Plant abandonment behavior and fitness of monarch larvae (Danaus plexippus) is not influenced by an intraspecific competitor

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Abstract
Integrating aspects of larval lepidopteran behavior that enhance survival into conservation plans could increase the overall impact of the efforts. We previously recommended that where possible, maintaining 2–4 ramets of closely-spaced common milkweed would support the development of at least one monarch through pupation, based on a seemingly innate behavior in which monarch larvae (Danaus plexippus) abandon their natal milkweed ramet (Asclepias sp.). Here, we explored the impact of intraspecific competition on larval ramet abandonment behavior and fitness of monarch larvae in small artificial milkweed patches.

We observed larvae reared under direct and indirect intraspecific competition, and larvae reared alone. We found no influence of intraspecific competition; however, our study provides further support that milkweed ramet abandonment is a seemingly innate behavior. This behavior occurs before all of the available leaf biomass on a ramet is consumed and prior to the pre-pupal wandering stage.

Implications for insect conservation: Results from our study suggest that in the absence of predation, parasitism, and interspecific competition, and when sufficient plant biomass is present to support larval development, the presence of an intraspecific competitor does not influence larval behavior or fitness. Based on milkweed ramet abandonment behavior, we continue to suggest maintaining small patches of 2–4 milkweed ramets when possible.

Keywords Monarch · Danaus plexippus · Common milkweed · Asclepias syriaca · Larval movement behavior · Larval host plant abandonment · Intraspecific competition

Introduction
Monarch butterflies (Danaus plexippus) are a charismatic lepidopteran species, known for their characteristic orange and black coloration, annual multi-generational migration across North America, and obligate host relationship with milkweed (Asclepias spp.). Since the 1990s, a significant population decline has been observed in association with loss of overwintering habitat in Mexico, loss of breeding and forage habitat in the Southern and Midwestern USA, pesticide use, and extreme weather conditions (Brower et al. 2012, Flockhart et al. 2015, Inamine et al. 2016, Oberhauser et al. 2017, Thogmartin et al. 2017, Grant et al. 2022). In the Midwestern USA, conservation efforts are underway to restore breeding and forage habitat (Midwest Association of Fish and Wildlife Agencies 2018).

Generally, larval lepidopteran survival is low, with larval monarch survival estimates of 3.6% (Grant et al. 2022), 7–10% (Nail et al. 2015), and 14–30% (Geest et al. 2019) from neonate until pupation. As such, aspects of conservation strategies aim to incorporate habitat restoration and maintenance practices that enhance larval survival (Haan and Landis 2019, Myers et al. 2019). Integrating larval behavior into conservation plans could increase the overall impact of habitat restoration efforts. Based on the results of a controlled laboratory study (Zalucki and Brower 1992), greenhouse study (Fisher et al. 2020), and field studies (Urqhart 1960, Rawlins and Lederhouse 1981, Borkin 1982, Zalucki and Rochester 2004, De Anda and Oberhauser 2015), monarchs perform a seemingly innate behavior in which larvae...
abandon their natal ramet of common milkweed, and subsequent ramets, before all of the available leaf biomass on a ramet is consumed and prior to the pre-pupal wandering stage. Although motivations for milkweed ramet abandonment by monarch larvae remain unknown, these findings suggest that where possible (i.e., backyard gardens), maintaining at least two to four ramets of closely-spaced common milkweed would support the development of at least one monarch through pupation (Fisher et al. 2020). Similarly, in urban gardens, Baker and Potter (2019) found more monarch eggs and larvae on spatially isolated milkweeds as compared to milkweed intermixed with non-host plants.

While in a controlled environment, without predation, interspecific competition, or intraspecific competition, our recommendation seems appropriate. Under field conditions, top-down forces could modify these findings. Specifically, although isolated milkweed ramets appear to be favored for oviposition, with up to ten monarch eggs observed per plant (Zalucki and Kitching 1982), the resulting larvae will likely encounter intraspecific competition. High densities of eggs (i.e., up to 50 eggs caged on ten milkweed ramets) can also result in increased infection probability by the protozoan parasite *Ophryocystis elektroscirrha*, reduced survival rates, smaller body size, shortened developmental rates, and reduced adult longevity in comparison to monarch larvae grown in isolation (Lindsey et al. 2009, Flockhart et al. 2012). Currently, there is minimal research exploring the influence of intraspecific competition on behavior (Flockhart et al. 2012).

Here, we explore the impact of intraspecific competition on larval ramet abandonment behavior and fitness of monarch larvae reared on milkweed in cages under greenhouse conditions as described by Fisher et al. (2020) in comparison to control larvae reared alone. We hypothesized that in the presence of a potential intraspecific competitor on the same ramet, natal ramet abandonment behavior would occur earlier in development than when there was only one larva per plant. Additionally, we hypothesized that more subsequent ramet abandonments would occur with two larvae co-located in a cage in comparison to larvae reared alone. Finally, we hypothesized that the presence of an intraspecific competitor would have a negative impact on developmental rates, body size, and leaf consumption, as other studies have shown (Lindsey et al. 2009, Flockhart et al. 2012).

