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ORIGINAL PAPER

Aphid abundance and monarch butterfly oviposition in urban gardens

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Abstract
Monarch butterflies (*Danaus plexippus*) have suffered dramatic declines and, as of 2025, are being considered for listing as a threatened species under the U.S. Endangered Species Act. Monarch declines have been explained, at least in part, by the loss of milkweeds (*Asclepias* spp.), their larval host plant. Increasing milkweeds in urban gardens may aid in monarch conservation efforts but concerns have been raised regarding negative interactions between monarchs and aphids co-occurring on milkweeds in these gardens. We made 934 observations on approximately 150 *Asclepias syriaca* (common milkweed) stems in garden beds in a highly urbanized landscape in Chicago, IL, USA over two summers. Using generalized linear mixed-effects models, we found that the number of monarch eggs and larvae was either not correlated or positively correlated with aphid abundance, indicating that aphid infestation did not deter oviposition by monarch butterflies on milkweed stems. Implications for Conservation: Planting milkweeds in urban gardens may aid in monarch population recovery, but aphid milkweed specialists often occur at high densities in urban gardens. We did not find that stems with high aphid abundance had fewer monarch eggs and larvae, suggesting that aphids may not reduce the value of native urban milkweeds for monarch oviposition as previously suggested.

Keywords Aphis · Myzocallis · *Danaus plexippus* · Urban gardens · *Asclepias syriaca* · Milkweeds

Introduction

The precipitous decline of the monarch butterfly, *Danaus plexippus*, in North America has roused public interest in conservation efforts and sparked wide-ranging research to investigate the underlying causes. The eastern North American population of monarch butterflies are long-distance migrants, traveling 4000 km or more from breeding grounds in the USA and Canada to overwinter in a small region of central Mexico where monarchs congregate on oyamel fir trees, *Abies religiosa*. The decline of the migratory population is seen most markedly at the overwintering sites, where the area occupied by monarchs has declined dramatically since the mid-1990s (Brower et al. 2012; Vidal and Rendón-Salinas 2014; Saunders et al. 2019). The continental scale of the monarch life cycle contributes to the difficulty of identifying its primary threats, and there is vigorous scientific debate regarding the relative importance of the various proposed pressures (Saunders et al. 2019; Crossley et al. 2022; Pleasants et al. 2024). These include loss of forests at the overwintering grounds (Brower et al. 2012; Vidal and Rendón-Salinas 2014), diminished floral resources along the migratory route (Castañeda et al. 2019; Saunders et al. 2019), climate change (Zylstra et al. 2021), and loss of milkweeds, especially in agricultural areas (Pleasants 2017).

A leading explanation for monarch declines centers on the milkweed limitation hypothesis (Pleasants and Oberhauser 2013), driven by reduced availability of milkweeds (Asclepiadoideae, and especially the genus *Asclepias*). Monarch butterfly larvae are specialist herbivores of milkweeds and adult females oviposit exclusively on milkweed plants. Milkweeds produce cardenolides as a defense against

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herbivory and monarch larvae sequester cardenolides while feeding on milkweeds, which confers toxicity to both larvae and adult monarchs. Widespread application of glyphosate herbicides in agricultural fields of the Midwest following the introduction of glyphosate-tolerant soybeans and corn has resulted in dramatic loss of milkweeds over the past three decades (Pleasants 2017; Zaya et al. 2017). This has led to efforts to increase milkweed stems in non-agricultural habitats (Thogmartin et al. 2017), including natural areas (Zaya et al. 2017), energy and transportation right-of-ways (Kasten et al. 2016; Cariveau et al. 2019) and residential gardens (Geest et al. 2019). One study suggests that urban areas have the potential to provide millions of milkweed stems in support of monarch conservation (Johnston et al. 2019).

