Monarch Butterflies Show Differential Utilization of Nine Midwestern Milkweed Species

Victoria Marie Pocius[1]*, John M. Pleasants[2], Diane M. Debinski[2,3], Keith G. Bidne[4], Richard L. Hellmich[4], Steven P. Bradbury[5] and Sue L. Blodgett[5]

[1] Department of Entomology, The Pennsylvania State University, University Park, PA, United States, [2] Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA, United States, [3] Department of Ecology, Montana State University, Bozeman, MT, United States, [4] Corn Insects and Crop Genetics Research Unit, United States Department of Agriculture, Agricultural Research Station, Department of Entomology, Iowa State University, Ames, IA, United States, [5] Departments of Natural Resource Ecology and Management and Entomology, Iowa State University, Ames, IA, United States

Monarch butterfly overwintering numbers have declined over the past 20 years. Restoring habitat that includes milkweeds, the only host plants for larval monarch butterflies, is necessary to increase monarch numbers within the breeding range. The value of different milkweed species for restoration will depend, in part, on the extent to which they are utilized by ovipositing females. The number of eggs laid on different species over a season will be a function of plant size and phenology as well as female preference. We examined seasonal egg deposition and females' oviposition choices by comparing the number of eggs laid by free-flying wild monarchs on each of nine native milkweed species occurring in Iowa (*Asclepias syriaca, Asclepias tuberosa, Asclepias incarnata, Asclepias verticillata, Asclepias exaltata, Asclepias hirtella, Asclepias speciosa, Asclepias sullivantii,* and *Cynanchum laeve*). One plot, consisting of clusters of each of the nine species, was established at each of 14 sites across the state of Iowa. Eggs were counted weekly in June, July and August 2015–2017. The highest egg totals were recorded on *A. incarnata* and *A. syriaca* in all years. Fewer eggs were counted on *A. exaltata, A. hirtella, A. tuberosa, A. verticillata,* and *C. laeve*. Our results show that monarchs prefer some milkweed species over others, but that they can use all nine native milkweed species for oviposition.

Keywords: *Danaus plexippus*, milkweed species (*Asclepias spp*), oviposition preference, habitat restoration, conservation

INTRODUCTION

Habitat loss is one of the leading causes of species decline for many taxa, (Means and Simberloff, 1987; Wilcove et al., 1998; Pimm and Raven, 2000; Ceballos and Ehrlich, 2002,?; Kerr and Cihlar, 2004; Venter et al., 2006; Xu et al., 2018). Over the past 20 years, monarch populations have experienced a significant decline in overwintering numbers (Brower et al., 2012; Espeset et al., 2016; Inamine et al., 2016; Schultz et al., 2017). Loss of milkweed within the breeding range is considered by many scientists to be the leading cause of the decline of the monarch population east of the Rocky Mountains (Pleasants and Oberhauser, 2013; Flockhart et al., 2015; Pleasants, 2017; Zaya et al., 2017). Restoration of Midwestern monarch habitat is essential to increase

(population numbers Oberhauser et al., 2016 as many of the monarchs that overwinter in Mexico originate from this area Wassenaar and Hobson, 1998; Flockhart et al., 2017. Organizations federal, state, and non-profit) have started efforts to establish monarch habitat, especially adding milkweeds to the landscape in critical land cover/land use categories to enhance monarch reproduction (Thogmartin et al., 2017).

Knowledge of what species to include in habitat restoration is necessary to develop and implement an effective conservation program. Although monarch butterflies (*Danaus plexippus*) are dependent upon milkweeds (*Asclepias* spp.) as larvae, there are over 100 species of milkweeds in the U.S. (Woodson, 1954) and we need to know how available each species is throughout the season, which ones are better for larval growth and on which ones monarch females choose to lay eggs. Currently, the majority of monarchs in population east of the Rocky Mountains feed on *Asclepias syriaca* in the summer (Wassenaar and Hobson, 1998). Rather than reflecting a preference, this may be because disturbance from modern agricultural has made *A. syriaca* the dominant species on the landscape (Martin and Burnside, 1980). This species may not have been as prevalent in historic landscapes (Hayden, 1919; Pleasants, 2015). More information is needed about monarch butterflies' use of other native milkweed species both as larvae and adults beyond *A. syriaca,* the milkweed on which all current conservation recommendations are based (Landis, 2013; Pleasants and Oberhauser, 2013; Pleasants, 2017).

