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ARTICLE

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Struggling to survive: A comparison of *Vanessa cardui* larval survivorship on putative host plants

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Abstract

The painted lady butterfly (*Vanessa cardui*) is a generalist herbivore with a global distribution. In North America, over 100 species have been identified as *V. cardui* larval host plants. This cosmopolitan species is commercially available in all life stages and can be reared on an artificial diet. As a result, *V. cardui* commonly serves as a model organism for education and outreach. However, gaps in our knowledge remain with regard to *V. cardui* ecology and larval host plant suitability for supporting complete development of larvae to reproductive adulthood. In a laboratory setting, we tested host plant suitability of five reported host plants commonly found in California sage scrub ecosystems by assessing survival of *V. cardui* caterpillars in its entirety. We also assessed how commercially sourced larvae survived on artificial diet: both raising the caterpillars exclusively on artificial diet as well as switching diets from artificial to thistle (a commonly reported host plant) and switching from thistle to artificial diet. We found that all commercially sourced caterpillars exhibited both high larval mortality and low pupation rates when reared on host plants, although larvae reared on *Malacothamnus fasciculatus* and *Sphaeralcea ambigua* survived longest. Moreover, *M. fasciculatus* and *S. ambigua* were the only host plants tested that supported successful pupation. This contrasted with 63% higher survival of wild-collected larvae. Our findings suggest that commercially obtained *V. cardui* may struggle to utilize wild host plants and that future investigations into host plant suitability in wild populations are needed. Additionally, future research using commercial larvae should consider the implications for interpreting host plant suitability as larvae may exhibit adaptations to artificial diet or the loss of adaptation to consuming plant material.

KEYWORDS
California sage scrub, generalist, host plant suitability, Nymphalidae

INTRODUCTION

Host plants play a key role in early lepidopteran development by providing nutrients and shelter. Additionally, host plant toxins sequestered by larvae help protect against predation throughout development and into adulthood (Brower, 1969). However, climate change and anthropogenic activities are altering plant communities

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worldwide, which may impact codependency between plants and butterflies (Sánchez-Bayo & Wyckhuys, 2019). Shifts in plant phenology may affect host plant quality (Yang et al., 2020) and availability—with subsequent impacts on larval development (Friberg & Wiklund, 2010). Such observations have resulted in a growing interest to increase monitoring of butterfly populations globally. While host plant resources may be stronger predictors of butterfly abundance than nectar plants (Curtis et al., 2015), detailed host plant information is often missing or incomplete. Even less understood is the suitability of host plants for larval survival despite the critical need for this information to inform butterfly conservation and habitat management strategies.

The painted lady butterfly (*Vanessa cardui*) is a cosmopolitan species with one of the broadest ranges of reported plants as nectar and larval host sources (Graves & Shapiro, 2003; Scott, 1986). The species is commercially available in all life stages, and larvae readily develop on artificial diet. The availability and ease of rearing makes *V. cardui* a favorite for scientific studies and for school projects. Similarly, it is often used as a model organism for studies in evolution and adaptation, and for investigating potential trade-offs associated with polyphagy (Audusseau et al., 2016; Briscoe et al., 2003; Ellis & Bowers, 1998; Garrigan, 1994; Graves & Shapiro, 2003; Janz, 2005; Janz et al., 2007). Despite its large geographic distribution and model organism status, research on wild host plants and their suitability to support development into adulthood is limited.

Painted lady butterflies utilize a diversity of nectar plant species throughout California (J. Caldwell, unpublished manuscript; Saldivar et al., 2022; Shapiro, 2002), and well over 100 species in North America have been reported as host plants (J. Caldwell, unpublished manuscript; Williams, 1970). While there are many observational records of *V. cardui* larvae feeding on plants, data are limited as to whether these plants are suitable for the caterpillars to complete development (Hanson, 1983). To date, larval survivorship and pupation rates have been quantified on only a few host plant species (e.g., Audusseau et al., 2016; Ellis & Bowers, 1998; Garrigan, 1994; Janz, 2005). Additionally, few studies have followed caterpillar survivorship beyond a specific age (in days), and when survivorship is low, detailed information is often not reported directly. This makes it challenging to assess how host plant identity impacts overall survivorship and makes building upon existing work difficult.

