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Neither Copy nor Avoid: No Evidence for Social Cue Use in Monarch Butterfly Oviposition Site Selection

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Abstract Time spent assessing host plant quality during oviposition for phytophagous insects represents an energy-fitness tradeoff affecting future reproduction and offspring survival. In situations where resources are scarce or unattractive, organisms can utilize social information, including cues left behind by conspecific individuals, to inform decisions. In invertebrates, eggs deposited by previous females could signal a desirable resource, or alternatively females might avoid ovipositing near conspecific eggs to reduce offspring competition. Here, we show that monarch butterflies (*Danaus plexippus*) display the same pattern of oviposition across milkweed (*Asclepias incarnata)* stalks of differing quality, ignoring potential social cues and competition pressure imposed by conspecific eggs. Female monarchs preferentially laid eggs on healthy-looking, intact milkweed relative to water-stressed or herbivory-damaged stalks and exhibited differential post-alightment behavior on the three stalk types. Despite this apparent assessment of host plants for suitability, females failed to respond to social information in the form of conspecific eggs. Contrary to expectations that females would avoid healthy-looking, intact stalks with high egg numbers and prefer less desirable stalks with moderate egg numbers, the number of eggs laid by focal females did not depend on the number of prior conspecific eggs per stalk, regardless of stalk type. Our results suggest that monarchs neither avoid nor prefer stalks with conspecific eggs- perhaps due to low egg densities and larval survival in the wild, making discrimination based on conspecific eggs impractical when milkweed is abundant. Alternatively, egg clustering by females may be an adaptive oviposition strategy when host plant options are few, regardless of quality.

Keywords *Danaus plexippus* · oviposition · conspecific · *Asclepias incarnata* · host plant · ovipositor

Introduction

Organisms must constantly make choices that either improve or reduce their fitness in unpredictable or changing environments. Environmental information used for decision-making can be gathered by individuals using visual, olfactory, or other cues. Some animals also rely on the continual collection of social information in the form of cues from conspecific or even heterospecific individuals (Seppänen et al. 2007). Social information use and learning by invertebrates is extensive, and its impact on behavior

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has been observed across a multitude of species, including social insects like ants and bees, and gregarious species such as tent caterpillars (Colasurdo and Despland 2005; Provecho and Josens 2009; von Frisch 2013). Utilization of these social cues is often an adaptive behavior, as it allows for decision-making with less individual investment in the collection and processing of information. However, relying solely on socially-acquired information can lead to incorrect decisions and can be costly in other ways (Dall et al. 2005; Rieucau and Giraldeau 2011). There is growing evidence that invertebrates are selective about their use of social information over individual information, and the type of information utilized can depend on environmental context, resource quality, or other factors (Papaj and Messing 1996; Grüter and Leadbeater 2014; Otake and Dobata 2018).

Some of the most important fitness decisions organisms make surround reproduction and can benefit from social information. This includes assessing the quality of potential mates (Valone and Templeton 2002), the number of mates chosen (Cory and Schneider 2018), and selecting nesting sites and egg-laying substrates (Sarin and Dukas 2009; Raitanen et al. 2013; Duménil et al. 2016; Otake and Dobata 2018). In Lepidoptera, since larvae typically remain on their natal host plant from hatching until late-stage larval instars (Borkin 1982; De Anda and Oberhauser 2015; Fisher et al. 2020), the site that an organism chooses for oviposition can impact survival, competition, growth rate, and defenses of offspring from predation and parasitism (Ladner and Altizer 2005; Jones and Agrawal 2019).

Monarch butterflies (*D. plexippus*) are milkweed specialists, utilizing only plants from the Apocynaceae as larval host plants. Females typically lay eggs singly on the underside of leaves near the tops of plants (Zalucki and Kitching 1982), with each female laying around 300-400 eggs in the wild over a period of 2-4 weeks (Oberhauser and Solensky 2004). All larval development and pupation take place on the milkweed host, and nutrient consumption during this time affects adult size, longevity and reproduction. Since larval host plants have such important fitness implications, it was thought that females oviposit in line with the preference-performance hypothesis (PPH) (Jaenike 1978), wherein options would be assessed carefully using all available information to maximize offspring success. However, observed oviposition behavior in monarchs often varies from the PPH (Thompson and Pellmyr 1991; Jones and Agrawal 2019).

