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ORIGINAL PAPER

Fantastic feasts and where to find them: mosquito (Diptera: Culicidae) sugar feeding and survivorship on endemic flowers of arid scrublands

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Abstract

Mosquitoes, like many other insects, are dependent on plant-derived nutrients as adults. Arid lands in particular create a challenge for mosquitoes to find resources consistently. In the United States, the arid, high elevation floodplains around the Great Salt Lake present a rich environment where salt desert shrublands meet alkaline freshwater wetlands, while plant communities contain a diversity of native and invasive flower species. We investigated survivorship on 15 flowering plants representing the common ephemeral wildflowers found through the aforementioned habitats using local *Culex pipiens* (L.) under laboratory conditions. Four native angiosperm species, *Cleome serrulata* Pursh (Brassicales: Cleomaceae), *Asclepias incarnata* L. (Gentianales: Apocynaceae), *Asclepias speciosa* Torrey, and *Verbena hastata* L. (Lamiales:Verbenaceae) had the highest mosquito mean percent survival in 10-day assays. Mosquito survival was significantly better on native flowers than on non-native flowers. Endemic mosquitoes in the field were also sampled for frequency of sugar feeding at six sites across 11 weeks. Flower phenology data of the aforementioned four flowers with highest mosquito mean percent survival were taken from iNaturalist and compared to the abundance of sugar-fed mosquitoes from the wild. Flower phenology and sugar-fed mosquito abundance followed the same trends, with increased flower sightings co-occurring with increased sugar feeding. The short-lived blooming intervals in the arid landscape result in time periods when both flower sightings and sugar feeding in mosquitoes are low, highlighting elevated risks to exposure and malnutrition for wild populations. Sustainable research and management of mosquitoes require answers to basic biological and ecological questions such as flower dependence and resource scarcity in the field.

Keywords Nectar · Plant · *Culex* · *Aedes* · Ultraviolet · Anthrone

Introduction

Mosquitoes access to plant -sugars affects survivorship in the wild and pathogen transmission potential (Gu et al. 2011; Sissoko et al. 2019). For mosquitoes, a source of sugar will be the first thing adults seek upon emergence from larval aquatic habitats (Foster and Takken 2004; Takken et al. 2013). Studies in fragmented landscapes suggest that *Anopheles* mosquitoes living in lush, sugar-rich sites have larger population sizes with higher survival rates and shorter gonotrophic cycles than mosquitoes in sparse, sugar-poor areas (Gu et al. 2011). Even mosquito species such as *Aedes aegypti* (L.), which have the ability to convert blood into glycogen and triglycerides for energy (Nayar and Sauerman 1997), will readily seek sugar sources in the wild, if available (Sissoko et al. 2019).

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Furthermore, studies on diurnal rhythms of sugar feeding by *Aedes* (Sissoko et al. 2019), *Anopheles* (Müller et al. 2017), and *Culex* (Andersson and Jaenson 1987; Peach and Gries 2016) suggest that mosquitoes feed multiple times on sugar (at the beginning and end of activity phases) as long as sources are available. In most mosquito species, both males and females rely solely on sugar feeding for energy requirements (Foster 1995). Mosquitoes have been shown to obtain sugar from a variety of sources such as floral and extrafloral nectaries (Haeger 1955; Mogi and Miyagi 1989; Foster 1995; Peach and Gries 2020), aphid honeydew (Haeger 1955; Patterson et al. 1969) fruit/seedpods and tree sap (Joseph 1970; Nasci 1986; Yu et al. 2017), sweet food waste (Dieng et al. 2017), and fresh plant herbivory sites (McCrae 1969; Mogi and Miyagi 1989). While mosquitoes can also feed by directly piercing tissues of plants, they likely only do so when other resources are not readily available (Müller and Schlein 2005) or if a plant is stressed/damaged (Stone and Foster 2013). Moreover, floral nectar has been shown to be the most abundantly utilized source of sugar for mosquitoes (Foster 1995; Peach and Gries 2020). With mosquitoes' reliance on sugar sources for survival, understanding local flowering communities could aid in pinpointing spatial mosquito accumulations, determining corridors of mosquito movement (Qualls et al. 2016), or facilitating interception of the population at large (Beier et al. 2012; Khallaayoune et al. 2013).

Studies involving mosquito–plant interactions are often investigated in the context of mosquito control to determine methods for exploitation; ecological discoveries often being a byproduct. For example, vegetation dependence in mosquitoes is often exploited using residual applications of contact insecticide as an area-wide approach (Stoops et al. 2019). However, a point-source approach of attractive targeted sugar baits (ATSB), a formulation platform exploiting sugar drive in mosquitoes, have been studied against *Culex pipiens* (L.) and *Anopheles sergentii* (Theobald) in Israel (Schlein and Müller 2008; Müller et al. 2010a; Beier et al. 2012), as well as *Ae. aegypti* and *Anopheles gambiae* s.l. (Müller et al. 2010b; Sissoko et al. 2019) in Mali. Despite sugar-baiting studies in arid scrubland habitats of Asia and Africa (Müller and Schlein 2006), the evidence for utility of ATSBs in the United States remains low (Fiorenzano et al. 2017), which also translates to low secondary gains in mosquito-plant ecology in arid lands of North America.

A useful study system is present in north America, whereby the floodplains surrounding the Great Salt Lake are characterized by salt desert shrublands and alkaline mudflats at an elevation of approximately 1300 m (Welsh et al. 2015). The vegetation contains a mix of arid adapted native and non-native flowering plants (Welsh et al. 2015). Throughout most of this region, pestiferous mosquitoes such as *Culex tarsalis* (Coquillett), *Aedes dorsalis* (Meigen), and *Aedes vexans* (Meigen) are responsible for explosive eruptions of biting mosquitoes impacting human quality of life (Nielsen et al. 2002), while *Cx. tarsalis* and *Cx. pipiens* are the primary vectors of mosquito-borne pathogens, such as West Nile virus, which impact public health (Rochlin et al. 2019).

