takes 3–5 days to hatch, could be counted once or twice. Accordingly, this study tracked abundance, not individuals, so the number of eggs and larvae is not only a reflection of monarch oviposition preferences but also of egg and larva survival and larval movement.

The role of morphological characteristics (stem length, width, stem count, number of blooming umbels, and leaf shape) was determined by grouping species with similar morphologies together to test the null hypothesis that ovipositing monarchs searching for a certain characteristic would lay similar amounts of eggs on all species with that characteristic. For example, if monarchs prefer to lay eggs on medium-leaf species, then the hypothesis that there is no significant difference in oviposition between all medium-leaf species in this study would be

supported by statistically similar egg counts on all species with medium leaves. Morphology was analyzed separately for each year, and means were compared using one-way ANOVA. Morphology was not analyzed for larval counts due to the dependence of larval presence on oviposition.

## RESULTS

A ZIP regression showed that the interaction of milkweed species, date, and year was a significant predictor of the number of eggs ($\chi^2 = 51.531$, $p < 0.0001$, df = 17) and larvae found per plant ($\chi^2 = 72.417$, $p < 0.0001$, df = 17) overall. *A. incarnata* received the most eggs in all three years of the study, followed by *A. speciosa* and *A. syriaca* in 2021 and 2022 and *A. syriaca* and *A. subverticillata* in 2023 (Figure 2). *A. incarnata* also had the most larvae in all three years of data collection, but the other species with the most larvae changed over time. The interaction effects of date with species and year with species were also significant for eggs ($\chi^2 = 147.521$, $p < 0.0001$, df = 17; $\chi^2 = 149.907$, $p < 0.0001$, df = 17) and larvae ($\chi^2 = 74.609$, $p < 0.0001$, df = 17; $\chi^2 = 37.057$, $p = 0.003$, df = 17). Accordingly, data were analyzed separately for each year of the study.

### 2021

Date ($\chi^2 = 6.419$, $p = 0.0113$, df = 1) and species ($\chi^2 = 1.384e+23$, $p < 0.0001$, df = 8) were significant predictors of egg counts throughout the season, but the interaction of date and species ($\chi^2 = 0.837$, $p = 0.991$, df = 8) was not. The mean number of eggs per plant peaked on 7/19/2021 with a mean of 0.122 eggs per plant overall (Figure 3A). Cumulatively during 2021, *A. incarnata* received the highest mean number of eggs per plant, followed by *A. syriaca* and *A. speciosa* (Figure 2A).

Date ($\chi^2 = 7.65$, $p = 0.006$, df = 1) and species ($\chi^2 = 86.83$, $p < 0.0001$, df = 8) were significant predictors of larval counts in 2021, but the interaction of date