California's sage scrub habitats support resident and migratory *V. cardui* populations, but only a small fraction of their reported native and non-native host plants occur there (J. Caldwell, unpublished manuscript; Scott, 1986). As southern California sage scrub ecosystems are increasingly threatened by habitat destruction and plant invasions (Cleland et al., 2016; Westman, 1981), it is critical to understand patterns of larval host plant suitability in this common *V. cardui* habitat. To address this knowledge gap, we selected several putative host plant species found in California sage scrub and assessed their suitability as *V. cardui* host plants by quantifying larval development and survivorship.

METHODS

As commercially sourced larvae are commonly used in lab studies (see Appendix S1: Table S1), we obtained the larvae used in our survival assays from commercial sources either as eggs ($n = 1307$) or eggs laid by mated females ($n = 377$) reared from commercially sourced larvae (Carolina Biological Supply Company [Burlington, NC] and Educational Science Supply [League City, TX]). Eggs were manually placed onto the adaxial surface of plant leaves. One shipment of eggs ($n = 270$) contained a few hatched larvae upon arrival, but all other egg orders arrived unhatched. When obtained as larvae, we raised all caterpillars on an artificial diet through pupation and adult emergence; we then allowed the resulting butterflies to mate. We randomly assigned each mated female to a diet treatment (Table 1) and placed each individual inside a mesh cage (39.9 × 39.9 × 59.9 cm) to oviposit on their respective plant. All larvae were maintained at 24°C ± 0.1 (mean ± SE) and 51.5% ± 0.2 (mean ± SE) relative humidity. All equipment was cleaned and sanitized in between uses.

Larval survivorship on a constant diet

Since *V. cardui* occur in California sage scrub year-round, we selected reported host plants with a range of vegetative phenologies. The larval host plant species included native Malvaceae—*Abutilon palmeri* (Palmer's Indian mallow), *Malacothamnus clementinus* (San Clemente Island bushmallow), *Malacothamnus fasciculatus* (chaparral mallow), and *Sphaeralcea ambigua* (apricot mallow)—and non-native *Cirsium vulgare* (bull thistle; Asteraceae) and *Nicotiana glauca* (tree tobacco; Solanaceae) (Figure 1). All plants were sourced from local, native plant nurseries except for *C. vulgare* and *N. glauca*, which were wild-sourced. Nursery plants and *N. glauca* were kept in the pots during feeding trials (Appendix S1: Figure S1) while larvae were initially provided with *C. vulgare* cuttings until we sourced and potted whole plants collected from the wild. Additionally, nursery plants appeared to be around the same age upon

TABLE 1 Larvae longevity (in days) and mortality by diet treatment.

Diet category	Diet treatment	*N*	Longevity (days)		Larval mortality (%)
			Mean ± SE	Range	
Plant diets only	*Abutilon palmeri*[a]	215	3.1 ± 0.55	2–4	100
	Malacothamnus clementinus[a]	240	2.5 ± 0.05	1–4	100
	Malacothamnus fasciculatus[a]	272	4.6 ± 0.27	1–36	99
	Nicotiana glauca[b]	235	3.8 ± 0.12	1–18	100
	Sphaeralcea ambigua[a]	192	6.3 ± 0.60	1–40	99
Artificial diets	Artificial diet to *Cirsium vulgare*[b]	210	8.1 ± 0.43	2–27	100
	Cirsium vulgare[b] to artificial diet	210	5.4 ± 0.28	2–35	100
	Artificial diet only	110	9.2 ± 0.23	2–13	100

[a]Native plant.
[b]Non-native plant.

purchase when comparing within species, but the ages of wild-collected plants varied as they were collected opportunistically. As a control, we also raised a subset of larvae on an artificial diet (#AD203, Educational Science). All larvae were reared in low-density groups with the average starting group size of 30.5 ± 0.93 larvae (mean ± SE); larvae were provided fresh potted plants and cuttings as needed. We followed the fate of each larva, assessing pupation success and survival daily.