Monarchs are characterized as solitary insects during the breeding season in North America: sightings of multiple caterpillars on the same plant, or multiple adults together are relatively rare (Kasten et al. 2016; Pleasants et al. 2017). In some circumstances, monarchs can be observed collectively under patchy resources, meaning there is opportunity for conspecific interaction, particularly in urban and suburban areas, and at locations where monarchs breed year-round (Lindsey et al. 2009; Satterfield et al. 2015; Majewska et al. 2019a). A large body of research suggests that female monarchs use host plant chemistry, particularly milkweed cardenolides (plant secondary metabolites that deter herbivory) in host plant choice (Cohen and Brower 1982; Zalucki et al. 1990). Monarch caterpillars can sequester cardenolides and use them to deter predators, but high cardenolide concentrations are toxic to caterpillars (Malcolm 1994). Other work shows that females preferentially oviposit on smooth-leaved low-latex species such as *A. incarnata* over *Asclepias* species with high latex and trichomes (Haribal and Renwick 1998; Ladner and Altizer 2005; Pocius et al. 2018). Other physical characteristics like plant height, size, and flowering also affect host plant choice by female monarchs (Cohen and Brower 1982; Zalucki et al. 1990). Using chemo-receptor sensilla on the antennae and forelegs, females have been observed to exhibit distinct post-alightment behavior on plants of differing characteristics and quality (Zalucki et al. 1990; Haribal and Renwick 1998), suggesting that female monarchs spend time assessing host plants for suitability. However, it is not understood whether monarchs utilize social information, in the form of cues from other females, to help gauge the quality of host plant options.

The goal of our study was to assess whether female monarchs utilize social information in the form of conspecific eggs to inform host plant selection, and to examine if monarchs preferentially lay eggs on milkweed stalks with conspecific cues as host plant quality decreases. In this study, stalks of *A. incarnata* (swamp milkweed) were physically manipulated to simulate herbivory damage or water stress, as two states that might be less preferred by ovipositing females. In the first experiment, stressed and damaged stalks were presented to naive females alongside intact (undamaged, unstressed) stalks to gauge female oviposition preference, based on behavior and number of eggs laid per stalk. In a second experiment, three stalks of the same treatment, one of which contained social information in the form of conspecific eggs (focal stalk), were presented to naive females, and we again recorded the number of eggs laid per stalk. We hypothesized that among the three stalk treatments, female monarchs would preferentially oviposit on healthy-looking, intact stalks over damaged and water-stressed stalks, to increase the survival and development of future offspring. When presented with three intact stalks (one containing eggs), we predicted that females would avoid stalks with higher numbers of conspecific eggs, to reduce resource-based competition. Based on findings from other insect oviposition choice studies, we expected this to change as milkweed quality decreased, with females utilizing social information and exhibiting conspecific attraction in situations where their host plant options are unattractive. The presence of conspecific individuals or cues left behind by those individuals (eggs in this case) can be an indicator of desirable resources (Papaj and Messing 1996; Raitanen et al. 2013; Otake and Dobata 2018).

Materials and Methods

Monarch and Milkweed Sources

To obtain adult butterflies for the experiments, monarch caterpillars were reared indoors at 26-28 °C under ambient light supplemented by overhead fluorescent lighting set to a 16-hour day. Caterpillars hatched from eggs laid by non-inbred F1 descendants of wild-caught spring migrants collected from Athens, GA in Apr-May 2021. We obtained 8-10 outcrossed genetic lineages of monarchs per experiment. Prior to mating and oviposition, adults were examined for the protozoan parasite *Ophryocystis elektroscirrha*, and any infected adults were excluded from further study (Altizer et al. 2000).

After eggs hatched, caterpillars remained on natal stalks until late second instar, and were then transferred to 1.4 L plastic containers with mesh screen lids, 6 caterpillars/container, and fed fresh cuttings of greenhouse-raised *A. incarnata* daily. Following emergence, uninfected adults were kept individually in glassine envelopes at 12 °C for 5-14 days. To obtain mated females for the oviposition experiments described below, adult males and virgin females were placed into 0.6m^3 mesh screen cages for 5-7 days, until each female had mated (10 M and 10 F per cage, from outcrossed parentage). Mated females were removed from cages and held at 26 °C in glassine envelopes prior to oviposition choice studies and fed 20% honey water to satiation every second day.

The milkweed used in these experiments was cultivated from seed (Prairie Moon Nurseries) in a greenhouse set to 31 °C day and 26 °C night. Greenhouse lights were set to a 14-hr day length. Milkweed (*A. incarnata*) was sown in a bulk pine bark soil mix, in 6″ diameter pots, and plants were 6 months of age when trials began in late June. One tablespoon per pot of time-release fertilizer 15-9-12 NPK) was applied every 3 months. Seedlings were given Jack's Professional Peat Lite 20-10-20 NPK liquid feed at a rate of 200 ppm after sprouting, which was repeated monthly.