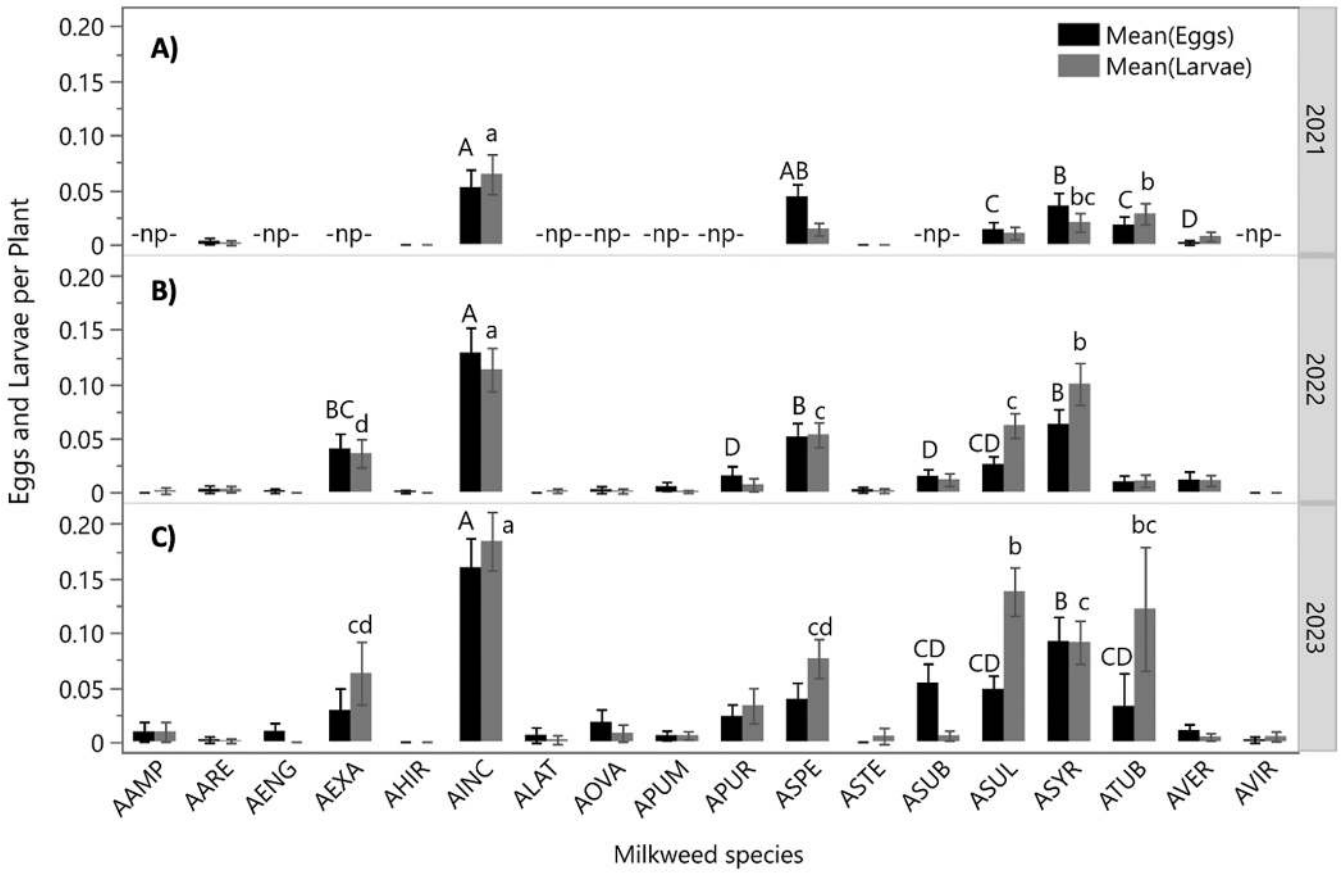



**FIGURE 2** The cumulative number of eggs and larvae per plant per species for (A) 2021, (B) 2022, and (C) 2023 (mean ± SE). Means were compared to level D, d, and not lower for clarity purposes. Uppercase letters represent means for eggs, and lowercase letters represent means for larvae. "-np-" Indicates no plant or that this species was not planted in 2021. See Figure 1 for explanations of species abbreviations.