Prior work has contributed to our understanding of monarchs' oviposition choices and use of different milkweed species (Cohen and Brower, 1982; Malcolm et al., 1989; Zalucki et al., 1990; Haribal and Renwick, 1996, 1998a,b; Calvert, 1999; Bartholomew and Yeargan, 2002; DiTommaso and Losey, 2003; Ladner and Altizer, 2005; Casagrande and Dacey, 2007) as well as larval survival on different species (Cohen and Brower, 1982; Zalucki et al., 1990; Zalucki and Brower, 1992; Ladner and Altizer, 2005; Yeargan and Allard, 2005; Robertson et al., 2015; Baker and Potter, 2018). These studies have not compared larval survival and oviposition preference patterns across the same set of co-occurring milkweed species in both laboratory and field settings.

In our prior work (Pocius et al., 2017b, 2018), we compared larval survival on nine milkweed species and oviposition preference on four of these species in a laboratory setting. These nine species are native to Iowa, which is a high priority area for Midwestern conservation efforts (Flockhart et al., 2015; Thogmartin et al., 2017). Most milkweed species native to the Midwest have not been evaluated in field experiments. The species we tested included: *A. syriaca* (common milkweed)*, Asclepias incarnata* (swamp milkweed)*, Asclepias tuberosa* (butterfly milkweed)*, Asclepias verticillata* (whorled milkweed), *Asclepias speciosa* (showy milkweed)*, Asclepias exaltata* (poke milkweed)*, Asclepias sullivantii* (prairie milkweed)*, Asclepias hirtella* (tall green milkweed), and *Cynanchum laeve* (honeyvine milkweed). These milkweeds have overlapping ranges (Woodson, 1954; Kaul et al., 1991; Eilers and Roosa, 1994), but varying habitat needs as well as differing concentrations of phytochemicals including cardenolides (Roeske et al., 1976; Malcolm, 1991; Rasmann and Agrawal, 2011); and quercetin glycosides (Haribal and Renwick, 1996). The species also have

different plant architecture (stem height, leaf width, leaf shape, stem branching, etc.; Woodson, 1954).

Our laboratory results suggest that monarch larvae will consume, survive, and eventually pupate on all nine Midwestern milkweed species (Pocius et al., 2017b); however, fewer larvae reached adulthood when they fed on *A. hirtella* and *A. sullivantii* (Pocius et al., 2017b, see **Table 1**). Larval survival was not significantly different among the other seven milkweed species; these species may provide equal benefits for larvae when included in habitat restorations within the native range of each milkweed species (Pocius et al., 2017b). Our laboratory oviposition results, using just *A. incarnata, A. syriaca, A. tuberosa,* and *A. verticillata,* suggest that monarch butterflies prefer to oviposit on *A. incarnata* and *A. syriaca* although they will utilize all four species (Pocius et al., 2018-see also Baker and Potter, 2018). Here, we build on prior laboratory work with a report of field oviposition using all nine milkweed species. We compare the total number of eggs laid on each species in June and July, in 2015 and 2016, to compare females' choices when all nine species were present, before senescence of three of the species. We also compared the total number of eggs laid on each of six species present in July and August, in 2015 and 2016, to capture females' choices during peak oviposition. Finally, we compare the total number of eggs laid on each species during the entire summer season, in 2015–2017, to provide estimates of monarch utilization of each milkweed species for habitat restoration purposes.

MATERIALS AND METHODS

Field Oviposition

Experimental Milkweed Plots and Site Establishment

Midwestern ecotype milkweed seeds of *A. exaltata, A. hirtella, A. incarnata, A. speciosa, A. sullivantii, A. syriaca, A. tuberosa, A. verticillata,* and *C. laeve* (Prairie Moon Nursery, MN, USA) were stratified in wet sand for 6 weeks. After stratification, seeds were sown into 128-cell plug trays (Landmark Plastics, Akron OH, USA) and transplanted into 8.9 cm^2, deep perennial pots (Kord, Ontario Canada) at approximately 6 weeks following germination. When milkweed plants were 12 weeks old, five young plants of each species were transported to each location. Sites were established at ten Iowa State Research and Demonstration Farms (Newell, IA; Lewis, IA; Boone, IA; Ames, IA; Chariton, IA; Nashua, IA; Kanawha, IA; Sutherland, IA; and Castana, IA), Luther College (Decorah, IA), Pella High School (Pella, IA), Central College (Pella, IA), and on the Sorenson-Powell property (Adel, IA). At least one site was located in each quadrant of the state. Plants were distributed to each site and planted by the second week of June 2015.

Each of nine milkweed species was randomly assigned to a 1 m^2 plot within a single row at each site. Each plot consisted of 5 plants for a total of 45 plants at each site. Plots were separated from each other by a 1 m wide grass or stone path. Any plants that did not survive were replaced with young plants (6–8 weeks old) twice during the summer of 2015 and at the beginning of the

TABLE 1 | Summary of the utility of nine milkweed species examined in the current study.