Plant Treatments

Oviposition trials took place in 0.6m^3 mesh cages, and were conducted indoors in a room exposed to ambient light, with four artificial fluorescent tube lights (set to 16-hr day) at 26-28 °C. Cuttings of *A. incarnata* were immediately placed into 0.6 L plastic bottles and provided as an egg-laying substrate in each cage. Stalks selected for the experimental trials were standardized in height (range 45-56 cm from the bottom of each bottle to the top of the stalk) and leaf number (16-24 leaves per stalk). Prior to trials, the milkweed stalks were manipulated to create one of three treatments: (i) intact stalks (fresh and healthy-looking with no signs of herbivory or water stress), (ii) herbivory damage, or (iii) water stress. To simulate herbivory damage, we punched round holes in milkweed stalks (3 mm diameter) after cuttings were placed in plastic bottles, with 4-10 holes per leaf, depending on leaf size. Water stress was simulated by removing cut stalks from water approximately 5 hours before presenting to females, to allow wilting; water removal was continued throughout the duration of oviposition (24 hours).

Experiment 1: Plant Treatment Preference

To establish oviposition preference among the three *A. incarnata* stalk treatments, three stalks in total, one from each treatment (intact milkweed, water-stressed, and herbivory damaged), were placed in each laying cage (0.6m^3 mesh screen) (Fig. 1). The position of each stalk type within each cage was randomized. We placed a single female monarch into each cage at 9 AM, and allowed females to oviposit for 24 hours, after which the number of eggs laid by each female on each milkweed stalk was recorded. We set up 10 cages per day, over 6 days, to test a total of 60 females. If fewer than 10 eggs were laid across all three stalks (combined), data from that female was excluded from further analysis (N = 11). Females were randomly chosen from one of 10 genetic lineages (full-sib family lines), with 5-7 females per lineage.

Oviposition behavior of each female was observed for one hour, following a minimum 1-hr acclimation period. During the hour of observation, we recorded each time a female alighted on a stalk, drummed forelegs or antennae on a leaf (drumming), or curled the abdomen to reach the underside of leaves (from here on referred to as dabbing; Fig. A1; (Zalucki et al. 1990). If a female did not land, drum, or dab on any plants during the observational period, that female was excluded from behavioral analyses (N = 18).

Experiment 2: Social Cue Use during Oviposition Site Selection

Here, we sought to establish whether female monarchs utilize social cues in the form of conspecific egg presence on milkweed stalks during oviposition, and if females display a differential use of social cues corresponding to environmental condition. We provided naive females in this experiment with three *A. incarnata* stalks of the same treatment type. One of the 3 stalks contained eggs laid by another female the day before. Since we found no significant difference between the intact and herbivory stalk treatments during experiment 1, we conducted experiment 2 using only intact and water-stressed stalks. To create stalks with conspecific eggs (focal stalks) prior to the start of this experiment, females from the previous preference trials were presented with intact milkweed stalks, and allowed to lay for 24 hours, until 10-100 eggs were present on each focal stalk. These focal stalks were then assigned to their treatment (intact or water-stressed) (Fig. 1), and water was removed from water-stressed treatment stalks 5 hours prior to trials.