**Methods**

**Experimental design**

As described by Fisher et al. (2020), individually potted common milkweed (*Asclepias syriaca*) ramets were grown from locally sourced seed (Ames, IA, USA) under greenhouse conditions (sodium light-augmented 16:8 L:D cycle, approximately 56% RH, windows opened when temperatures exceeded 21 °C). When ramets were between 10 and 35 cm tall with seven to 24 leaves, four potted ramets of comparable size were arranged in the corners of 54 cages (57 × 37 × 55 cm; Honey-Can-Do HMP-03891 Mesh Hamper with Handles, Walmart, Rogers, AK and “no-see-em” netting Arrowhead Fabric Outlet, Duluth, MN) and covered with potting soil to provide a uniform surface at the base of the ramets (Fig. 1). Within 5 h of hatching, colony-reared monarch neonates were acquired from the United States Department of Agriculture, Agriculture Research Service, Corn Insects and Crop Genetics Research Unit (USDA-ARS-CICGRU, Ames, IA, USA) and placed in the cages in random order. The location of neonate placement within the cages were the experimental treatments, including (1) control with one neonate on a randomly selected milkweed ramet (Fig. 1a), (2) two neonates on different leaves of the same randomly selected milkweed ramet (Fig. 1b), and (3) one neonate on a randomly selected ramet and one neonate on a ramet diagonal to the original ramet (Fig. 1c). Cages were arranged in a randomized complete block design. Experiments were replicated with three cohorts of milkweed ramets and monarch larvae, with trials initiating on April 30, May 21, and June 11, 2019 (162 total cages; 54 cages per treatment).

Cages were monitored twice daily (approximately 0600 and 1600 h) for the duration of larval development. Larval developmental stages present and ramets occupied during the observation periods were recorded until pupation. When two larvae were observed occupying the same ramet, it was noted if they were located on the same leaf. The first ramet abandonment was identified when at least one larva in the cage was first observed off its initial ramet. Twenty-four hours after all larvae in the cage pupated, pupae were collected and weighed. At this time, the number of leaves with and without evidence of feeding on each ramet in the cage was recorded. We did not observe stem feeding.

**Statistical analyses**

All statistical analyses were conducted in RStudio version 4.0.3 (R Core Team 2020, RStudio Team 2020). The percent of larvae that survived to pupation was analyzed by treatment (control, two larvae initiated on same ramet, two larvae initiated on different ramets) and by the number of larvae in the cage (1 vs. 2) with chi-square tests for probabilities (chisq.test). Our experimental treatments depended on survival of larvae until pupation within a cage. Cages in which a larva died were removed from further analyses, leaving 45, 33, and 30 cages from the one larva control,
two larvae on the same plant, and two larvae on different plant treatments, respectively. The average instar in the cage at the first ramet abandonment, the number of days elapsed prior to the first ramet abandonment within a cage, the total number of ramet abandonments observed within a cage, the number of times two larvae were observed on the same plant were analyzed by treatment with generalized linear models that incorporated cohort using the package' emmeans' (Lenth et al. 2020). When evidence of feeding was noted in these treatments, the logit transformed proportion of leaves consumed per larva was analyzed with a generalized linear model. Pupal masses and the total days of development until pupation were analyzed by treatment using generalized linear models that incorporated cohort.

Results

Survival until pupation was not influenced by treatment ($\chi^2 = 3.1, df = 2, p = 0.2122$) or by the number of larvae within a cage ($\chi^2 = 1.6095, df = 1, p = 0.2046$). Overall, 78.7% of larvae in our experimental trials survived until pupation.

At least one milkweed ramet abandonment event was observed in 97.2% (105/108) of cages where all larvae survived until pupation. There was no effect of treatment on the time ($df = 2, 102; f = 2.347, p = 0.0956$) or instar ($df = 2, 102; f = 2.062, p = 0.1272$) at the first ramet abandonment. On average, the first ramet abandonment within a cage occurred after 6.7 ± 2.5 days. While the first ramet abandonment was most often initiated by a 4th instar larva ($n = 50$ occurrences), the first ramet abandonment was observed 4, 9, 32, and 10 times during the 1st, 2nd, 3rd, and 5th instars, respectively. Because we could not differentiate larvae within a cage, the total number of ramet abandonments observed in each cage was an artifact of the number of larvae in the cage. After the first ramet abandonment, when two larvae were in a cage, an additional 2.3 ± 1.2 ramet abandonments per larva occurred, which was not significantly different from the 2.5 ± 1.7 ramet abandonments per larva occurred, which was not significantly different from the 2.5 ± 1.7 ramet abandonments that were observed when one larva was in a cage ($df = 1, 103; F = 0.226; p = 0.6348$).