Larval survivorship on a changing diet

We further tested the ability to switch diet types by providing larvae with either artificial diet or *C. vulgare* for the first six days following egg hatching. At day seven, they were switched to either *C. vulgare* or artificial diet. As previously described, we assessed pupation success and survival of each larva. *C. vulgare* was selected for these tests because it is a key host plant in the sub-Saharan range of the Palearctic-African *V. cardui* migration (Stefanescu et al., 2017; Talavera et al., 2023). Additionally, *C. vulgare* is commonly found in California sage scrub despite being non-native.

Using wild-collected live specimens for comparison

In the spring of 2023, we collected 27 larvae and 16 adult butterflies from the wild (Riverside, CA). Second and third instar larvae were collected opportunistically from *Amsinckia menziesii*, *C. vulgare*, or *Carduus pycnocephalus*. Wild butterflies were collected while exhibiting courtship behaviors. We reared wild larvae to adulthood (Table 2) with the goal of obtaining wild-sourced eggs for host plant suitability tests.

Statistical analyses

All statistical analyses were conducted in R v.4.2.2 (R Core Team, 2022). Survivorship curves were constructed using the Kaplan–Meier method and survival times between groups were compared using the "survdiff" function in package "survival" (Therneau, 2023). Survival rates were compared using the Cox proportional hazards model in the same package. We used a 95% CI for hazard ratios. Additionally, we calculated CVs in survival time for all host plant species tested and ran separate analyses for larvae in the treatments involving a changing diet or artificial only diet. We compared survival time CV ($CV_{survival}$) using a linear model that included fixed effects of plant species and trial number. We conducted post hoc comparisons of estimated marginal means ("emmeans" in the package emmeans) with a false discovery rate (fdr) correction for multiple comparisons (Lenth, 2021). All means are reported as ±SE.

RESULTS

We tested 1684 commercially sourced larvae on six plant species (Figure 1) and a commercially available artificial diet. Mean larval longevity was low across all plant treatments with 100% mortality by days 4 and 5 for *A. palmeri* and *M. clementinus*, respectively (Table 1). Similarly, larvae experiencing the changing diets and an artificial only diet exhibited low larval longevity and high mortality (Table 1). Overall, larval survivorship was extremely low (0.1%) despite visible feeding damage to plants (Appendix S1: Figure S2). Most larvae died during the first and second instars; only four (0.2%) larvae survived to pupation. If a chrysalis formed, pupation success was 50% (2/4). The two failed pupations involved the