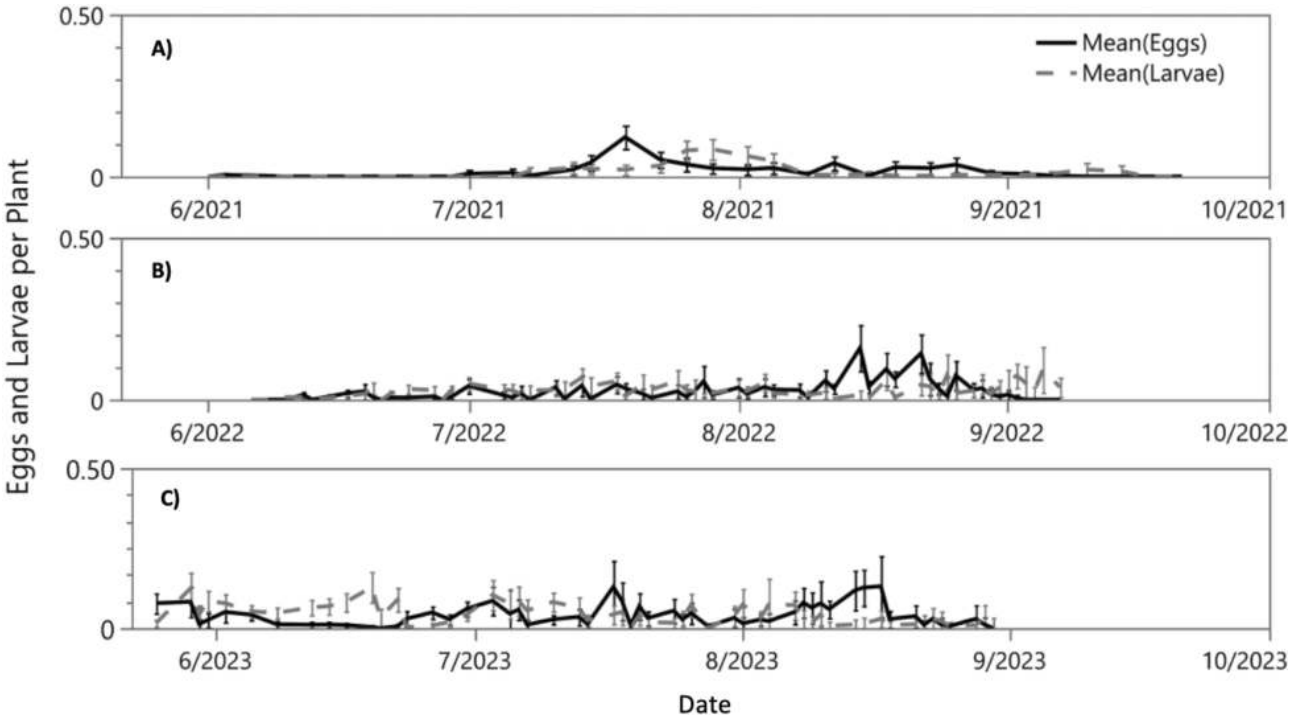



**FIGURE 3** Numbers of eggs counted per plant per day for all milkweed species throughout 2021, 2022, and 2023 (mean ± 95% CI).

and species ($\chi^2 = 4.94$, $p = 0.764$, df = 8) was not. The first larva of the season was found on 7/8/2021, and the mean number of larvae found per plant peaked on 7/29/2021 at a mean of 0.084 larvae per plant overall (Figure 3A). Over the course of the season, *A. incarnata* had the highest mean number of larvae per plant, followed by *A. tuberosa* and *A. syriaca* (Figure 2A).

## 2022

Milkweed species was a significant predictor of egg counts ($\chi^2 = 283.098$, $p < 0.0001$, df = 17), but not date ($\chi^2 = 0.0002$, $p = 0.989$, df = 1). However, the interaction of date and milkweed species was a significant predictor of egg counts ($\chi^2 = 51.483$, $p < 0.0001$, df = 17). Cumulatively over the course of the growing season, *A. incarnata* received the highest mean number of eggs per plant overall, followed by *A. syriaca, A. speciosa*, and *A. exaltata* (Figure 2B). The first egg was found on 6/12, and oviposition continued until 9/1. Monarchs laid significantly more eggs on *A. syriaca* than on *A. incarnata* until mid-July, indicating monarch preference for *A. syriaca* early in the season and *A. incarnata* later in the season (Figure 4). No eggs were found on *A. exaltata* until 7/19/2022.

Similar to eggs, milkweed species was a significant predictor of larval counts ($\chi^2 = 303.942$, $p < 0.0001$, df = 17), but not date ($\chi^2 = 0.0001$, $p = 1$, df = 1). However, the interaction of date and species was a significant predictor of larval counts in 2022 ($\chi^2 = 45.147$, $p < 0.0001$, df = 17). Over the course of the growing season, *A. incarnata* and *A. syriaca* received the highest number of mean larvae per plant, followed by *A. sullivantii* and *A. speciosa* (Figure 2B). Although *A. incarnata* and *A. syriaca* amassed a statistically similar total number of larvae by the end of data collection, significantly more larvae were found on *A. syriaca* than on *A. incarnata* until mid-July, and larval counts between the two species remained similar after mid-July until the last two weeks of data collection, when significantly more larvae were found on *A. incarnata* than on *A. syriaca* (Figure 4). Additionally, significantly more larvae were found on *A. speciosa* than on *A. syriaca* until 6/29 (Figure 4). More eggs were found on *A. speciosa* than on *A. sullivantii* until 7/21/2022 (Figure 4). No larvae were found on *A. exaltata* or any newly planted species until 7/22 (Figure 4).