Creative exploitation of mosquito ecology is predicated on studying their environmental interactions. For example, study of mosquito-nectar dependance could inform timed control applications during periods of sugar scarcity (Beier et al. 2012). These periods are determined by investigating the suitability of flowering plants for mosquito feeding, and flowering plant phenology and mosquito population dynamics. Therefore, understanding the mosquito dependencies on plants can help the understanding of environmental persistence and top-down pressures for migrant mosquitoes. Accordingly, we investigated the suitability of wild flowering plants as sugar sources for mosquitoes by studying the survival of a *Cx. pipiens* strain originating from the same geography and found in other arid environments (Müller et al. 2010a; Peach et al. 2019). We also sampled wild populations of mosquitoes for frequency of sugar ingestion over the course of the season. Mosquito sugar feeding was then compared to plant phenology field data from iNaturalist for the four flower species with the highest mosquito survival rates.

Materials and methods

Mosquito flower bioassays

Flowering plants representing 15 commonly encountered species were collected from wetlands in the west of Salt Lake City in the flood plains of the Great Salt Lake. Both native and introduced plant species were represented. Native flowers included Rocky Mountain beeplant, *Cleome serrulata* Pursh (Brassicales: Cleomaceae); swamp milkweed, *Asclepias incarnata* L. (Gentianales: Apocynaceae); showy milkweed, *Asclepias speciosa* Torrey (Gentianales: Apocynaceae); blue vervain, *Verbena hastata* L. (Lamiales:Verbenaceae); blue flax, *Linum perenne* L. (Malpighiales: Linaceae); Munroe's globemallow, *Sphaeralcea munroana* (Douglas) Spach (Malvales: Malvaceae); Woods' rose, *Rosa woodsii* Lindley (Rosales: Roseaceae); and dogbane, *Apocynum cannabinum* L. (Gentianales: Apocynaceae). Non-native flowering plants included tamarisk, *Tamarix chinensis* Louriero (Caryophyllales: Tamaricaceae); alfalfa, *Medicago sativa* L. (Fabales: Fabaceae); whitetop, *Cardaria draba* (L.) Desvaux (Brassicales: Brassicaceae); dalmatian toadflax, *Linaria dalmatica* (L.) Miller (Lamiales: Scrophulariaceae); purple loosestrife, *Lythrum salicaria* L. (Myrtales: Lythraceae); Russian olive, *Elaeagnus*

angustifolia L. (Rosales: Elaeagnaceae); and Russian knapweed, *Centaurea repens* L. (Asterales: Asteraceae) (Fig. 1). These plant species were selected due to several factors such as presence within local shrublands or wetlands, seasonality, abundance, and flower structure (Welsh et al. 2015). To estimate seasonal availability of flowering plants, 'verifiable' Utah entries pertaining to target flower species were extracted from iNaturalist (iNaturalist Community 2008).

Laboratory bioassays were conducted with a locally collected strain of *Cx. pipiens* colonized from wild-collected mosquitoes within the area served by the Salt Lake City Mosquito Abatement District (SLCMAD). Mosquitoes were reared and maintained in the SLCMAD insectaries in conditions of 28 ± 1 °C temperature and 70 ± 5% relative humidity. Adults were sustained on 10% sucrose solution ad libitum during rearing. Adults were allowed 5–10 days in mixed-sex cages before being used in survivorship assays. Cohorts of approximately 150 mixed-sex mosquitoes at an approximate 50:50 (M:F) sex ratio were transferred to bioassay cages ranging from 30 cm × 30 cm × 30 cm to 75 cm × 75 cm × 115 cm (BugDorm, MegaView Science Co., Taiwan, China), dependent on the space needed for each plant. Every bioassay cage was stocked with field collected, flowering plant material of one target flower species each (Fig. 2).

The amount of vegetative material presented was standardized across flower species based on the number of intact flowers that collectively fit withing a 12–18 cm^2 (4.72–7.09 in^2) area, rather than the entire amount of total vegetative matter of the cutting. This was to ensure a similar availability of flower nectaries, and flower material between all samples. Flower cuttings were placed in a receptacle of 10% sucrose solution, to preserve turgor pressure, and sealed with a parafilm membrane to prevent mosquito entry. Positive control bioassay cages were provided with a 10% sucrose solution in a in a vial with a cotton wick. Negative control bioassay cages were provided only with water with no sugar source. All mosquito cohorts were given a cup of shallow water and an additional dietary RO water source regardless of treatment level. Daily survival counts were taken for 10 consecutive days with flower material replaced every other day with fresh cuttings to avoid issues with turgor pressure, wilting, or depleted nectar expression. Three replicates were conducted for each flowering plant species.