With enthusiastic grass-roots efforts to plant "monarch waystations" and pollinator gardens, researchers have begun investigating the role small gardens could play in supporting monarch butterfly conservation. Evidence suggests that female monarchs can find even small patches of milkweeds in urban gardens and show high rates of oviposition (Cutting and Tallamy 2015; Baker and Potter 2018a; Geest et al. 2019). Investigations of milkweed species, garden locations, and configurations are providing evidence-based guidelines for increasing monarch oviposition in urban gardens (Baker et al. 2020; Baker and Potter 2018a, 2019; Nestle et al. 2020), but there is less information on monarch egg and larval survival in these gardens. The conservation value of urban gardens for monarchs depends not just on oviposition, but upon successful completion of all stages of metamorphosis. Urban gardens are artificial ecosystems that may support novel communities of arthropods, including competitors and predators of monarch eggs and larvae, and both native and nonnative species. Invasive paper wasps (*Polistes dominula*) killed most monarch larvae they encountered in urban gardens in Lexington, Kentucky (Baker and Potter 2020). Invasive Japanese beetles, *Popillia japonica*, feed on *Asclepias syriaca* (common milkweed), the main larval host plant for monarchs, and reduce fruiting and seed set (Baker and Potter 2018b).

Native species will also impact the survival of monarch eggs and larvae in urban gardens, especially if arthropod community interactions are altered (Dale and Frank 2018). Two native aphids specialize on milkweeds, *Aphis asclepiadis* and *Myzocallis asclepiadis*. An introduced species, *Aphis nerii*, frequently occurs on *Asclepias syriaca* (Smith et al. 2008). Milkweed aphids, especially *A. nerii*, often reach high densities on milkweeds in urban landscapes and can cause leaf damage and mold accumulation. *Aphis nerii* sequesters chemical defenses and has aposematic coloration. *Aphis asclepiadis* is nearly always tended by ants, while ants do not mutualistically tend the other two species (Mooney and Agrawal 2008; Smith et al. 2008). Phloem-sucking insects like aphids trigger the salicylic acid pathway in plants, whereas chewing herbivores like caterpillars induce the jasmonic acid pathway. These two pathways show a negative correlation when both aphids and monarch caterpillars are present (Ali and Agrawal 2014). Additionally, there is evidence of aphid presence reducing plant resistance to caterpillars, and monarch larvae growing faster on aphid-infested *A. syriaca* plants compared to aphid-free plants (Ali and Agrawal 2014). These findings are discordant with a study evaluating the impacts of *A. nerii* infestation on tropical milkweed (*Asclepias curassavica*); monarchs oviposited fewer eggs on aphid-infested plants (Mach et al. 2023). Monarch larvae also consumed less *A. curassavica* leaf material from aphid-infested plants, resulting in significantly lower larval weight (Mach et al. 2023). These findings may not extend to aphid infestation of native milkweeds. *Asclepias curassavica* has much higher levels of cardenolides than native milkweeds. Also, laboratory bioassays may not apply in the field, where females may demonstrate preferences for milkweeds with varying aphid levels, or confounding factors may drive any correlation between monarch and aphid abundance. Two field studies compared predator abundance, aphid abundance, and monarch oviposition in mowed and unmowed grassland patches (Haan and Landis 2019, 2020). These two studies found that predators and aphids were more abundant on milkweeds in unmowed areas, and first-instar larval survival was lower in unmowed areas. However, the studies did not directly compare aphid numbers and monarch survival. Overall, previous investigations of monarch and aphid interactions suggest complex indirect effects that differ depending on milkweed species and local arthropod communities.

We monitored *A. syriaca* individuals in small gardens for monarchs and aphid abundance over two summers during the monarch breeding season. Our gardens were on the University of Illinois Chicago campus in a highly urbanized landscape. To our knowledge, no studies to date have evaluated the relationship between monarch egg and larval densities and aphid abundance in gardens. Our goal was to determine if there was a relationship between their abundances and, if so, the direction of the relationship. Female monarchs may show oviposition preferences for milkweeds with higher or lower aphid counts, or particular milkweed stems may be more attractive to monarchs, aphids, or both. If urban gardens are to play a role in monarch conservation, it is critical to evaluate the impact of aphid communities on the monarchs that share these gardens.