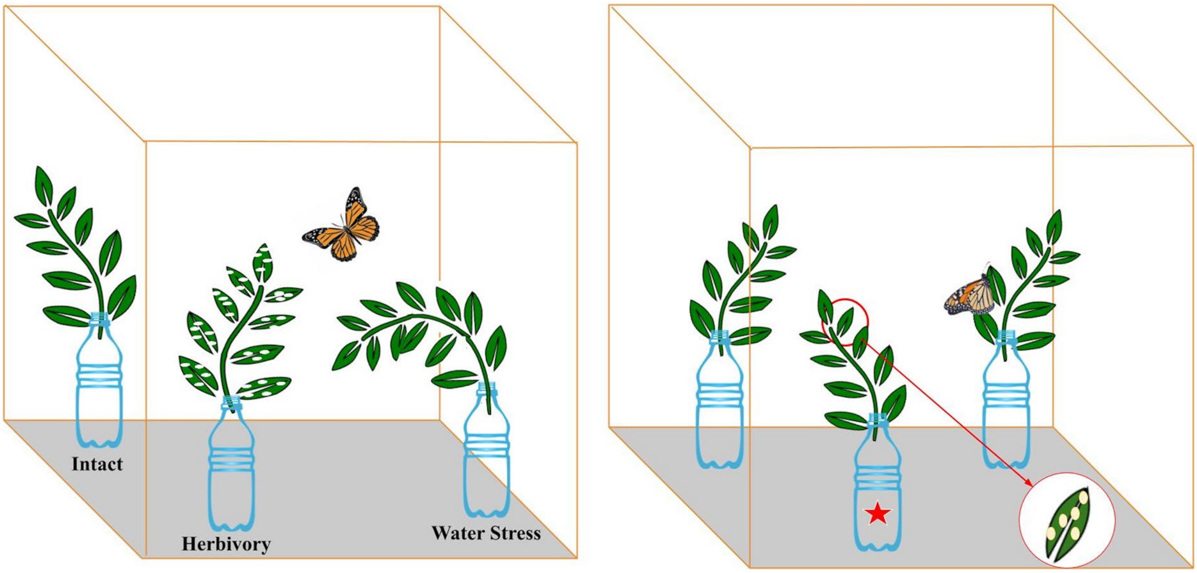

Fig. 1 Illustration of cage set up for experiments 1 (plant treatment preference, left) and 2 (social cue use, right). Each cage in experiment 1 contained a water-stressed stalk (left), herbivory-damaged stalk (middle), and intact stalk (right). In experiment 2, three stalks of the same treatment type (either herbivory or intact) were placed in each cage. The focal stalk (with eggs from a different female) is indicated with a star

The position of the focal stalk in each cage was randomized, and we recorded the number of eggs on the focal stalk prior to adding a single test female to each cage. As before, after 24 hours, the number of eggs laid by each test female on each milkweed stalk was recorded. We set up 10 cages per day, over 6 days, for a total of 55 females. If fewer than 10 eggs were laid across all three stalks (combined), data from that female was excluded (N = 10). Females were randomly chosen from one of 10 genetic lineages (full-sib family lines), with 2-12 females per lineage.

Data Analyses

In experiment 1, to test whether females discriminate based on host plant quality when laying eggs on milkweed, we examined the proportions of eggs laid on each of the three stalk treatment types. Proportions were square-root transformed prior to analysis to normalize error variance. We used a linear mixed model (LMER) with transformed proportions of eggs on each stalk type as our response variable, stalk treatment type as a fixed effect, and female ID as a random effect. To examine the behavior of females across milkweed treatments, we conducted three linear mixed models with the proportions of landings, drumming, or dabbing events per stalk as the response variable, stalk treatment type as a fixed effect, and female ID as a random effect. Proportions were again square-root transformed prior to analysis.

In the second experiment, the effect of monarch egg cues (number of initial starting eggs on each focal stalk) was tested by examining the proportion of eggs each female laid on the focal stalk, relative to the total number of eggs laid across all stalks combined. Proportions were square-root transformed prior to analysis. With transformed proportions as the response variable, we included plant treatment type (fixed effect), the starting number of eggs on the focal stalk (continuous covariate), and the interaction between the two as predictor variables.

Results

Experiment 1: Treatment Preference Trials

In the treatment preference experiment, stalk treatment type was a significant predictor of the proportions of eggs laid by females (F = 4.50, df = 2, $p = 0.0127$), suggesting discrimination based on milkweed quality. A post-hoc test showed that monarchs laid significantly more eggs on the intact milkweed stalks over the water-stressed stalks (Fig. 2; $p = 0.0129$). More eggs were laid on the intact stalks than herbivory-damaged stalks, but the difference between these two treatments was not significant ($p = 0.0773$), and there was not a significant difference between numbers of eggs laid on the two unattractive stalk types ($p = 0.7697$). The laying propensity of each female (the total number of eggs laid across all stalks) did not have a significant effect on treatment preference (Fig. A2; F = 0.347, df = 2, $p = 0.7076$).

Stalk treatment type was not a significant predictor of the proportion of landings per stalk (F = 1.443, df = 2, $p = 0.2401$), meaning females visited all stalk types relatively equally. The frequency of drumming antennae or forelegs differed significantly among stalk types (F = 5.650, df = 2, $p = 0.0045$), indicating different levels of post-alignment assessment by females depending on plant quality. Females were observed drumming significantly more often on herbivory-damaged stalks than intact stalks ($p = 0.0040$). Water stressed plants were also drummed upon more often than intact stalks ($p = 0.0460$), but we found no significant difference in drumming behavior between the two unattractive stalk treatments ($p = 0.680$). Treatment type was also a significant predictor of the number of abdomen dabs by females (Fig. 3; F = 5.973, df = 2, $p = 0.0033$). Monarchs dabbed (oviposition attempt) significantly more on intact plants than on water-stressed plants ($p = 0.0029$) and herbivory-damaged plants ($p = 0.0480$). There was no significant difference between female dabbing rates on water-stressed vs. herbivory stalks ($p = 0.5970$).