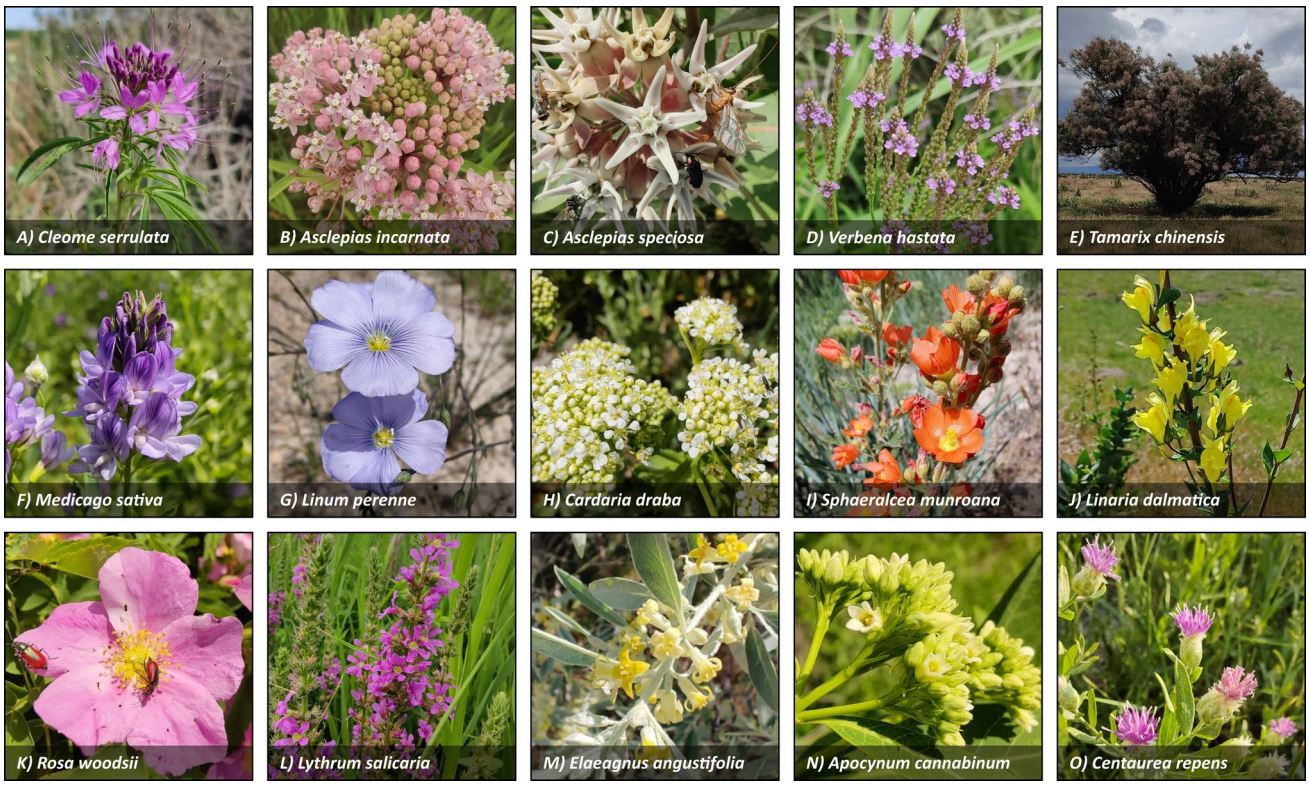

Fig. 1 Native flowers tested includes **A** Rocky Mountain beeplant **B** swamp milkweed **C** showy milkweed **D** blue vervain **G** blue flax **I** Munroe's globemallow **K** Woods' rose **N** dogbane. Non-native flowers tested includes **E** tamarisk **F** alfalfa **H** whitetop **J** dalmatian toadflax **L** purple loosestrife **M** Russian olive **O** Russian knapweed

Fig. 2 Examples of mosquito sugar feeding in trials. **A** Rocky Mountain beeplant **B** swamp milkweed **C** tamarisk **D** whitetop **E** dalmatian toadflax **F** purple loosestrife **G** dogbane **H** Russian knapweed. Some mosquitoes show visibly distended abdomens from sugar intake

Field sampling

To assess tendency of sugar feeding in the field, six surveillance locations already in use by the SLCMAD—Audubon, South Saratoga, Elephant Island, Noggin, Rudy, and a Recreational Athletic Complex (RAC)—were selected from within the Great Salt Lake wetlands representing a rural to urban gradient (Fig. 3). Audubon, South Saratoga, and Elephant Island are characterized by salt playas, palustrine flood plains, and salt desert shrublands. Of these three sites, South Saratoga was the most proximal to industrial development. Noggin, Rudy, and RAC were characterized by meadow seeps, saline wetlands, and riparian canals. Of these three sites, RAC was the closest to urbanized habitats. All six sites contained mixed flowering plant communities dominated by the plant species examined in this study.

To assess the relative abundance of sugar-fed mosquitoes, a 3D-printed CDC trap developed at SLCMAD (Bibbs et al. 2024b) was used with LED light modifications (Harker et al. 2024) and without CO_2. Traps were deployed in the early evening and allowed to operate 24 h at a time at the six field sites weekly for 11 weeks, covering the beginning and end of the observed wildflower season for the species being monitored for this study. Although CO_2 is commonly used in mosquito traps, it was not utilized in this study because sugar-fed mosquitoes are refractory to host-seeking cues in the magnitude used for conventional mosquito surveillance, since they are already engorged on a liquid source (Hill and Ignell 2021). Collected mosquitoes were taken back to the laboratory and identified to species using light microscopy and morphological keys (Darsie and Ward 2005).

Mosquitoes from the light trap collections were processed individually for detectable carbohydrate to estimate sugar consumption using the cold anthrone test. In this study, the cold anthrone reactions allow detection of sucrose or derivative fructose in the mosquito gut. Cold anthrone reactions were prepared accordingly (Nunes et al. 2008) and mosquitoes were handled using procedures from previous studies (Gu et al. 2011). Briefly, anthrone mixtures were prepared by adding technical grade H_2SO_4 (Hi Valley Chemical, Inc., Centerville, UT) to RO water until a 70% (w/v) concentration was obtained. Then, 25 mg of anthrone (ANTH25G, Chemsavers, Inc., Bluefield, VA) was added to 50 ml of the diluted acid. Prepared anthrone mixtures were brought to room temperature before use. After traps were collected from the field, mosquitoes were cold-anesthetized at − 80 °C, and mosquitoes were sorted within 1 h of collection into a 96-DeepWell plate (Nunc 96-well polypropylene DeepWell storage plate, ThermoFisher Scientific, Rochester, NY). One mosquito per well was crushed with a glass pestle to allow reagent penetration into tissues. Aliquots of 1 ml of the prepared anthrone mixture were immediately added to each mosquito. Following a 45-min incubation, an image was taken within the fume hood for every plate so that score records could be revisited. The assay was preliminarily tested on sugar-fed and starved *Cx. pipiens* from a colony to form baselines on the color change from yellow to blue. Scoring was performed on the image records of the finished