Methods

Study site

The study was conducted during the summers of 2023 and 2024 on the campus of the University of Illinois Chicago (UIC). We monitored milkweed stems in three garden beds in 2023 and three beds in 2024 for eggs and larvae of monarch butterflies, *D. plexippus*, and for aphids of any species. These garden beds are located in a highly urban, developed part of Chicago (coordinates: 41.8718º N, 87.6504º W) and were established and are maintained by the UIC Heritage Garden. The garden beds are in close proximity to each other (all within 100 m) in the center of campus and have well-established *A. syriaca* plants that are self-propagating, likely through cloning and possibly self-seeding. "Swallowtail Bed" was a raised bed that contained 10–17 *A. syriaca* stems. This garden was monitored in both years. Plant species in the same garden bed included *Allium tuberosum*, *Calendula officinalis*, *Echinacea purpurea*, *Ruta graveolens*, *Paeonia lactiflora*, *Amaranthus cruentus*. "Spiky Bed" was a raised bed that contained 11–16 *A. syriaca* stems, as well as *Oenothera biennis*, *Eryngium yuccifolium*, *Rubus idaeus*, *Rosa acicularis*, *Solanum dulcamara*, and *Fragaria* x *ananassa.* This bed was monitored in both years, but was not included in analyses for 2024 due to a lack of monarchs and aphids found on the milkweeds. "Aster Bed" was a raised bed that contained 11–13 *A. syriaca* stems in 2023 and 46 stems in 2024, as well as *Symphyotrichum pilosum*, *Echinacea pururea*, *Chenopodium album*, *Coriander sativum*, *Solanum lycopersicum*, *Agastache foeniculum*, and *Luffa aegyptiaca.* The "Bioswale" garden, an in-ground bed, was only monitored in 2024 and contained over 30 *A. syriaca* stems, as well as *Heliopsis helianthoides* and *Sporobolus heterolepis. Asclepias syriaca* was the only milkweed species in these gardens, although *A. incarnata* and *A. tuberosa* were found in the other nearby gardens.

Data collection

For each observation, the entire shoot of each *A. syriaca* stem was inspected and the number of *D. plexippus* eggs and larvae were recorded along with the growth stage of each larva. When aphids were present on a plant, the aphid number was estimated by counting aphids on one-quarter of each leaf and multiplying those counts by four, or by counting the exact number if very few were present. While counting aphids, we did not track aphid species, although the three specialist species (*Aphis nerii*, *A. asclepiadis*, *Myzocallis asclepiadis*) were all present during the monarch breeding season. In 2023, every *A. syriaca* stem was monitored weekly from June 12 to August 18, except that no data were collected during the fourth week, resulting in 9 points of data collection. In 2024, milkweeds were monitored weekly from June 12 through August 2, resulting in eight data collection points. In 2024, every *A. syriaca* stem was monitored except in the "Bioswale," where 30 stems were monitored. In both years, data were collected and analyzed at the level of an individual milkweed stem.

Data analysis

Our analysis aimed to test whether there was a relationship between the aphid abundance on a milkweed stem and the number of monarch eggs and larvae observed on that stem. Raw aphid counts were highly right-skewed, thus, we $\log(x+1)$-transformed the aphid counts in order to better model statistical relationships. For the monarch egg and larvae data, we only used counts for early stages (eggs, first, and second instars) since later instars may have moved from the plant they were oviposited on (Fisher et al. 2020) and may have been more than one week old and potentially double-counted. We used generalized linear mixed-effects models (GLMM) and analyzed the 2023 and 2024 data separately because of the large difference in monarch abundance; monarch eggs and larvae were relatively abundant in 2023 but much rarer in 2024. Mixed-effects modeling was implemented with the *lme4* package for R version 4.4.1 (Bates et al. 2015). Counts of monarch eggs and young larvae on individual stems for each date of data collection were modeled as a Poisson-family response variable. The raw data consisted of monarch and aphid counts from individual stems. We included random intercepts for two uncrossed random effects, garden and week of the survey. The fixed effect we explored was $\log(x+1)$-transformed aphid count. We compared statistical support for the model with log-transformed aphid count to a null model without any fixed effects. We then conducted model selection with the Akaike information criterion corrected for small sample sizes (AIC_C) to compare the two candidate models. Akaike weights were calculated and the best model was determined by the maximum weight value. Model assumptions regarding dispersion were checked and satisfied. The script used to conduct the statistical analyses is available as a supplement (Online Resource 1).