## 2023

Milkweed species was a significant predictor of egg counts ($\chi^2 = 4.582e{+}18$, $p < 0.0001$, df = 17), but not date ($\chi^2 = 0.236$, $p = 0.627$, df = 1). The interaction of date and species was a significant predictor of egg counts in 2023 ($\chi^2 = 4.582e{+}18$, $p < 0.0001$, df = 17). Overall, *A. incarnata* had the highest number of mean eggs per

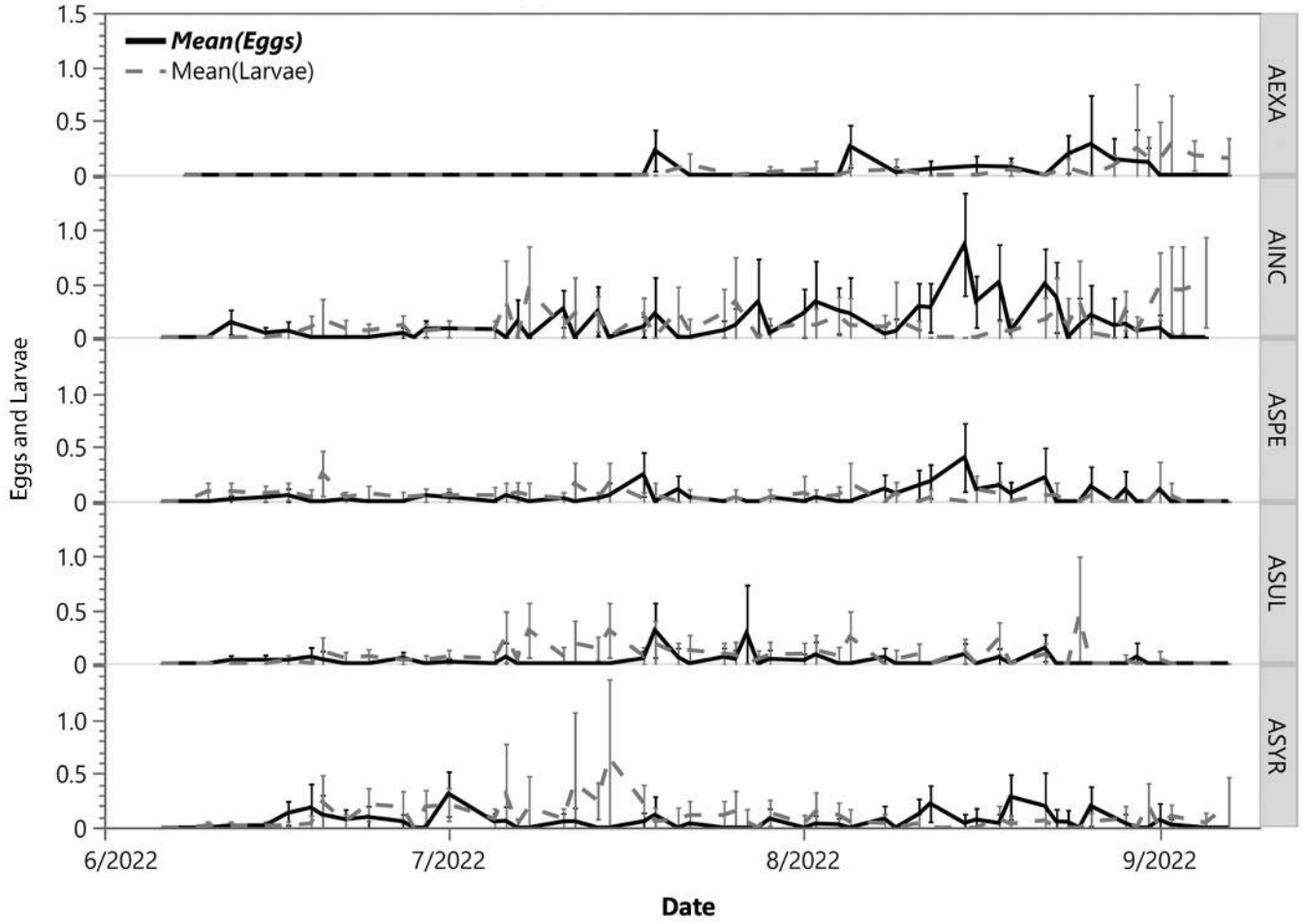



**FIGURE 4** Numbers of eggs and larvae per plant per day for *Asclepias exaltata*, *Asclepias incarnata, Asclepias speciosa*, *Asclepias sullivantii*, and *Asclepias syriaca* in 2022 (mean ± 95% CI). The gray dashed line represents larvae, and the black line represents eggs.

plant by the end of the season, followed by *A. syriaca*, then *A. subverticillata*, and *A. sullivantii* (Figure 2C). Oviposition began on 5/25 and continued through 8/29. In a similar trend to 2022, more eggs were found on *A. syriaca* than on *A. incarnata* until midseason (6/26, Figure 5), indicating a preference for *A. syriaca* earlier in the season and *A. incarnata* later in the season. More eggs were found on A. *speciosa* than on *A. subverticillata* until 8/18. No eggs were found on *A. subverticillata* until 7/17 (Figure 5).