Milkweed species	Common name	Habitat requirements	Larval survivorship	Oviposition use	Ease of establishment from plugs	Recommended for restoration
A. exaltata	Poke milkweed	Partial shade, woodland edges, upland woods	High	Medium	Difficult	No
A. hirtella	Tall green Milkweed	Full sun, prairie remnants, fields	Low	Medium	Difficult	No
A. incarnata	Swamp milkweed	Partial to full sun, wetlands, floodplains, marshes	High	High	Easy	Yes Wet locations only
A. speciosa	Showy milkweed	Full sun, roadsides, untilled fields, forest clearings	High	Medium	Easy	Yes, outside the range of *A. syriaca*
A. sullivantii	Prairie milkweed	Full sun, prairies, roadsides, field edges	High	Medium	Medium	Yes
A. syriaca	Common milkweed	Full sun, any disturbed areas	High	High	Easy	Yes
A. tuberosa	Butterfly milkweed	Full sun, prairies, open woodlands,	High	Low	Easy	Yes, as a late season larval host
A. verticillata	Whorled milkweed	Partial to full sun, disturbed areas, roadsides, prairies	High	Low	Easy	No
C. laeve	Honeyvine milkweed	Full sun, disturbed areas, prairies, cities	Low	Medium	Easy	No

Habitat information is summarized from Kaul et al. (1991) and (Eilers and Roosa, 1994). Larval survivorship designated as high if over 60% of larvae reached adulthood (Pocius et al., 2017b); under 60% survival is designated as low. Oviposition use is designated as high if species were in the top third for both laboratory (Pocius et al., 2018) and field oviposition experiments, medium if species were in the second third for both experiments, and low if the species were in the bottom third of egg totals for both experiments. Species are designated as easy to establish if over 60% survived within the demonstration plots from 2015 to 2017, and are recommended for restoration if plants were easy to establish, had high larval survivorship, and medium to high oviposition use. Larval survivorship and oviposition use were determined as low, medium or high from laboratory data Pocius et al., 2017a; Pocius et al., 2018.

season in 2016. *A. hirtella* plants were not replaced due to a lack of seed in 2016 and 2017.

Site Monitoring

Each site was monitored weekly from the first week of June 2015 through the end of August 2017 for a total of 42 visits to each site. Each week, the number of live milkweed plants, bloom presence, the number of blooms, the height of the tallest plant, the presence of seed pods, and the presence of mature seed pods was recorded for each milkweed species. Each plant was examined for the presence of monarch eggs, larvae, or other insects using a modified protocol from the Monarch Larva Monitoring Project (Oberhauser, 2013).

Statistical Analysis

The total number of eggs on each plot of five plants was summed across June, July, and August for each site and then averaged; the results were analyzed separately for each year. Only sites where observers recorded egg numbers for at least 8 weeks were included in the analysis of each year. Sites without any eggs during the summer within each year were removed from the analysis ($N = 12$ sites in 2015, $N = 13$ sites in 2016, and $N = 10$ sites in 2017). Egg counts were only reported for milkweed species with live plants at each site over the observation period. Differences in total egg counts in single years were determined using a Poisson regression with milkweed species (Pocius et al., 2018) as a fixed effect and site a random effect. Pairwise differences in egg counts

were determined by comparing least square means for each milkweed species (Pocius et al., 2018); *p*-values were adjusted using Tukey's range test for multiple comparisons (Pocius et al., 2018). Concordance was determined using a Kendall coefficient of concordance. Correlation between average egg counts and average plant traits were determined using a Pearson correlation. R version 3.3.3 (R Core Team, 2014) was used for all statistical analyses.

To address preference directly, the total number of eggs in each plot of five plants were summed across June and July in 2015 and 2016 when all nine species were available and prior to senescence of *A. exaltata, A. hirtella,* and *A. speciosa.* The total number of eggs in each plot were also summed across the six milkweed species present in across July and August in 2015 and 2016 to include the timing of peak oviposition in the analysis of these years. The year 2017 was excluded from preference analyses because some species had disappeared from the plots by then. Only sites where eggs were laid were included in the analysis ($N = 12$ in 2015 and $N = 11$ in 2016). Differences in total egg counts in each year were determined using a Poisson regression with milkweed species (Pocius et al., 2018) as a fixed effect and site as a random effect. Plant height and bloom count were not significant predictors of the number of eggs laid per species and were excluded from the final model. Pairwise differences in egg counts were determined by comparing least square means for each milkweed species (Pocius et al., 2018); *p*-values were adjusted using Tukey's range test for multiple comparisons (Pocius et al., 2018).