Larvae originally placed on the same plant were observed on the same milkweed ramet six times more frequently than larvae originally placed on different ramets ($df = 1, 61; f = 126.625; p < 0.0001$). This observation is consistent with early instars being less mobile than late instars; however, there was no difference in the proportion of times larvae were observed sharing a milkweed leaf ($df = 1, 51; f = 0.924, p = 0.3364$). Larvae were observed on the same milkweed leaf for ~13% of the observations when larvae were on the same plant.

Plant utilization was estimated based on the percent of total leaves consumed from the four milkweed ramets per number of larvae in the cage. When we assume that both larvae in one cage consumed the same amount of leaf tissue, there was no difference in the logit transformed percent of total leaves with evidence of feeding (glm; $f = 2.636,$ $p = 0.146$).
The motivations for milkweed ramet abandonment remain unclear. We hypothesize herbivory causes reduced plant quality, which initiates searching behavior for an alternative food source. Reduced plant quality could result from (1) preferential consumption of young vegetation, (2) induced cardenolides, (3) induced defenses including “call for help” compounds to attract predators and/or parasitoids, and/or (4) reduced leaf cover resulting in exposure to potential predators (Borkin 1982, Zalucki and Brower 1992, Fisher et al. 2020). We anticipated that intraspecific competition between two larvae in our experimental system would help shed some light on these hypotheses; however, since there were no differences in behavior or fitness characteristics, with and without competition, additional targeted studies are required.

In general, movement of larvae is more extensive than often thought (Dethier 1959, 1989) and is usually ignored. Integrating larval behavior into conservation plans could enhance larval survival and increase the overall impact of habitat restoration efforts. Results from our study suggest that in the absence of predation, parasitism, and interspecific competition, and when sufficient plant biomass is present to support larval development, the presence of an intraspecific competitor does not influence larval behavior or fitness. Based on milkweed ramet abandonment behavior, we continue to suggest maintaining small patches of at least 2–4 milkweed ramets when possible.

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Author contributions Both authors contributed to the study’s conception and design. Material preparation, data collection, and analysis were performed by Kelsey E. Fisher. The first draft of the manuscript was written by Kelsey E. Fisher. Both authors edited subsequent versions of the paper, read, and approved the final manuscript.

Declarations

Competing interest The authors declare that they have no conflict of interest.

Compliance with ethical standards This work is original and has not been submitted to any other journal for consideration. This is a complete study and has not been split into several parts to increase the number of submissions. Results are presented to the best of our knowledge without fabrication, falsification, or inappropriate data manipulation. No data, text, or theories by others were presented as if they were our own work; proper acknowledgments were given. All work

Discussion

Using a design similar to Fisher et al. (2020), we aimed to determine the influence of intraspecific competition on monarch larval behavior and fitness. We hypothesized that the presence of an intraspecific competitor would initiate ramet abandonment earlier, cause larvae to abandon their milkweed ramets more often in an attempt to avoid conspecifics, and negatively impact fitness characteristics. We found no influence of intraspecific competition during our experiment; therefore, we conclude that in the absence of predation, parasitism, and interspecific competition, and when sufficient plant biomass is present to support larval development, the presence of a single intraspecific competitor produces no measurable impact but additional intraspecific competitors could have an influence. Other studies found impacts of intraspecific competition on fitness (Lindsey et al. 2009, Flockhart et al. 2012); however, these studies used high densities of conspecifics per plant (5, 10, 20, 35 and 50). Additional research is exploring the influence of resource deprivation on larval behavior and potential cannibalism (Shryock 2021).

The results of this study are consistent with those of Fisher et al. (2020) in which there was no intraspecific competition. Both studies support the notion that ramet abandonment is an innate behavior. The average pupal mass was consistent in both studies (~1.3 g). In both studies, the natal ramet abandonment was initiated most frequently in the 4th instar (approximately 6 or 7 days after neonate placement). Likewise, evidence of an additional ~ two ramet abandonments per individual was observed in each study. In both studies, larvae abandoned milkweed ramets prior to the complete consumption of the occupied milkweed ramet, the completion of larval development, and the prepupal wandering stage. Although larval development was slightly longer in the present study (14.04 ± 1.1 days) in comparison to Fisher et al. (2020; 11.6 ± 1.60 days), the difference is likely due to differences in greenhouse temperatures during the two studies.

p = 0.0717). Each larva was estimated to consume ~20% of leaves (control: 20.3 ± 6.4%; same plant: 17.2 ± 4.6%; different plant: 19.0 ± 5.0%). In support of the assumption that larvae consumed an equal amount of leaf tissue, individual pupal masses were not influenced by treatment (df = 2, 168, t = 2.365, p = 0.0939), with an average pupal mass of 1.39 ± 0.14 g. Likewise, there was no difference in the number of days elapsed from neonate to pupation (df = 2, 168, ŷ = 1.619, p = 0.1980) with an average of 14.04 ± 1.1 days of larval development.

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here is well-intended. The author list is complete and will not change. Raw data or documents are publicly available through GitHub: https://github.com/kelseyefisher/larvalmonarchmovementandcompetition. This research was not conducted on human subjects and was consistent with the United States Animal Welfare Act.

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