Milkweed species was also a significant predictor of larval counts ($\chi^2 = 390.249$, $p < 0.0001$, df = 17), as well as date ($\chi^2 = 4.300$, $p = 0.0381$, df = 1). The interaction of date and species was a significant predictor of larval counts in 2023 ($\chi^2 = 43.117$, $p = 0.0005$, df = 17) as well. Overall, *A. incarnata* had the highest number of mean larvae per plant, followed by *A. sullivantii*, then *A. tuberosa*, and *A. syriaca* (Figure 2C). More larvae were found on *A. incarnata* than on any other species from early July to late August (Figure 5). *A. syriaca* had significantly more larval counts than *A. sullivantii* until 6/14 and *A. incarnata* until late June (Figure 5). *A. tuberosa* had the most larvae early in the season but only had one larval count after 6/8, likely a reflection of high *A. tuberosa* plant mortality in 2023.

## Morphology

Our results indicate that leaf shape has no bearing on monarch oviposition. A ZIP regression of egg counts within medium-leaf species (A. *hirtella, A. incarnata, A. tuberosa*, and *A. viridiflora*) revealed significant differences in the mean eggs per plant ($\chi^2 = 206.943$, $p < 0.0001$, df = 2). *A. hirtella*, *A. tuberosa*, and *A. viridiflora* had significantly lower egg counts than *A. incarnata*, suggesting that monarchs do not prefer medium-leaf plants; they prefer a particular species that has medium leaves. Analysis for narrow and wide leaf plants yielded similar results, with certain species within each group having significantly more eggs than others.