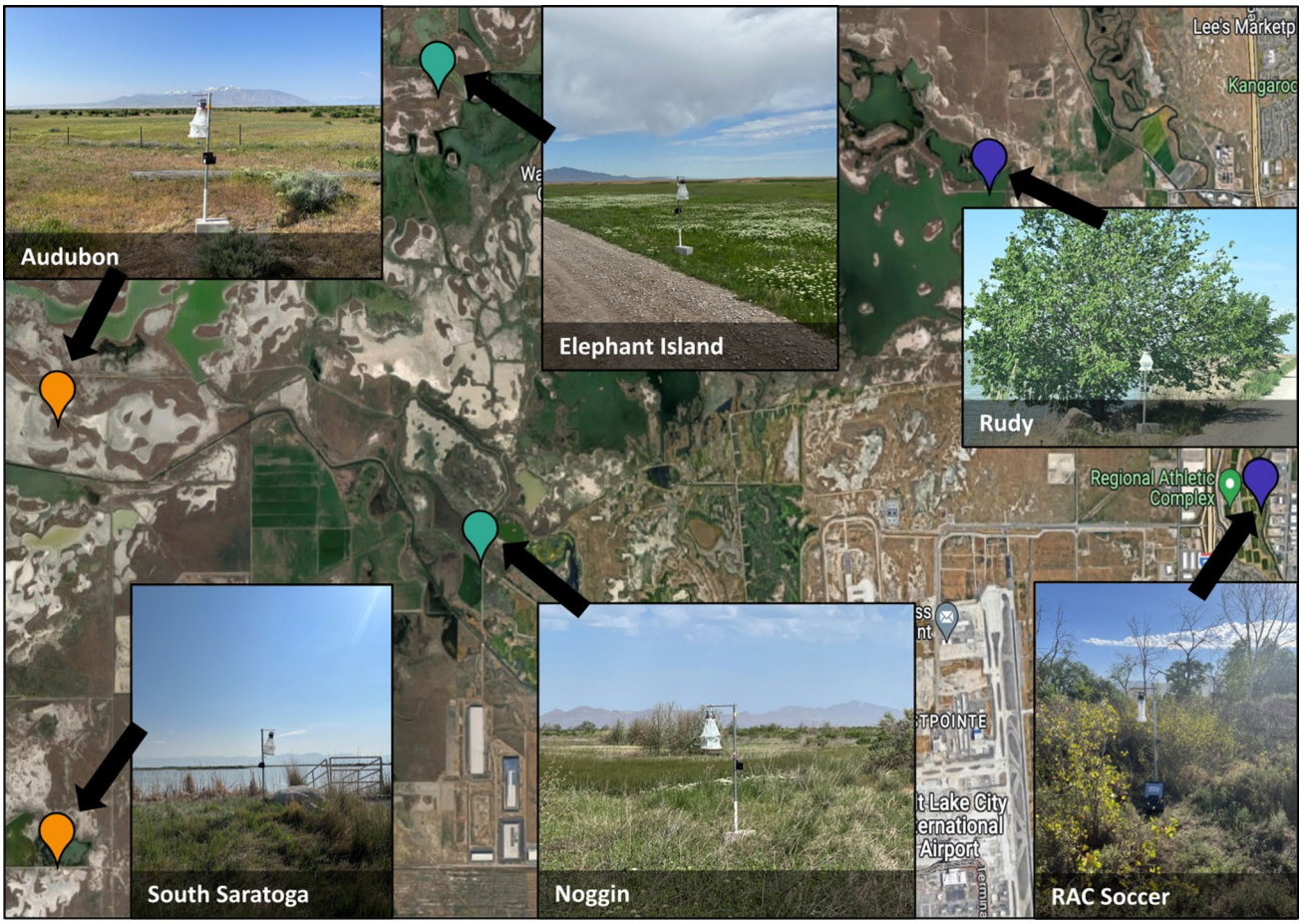

Fig. 3 Field site selection. Mosquitoes were collected along a rural–urban gradient and tested for sugar-feeding success among the wild population

reaction and rated for simple presence (blue) or absence (yellow) of carbohydrate (Fig. 4).

Data analysis

Data were analyzed using R statistical software (v.4.2.1, The R Foundation for Statistical Computing, Vienna, Austria) via RStudio (v. 3.3.0, RStudio PBC, Boston, MA). Survival in laboratory assays was analyzed with Kruskal–Wallis analysis of variance and post hoc two sample Wilcoxon test on the general groupings of native and non-native flowers. Using the outputs, quantiles were bracketed using 10th day survival from each flower species. Additional Kaplan–Meier survival functions were performed on survival over time.

iNaturalist observations of *C. serrulata, A. incarnata*, *A. speciosa*, and *V. hastata* from Utah observed from 15 May to 31 July across 2005 to 2023 were counted and grouped by week for a total of 11 weeks of data (iNaturalist Community 2008). Sugar phenology data was broken down into 11 weeks starting on the week of 15–21 May and ending on the week of 24–30 July.

Results

The foundational data set for this work was survivorship of the locally colonized *Cx. pipiens* strain on the breadth of common native and non-native flowering plants in the greater Salt Lake area (Table 1). Mosquito survival was significantly greater on the Utah native flowers as a whole as compared to non-native flowers ($W_{(24,21)} = 383$, $P < 0.003$) (Fig. 5). Mosquito survival on day 10 was significantly greater on sucrose, at a mean of ~ 75%, than either of the native flowers ($W_{(24,13)} = 52$, $P < 0.001$) or non-native flowers ($W_{(21,13)} = 18$, $P < 0.001$) (Fig. 5). The lowest survival was 0% on day 10 with *C. repens*. Quantiles derived from the 10th day laboratory mean percent survival data included (from the highest to the lowest mosquito survival): Quantile (1) 10% sucrose, *C. serrulata*, *A. incarnata*, *A. speciosa*, and *V. hastata* (Figs. 5, 6). Quantile (2) *T. chinensis*, *M. sativa*, *L. perenne*, and *C. draba* (Figs. 5, 6). Quantile (3) *S. munroana*, *L. dalmatica*, *R. woodsii*, and *L. salicaria* (Figs. 5, 6). Quantile (4) *E. angustifolia*, *A. cannabinum*, water, and *C. repens* (Figs. 5, 6).