Results

The number of aphids and monarchs observed on our milkweed stems differed dramatically between the summers of 2023 and 2024 (Fig. 1). In 2023, the peak abundance of monarch eggs and larvae was 3.3 (SE = 0.43) per milkweed plant, and this peak occurred during week six (around 26

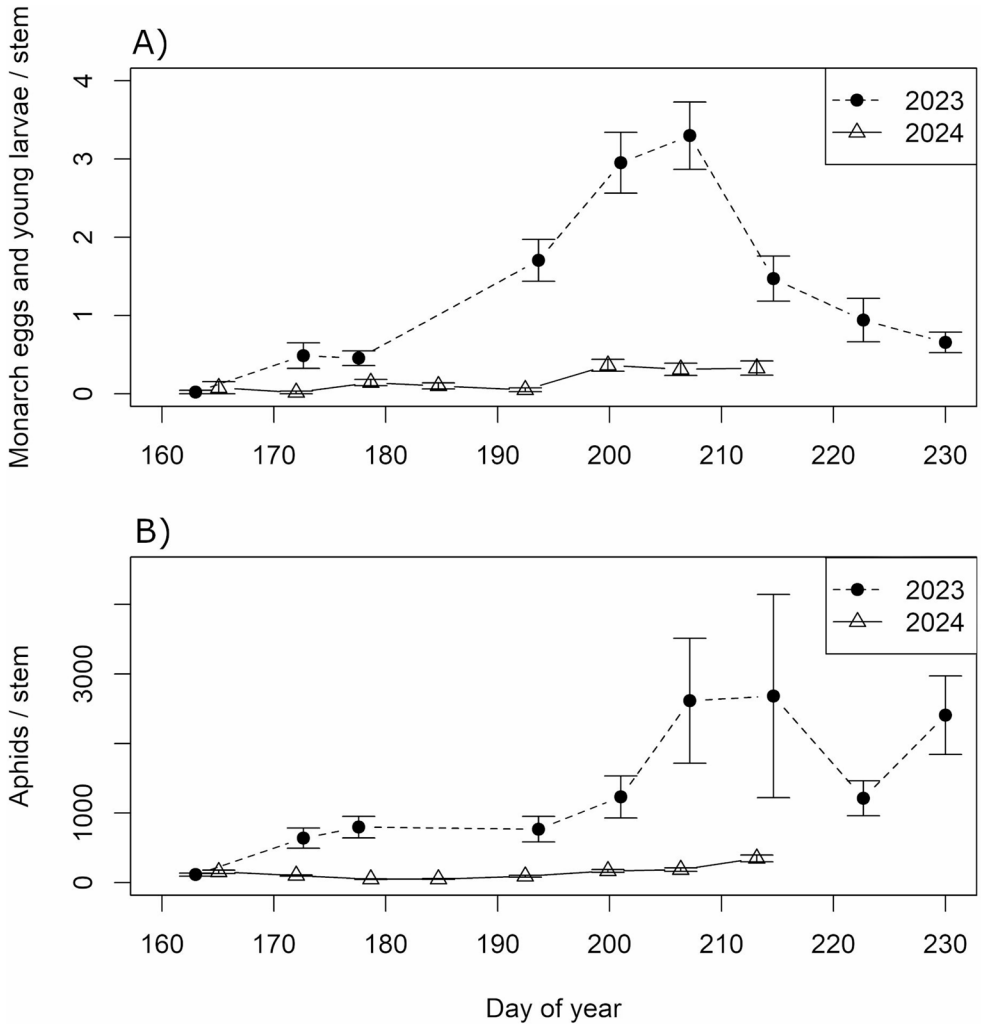


Fig. 1 Monarchs (**A**) and aphids (**B**) observed per milkweed during each round of sampling over two years. Young monarch larvae were those in the first two instar stages, which are most likely to be found on the same plant on which they were oviposited. Multiple species of aphids were encountered, and all observations are pooled

July). The number of eggs and larvae per plant was greater than one for four weeks in 2023. In contrast, during our 2024 surveys, we found far fewer monarchs, with less than one per plant throughout the season. The peak number in 2024 was 0.36 (SE = 0.076) eggs and larvae per plant, which occurred during week six (around 17 July). Similarly, aphid counts were much higher in 2023 compared to 2024. In 2023, the peak abundance of aphids was 2700 (SE = 1461) per plant, which occurred during week seven (around 2 August). Aphid abundance was over 500 per plant for all but the first week in 2023. In contrast, the number of aphids did not exceed 350 per plant for any week in 2024. We did not make separate counts of each species of aphid we observed, but qualitatively, *A. myzocallis* was observed at moderate level throughout the study period, *A. asclepiadis* made up most of the highest densities of infestation, and *A. nerii* was not seen frequently until later in the study period and at lower abundances. We also observed at least one additional aphid species (*Aphis fabae*) that is not a milkweed specialist.