RESULTS

Field Oviposition

2015

Milkweed species had a significant effect on the total number of eggs laid per milkweed species. *A. incarnata* had the highest egg totals when counts from all sites were combined across the entire breeding season (**Figure 1A**). Females laid 1.3 times more eggs on *A. incarnata* than *A. syriaca,* although this difference was not significant ($z = 2.12, p > 0.4$). One of the largest differences in total egg counts was between *A. incarnata* or *A. syriaca* and *A. exaltata.* Females laid 6.8 times more eggs on *A. incarnata* ($z = -4.04, p < 0.001$) and 5.4 times more eggs on *A. syriaca* ($z = -6.59, p < 0.001$) than on *A. exaltata* (**Figure 1A**). All other significant pairwise comparisons are shown in **Supplementary Table 1**.

For June-July, when all species were present, *A. incarnata* and *A. hirtella* had the highest average egg totals per site (**Figure 2A**). *A. incarnata* had significantly higher egg counts compared to *A. exaltata, C. laeve, A. tuberosa,* and *A. verticillata* (**Figure 2A**, **Supplementary Table 2**). *A. exaltata* had significantly lower egg counts than *A. hirtella* and *A. sullivantii* (**Figure 2A**, **Supplementary Table 2**). The number of eggs laid on *A. syriaca* was not significantly different from *A.*

incarnata. All other significant pairwise comparisons are shown in **Supplementary Table 2**.

When the period from July through August was examined, with *A. exaltata, A. hirtella,* and *A. speciosa* removed due to senescence, *A. incarnata* and *A. syriaca* had the highest average egg totals per site (**Figure 3A**). The largest differences in egg counts were between *A. incarnata* and *C. laeve* ($z = 7.02, p < 0.0001$), *A. tuberosa* ($z = 5.86, p < 0.0001$), and *A. verticillata* ($z = 6.49, p < 0.0001$). *A. verticillata* ($z = 5.02, p < 0.0001$), *A. tuberosa* ($z = 4.28, p = 0.0003$), and *C. laeve* ($z = -5.65, p < 0.0001$) also had significantly fewer eggs than *A. syriaca* although *A. sullivantii* and *A. syriaca* were not significantly different from each other. All other significant pairwise comparisons are shown in **Supplementary Table 3**.

2016

Milkweed species had a significant effect on the total number of eggs laid per milkweed species. *A. syriaca* had the highest average egg totals followed by *A. incarnata* (**Figure 1B**). Females laid 1.4 times more eggs on *A. syriaca* than *A. incarnata* although this difference was not significant ($z = -1.55, p > 0.8$). The largest difference in egg counts was observed between *A. syriaca* or *A. incarnata* and *A. exaltata.* Females laid over twenty times more eggs on *A. syriaca* ($z = -4.21, p < 0.01$) and *A. incarnata* ($z =$
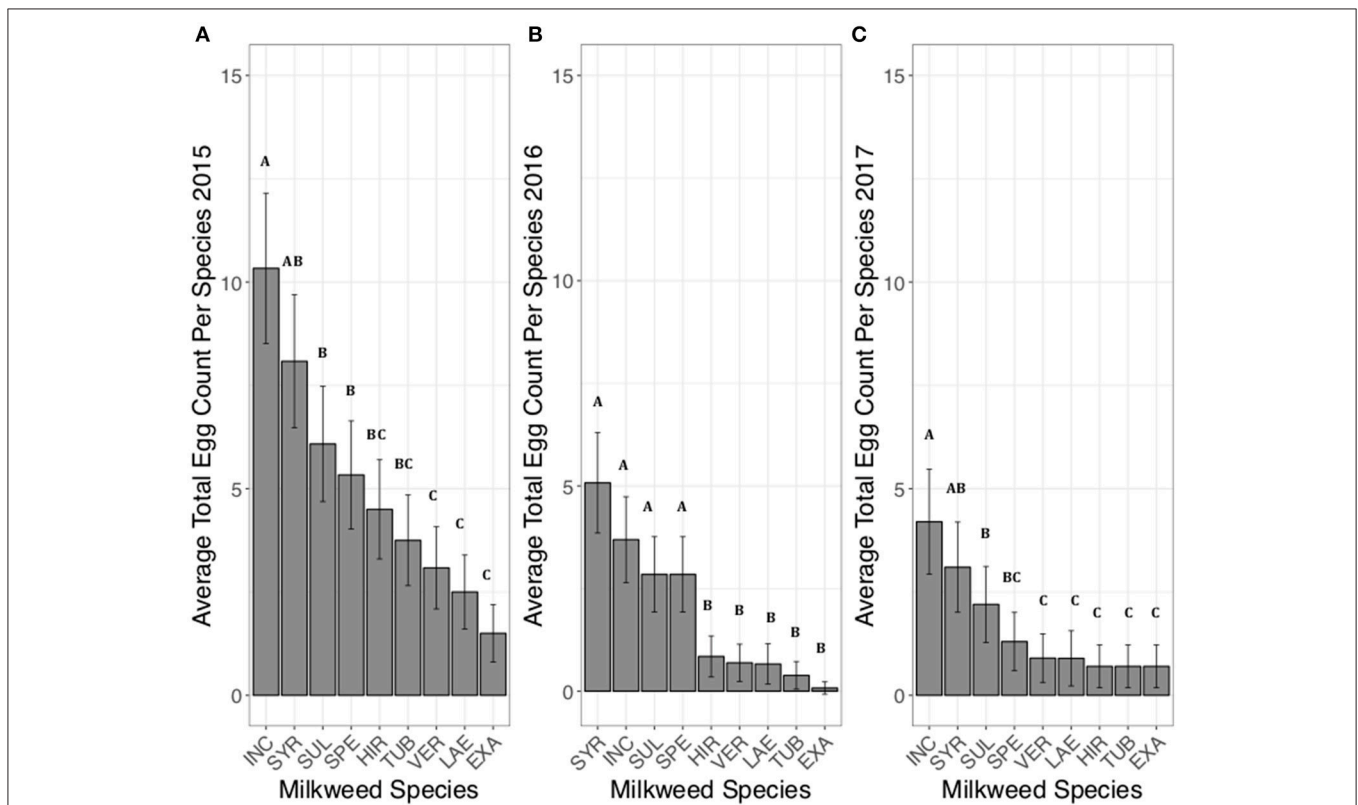