Fig. 4 **A** A native, sugar-fed, *Culiseta inornata* (Williston) feeding on *Asclepias speciosa* Torrey (showy milkweed) in the field. **B** Example record for anthrone reactions: Arrow 1: No sugar meal detected, bright/pale background (scored as unfed). Arrow 2: Partially reacted or small sugar meal, dark reaction mixed with bright/pale background (scored as sugar-fed). Arrow 3: Complete reaction or large sugar meal, dark reaction (scored as sugar-fed)

The iNaturalist observations (iNaturalist 2008) average estimated flower activity of the highest survival Quantile 1 flowers in Utah ascends to week 4 (15 May–11 June), falls slightly to week 5 (12–18 June), rises to week 6 (19–25 June) falls to week 7 (26–2 July), rises to week 9 (3–16 July), falls to week 10 (17–23 July), and rises again to week 11 (24–31 July) (Fig. 7). Data collected from the six field sites show that mosquito sugar activity generally descends to week 2 (15–28 May), rises to week 4 (29 May–11 June), falls to week 7 (12 June–2 July), rises to week 10 (3–23 July), and falls slightly to week 11 (24–31 July) (Fig. 7). The general composition of the field collections was predominantly (75% and greater) *Ae. dorsalis, Cx. pipiens, and Cx. tarsalis* with intermittent (25% or less) collections of *Aedes increpitus* Dyar and *Culex erythrothorax* Dyar. Rarely (1% or less), collections included *Ae. vexans* and *Anopheles freeborni* Aitken. The abundance of sugar-fed mosquitoes at the six field sites and the flower projections derived from iNaturalist both exhibited multiple peaks and valleys.

Discussion

Of the 15 flowering plant species tested, native flowers supported higher mosquito survival as a group compared to non-native plants. Four flowering species, all native, supported the highest mosquito survival—*C. serrulata, A. incarnata*, *A. speciosa*, and *V. hastata*. Flowers from these plants span various sizes and shapes with hues of bright purples and bright and pale pinks. Bright colored flowers generally attract diurnal insects, while pale colored flowers attract diurnal and nocturnal insects, and white flowers with strong fragrances attract nocturnal insects (Baker 1961). Mosquito behavior generally seems in agreement with these parameters, particularly with fragrant flowers in arid environments where flowering windows are short (Müller and Schlein 2006).

Many flowering plants possess secondary compounds that are toxic to insects (Adler 2000). Three of the plants tested, *A. incarnata*, *A. speciosa*, and *A. cannabinum* are from the

Table 1 Flowers used in laboratory assays with 10th day survival (±SEM) of *Culex pipiens* mosquitoes

Flower species/ treatment	Binomial synonyms	Common name	Common synonyms	Status	Day 10 survival (%)	Quantile
Sucrose	N/A	N/A	N/A	N/A	65.5 ± 7	1
Cleome serrulata	- *Peritoma serrulata* DC - *Cleome integrifolia* Torr. & Gray	Rocky Mountain Beeplant	- Bee Spider Flower - Stinking Clover	Native	63.8 ± 1.2	1
Asclepias incarnata	- *Acerates incarnata* (L.) Decne	Swamp Milkweed	- Rose Milkweed - Rose Milkflower	Native	62 ± 3.2	1
Asclepias speciosa	N/A	Showy Milkweed	N/A	Native	54.9 ± 13.5	1
Verbena hastata	N/A	Blue Vervain	- American Vervain - Swamp Verbena	Native	50 ± 2.9	1
Tamarix chinensis	- *Tamarix pentandra* Pall	Tamarisk	- Salt Cedar - Five Stamen Tamarisk - Chinese Tamarisk	Non-Native	25.4 ± 11.1	2
Medicago sativa	- *Medica sativa* Lam	Alfalfa	- Lucern	Non-Native	25.3 ± 3.1	2
Linum perenne	- *Linum lewisii* Pursh - *Linum perenne* var. *lewisi* Pursh - *Adenolinum lewisii* Kellogg	Blue Flax	- Lewis Flax - Prairie Flax	Native	23.1 ± 3.5	2
Cardaria draba	- *Lepidium draba* L	Whitetop	- Hoary Cress	Non-Native	19 ± 14.5	2
Sphaeralcea munroana	N/A	Munroe's Globemallow	- Munro's Globemallow - Munro's Desert Mallow	Native	16.6 ± 8.8	3
Linaria dalmatica	- *Antirrhinum dalmaticum* L - *Linaria genistifolia* var. *dalmatica* (L.) Maire & Petitm	Dalmatian Toadflax	- Balkan Toadflax - Broadleaf Toadflax	Non-Native	16.2 ± 2.3	3
Rosa woodsii	N/A	Woods' Rose	- Common Wild Rose - Prairie Rose	Native	14.9 ± 4.2	3
Lythrum salicaria	N/A	Purple Loosestrife	- Spiked Loosestrife - Purple Lythrum	Non-Native	12.4 ± 2.7	3
Elaeagnus angustifolia	- *Elaeagnus caspica* (Sosn.) Grossh - *Elaeagnus hortensis* M.Bieb - *Elaeagnus oxycarpa* Schltdl	Russian Olive	- Oleaster - Wild Olive - Silver Berry	Non-Native	11.1 ± 4	4
Apocynum cannabinum	- *Apocynum cannabinum* var. *typicum* Bég. & Belosersky - *Cynopaema cannabinum* (L.) Lunell	Dogbane	- Hemp Dogbane - Prairie Dogbane - Indian Hemp	Native	6.1 ± 1.1	4
Water	*N/A*	N/A	N/A	N/A	2 ± 1.4	4
Centaurea repens	- *Rhaponticum repens* (L.) Hidalgo - *Acroptilon repens* (L.) DC - *Leuzea repens* (L.) D.J.N.Hind	Russian Knapweed	N/A	Non-Native	0.7 ± 0.7	4