In 2023, there was a positive correlation between the number of young monarch neonates and our estimates of the number of aphids on individual stems (Fig. 2a). The positive relationship with the aphid estimates was weak and had weak statistical support (Online Resource 2, Table S1a); the model that included aphid as a fixed effect had more support than the null model (Akaike weight = 0.63, $\Delta AIC_C = 1.0$).

We repeated the statistical analysis using only data from the two weeks with the highest neonate counts in 2023 (19 July to 28 July) in order to more closely explore the association between aphids and monarchs when monarchs were most abundant. Additionally, concentrating on a shorter time period helps to explore the association with fewer uncontrolled temporal variables, such as aphid phenology. When working with the smaller dataset with more monarch observations, we found a stronger positive relationship between monarch counts and aphid estimates (Fig. 2b). The model that included aphid counts had much more statistical support than the null model (Akaike weight = 0.93, $\Delta AIC_C = 5.1$; Online Resource 2, Table S1b).

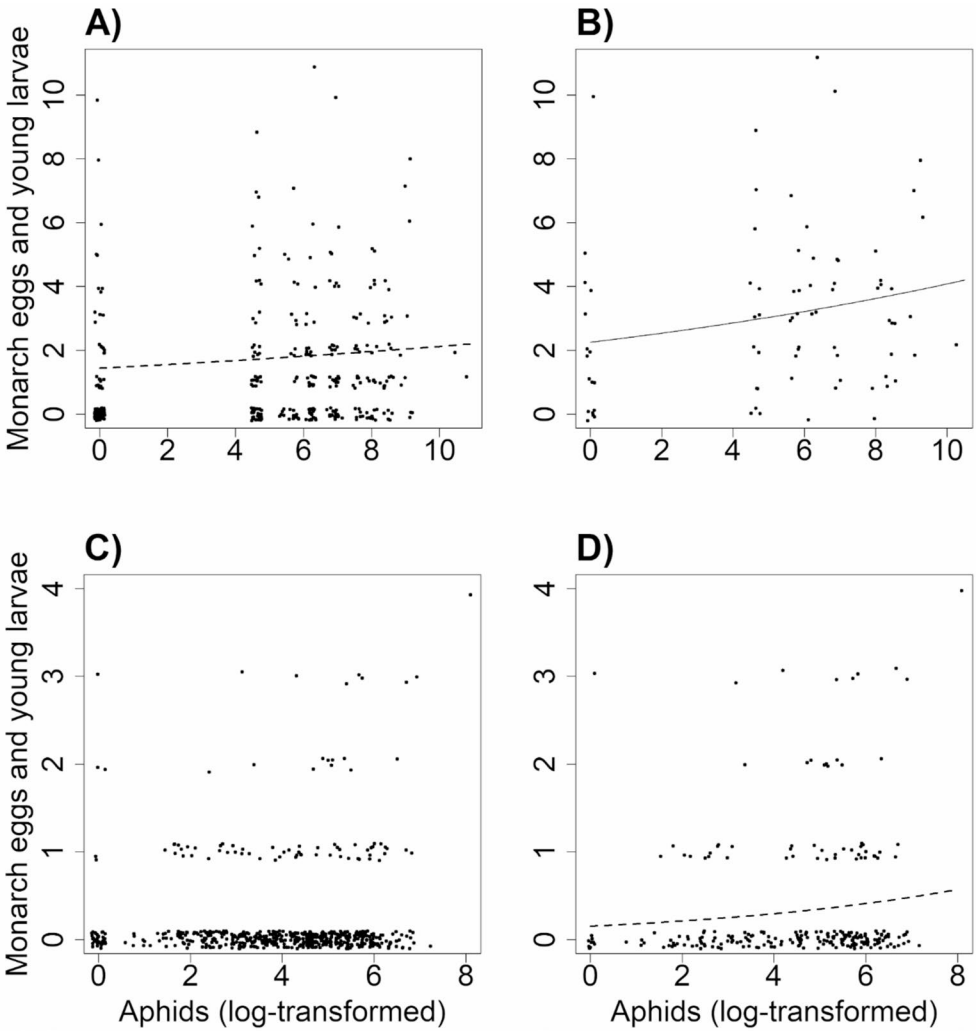


Fig. 2 Relationship between monarchs per milkweed and aphids per stem. **A** All observations in 2023, **B** observations from the two weeks with the most monarchs in 2023, **C** all observations in 2024, **D** observations from the three weeks with the most monarchs in 2024. Monarch counts include eggs and young larvae (first and second instar). Aphid counts were log(x+1)-transformed. Values in both axes were randomly offset for clearer visualization of clustered and overlapping datapoints. Curves indicate the predicted values from the statistical model for aphids predicting monarch counts, using typical random intercepts. Dashed curves indicate weaker associations ($\Delta AIC_C < 2$), and no curve indicates that there was no support for the hypothesized association

In 2024, when considering the entire dataset, we found that there was no association between neonate count and aphid counts (Fig. 2c). The null model had more statistical support than the model that included aphid count (Akaike weight = 0.73, $\Delta AIC_C = 2.0$; Online Resource 2, Table S1c).

There were extremely low numbers of monarchs observed during the early summer of 2024 (Fig. 1a). When we concentrated on the three periods of data collection with the most monarchs (17 July to 2 August), we found a weak positive association with aphid counts (Fig. 2d). The model that included aphid estimate as a fixed effect had more support than the null model, but the statistical support was relatively weak (Akaike weight = 0.63, ΔAICC = 1.0; Online Resource 2, Table S1d).

Discussion

Our study aimed to investigate the relationship between monarch butterflies and aphids in urban gardens. Milkweed plants in urban gardens are often colonized by aphids, and it is important to understand what impact this may have on monarch oviposition. While we included no measure of monarch survival in our analysis, we present evidence that in an urban setting, aphid infestation on milkweeds is not associated with reduced monarch oviposition on individual stems. In fact, when an association was found, it was positive. We found support for a positive association in 2023 across the entire season. In 2024, a year with low monarch abundance in Chicago, we found no relationship when we used data from across the whole season. When we included only the weeks of the study when the most monarch neonates were observed, there was again a weak positive relationship between aphid and monarch abundance. None of our analyses identified a negative association. Taken together, our