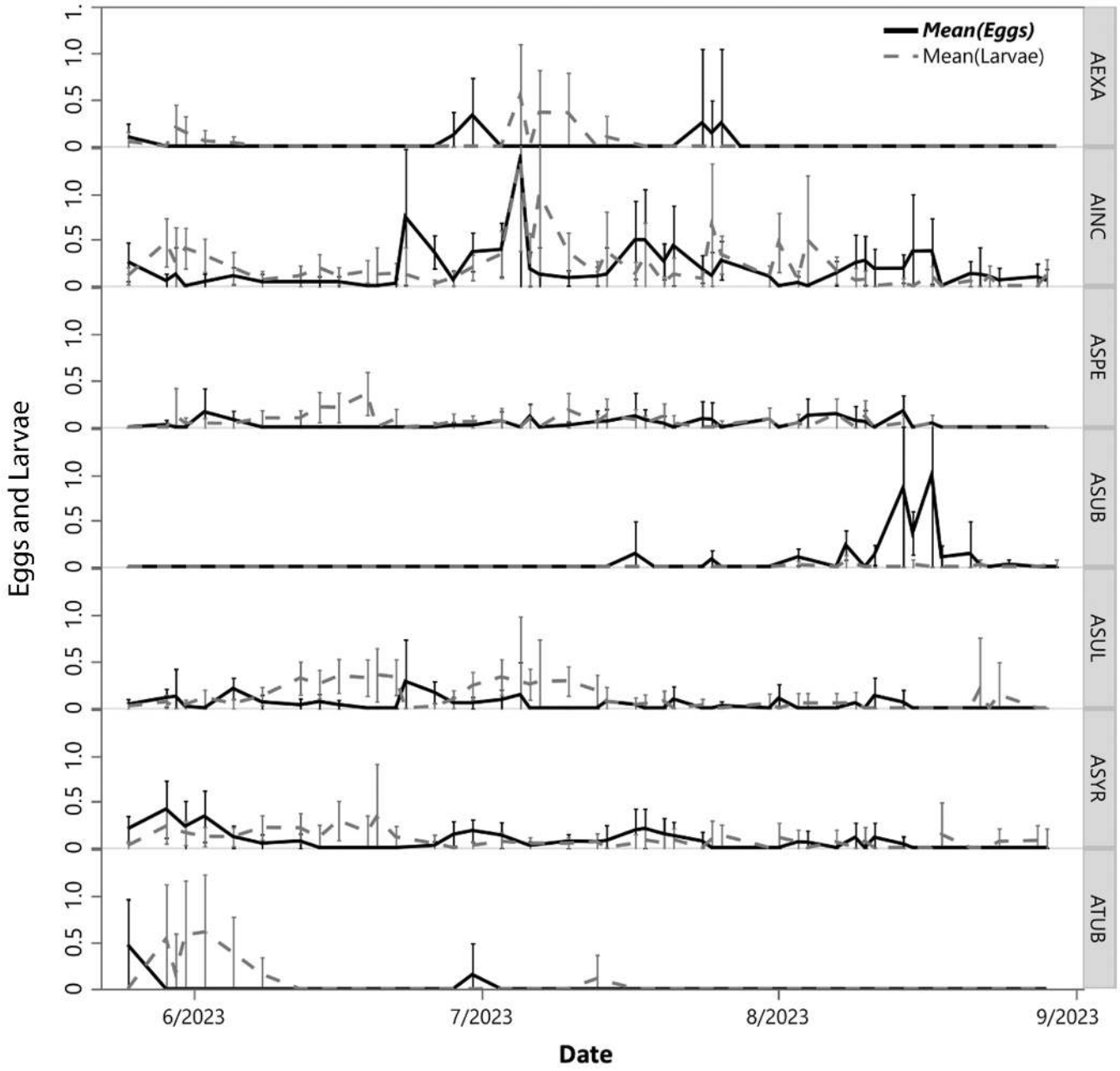



**FIGURE 5** Numbers of eggs and larvae per plant per day for *Asclepias exaltata, Asclepias incarnata, Asclepias speciosa*, *Asclepias subverticillata*, *Asclepias sullivantii*, *Asclepias syriaca*, and *Asclepias tuberosa* in 2023 (mean ± 95% CI). The gray dashed line represents larvae, and the black line represents eggs.

Our results suggest that stem length is not a factor in monarch oviposition preference. In 2021, *A. incarnata* had a significantly longer average maximum stem length (90.55 cm) than *A. speciosa* (55.64 cm), but the two species did not receive a significantly different number of eggs (Table 2, Figure 3A). Furthermore, the average maximum stem length of *A. tuberosa* (40.91 cm) was not significantly different from the average maximum stem length of *A. verticillata* (40.11 cm), but *A. tuberosa* received significantly more mean eggs per plant than *A. verticillata* (Table 2). *A. tuberosa* also had significantly longer stems than *A. sullivantii* (17.32 cm), but the two species had similar egg counts, suggesting that ovipositing monarchs may prefer to lay eggs on certain species of milkweed, rather than preferring taller plants overall. In 2023, *A. incarnata* and *A. syriaca* had similar average maximum stem lengths (87.49 and 82.91 cm respectively), but *A. incarnata* received significantly higher egg counts than *A. syriaca* (Table 2, Figure 3C). *Asclepias subverticillata* had a similar mean number of

eggs per plant to *A. speciosa* and *A. sullivantii*, but it had a significantly shorter average maximum stem length (16.58 cm) than *A. speciosa* (62.25 cm) and *A. sullivantii* (53.37 cm, Table 2). Overall, the significant differences in egg counts between species of similar maximum stem lengths and similar egg counts between species of significantly different maximum stem lengths indicate that monarchs do not prefer to oviposit on longer stems; they prefer to oviposit on certain species of milkweed.

The width of the plant was also not a factor in monarch oviposition. In 2021, *A. syriaca* and *A. incarnata* had similar average maximum widths (70.29 and 67.09 cm respectively), but *A. incarnata* had significantly higher egg counts than *A. syriaca* (Figure 3A). *A. subverticillata* had a significantly lower average maximum width (16.85 cm) than *A. speciosa* (49.36 cm), but both species had similar egg counts. Overall, our results indicate monarch preference for *A. incarnata* and *A. syriaca*, which are species that can grow wider than others, rather than monarch preference for wider plants overall. Data were analyzed for width in 2023 due to establishment challenges by newly planted species in 2022. Data on width were not collected in 2021.