FIGURE 1 | Average eggs counted on each milkweed species over the course of the summer breeding season in 2015 **(A)**, 2016 **(B)**, and 2017 **(C)**. Each bar represents one milkweed species. EXA, *A. exaltata*; HIR, *A. hirtella*; INC, *A. incarnata*; LAE, *C. laeve*; SPE, *A. speciosa*; SUL, *A. sullivantii*; SYR, *A. syriaca*; TUB, *A. tuberosa*; VER, *A. verticillata;* error bars represent 95% confidence intervals. *N* = 12 sites in 2015, 12 sites in 2016, and 10 sites in 2017. Bars that do not share a letter within each panel are significantly different from each other. Females laid more eggs on *A. incarnata* and *A. syriaca* than on *A. exaltata, A. hirtella, C. laeve, A. tuberosa,* and *A. verticillata* in all years ($p < 0.05$). *P*-values were adjusted using the Tukey method for multiple comparisons.
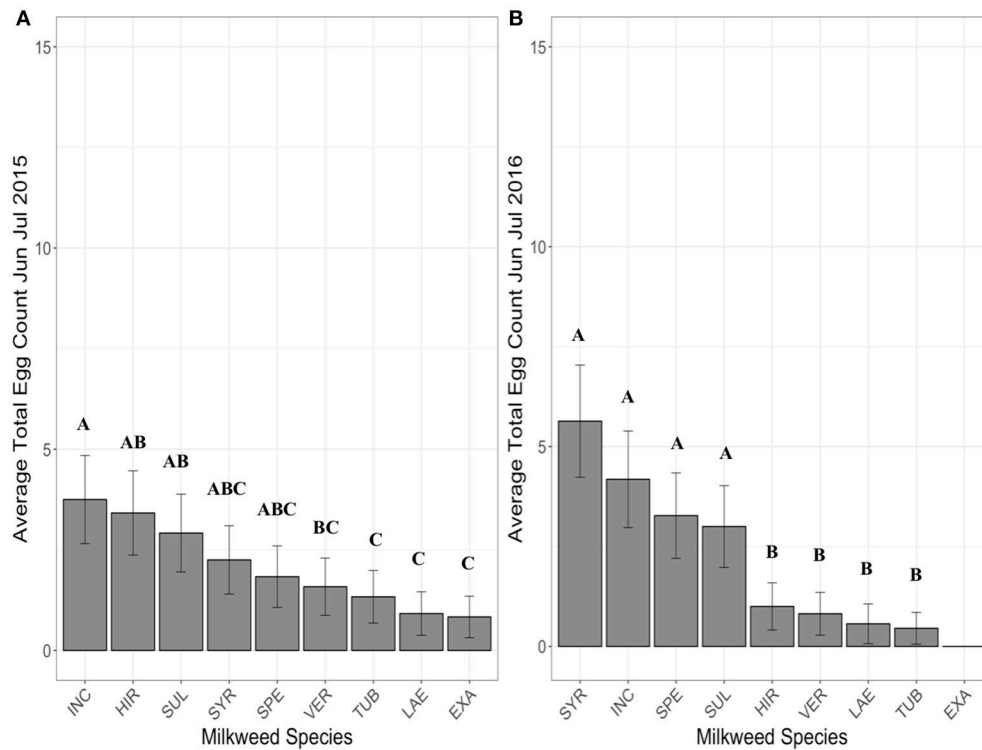
FIGURE 2 | Average eggs counted on each milkweed species in June and July in 2015 **(A)**, 2016 **(B)** when 5 plants of each species were present in each research plot. Each bar represents one milkweed species. EXA, *A. exaltata*; HIR, *A. hirtella*; INC, *A. incarnata*; LAE, *C. laeve*; SPE, *A. speciosa*; SUL, *A. sullivantii*; SYR, *A. syriaca*; TUB, *A. tuberosa*; VER, *A. verticillata;* error bars represent 95% confidence intervals. *N* = 11 sites in 2015, and 12 sites in 2016. Bars that share a letter within each panel are not significantly different from each other. Females laid more eggs on *A. incarnata* than on *A. exaltata, C. laeve, A. tuberosa,* and *A. verticillata* in both years (*p* < 0.05). The number of eggs laid on *A. syriaca* was not significantly different from *A. incarnata*. *P*-values were adjusted using the Tukey method for multiple comparisons.