Experiment 2: Focal Stalk Trials

Females did not show evidence for avoidance (fewer eggs on egg-laden focal stalks) or attraction (more eggs on egg-laden focal stalks) in either the intact or water stressed stalk treatments (Fig. 4; F = 0.0001, df = 1, $p = 0.9907$). The number of initial conspecific eggs per focal stalk was not a significant predictor of the proportions of eggs laid by females on the focal stalk (Fig. 5; F = 0.0520, df = 1, $p = 0.8208$), regardless of treatment (intact stalks: $R^2 = 0.009$; Beta = −0.0009; F = 0.19; $p = 0.6710$) (water

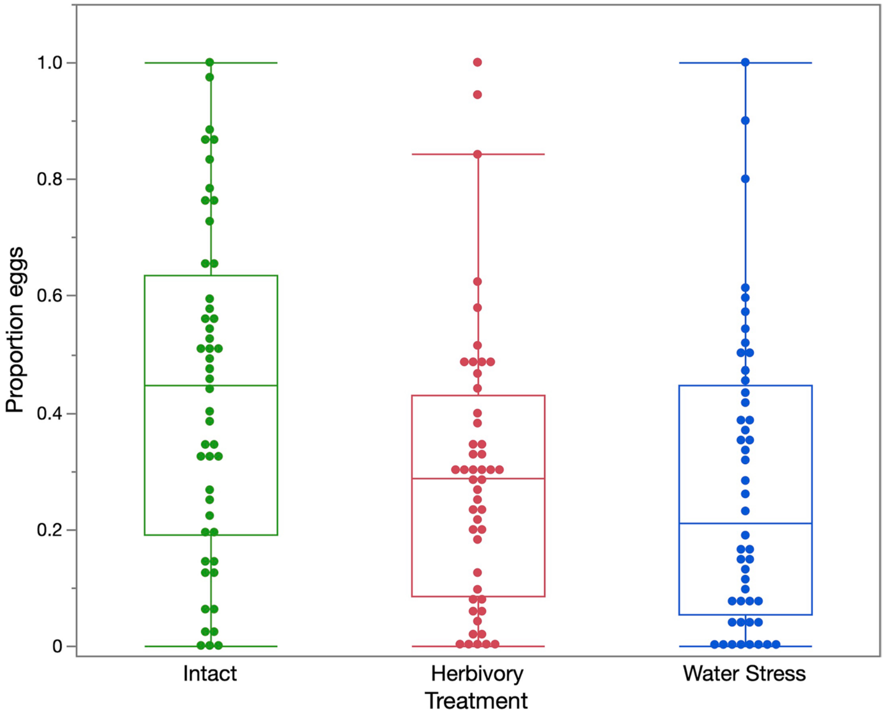

Fig. 2 Proportions of eggs laid by each female across each milkweed treatment type in Experiment 1. Intact stalks had significantly more eggs than water stressed stalks, but no other pairwise differences between treatments were significant

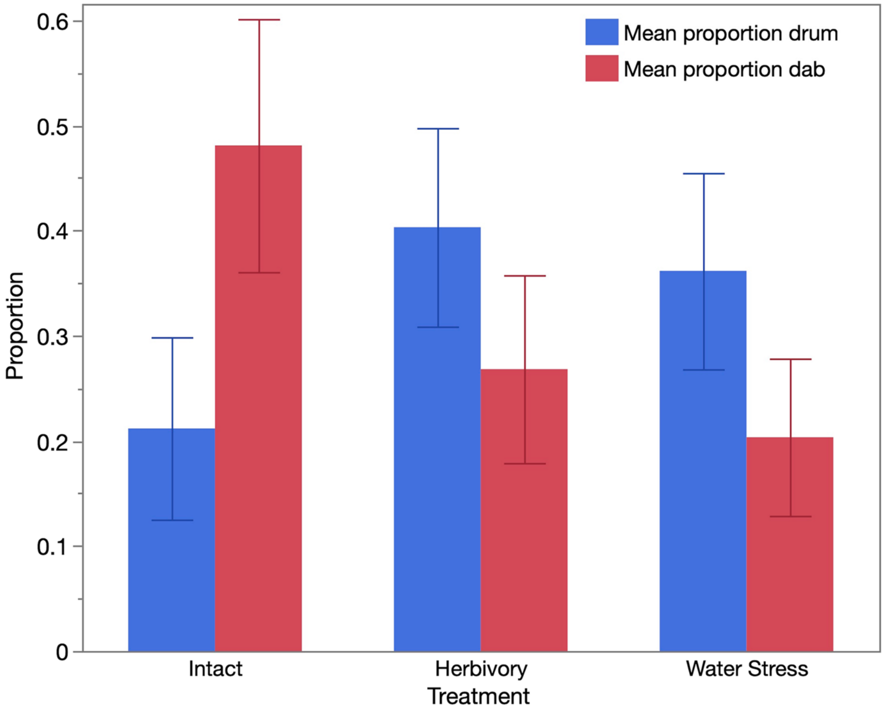

Fig. 3 Mean proportion of observed drumming (blue) and dabbing (red) behavior by females after landing across each milkweed treatment type in Experiment 1. Intact stalks were drummed upon with antenna and forelegs significantly less than the other stalk treatments, and were dabbed upon significantly more often