Blooms: Our results indicate that the number of blooming umbels does not influence monarch oviposition. In 2023, *A. incarnata* had the highest mean number of blooms (20.59), but *A. pumila* and *A. verticillata* had the second highest mean number of blooms (7.86 and 6.79 respectively) and significantly lower egg counts than species with a significantly lower average number of blooms, such as *A. syriaca* (1.65), *A. speciosa* (0.70), and *A. sullivantii* (0.52).

Stems: The number of stems was not a significant predictor of egg counts in 2023 ($\chi^2 = 0.00292$, $df = 1$, $p = 0.957$). Data were not analyzed for 2021 and 2022 due to plant establishment struggles.

# DISCUSSION

The goal of this project was to examine monarch oviposition and larval presence on all species of milkweed native to the Northern Great Plains region of the United States. Our results agreed with prior research done on monarch oviposition preferences, namely that ovipositing monarchs prefer to lay eggs on *A. incarnata* and on *A. syriaca* (Baker & Potter, 2018; Pocius, Pleasants, et al., 2018). We also found some notable differences, namely that some species did not receive any eggs at all or, species that received a high number of eggs and relatively few larvae, suggesting that monarchs do not always choose the most suitable milkweed for their offspring. Monarchs laid more eggs on taller milkweed species, supporting the results of Baker and Potter (2018) and Cohen and Brower (1982), but it is unclear whether stem length is a morphological preference of ovipositing monarchs or whether increased oviposition on taller plants is species-driven.

## Larval and egg abundance

Our larval count data from all three years show that monarch oviposition does not necessarily reflect larval abundance. Species with more eggs would be expected to have more larvae, but we did not always find this to be the case. In 2022 and 2023, more larvae were found on *A. sullivantii* than eggs, suggesting either higher larval survival rates on *A. sullivantii* or larvae were moving to *A. sullivantii* from other species (Figure 3A,B). The higher number of larvae on *A. sullivantii* in 2022 and 2023 is interesting in light of other research on larval ontogeny, which has found lower larval survival rates on *A. sullivantii* than most of the other species they tested (Pocius et al., 2017). Our study used an outdoor field setting that may have provided factors that lab-reared monarchs or laboratory studies have not, but there is no clear reason for the relatively high larva to egg ratio on *A. sullivantii*. Our data also reflected a higher ratio of larvae to eggs on *A. tuberosa* compared to other species with more eggs, possibly due to lower latex and cardenolide concentrations in *A. tuberosa* than other milkweed species (Agrawal et al., 2012; Jones et al., 2019; Pocius et al., 2017). The number of eggs found on each plant is not only a measure of monarch oviposition but also of predation and the ability for researchers to locate them (which is more challenging on a large plant with many leaves than a small plant with few leaves). This study checked each plant every 2–4 days, leaving opportunities for eggs to be laid and predated without being recorded, and different species of milkweed may be more subject to egg predation than others. The number of larvae found on each plant is also a reflection of death, predation, and larval movement since fourth and fifth instar larvae may seek out other plants. We did not find significant differences in species with the most larvae when fourth and fifth instar caterpillars were analyzed separately from first, second, and third instar caterpillars.

## Trends over time

Monarchs laid significantly different numbers of eggs on different species at different times of year, suggesting a phenological signal, or in other words, that oviposition preferences change throughout the growing season. In