results suggest that female monarchs were not deterred from ovipositing on aphid-infested milkweeds at our study site.

Our study was observational and therefore did not allow us to identify the mechanisms underlying the patterns we found. If a positive association exists, it is possible that female monarchs and aphids are attracted to the same plant traits (e.g., taller stems) without directly influencing one another, or that the presence of either attracts the other. Manipulative experiments would be needed to distinguish the mechanisms at play. It is also important to note that our counts of eggs and larvae reflect a combination of oviposition and mortality, and we do not know the relative strength of these processes; some eggs and larvae will have been predated before we observed them. Aphid abundance may impact other important elements of the monarch life cycle we did not measure, such as survival in later larval stages, rate of development, movement between milkweed stems, pupation success, and final body size. Finally, we did not make separate counts of each aphid species, and different aphid species likely have different interactions with monarch oviposition and larval survival. Despite these caveats, the neutral or positive relationship we observed between monarch oviposition and aphid abundance is an important pattern not previously reported.

Previous research, in fact, suggested that we might find the opposite results due to antagonistic relationships between aphids and monarchs. Studies have reported that aphids attract monarch predators, negatively impact monarch survival, lower milkweed nitrogen levels, reduce the quality of milkweed, and reduce attraction of ovipositing female monarchs (De Roode et al. 2011; Mach et al. 2023). These findings predict that female monarch butterflies would, or at least should, avoid aphid-infested stems for oviposition. Indeed, Mach et al. (2023) report that monarchs deposited three times more eggs on aphid-free versus aphid-infested milkweeds. However, Mach et al. (2023) used *Asclepias curassavica* in their bioassays, which may not be directly comparable to our study system because *A. curassavica* is a nonnative species that may disrupt monarch migration (Clement and Crawford 2020), has elevated cardenolide levels (Agrawal et al. 2021), and may increase pathogen and parasite exposure for monarchs (Satterfield et al. 2015). Also, Mach et al. (2023) studied *Aphis nerii*, which were a minority of the aphids we encountered. The study by Haan and Landis (2019) may be more relevant because they examined the effects of mowing patches of *A. syriaca* on monarch oviposition. They found more monarch eggs in mowed patches and the regenerating milkweeds in these patches had fewer predators and fewer aphids.