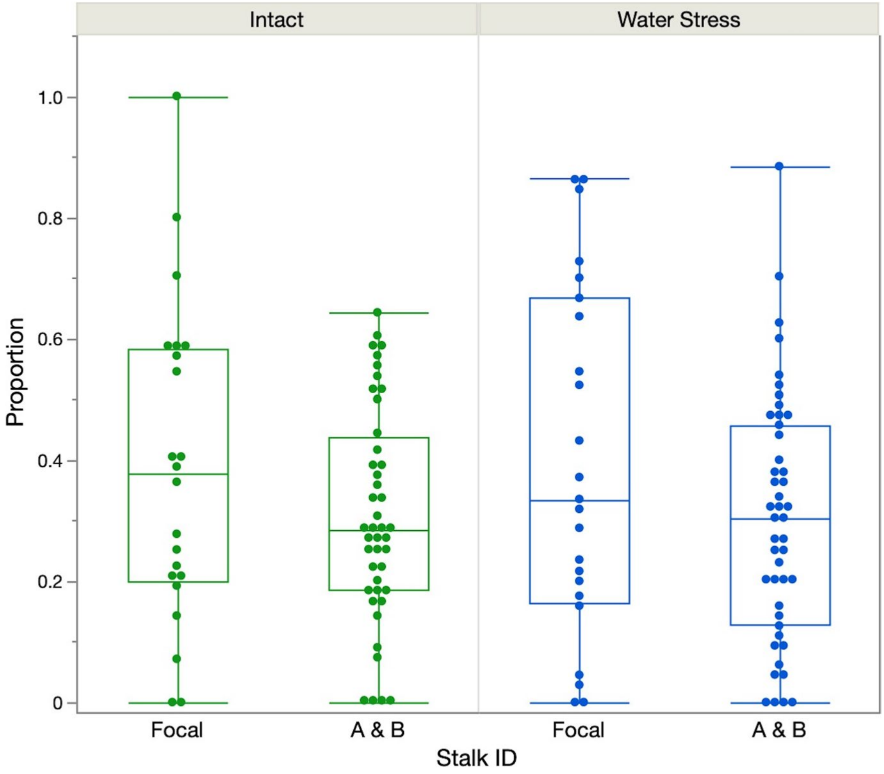

Fig. 4 Proportions of eggs laid by each female across each of the three milkweed stalks in Experiment 2. Females did not display avoidance of or attraction to egg-laden focal stalks in either stalk treatment type. There was no significant difference in the proportions of eggs laid by females on focal stalks versus the two plain stalks (A and B). Each point represents the proportion of total eggs per stalk type by one female

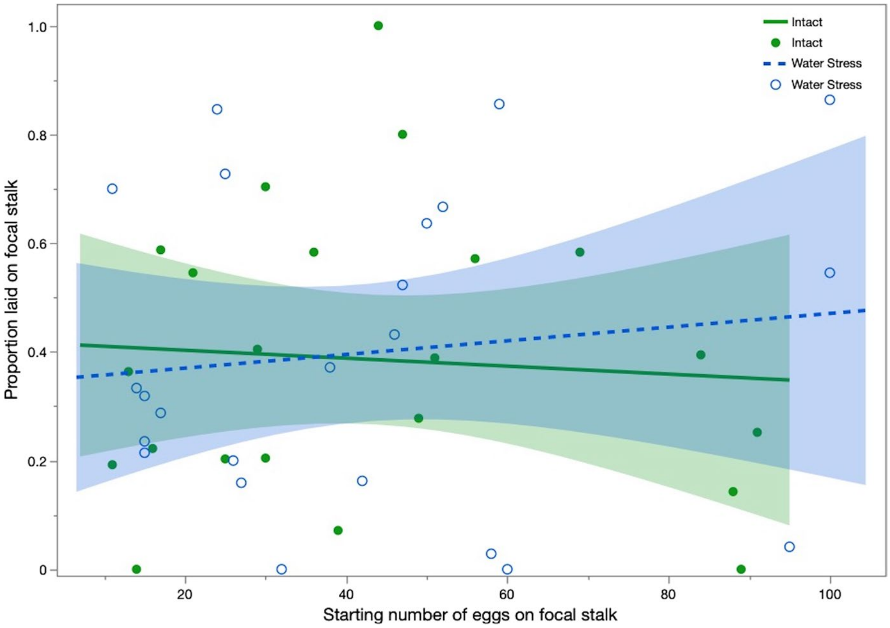

Fig. 5 Proportions of eggs laid on focal stalks during trials (y-axis) did not depend on the starting number of eggs on focal stalks (x-axis) in Experiment 2, regardless of stalk treatment (green = intact, blue = water stress). Each point represents the proportion of total eggs per focal stalk by one female

stressed stalks: R^2 =0.000; Beta = 0.0002; F = 0.01; $p = 0.9441$). We also found no effect of an interaction between starting focal egg number and stalk treatment (F = 0.1216, df = 1, $p = 0.7291$) on the proportion of eggs laid on the focal stalk.