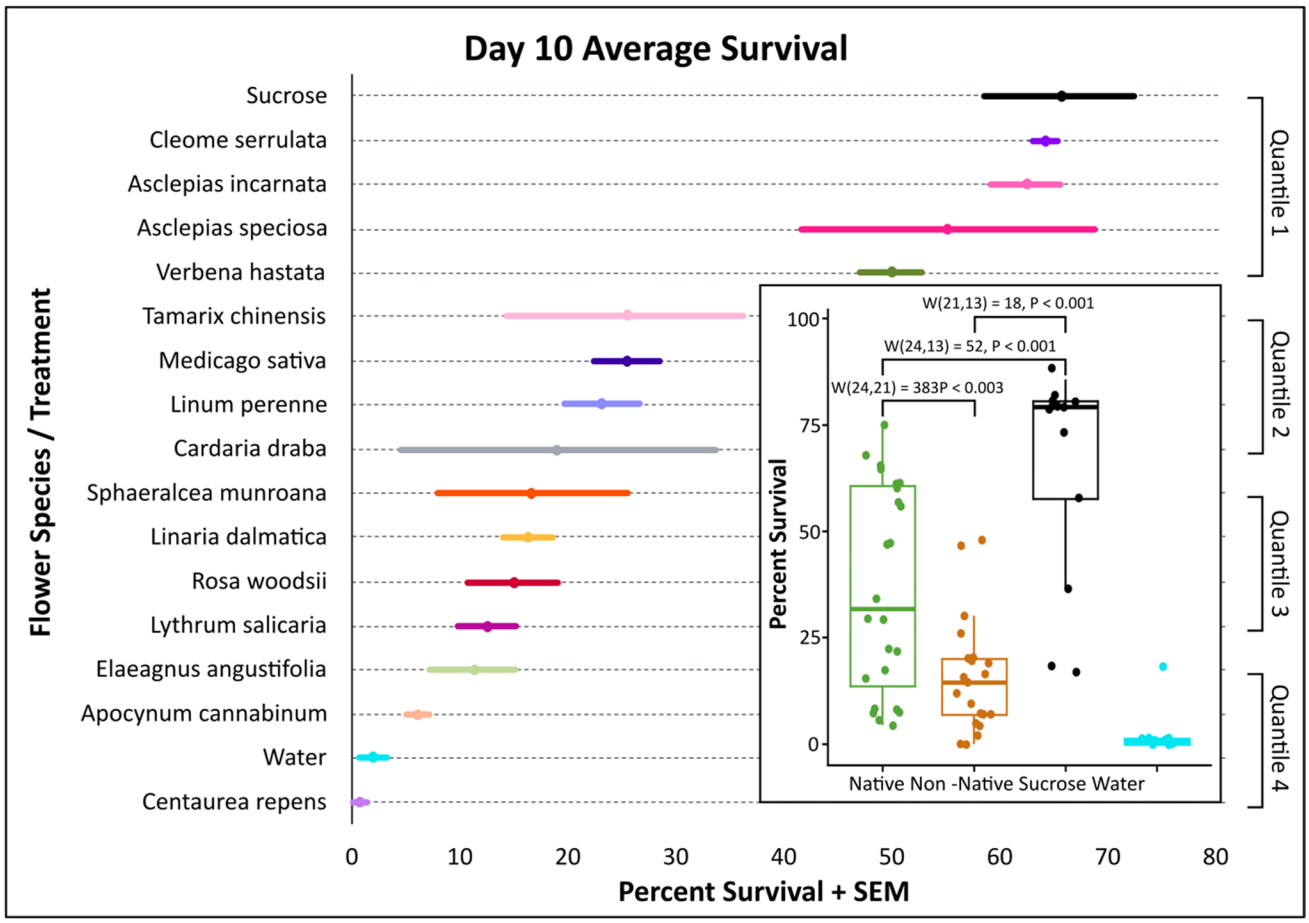

Fig. 5 10th day mosquito mean percent survival + SEM across various flower species/treatments. Clear delineation of Quantile 1 from the other quantiles. Mosquito mean percent survival was significantly greater on natively occurring flowers compared to non-native flowers ($W_{(24,21)} = 383$, $p < 0.003$). Mosquito mean percent survival was significantly greater on sucrose than either of the native flowers ($W_{(24,13)} = 52$, $p < 0.001$) or non-native flowers ($W_{(21,13)} = 18$, $p < 0.001$)

family Apocyanaceae, a family known to have many members with toxic secondary compounds (Patil et al. 2023); some members, such as *Asclepias*, specifically having toxins in their nectar (Manson et al. 2012; Adler 2000). Mosquitoes feeding on *A. cannabinum* stand apart from the rest of their quantile 4 counterparts. While mosquitoes feeding on *E. angustifolia*, *C. repens*, and water had steep survival drop offs around day 2, *A. cannabinum* stayed consistent with quantile 1 survival until around day 5 where deaths began to increase, likely due to a buildup of toxins in the mosquito from repetitive ingestion of toxic secondary compounds while sugar feeding (Jones and Agrawal 2016).

Although likely not a staple, *A. cannabinum* still may be utilized sporadically by mosquitoes in the wild as it is common for mosquitoes to feed on a variety of plants (Sandholm and Price 1962). Although many *Asclepias* species similarly have high levels of toxic secondary compounds, specifically cardenolides, this is not the case for all (Manson et al. 2012). The plants *A. incarnata* and *A. speciosa* possess very low levels of cardenolides (Rasmann and Agrawal 2011; Manson et al. 2012), and thus, are lower risk for causing large buildup of toxins in mosquitoes. Another species *C. repens*, had lower mosquito survival rates than that of the negative control of water only. Other species in the genus *Centaurea* contain cytotoxic compounds, which may explain survivorship being worse than a starvation control when mosquitoes only had access to this invasive plant (Shoeb 2005). Though we did physically observe abdomens becoming distended with nectar when feeding on the various aforementioned plants, we lack clear evidence for the causes of reduced survivorship. Future work would need to characterize the liquids from those plants either experimentally or biochemically to clarify the relationships.