−3.87, *p* < 0.01) than on *A. exaltata* in 2016. All other significant pairwise comparisons are shown in **Supplementary Table 4**.

For June-July, when all species were present, species had a significant effect on the average total number of eggs laid per milkweed species (**Figure 2B**). No eggs were laid on *A. exaltata* during this time period (**Figure 2B**). *A. incarnata* and *A. syriaca* had the two highest average egg totals (**Figure 2B**). *A. syriaca* had significantly higher egg counts than *A. hirtella, C. laeve, A. tuberosa*, and *A. verticillata* (**Figure 2B**, **Supplementary Table 5**). *A. speciosa* and *A. sullivantii* had comparable egg totals to *A. incarnata* and *A. syriaca* (**Figure 2B**). All other significant pairwise comparisons are shown in **Supplementary Table 5**.
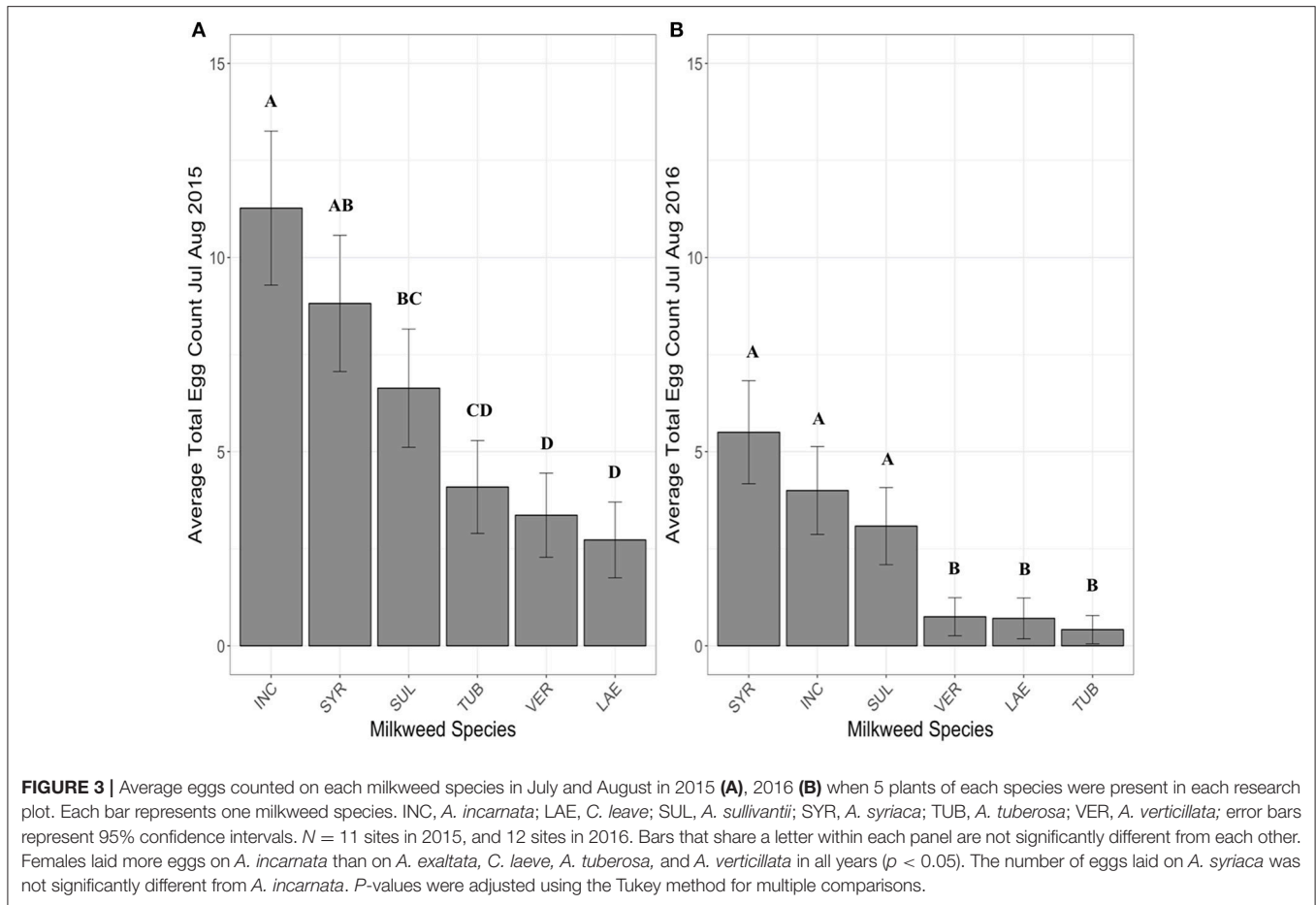
When the period from July through August was examined, with *A. exaltata, A. hirtella*, and *A. speciosa* removed due to senescence, *A. incarnata* and *A. syriaca* had the highest average egg totals (**Figure 3B**), but the largest differences in egg counts were between *A. syriaca* and *C. laeve* (*z* = −5.23, *p* < 0.0001), *A. tuberosa* (*z* = 5.63, *p* < 0.0001), and *A. verticillata* (*z* = 5.68, *p* < 0.0001). *A. verticillata* (*z* = 4.67, *p* < 0.001), *A. tuberosa* (*z* = 4.88, *p* < 0.001), and *C. laeve* (*z* = 4.35, *p* = 0.0002) also had significantly fewer eggs than *A. incarnata*. *A. incarnata, A. syriaca*, and *A. sullivantii* are not significantly different from each other. All other significant pairwise comparisons are shown in **Supplementary Table 6**.