Discussion

Our study showed that female monarchs preferentially laid eggs on healthy-looking, intact milkweed stalks over those that were water stressed or with simulated herbivory damage. Females did not change their oviposition behavior in response to social cues, and neither avoided nor preferred stalks containing the eggs of conspecifics. The lack of social cue response was similar for both preferred (intact and healthy-looking) and nonpreferred (water-stressed) stalk types. This suggests that while monarchs use a combination of physical and chemical plant traits in selecting oviposition sites, they do not appear to copy the host plant selection behavior of other females when presented with poor resources, nor do they avoid plants selected by previous females when presented with high quality host plants.

Females were observed visiting all stalk types relatively equally in Experiment 1 but exhibited differential post-alightment behavior between preferred and nonpreferred stalk types. On healthy-looking stalks, females were often observed dabbing to lay an egg almost immediately after landing, with infrequent or brief drumming of antennae or forelegs on the leaf surface. On the lower quality water-stressed and herbivory-damaged stalks, however, females spent more time assessing the suitability of the plants by drumming chemoreceptor sensilla on antennae and forelegs against the leaves. Despite being landed upon an equal amount, stalks of lower quality received fewer eggs, particularly water-stressed stalks. This suggests that these stalks were rejected (female leaves the plant without laying) more frequently than intact stalks. Past research also found that females used antennae, midlegs, and forelegs most extensively on the host plant options that ultimately received the fewest eggs (Haribal and Renwick 1998), which aligns with our observations. Our findings indicate that visual cues may not be the primary tool used by females when selecting a host plant at a close range, and that host plant suitability is investigated after landing. This further differentiation between host plant options involves female examination of leaf nutrient availability, latex levels, cardenolide concentrations, and water content (Zalucki et al. 1990). Discrimination based on the water content of leaves is likely why the wilted, water-stressed stalks consistently contained the fewest eggs after 24 hours.

Interestingly, herbivory-damaged stalks were drummed on most frequently and contained nearly as many eggs as intact stalks after 24 hours. The high levels of drumming by females suggests a lengthy period of plant assessment, but ultimately most females were not dissuaded from depositing eggs. In past research, female monarchs have been observed to exhibit a strong avoidance of plants containing conspecific larvae, but it was unclear whether this was in response to visual or chemical cues produced by the larvae itself, or to plant volatiles released through physical herbivory damage (Wason et al. 2013; Jones and Agrawal 2019). When milkweed leaves are damaged, the plant exudes latex, which is known to developmentally hinder early-instar larvae and increase mortality (Zalucki et al. 1990; Zalucki and Malcolm 1999; Van Zandt and Agrawal 2004; Ladner and Altizer 2005). Our results suggest that female monarchs may exhibit competition avoidance only when larvae (or their pheromonal cues) are physically present on host plants, and don't respond to plant volatiles alone. It is important to note that the use of cut stalks as opposed to intact plants likely limited latex flow, but exposed latex was still present on leaves after the mechanical damage was completed.

Despite evidence that females assessed host plants prior to oviposition, we found no indication that females either avoided or were attracted to stalks with conspecific eggs. Assuming that females could, in fact, detect the conspecific eggs on focal stalks, results observed here suggest that oviposition strategies of monarchs do not utilize social information. There is growing documentation of color vision (Stavenga and Arikawa 2006) and learning in monarchs and other Lepidopteran species, particularly as it pertains to nectar foraging (Kinoshita et al. 1999; Arikawa 2003; Rodrigues et al. 2010; Blackiston et al. 2011; Rodrigues 2016; Gegear 2021), and host plant selection (Stanton 1984; Traynier 1984; Cunningham et al. 1998). However, given that visual perception in monarchs is thought to rely heavily on high-contrast color information (Papaj 1986; Mackay and Jones 1989; Cepero et al. 2015), conspecific eggs on the undersides of leaves may be hard for females to visually detect. Further, many lepidopteran species have excellent distance-based vision and estimated perceptual ranges varying between 8 m to 50-100 m (Harrison 1989; Haddad 1999; Schultz and Crone 2001; Schtickzelle et al. 2007; Merckx and Van Dyck 2007; MacDonald et al. 2019), but may not be able to perceive certain visual cues at a close range. While monarchs have an estimated visual perceptive range of only a few meters (Garlick 2007), the small size of our experimental cages ($0.6m^3$) may also have limited the monarchs' ability to visually detect physical differences in the host plants or the presence of conspecific eggs. This could also explain why monarchs landed on all treatment types equally, despite the distinct physical variation between intact stalks and those that were heavily wilted or damaged by herbivory. Their discrimination between treatments occurred post-alightment, after drumming of antennae and forelegs on the tops of leaves.