2022, no eggs were found on the newly planted species until mid-July, partially explaining the significant interaction between date and species in monarch oviposition in 2022: no eggs were found on 9 of the 18 species in the site until they had grown beyond the seedling stage, perhaps because the older, more established plants were larger or more appealing for some other reason. More eggs were found on *A. syriaca* than on any other species from mid-June to early July, suggesting that early-season monarchs prefer to lay eggs on *A. syriaca*. A similar pattern occurred in 2023, reinforcing the suggestion that monarchs prefer to lay eggs on *A. syriaca* at the beginning of the season and *A. incarnata* toward the middle and end of the season. Most eggs found at the very beginning of the 2023 season were found on *A. tuberosa*, but almost all *A. tuberosa* plants were dead by the end of June, so these numbers reflect only the early part of the season and may not accurately represent monarch oviposition preferences on this species. Trends that occurred over time, such as higher egg counts on *A. incarnata* and *A. subverticillata* later in the season, may be caused by changing availability of appealing plant tissue as the growing season progresses. Most species of milkweed in this study typically grew by producing individual stalks with little to no branches, so all new growth is produced from the two apical leaves. Each *A. incarnata* plant produced stalks with a branching pattern, so each branch provided more apices per stem for new growth. Research has shown that strategic mowing of common milkweed (*A. syriaca*) can increase monarch oviposition by creating vigorous new growth from the cut stems, and the abundant new growth throughout the season provided by *A. incarnata's* branching pattern may have provided more appealing foliage for ovipositing monarchs (Alcock et al., 2016; Fischer et al., 2015; Haan & Landis, 2019; Knight et al., 2019). Monarchs also tend to oviposit on newer leaf tissue than on older leaf tissue, making species with more new growth more appealing to ovipositing females (Zalucki & Kitching, 1982). Like *A. incarnata*, *A. subverticillata* also provided new forage later into the season by continuing to grow later into the summer and producing flowers once most of the other species in this study had shifted into seed production. *A. subverticillata* is most often found in the American Southwest, so it may have been better adapted to continue producing new growth in the hotter, dryer months of late summer in South Dakota (USDA, BONAP). The new growth produced by *A. subverticillata* later in the summer when most other species were shifting from growth to seed production may have made *A. subverticillata* more appealing to ovipositing monarchs than other species of milkweed at that time. Concerningly, however, very few larvae were found on *A. subverticillata* relative to the number of eggs it received, suggesting high larval death rates on this species, potentially making it a trap species for monarchs (Battin, 2004, Figure 3C).

## Morphological factors

Our results indicate an overall oviposition preference for *A. incarnata* and *A. syriaca*, not for plants of greater or lesser stem lengths and plant widths. *A. incarnata* and *A. syriaca* are disturbance-tolerant, and some of the more sensitive species included in this study may have been stunted due to stress caused by less-than-ideal field conditions and provided less appealing foliage for ovipositing monarchs as a result. For example, *A. hirtella* can grow up to a meter in height but had an average maximum stem length of 12.41 cm in 2023, suggesting that this species may have struggled to survive in our field (Wisconsin DNR). Furthermore, monarch oviposition rates increase throughout the season as the mating population builds, leading to higher oviposition rates as the milkweed grows taller. We conclude that milkweed must be large enough to be noticeable to the ovipositing monarch, but that the factors that influence oviposition in monarchs are overwhelmingly species driven (Pocius, Debinski, et al., 2018; Pocius, Pleasants, et al., 2018). It is important to consider that our site did not necessarily provide the ideal growing conditions for all 18 species of milkweed represented in this study. The factors that may influence monarch oviposition, including phenology, stem length, and factors we did not test for such as leaf nitrogen, may cause different species to be more or less appealing to ovipositing monarchs under different conditions; however, providing different conditions would prevent different species from being directly compared.

Other morphological factors can influence larval survival rates. The higher number of larvae found on *A. sullivantii* may be explained by the species' lack of trichomes. Trichomes pose a mechanical challenge for herbivory in young monarch caterpillars, and the glabrous exterior of *A. sullivantii* may have increased the larval survival rate compared to larvae on other species of milkweed with trichomes (Jones & Agrawal, 2019). The other glabrous species included in this study was *A. amplexicaulis*, which struggled to survive in our field settings.

# CONCLUSION

Our results indicate that *A. syriaca* is the most appealing species of milkweed to ovipositing monarchs in the early

part of the season and *A. incarnata* is the most appealing species of milkweed to ovipositing monarchs in the middle and later parts of the season. To support monarch larvae, we recommend planting *A. sullivantii* and *A. tuberosa* because these species had a higher larva to egg ratio, indicating higher larval survival rates than other species. These milkweeds grow in dry and mesic prairie sites. If a restoration site is shady or wet, *A. exaltata* and *A. purpurascens* might be good choices. *A. exaltata* and *A. purpurascens* did not thrive in our site conditions but performed comparatively well to other species in our plots. Despite relatively high egg counts in 2023, we cannot recommend planting *A. subverticillata* because it had low larval counts, which could indicate a low larval survival rate. Some species in this study did not receive any eggs or received very few, but they can still be valuable in restoration projects for other pollinators and to increase biodiversity; for example, *A. stenophylla, A. purpurascens*, *A. amplexicaulis*, and *A. hirtella* are threatened or endangered in some states and are worth restoring themselv.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Perkins & Damiano, 2025) are available from the South Dakota State University Open PRAIRIE: https://doi.org/10.62812/PWKT6974.

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