2017

Milkweed species had a significant effect on the number of total eggs laid per milkweed species. *A. incarnata* had the highest egg totals while *A. syriaca* had the second highest egg counts when eggs from all sites were combined (**Figure 1C**). Females laid about 1.3 times more eggs on *A. incarnata* than *A. syriaca*, although this difference was not significant (*z* = 1.29, *p* > 0.9). Females laid eight times more eggs on *A. incarnata* than on *A. exaltata* (*z* = −4.44, *p* = 0.0003) and six times more eggs on *A. incarnata* than on *A. hirtella* (*z* = −4.44, *p* = 0.0003) in 2017. All other significant pairwise comparisons are shown in **Supplementary Table 7**.

Comparison Among Years

During each of the 3 years, over the entire summer season, female monarchs laid eggs on all nine milkweed species but a greater number of eggs were laid on some milkweed species than others (**Figure 1**). The species order of the number of eggs laid was highly concordant across years (*W* = 0.94). Across years the overall utilization of each species is summarized in **Table 1**. There was no significant correlation between the average number of blooms per plant and the average number of eggs per plant (*r* = 0.18, *p* = 0.25) or the average number of eggs per plant and species plant height (*r* = −0.07 to 0.09, *p* > 0.05). The total

FIGURE 3 | Average eggs counted on each milkweed species in July and August in 2015 **(A)**, 2016 **(B)** when 5 plants of each species were present in each research plot. Each bar represents one milkweed species. INC, *A. incarnata*; LAE, *C. leave*; SUL, *A. sullivantii*; SYR, *A. syriaca*; TUB, *A. tuberosa*; VER, *A. verticillata;* error bars represent 95% confidence intervals. $N = 11$ sites in 2015, and 12 sites in 2016. Bars that share a letter within each panel are not significantly different from each other. Females laid more eggs on *A. incarnata* than on *A. exaltata*, *C. laeve*, *A. tuberosa*, and *A. verticillata* in all years ($p < 0.05$). The number of eggs laid on *A. syriaca* was not significantly different from *A. incarnata*. *P*-values were adjusted using the Tukey method for multiple comparisons.

number of eggs laid was 542 (41.7 eggs per site) in 2015, 221 (13 eggs per site) in 2016 and 136 (10.5 eggs per site) in 2017. When species were compared during a subset of the summer, species order of preference was moderately concordant between June-July 2015 and 2016 ($W = 0.50$) and highly concordant between July-August 2015 and 2016 ($W = 0.70$).

DISCUSSION

The findings of our field-based oviposition preference experiment (June through July counts) were consistent across 2015–2016 and suggest that while monarch butterflies will oviposit on all milkweed species tested, some species consistently received fewer total eggs in the research plots; *A. exaltata* received few eggs across all years. The species on which females chose to oviposit in the June-July period, *A incarnata* and *A. syriaca*, were also preferred in July-August. *A. incarnata* and *A. syriaca* also had higher egg totals in the field study by Baker and Potter (2018). These two species were also preferred in the laboratory experiment which also included *A. verticillata* and *A. tuberosa* (Pocius et al., 2018). Contrary to Zalucki and Kitching (1982) and Baker and Potter (2018), we did not see an increase in egg counts with plant height within species in any year or an increase in the number of eggs laid with increasing bloom count.