If omitting plant defenses and other toxins that can confound survivorship (Jones and Agrawal 2016), some literature supports that invasive plant species may aid mosquito survival and disease transmission because they are more abundant and bloom longer in the areas they

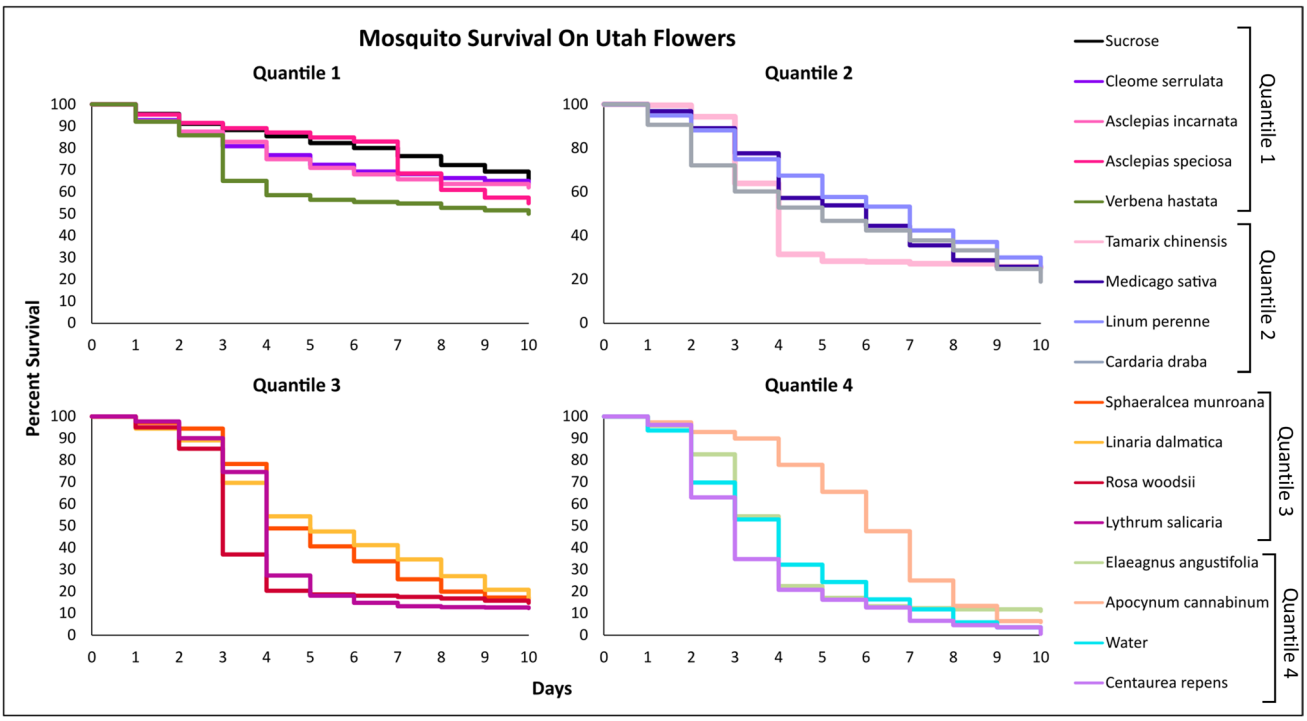

Fig. 6 Kaplan–Meier mosquito mean percent survival curves on flower species/treatment across 10 days. Quantile (1) 10% sucrose, *Cleome serrulata* Pursh, *Asclepias incarnata* L., *Asclepias speciosa* Torrey, and *Verbena hastata* L. Quantile (2) *Tamarix chinensis* Lourier, *Medicago sativa* L., *Linum perenne* L., and *Cardaria draba* (L.). Quantile (3) *Sphaeralcea munroana* (Douglas), *Linaria dalmática* (L.), *Rosa woodsii* (Lindley), and *Lythrum salicaria* L. Quantile (4) *Elaeagnus angustifolia* L., *Apocynum cannabinum* L., water, and *Centaurea repens* L

invade while displacing native species (Roberts et al. 2013; Müller et al. 2017). Two common invasive species tested, *T. chinensis* and *C. draba*, were placed into quantile 2 in terms of mosquito survival. Although appearing not as suitable for supporting high mosquito survival, these flower species may still serve as important sugar sources for wild mosquitoes due to their ubiquity in many sites, especially as land cover adjacent to human infrastructure. Anecdotally, wild mosquitoes flying at Elephant Island and RAC were observed feeding on *C. draba*, a plant possesing UV dark flowers (Blum and Rørslett 2013); a feature possessing attractive qualities to species such as Cx. pipiens (Peach et al. 2019). It has also been observed previously that *T. jordanis* is highly attractive to *Cx. pipiens* (Schlein and Müller 2008) and *Aedes albopictus* Skuse (Müller et al. 2011). Cuttings of *T. chinensis* and *C. draba* from our study tended to desiccate quickly despite being replaced frequently, and the poor condition of the flowers likely confounded mosquito survival in our experiments.

Low UV reflectance across the flower was previously identified as an indication that mosquitoes can favor flower type, as it correlates to nocturnally available nectar supplies (Peach et al. 2019), likely working in tandem with strong odor cues (Baker 1961; Müller and Schlein 2006). Attraction to UV dark or contrast in other contexts has been documented for oviposition in *Aedes* spp. with specific allusion to UV filtering pigments, such as betacyanin in beets (Melo et al. 2020; Bibbs et al. 2024a) and anthocyanin (Bibbs et al. 2024a). The shared utilization of UV light, while in different contexts, supports the importance of UV across mosquito genera. Within flowers supporting the highest mosquito survival, there was a tendency toward UV dark flowers, for example as in *A. speciosa* (Eby et al. 2013) and *Verbena* sp. (Blum and Rørslett 2013). Flowers with UV reflectance, such as *Linum* sp., *C. draba*, *Sphaeralcea* sp., *Rosa* sp., and *L. salicaria* (Blum and Rørslett 2013) tended to exhibit lower mosquito survival.