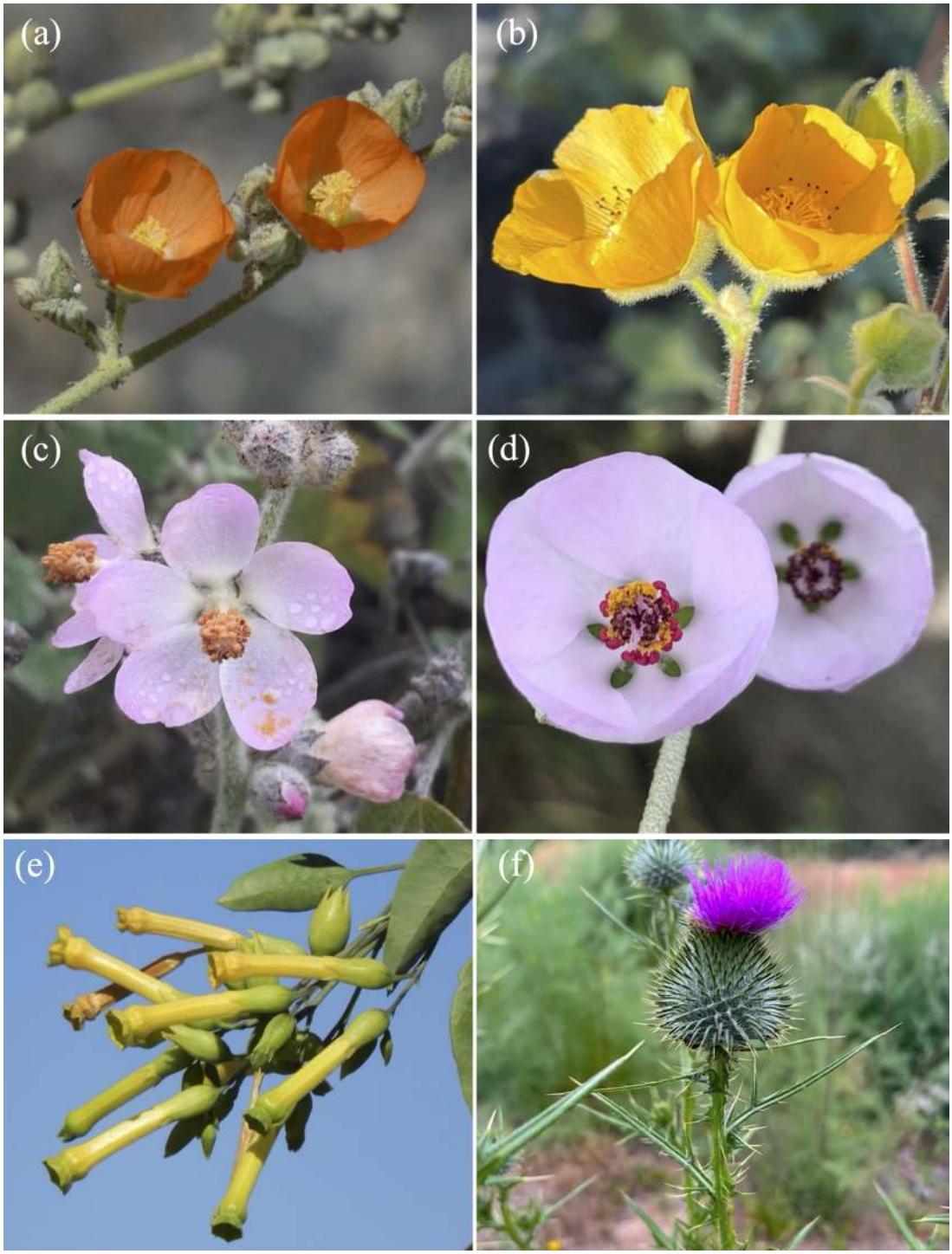


FIGURE 1 Putative *Vanessa cardui* host plants used in this study. (a) *Sphaeralcea ambigua*. (b) *Abutilon palmeri*. (c) *Malacothamnus clementinus*. (d) *Malacothamnus fasciculatus*. (e) *Nicotiana glauca*. (f) *Cirsium vulgare*. Photo credit: (a, d, e) David Rankin, (b) iNaturalist user e-meling (CC BY), (c) iNaturalist user serpophaga (CC BY-NC), and (f) Jo'lene A. Saldivar.

prepupae dying before forming the chrysalis ($n = 1$ on *S. ambigua*, $n = 1$ on *C. vulgare*-to-artificial diet).

Larval survivorship varied with diet treatment: The host plant species had an effect on proportion surviving over time ($\chi^2_4 = 169$, $p < 0.0001$). Survival rates on *S. ambigua* were significantly higher than on *A. palmeri* (HR = 1.72, 95% CI = [1.39, 2.14], $Z = 4.94$, $p < 0.0001$) and *M. clementinus* (HR = 2.80, 95% CI = [2.27, 3.46], $Z = 9.57$, $p < 0.0001$) but did not differ from that on *M. fasciculatus* (HR = 0.95, 95% CI = [0.78, 1.15], $Z = -0.52$, $p = 0.61$) or *Nicotiana glauca* (HR = 1.08, 95% CI = [0.88, 1.33], $Z = 0.74$, $p = 0.46$) (Figure 2a). For artificial

TABLE 2 Development of wild-collected *V. cardui* larvae on select California host plants.

