# LOW SEED VIABILITY OF A RARE ASTER

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**Abstract**—The reproductive ecology of rare plants is often unknown, yet the persistence of most plant populations depends on successful interactions with pollinators and favourable environmental conditions. Sexual reproduction maintains genetic diversity within plant populations using pollinators to transport pollen grains among plants of the same species and producing seeds. We investigated the reproduction of *Yermo xanthocephalus* Dorn (Desert yellowhead), a perennial member of Asteraceae endemic to central Wyoming, USA, which grows in only two locations within 8 km of each other. Our objectives were to assess the pollination and seed-set of *Y. xanthocephalus*. We conducted seed-set experiments in both populations to measure self-pollination and estimate if pollinating insects limited seed production. We used vane traps and pan traps to capture pollinators, and we examined pollen carried on bees. *Yermo xanthocephalus* can self-pollinate, but seed-set was extremely low. The number of viable seeds produced in flowerheads pollinated by insects did not differ from those produced by capitula hand-pollinated with excess pollen, indicating that pollinators did not limit seed production that year. Pollen from *Y. xanthocephalus* was carried by nine bee genera, suggesting that no one specific insect pollinates this plant. Only 12% of ovules produced viable seeds in the main population and 0% were viable in the other population, suggesting that something beyond pollinators limited seed-set. We recommend continued research to address what is limiting seed production to advance the knowledge and management of this declining plant species.

**Keywords**—Pollination biology, phenology, seed biology, plant reproduction, endemic

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## INTRODUCTION

Rare plant species provide vital services in the habitats and ecosystems in which they live (Xu et al. 2020), but little is typically known about these unique species. Rarity can be associated with a restricted geographic range, high habitat specificity, or low local population size in most places a species occurs (Rabinowitz 1981). Regardless, rare species often have a distinct combination of traits and are more likely to support the more vulnerable ecological functions in their communities (Mouillot et al. 2013; Leitão et al. 2016). Therefore, rare species not only increase biodiversity, they also increase a diversity of ecosystem functions (Mouillot et al. 2013; Leitão et al. 2016). Despite their critical roles, little is typically known about the ecology of rare plant species (Burmeier & Jensen 2008; Miller et al. 2019) leaving conservation managers with little information upon which to base decisions. Global biodiversity is decreasing and the number of plant species in danger of extinction is increasing (Kempel et al. 2020). Investigating vital life history characteristics of rare plants, such as their life cycle, reproduction, pollination, and seed production, are essential for making informed management decisions (USDI [United States Department of the Interior] 2001, 2010).

Knowledge of a plant's reproduction is crucial to understand a species' current trajectory and their ability to persist (Willemse 2009). Plants can reproduce through two main methods, asexual and sexual reproduction. Asexual reproduction can occur by producing ramets, which are genetically-identical to the parent plant, through rhizomes or similar structures. Sexual reproduction predominantly occurs through seed production, where pollen is usually transferred from another plant resulting in increased genetic diversity (Jabis et al. 2011). Notably, 79-90% of plants globally rely on animals to transport pollen among individuals of a plant species to maintain genetic diversity (Ollerton et al. 2011; Rodger et al. 2021; Tong et al. 2023). Plants that can reproduce asexually and sexually may be more likely to be self-incompatible in order to maintain genetic diversity (Aigner 2004). For example, higher genetic diversity among nearby groups of clones of *Dithyrea maritima* (Beach spectacle pod), a rhizomatous member of Brassicaceae endemic to the coastal sand dunes in southern California, resulted in more seed production upon cross pollination (Aigner 2004). Also, the pollen from nearby asexually produced clones of *Calystegia collina* (Coast Range false bindweed), a clonal member of Convolvulaceae endemic to serpentine outcrops in northern California, was incompatible with the neighbouring genetically identical plants (Wolf et al. 2000). Sexual reproduction increases the genetic diversity within populations making them more likely to survive adverse conditions (Jabis et al. 2011). Conversely, asexual reproduction produces new plants that are genetically identical to the parent plant creating populations that are in theory less resilient (Agrawal 2001).