Other studies suggest that the milkweed-mediated interaction between aphids and monarchs could benefit monarch survival, mass gain, and possibly oviposition. Multiple studies have established an interaction between the jasmonic acid and salicylic acid hormonal defense pathways when both aphids and monarchs are present on the same milkweed plant (reviewed in Agrawal et al. 2014). Bioassays have shown that aphids reduce the induction of the jasmonic acid pathway, which is a defense against chewing herbivores like monarchs (Ali and Agrawal 2014). Although it is unclear whether female monarchs can detect defense compound concentrations in milkweeds, this indirect aphid interaction could potentially explain weak positive associations with oviposition rates. Gathering data on larval survival would provide additional insights into indirect effects between aphids and monarchs. Alternatively, aphids may be attracted to stems with monarch larvae because of reduced induction of the salicylic acid pathway. There may also be unidentified characteristics of different milkweed stems that are more important in monarch oviposition preference than aphid abundance. Aphids and monarchs could be more abundant on the same stems due to traits of individual plants, making them more attractive to both monarchs and aphids.

We estimated total aphid numbers, but this included at least four species, *A. asclepiadis*, *M. asclepiadis*, and *A. nerii*, mostly existing on milkweed, and *A. fabae*, a generalist species. The three milkweed-feeding aphid species have been reported to be more abundant at different times of the season (Smith et al. 2008) and may have different interactions with monarchs. Only *Aphis asclepiadis* is consistently tended by ants, and ants may act as monarch predators (and/or deterrents to other predators). While the focus of our study was aphid interactions with monarchs, aphids may also impact other lepidopterans that use milkweeds as host plants, including *Euchaetes egle*, *Cycnia tenera*, and *Cycnia inopinatus*. The two *Cycnia* moths are unlikely to encounter milkweed stems with aphid abundances as high as the ones in our study since they are uncommon in urban environments. Milkweeds have such distinctive chemical defenses that it is difficult to compare our findings to aphid and lepidopteran interactions on other host plant species, though negative associations have been found in other systems (e.g., Layman and Lundgren 2015).

Data on monarch neonate survival are also needed to clarify the interactions between aphids and monarch neonates. We intended to collect data on neonate survival in 2024 by monitoring individual stems every week and tracking the fate of eggs and young larvae but the scarcity of eggs and larvae that summer prevented us from collecting sufficient data for statistical analysis. Tracking later instar stages is also needed for estimating larval survival until pupation, although this is difficult since older larvae are mobile enough to move between milkweeds (Fisher et al. 2020; Myers et al. 2020). Investigations of the relationship between milkweed plant density with both aphid abundance

and monarch oviposition would be informative, as well as garden composition, garden layout, and surrounding physical structures, which have been shown to alter monarch oviposition rates (Baker and Potter 2019). It is feasible that these factors could also affect aphid abundance or shift the relationship between monarchs and aphids. Finally, assessing morphological, phenological, and chemical characteristics of individual milkweed stems or genets with differing numbers of aphids and monarchs would help determine whether plant traits mediate the interactions of milkweed herbivores.

Our findings indicate that female monarch butterflies do not actively avoid aphid-infested stems for oviposition in an urban setting. While it has been reported that urban gardens have higher rates of aphid infestation (Hall and Ehler 1980; Mach et al. 2023), this has not been thoroughly investigated. Comparing aphid abundances on milkweeds in different landscapes would elucidate whether aphid abundance and potential interactions with monarchs are more prominent in urban environments. Some of the milkweed stems in our study had extremely high levels of aphids and still were used for oviposition. Urban gardeners and conservationists should be encouraged to plant and maintain these habitats in support of monarchs and other native insects facing population decline despite the presence of aphids.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-025-00720-5.

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Author contributions All authors contributed to the study design. Data was collected by EQ and data was analyzed by EQ and DNZ. EQ and MVA drafted the manuscript, and all authors revised and approved the final version.

Data availability All data used in this manuscript are available from the Illinois Data Bank, Quiroz E, Ashley MV, Zaya DN (2025) Data for Aphid Infestation and Monarch Butterfly Oviposition in Urban Gardens. University of Illinois Urbana-Champaign. https://doi.org/10.13012/B2IDB-2226372_V1.

Declarations

Conflict of interest The authors declare no competing interests.

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