Plant species collected from	*N* collected	Pupation (%)	Adult emergence (%)	Max longevity (days)
Amsinckia menziesii	9	100	83	20
Carduus pycnocephalus[a]	6	0	...	18
Cirsium vulgare	13	69	100	7

Note: Maximum longevity was measured from day of collection for larvae that failed to pupate.
[a]All larvae were reared on the plant species that they were collected on except for *Carduus pycnocephalus* which we raised on *Cirsium vulgare* due to limited availability. All cuttings were sourced from the wild. None of the wild butterflies were observed mating and zero eggs were laid.

diet treatments, survival differed across treatments ($\chi^2_2 = 45.3$, $p < 0.0001$). Larval survivorship was lower on *C. vulgare*-to-artificial diet (HR = 2.21, 95% CI = [1.74, 2.82], $Z = 6.40$, $p < 0.0001$) than artificial diet only treatment (Figure 2b). There were no differences in survivorship between artificial diet only and the artificial-diet-to-*C. vulgare* (HR = 1.26, 95% CI = [0.99, 1.60], $Z = 1.89$, $p = 0.06$).

Despite high mortality across all treatments, we observed high variability (CV) in larval survival times. Variability in larval survival time was highest on *S. ambigua* compared with all other plant species tested (Figure 2c, Appendix S1: Table S2). Moreover, there was no significant difference in variability of larval survival time in any diet involving artificial diet (Figure 2d, Appendix S1: Table S2). When comparing putative host plants with artificial diet, *S. ambigua* still showed significantly highest variability.

While the sample size for wild-collected larvae was limited, wild caterpillars exhibited higher survivorship to adulthood than those described above. Of wild-collected larvae, 63% (17/27) pupated successfully (Table 2), but the resulting butterflies did not mate despite surviving as adults for an average of 19 ± 0.3 days. Additionally, the larvae lived an average of 10.1 ± 3.9 days, which is more than twice as long as commercially sourced larvae reared on plants (Table 1). The butterflies collected from the wild also did not mate during their lifespan.

DISCUSSION

Identifying which host plants support high larval survivorship and successful development is critical to promoting stable, healthy butterfly populations. Here, we observed extremely high mortality of commercially sourced *V. cardui* on known host plants and artificial diet treatments. Several factors may have contributed to these low survival rates. The high mortality observed in this study may have been in part due to large-scale commercial rearing selecting for larvae adapted to an artificial larval diet. This may have led to changes to the larval microbiome. As gut microbiomes are known to influence an herbivore's ability to respond to or overcome plant defenses (e.g., Chung et al., 2017; Mason, 2020), larvae adapted to artificial diet may be unable to properly metabolize plant defense chemicals or materials. We identified 12 additional studies that similarly used commercially obtained *V. cardui* eggs or larvae, provided diet details, and reported larval survival or survival to pupation (Appendix S1: Table S1). These authors also reported low larval survival when raised exclusively on plants (Appendix S1: Table S1; mean $\text{survival}_{\text{plants}}$: 26.9% ± 8.3%), while higher survival rates resulted from feeding artificial diet only (Appendix S1: Table S1: mean $\text{survival}_{\text{artificial diet}}$: 87.4 ± 4.1%). If commercially sourced larvae are adapted to artificial diets, such larvae may be less suited to develop on wild plant diets (Symanski & Redak, 2021) and thus may not be representative of how wild larvae respond to wild plants (Ellis & Bowers, 1998). More research is needed to investigate whether adaptations to artificial diet are occurring. Future studies using commercial organisms should include a control treatment of wild organisms for comparison or explicitly address concerns as to any potential adaptation to artificial diets.