Generally, the flower phenology data obtained from iNaturalist is an estimated time window based on prior years. Consequently, the exact timings may not align with our local fluctuations even if the general trends are similar between them. Particular species like *A. speciosa*, had higher numbers of observations within the iNaturalist database, possibly due to the popularity of the flower among outdoor enthusiasts. Hence, general proportions of total observations are more informative than the quantity of observations, as they may be biased by the observers. When flower availability is low, sugar availability for mosquito feeding also tends to be low

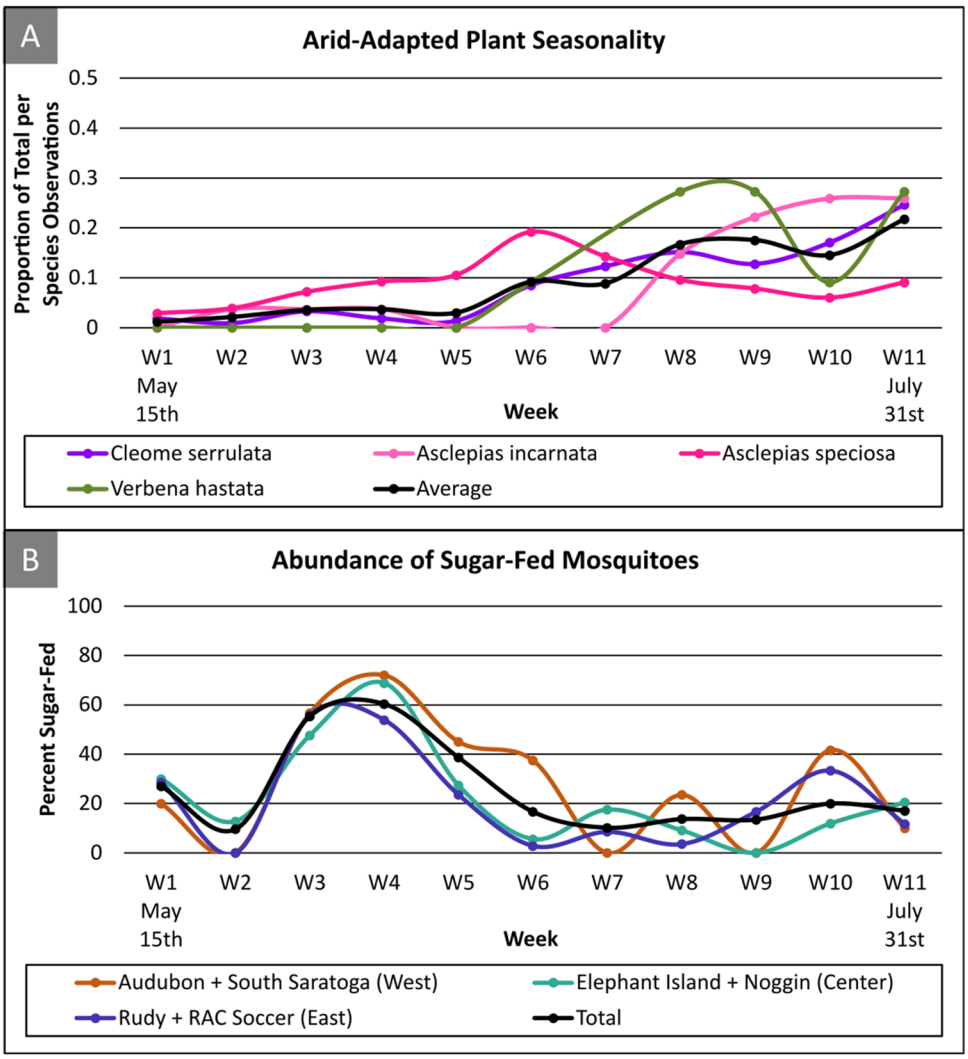

Fig. 7 **A** Flower phenology of plants with the highest mosquito survival: *Cleome serrulata* Pursh, *Asclepias speciosa* Torrey, *Asclepias incarnata* L., and *Verbena hastata* L. (iNaturalist Community 2008). **B** Relative abundance of sugar-fed mosquitoes (percent sugar fed per total collected using light traps)

(Martinez-Ibarra et al. 1997; Takken et al. 2013). However, the phenology data had several limitations including reliance on multi-year flower phenology obtained from iNaturalist records and the fact that particular species, such as *A. speciosa* are more charismatic than the others, resulting in biased observations. More research needs to be conducted to ascertain peak flowering times.

The techniques optimized for this study can indicate the low sugar abundance period in real time to inform changes in the mosquito resources in the field. We also identified four plants on which *Cx. pipiens* survival was optimal, all of which were natively occurring species, giving some context as to land use by the mosquitoes. Future experiments could utilize plant-DNA extractions from nectar meals imbibed by a mosquito, which could validate our plant-usage data from this study. This step is critical in cementing the mosquito's nutritive relationship to the plants in the field, as the current body of knowledge can only draw inference on field interactions by using behavioral studies to help deduce probable links. Furthermore, investigating what characteristics make *C. serrulata*, *A. incarnata*, *A. speciosa*, and *V. hastata* attractive, such as the most useful odorants and characteristics or signs of UV reflectance, could provide more insights into understudied mosquito behaviors. These investigations provide further insight into cryptic habits of mosquito species, potentially leading to enhanced integrated management measures for public health protection.

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supplies, resources, manuscript editing. CSB: Ideation, data curation, data interpretation, project aims, methods development, manuscript preparation/editing, project supervision.

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Data availability Data are externally available at Harvard Dataverse at https://doi.org/10.7910/DVN/SV3F9I.

Declarations

Conflict of interest Not applicable.

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