Monarchs from the populations both east and west of the Rocky Mountains also have exhibited the same oviposition choices when exposed to the same array of milkweed species (Ladner and Altizer, 2005). Although monarchs exhibited egg-laying patterns in this study, they did lay eggs on all nine species each year. This indicates that although monarchs make oviposition choices, they do not specialize on a single milkweed species. This is important for a species that encounters different sets of milkweed species on the landscape during its annual cycle (Zhan et al., 2014; Agrawal, 2017).

Interestingly, the species on which larvae performed well and those with high egg totals were not always correlated (Mayhew, 1997, 2001; Berdegué et al., 1998; Gratton and Welter, 1998 see **Table 1**). For example, both *A. tuberosa*, and *A. verticillata* were good larval food sources (Pocius et al., 2017b), but fewer eggs were laid on these species in the lab (Pocius et al., 2018) and in the field. This suggests that the factors that female monarchs use to make egg-laying decisions can be different from those that determine larval success.

We saw more eggs on all species in 2015 than 2016 and 2017. These higher egg totals could be due to the young plant age and smaller stature of first-year plants which made them more attractive (Zalucki and Kitching, 1982). Alternatively, the 2015 observations were reflective of the higher level of egg laying in the Midwest in 2015 as compared to 2016 and 2017 (J. Pleasants

pers comm.). Eggs were not present at all sites each year, but no site had zero eggs in 2 consecutive years, demonstrating the variability of egg distribution across Iowa during these 3 years. These differences could be related to varying adult recruitment rates in the spring and subsequent habitat utilization across the state later in the summer.

Across years, fewer monarch eggs were deposited on *A. exaltata*, *A. tuberosa*, and *C. laeve* when compared to *A. incarnata and A. syriaca*. Both *A. exaltata* and *A. hirtella* were difficult to establish in these Iowa sites (**Table 1**). Only four sites had five live plants of both species by August 2017, but the differences in egg counts are apparent in 2015 and 2016 when each site still had 5 live plants of each species. *A. exaltata* senesced by late July in all years, before peak oviposition occurred. This is likely the primary explanation for its lower overall egg count. The few eggs that we did observe on *A. tuberosa* were located on flower buds; however, we saw 4th and 5th instars feeding on this species in August. Older larvae may have moved to these plants from the other milkweed species within the site. Because *A. tuberosa* was in better condition (greener leaves, no visible senescence) compared to *A. incarnata, A. speciosa*, and *A. syriaca* late in the growing season, *A. tuberosa* may be more valuable as a late-season larval food source than for oviposition in August. The utility of *C. laeve* may be underestimated in our analysis; we observed more eggs on this species anecdotally in September in central Iowa after plot monitoring across the state ended; data from September were not included here. However, it is unlikely that eggs laid that late will successfully produce adults that migrate to Mexico (Orley Taylor *pers comm*). There is also inherent variation because of the various locations of the research plots. An examination of these site differences is outside the scope of this study.

Annual and inter-annual variation of temperature and precipitation can affect milkweed quality. High-quality milkweed is essential for both larvae and ovipositing females throughout the breeding season. Because some milkweeds thrive in wet conditions (*A. incarnata*), and others grow well in drier conditions (*A. hirtella* and *A. tuberosa*), specialization on one milkweed species is not a viable strategy for ovipositing female monarchs because plant quality is highly variable across the landscape and the duration of the breeding season. Future work should investigate milkweed phenology, milkweed survival after planting, and monarch use across critical areas of the breeding range because the timing for peak oviposition and larval feeding likely differs by location. More information is needed about how monarchs find and use mature, naturally occurring milkweed plants. Understanding how females utilize these mature patches will allow researchers and managers to assess the worth of different milkweed species and the configuration of milkweed patches within habitat restoration sites.

As a whole, the results show that there are a few species that are most preferred for oviposition and would be best to use for restoration purposes (**Table 1**). Other considerations in choosing a species for restoration include matching the habitat preferences of species with the environmental conditions of the restoration site. Planting several milkweeds species with different habitat preferences may allow the persistence of milkweeds at a site despite variable weather conditions within and between

years. Because larval survivorship is high on most species, with the exception of a couple (**Table 1**), planting a few species that are less preferred for oviposition will not compromise larval survival. See **Table 1** for a summary of milkweed species' habitat requirements, ease of plug establishment, and utility for larvae and ovipositing females. We designate a species as recommended for restoration if plugs were easy to establish, had high larval survivorship, and medium to high oviposition use.

AUTHOR CONTRIBUTIONS

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00169/full#supplementary-material

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