Another factor that could contribute to low survivorship is the placement of eggs on the experimental plants. While eggs laid by female butterflies varied in location (adaxial leaf surface, abaxial leaf surface, stem, soil, or on the cage itself), we placed all commercially purchased eggs onto the adaxial surface of leaves. As eggs and early larval instars are small and vulnerable, initial feeding position may mediate successful establishment (Janz, 2005). Testing initial larval positioning may help to determine protocols to maximize larval establishment.

It is important to note that we obtained *V. cardui* from multiple commercial sources and in multiple batches over an 18-month period—all of which exhibited high mortality. Because we were able to concurrently raise wild-caught larvae, the observed high levels of mortality were unlikely to be the result of a "bad batch" or environmental conditions. The protocols in place to promote larval hygiene (e.g., keeping cages clean) and

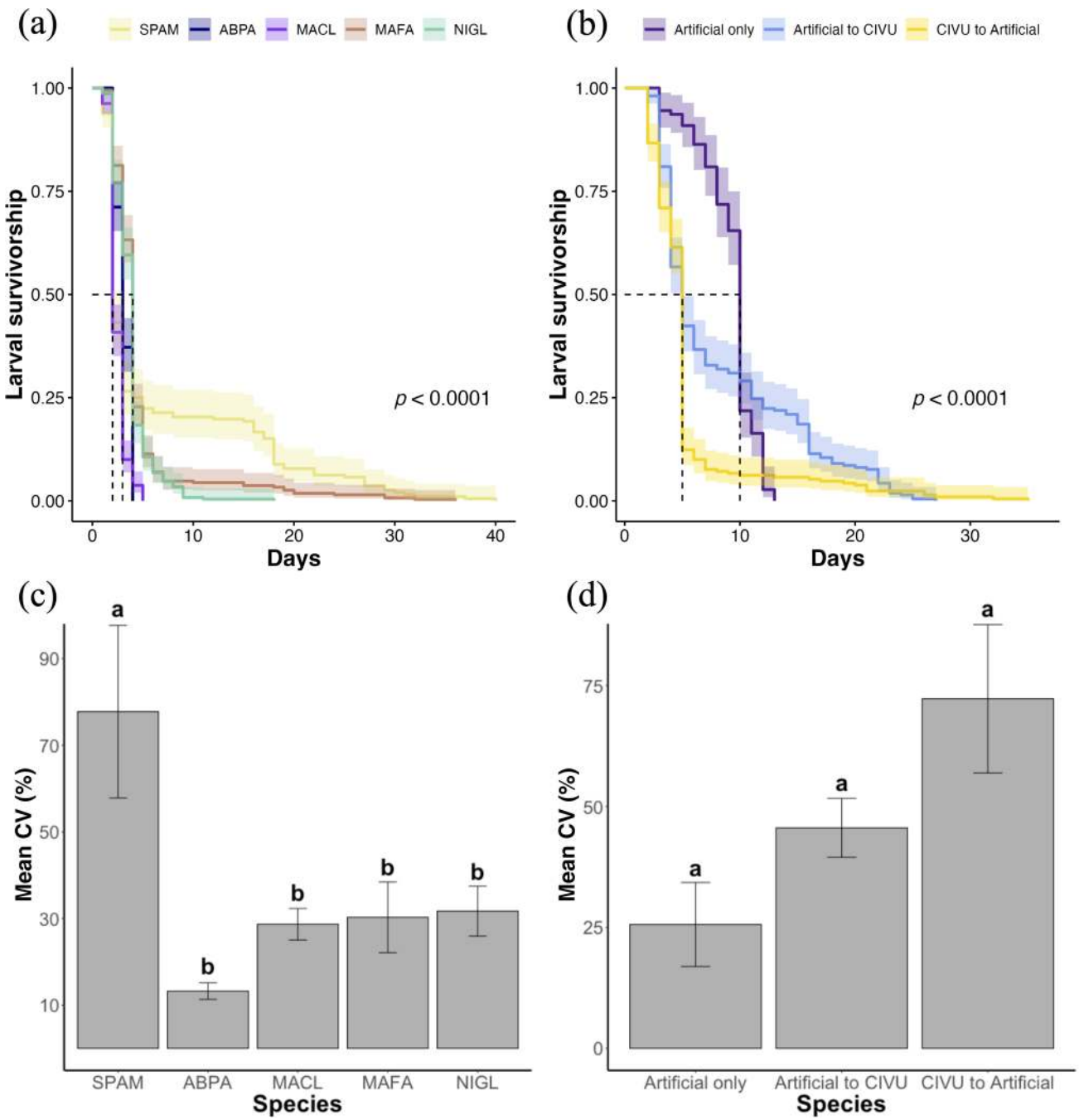


FIGURE 2 Effect of diet treatment on larval survival and longevity. Larval survivorship for (a) larvae reared on a single potted plant and (b) larvae tested with either artificial only or switched after 6 days from one diet to another. Shaded areas delimit the 95% CIs. Mean CVs for larval longevity (in days) for (c) larvae reared on a single potted plant and (d) larvae tested with artificial only or switched diets. Different letters indicate significance at $p < 0.05$ after correcting for multiple comparisons. ABPA, *Abutilon palmeri*; CIVU, *Cirsium vulgare*; MACL, *Malacothamnus clementinus*; MAFA, *Malacothamnus fasciculatus*; NIGL, *Nicotiana glauca*; SPAM, *Sphaeralcea ambigua*.