It is equally likely that monarchs were able to detect the conspecific eggs (visually or chemically), but do not utilize egg-based social information in their oviposition process. Female monarchs typically deposit eggs singly, and milkweed plants in core regions of the migratory breeding range are highly abundant, such that numbers of eggs per milkweed rarely exceed 1 egg per stem, and egg densities are often much lower (Stenoien and Nail 2015). In the field, females have been shown to travel an average distance of 23 m between landing on milkweed plants, passing many viable options in the process (Zalucki et al. 1990). In areas with such abundant resources, monarchs may choose to disperse eggs widely with little or no plant assessment, since the probability that any given host plant will receive more than 2 eggs is very low, and therefore conspecific eggs will have a minimal impact on overall fitness.

In areas with limited or highly patchy milkweed resources, monarchs might show a different oviposition strategy. An observational study in southwestern Ontario, Canada saw females deposit more eggs per plant in areas with a low density of milkweed plants (Pitman et al. 2018). Another study conducted in Queensland, Australia reported a decrease in eggs per plant as the number of plants per patch increased, with isolated plants receiving the most eggs (Zalucki and Kitching 1982). This suggests that females may be more likely to 'egg dump' when their host plant options are few. Such conditions could occur in urban settings and in regions like the southeastern United States where milkweed occurs at much lower densities. When host plant options are limited, females might need to lay eggs on milkweed stalks already containing eggs from a previous female, a practice observed in *Pieris rapae L.* (Ives 1978). Because females in our experiments were presented with only three milkweed stalks, this could explain why some females chose to lay additional eggs on stalks already containing high densities. For example, one female deposited an additional 91 eggs on a stalk that contained 51 conspecific eggs at the beginning of the trial. Our focal stalks contained a range of 10-100 eggs prior to trials, a number similar to that used by Zalucki and Kitching (1982), who found no evidence for female monarch avoidance of milkweed plants containing eggs. It therefore seems likely that the high fecundity of monarchs, combined with low egg and early-instar survival rates, make egg clustering by multiple females an appropriate alternative to searching for unexploited resources when milkweed abundance is low.

It is important to note that the transmission of a debilitating protozoan parasite (*Ophryocystis elektroscirrha*) in monarchs occurs during oviposition, and infection risk to offspring increases when females lay eggs on plants previously visited by infected monarchs. This parasite forms spores on the outside of the body of adults, and infection occurs when caterpillars ingest parasite spores (McLaughlin and Myers 1970). Parasite spores can be transmitted from females to their offspring during oviposition (Altizer and Oberhauser 2004). In addition, adults can scatter spores onto milkweed leaves which are later consumed by unrelated caterpillars (de Roode et al. 2009; Majewska et al. 2019b). Analysis of volunteer- and field-based monitoring data show that parasite transmission increases with greater egg, larval, and adult densities in milkweed patches (Bartel et al. 2011; Majewska et al. 2022). Thus, females could benefit from avoiding milkweed already visited by other females when monarch densities and parasite infection risk is high. Further work could examine whether healthy females might respond differently to the presence of conspecific eggs laid by infected females, which would carry the benefit of disease avoidance.

In sum, our study showed that monarchs prefer to oviposit on healthy-looking, intact milkweed stalks and exhibit post-alightment assessment behaviors. However, monarchs did not use social information in the form of conspecific eggs to inform oviposition and showed no preference or avoidance of stalks with eggs laid by prior females. That conspecific eggs did not deter monarch oviposition is surprising, given the strong competition pressure that would occur between caterpillars feeding on the same host plant. Further work is needed to examine the mechanisms by which females detect the presence of conspecific eggs and larvae; see Wason et al. (2013) and Jones and Agrawal (2019); and to explore whether other aspects of monarch reproduction, such as mate choice, might respond to social information.

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Author Contribution All three authors conceived the study and designed the experiments. Data collection was led by C. Aikins, C. Aikins and S. Altizer wrote the main manuscript text, and T. Sasaki assisted with statistical analyses and figure preparation. All authors reviewed the manuscript.

Declarations

Competing Interests The authors have no competing interests as defined by Springer, or other interests that might be perceived to influence the results and/or discussion reported in this paper. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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