sterilization of equipment (e.g., cages and paintbrushes) in between uses minimized the opportunity for larval mortality due to environmental contamination. Comparing the observed rates of mortality to the literature, the highest levels of mortality on host plants were observed in the most recent publications on this topic (Appendix S1: Table S1; Gompert et al., 2022; this study). While the larvae only fed artificial diet exhibited higher longevity than any other treatment, this performance was lower than we would have expected from studies from the pre-COVID era (Appendix S1: Table S1). Thus, future studies could assess the health of commercially sourced larvae by screening dead larvae for pathogens or diseases.

While most of our larvae were sourced from commercial providers, we observed low caterpillar survivorship of both wild and commercially sourced *V. cardui* larvae on native and non-native plants. In a pilot trial, we transferred 15 commercial larvae as third instars onto wild-sourced *Malva assurgentiflora* (island tree mallow; Malvaceae). We observed 27% pupation success and mean larval longevity of 5.8 ± 1.2 days, which is among the highest for all other plant treatments. This corresponds with our changing diet results, where survival on artificial-diet-to-*C. vulgare* was significantly higher than on *C. vulgare*-to-artificial diet. Such observations suggest that artificial diet may be particularly important for early instars of commercially sourced individuals.

Variation in survivorship for wild and commercially sourced *V. cardui* larvae is also observed with larvae reared on common agricultural plants. When field-collected larvae were reared on soybeans (*Glycine max*) along a temperature gradient, Poston et al. (1977) reported mortalities of 21.8% (75°F, 23.8°C) to 100% (55° and 60°F, 12.7° and 15.5°C). On the other hand, commercial larvae reared on alfalfa (*Medicago sativa*) exhibited initially relatively high larval survival of ~40% to day 14, but *none* survived to pupation or adulthood (Gompert et al., 2022). For our larvae collected from and reared on the native annual forb, *Amsinckia menziesii*, there was 100% survival and nearly all pupae emerged as butterflies. Such findings highlight the need to further test the suitability of host plant from wild-collected larvae.

High variation in *V. cardui* mortality and differing methodologies among published studies limit our ability to draw general conclusions about host plant suitability, particularly when larvae are from multiple sources. While adults that developed from commercially obtained eggs or larvae successfully mated and laid eggs in the lab environment, we struggled to obtain similar success with wild-caught adults or adults developing from wild-caught larvae under the same conditions. This was in spite of the fact that wild adults were caught while courting. Although there has been work on courtship behaviors for several other Nymphalid species (Klein & de Araújo, 2010; Pliske, 1975), future studies could investigate what conditions or cues best elicit courting and mating behavior in *V. cardui* butterflies under wild and captive conditions.

Many reports of *V. cardui* host plants come from field guides, which often lack a clear account as to how the author is defining a host plant—whether a larva was just observed on the plant or observed consuming the plant. Furthermore, many sources lack details as to the life stage observed on the plant. Some *V. cardui* host plants may also serve as nectar plants, which may increase the likelihood of females ovipositing opportunistically (Janz, 2005). In California, there is a ~20% overlap in reported *V. cardui* host and nectar plants (J. Caldwell, unpublished manuscript) with the potential for more species as community science efforts continue to increase our knowledge of nectaring plant use (Saldivar et al., 2022). Alternatively, larvae may not survive to pupation on the observed plant due to nutritional deficiencies or plant chemical defenses (Awmack & Leather, 2002; Roeder & Behmer, 2014). For larvae from captive lab-reared colonies, the inability to thrive on wild plants may lead to such plants serving as ecological traps—further suggesting releasing adults from such lab-reared sources may not contribute to wild butterfly population growth. While pesticide residues in plant tissue could contribute to larval mortality, this was unlikely in the current study as we obtained plants from sources that do not use neonicotinoids. Moreover, we observed herbivorous and leaf-mining insects feeding, pupating, and emerging as adults on these host plants (Appendix S1: Figure S3). Furthermore, there was no difference in mortality on plants from nurseries and plants wild-sourced. Taken together, these suggest that pesticides did not contribute to the mortality levels in our study.

The low survivorship of *V. cardui* larvae on a variety of plant species from several different families from our study and those in Appendix S1: Table S1 have potential implications for butterfly releases. The public may be drawn to purchase and captive rear Lepidoptera from online retailers to release for ceremonial events (New, 2008) or for conservation and public education (Davis et al., 2020; Tenger-Trolander et al., 2019; Wilcox et al., 2021). There have been concerns that releases may be detrimental to the released individuals because they may not be able to locate or survive on wild plants and also potentially harm biodiversity by spreading diseases (Boppré & Vane-Wright, 2012; Brower et al., 1995). The most commonly available butterflies, monarchs (*Danaus plexippus*) and painted ladies (New, 2008), are also migratory. Additional concerns have been expressed over releases affecting the butterfly's natural migration behavior (Davis et al., 2020; Tenger-Trolander et al., 2019), although recent studies suggest some of these effects may be transitory in nature (Wilcox et al., 2021). Appendix S1: Table S1 highlights a real uncertainty for those hoping to promote butterfly populations through release of commercially available *V. cardui*. Larvae from these captive-reared butterflies likely face high mortality because survivorship on non-artificial diets is extremely low. Conservation efforts for *V. cardui* in the short term may be better allocated to promoting nectar and host plants and stable habitats for wild butterfly populations.

Our work provides new insights into larval survivorship for one of the most polyphagous butterfly species and identifies avenues for future research on larval diet

adaptations. Through testing larval survival on putative host plants common in California's sage scrub and artificial diet configurations in lab experiments, we show that survival is highly variable, and overall high mortality occurred when diets consisted only of a single plant species. This study demonstrates that not all host records likely represent suitable host species. Future studies could continue to assess and compare survival across putative host plants, and with direct comparisons between commercially obtained and wild-raised individuals.

AUTHOR CONTRIBUTIONS

All authors contributed to data collection. Jo'lene A. Saldivar made the figures, conducted statistical analyses, and wrote the first draft of the manuscript with feedback from Erin E. Wilson-Rankin. All authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Saldivar & Wilson Rankin, 2024) are available from Dryad: https://doi.org/10.5061/dryad.wdbrv15v5.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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