Pollinators, especially some bees and butterflies, are declining precipitously (Wagner 2020; Potts et al. 2010; Cameron et al. 2011; Abrol 2012; Goulson & Nicholls 2016; Rhodes 2018; Wagner 2020), and their decline will likely decrease the production of viable seeds because less pollen may be transported by pollinators (Potts et al. 2010). Rare plants that rely on specialist pollinators may be especially vulnerable to declining pollinators; however, many rare plants use common pollinators (Bascompte et al. 2003; Vázquez and Aizen 2004; Rasmussen et al. 2020). A few insect pollinators have been connected to the decline of several rare plants showing the critical mutualisms between them (Biesmeijer et al. 2006). The pollen loads on bees must be examined to understand which plant species bees actively collect pollen from (Popic et al. 2013); however, this method is infrequently done because of the effort needed. Examining the pollen on pollinators collected in the vicinity of a specific plant is one method of estimating which insects transport their pollen. Models predict drier conditions in many areas of North America (Overpeck and Udall 2020), which may hamper plant reproduction, blooming and the availability of floral resources to pollinators. Fewer pollinators could translate to less genetic diversity in plant populations from fewer viable seeds (Aigner 2004; Ramos-Jiliberto et al. 2020). Less genetic variation reduces biological fitness to confront changes in the environment (Agrawal 2001).

We studied the reproduction of a threatened plant to estimate the degree to which seed production was limited by pollinators, and if it could self-pollinate and self-fertilize. *Yermo xanthocephalus* Dorn (Desert yellowhead; Asteraceae) is endemic to central Wyoming, USA and grows in soil from volcanic sandstone, tuff and conglomerate (Van Houten 1964; Scott & Scott 2009; Heidel et al. 2011). *Yermo xanthocephalus* is known only from an area of 10 km$^2$, blooms from early June into mid-August, sets seed in mid-July into late September and lives in sparsely vegetated *Artemisia tridentata* (Big sagebrush), bunchgrass and cushion plant communities. Information about the reproductive ecology of *Y. xanthocephalus* is sorely lacking. We measured seed-set in three treatments and assessed which pollinators transferred pollen grains. Our specific questions were: 1) To what extent can *Y. xanthocephalus* self-pollinate and self-fertilize? 2) What proportion of seeds produced by *Y. xanthocephalus* are viable? 3) To what degree was seed production limited by pollinators? and 4) Which pollinators carry the pollen of *Y. xanthocephalus*? Results will provide information to managers about the level of seed production by this rare plant and what may limit its reproduction.

## MATERIALS AND METHODS

### STUDY SPECIES

*Yermo xanthocephalus* is an herbaceous perennial with a long taproot. The flower stalks are up to 3 dm tall, with 20 to over 100 flowerheads in a multiparous cyme. The cylindrical involucres are yellow, ca 1 cm tall, with 4 to 6 disk florets. The leaves are mostly in a basal cluster with alternate leaves along the flowering stem (Dorn 1991). Ramets may develop from the taproot. Individual plants do not bloom every year. *Yermo xanthocephalus* is only known from two populations located ~8 km apart in Fremont

County, Wyoming, USA (Fig. 1), discovered in 1990 at Sand Draw (Dorn 1991) and 2010 at Cedar Rim (Heidel et al. 2011). *Yermo xanthocephalus* is listed as Threatened under the US Endangered Species Act (USDI Fish and Wildlife Service 2002). The Sand Draw population is much larger (9,300-13,250 plants based on extensive annual grid censuses 1995-2004; Scott & Scott 2009) than the Cedar Rim population (~750 plants in 2016; Freeland, personal communication). The Sand Draw population is directly windward of the Cedar Rim population (Heidel et al. 2011). *Yermo xanthocephalus* grows in soils derived from the White River Formation. Most *Y. xanthocephalus* individuals grow in sparsely vegetated sagebrush steppe and cushion plant communities (Fertig 1995, Scott & Scott 2009, Heidel et al. 2011). The area receives an average of 25 cm of precipitation annually (Jeffrey City weather station; Western Regional Climate Center 2022).

### SEED-SET EXPERIMENTS

We measured seed-set in three treatments to estimate the contribution of self- and cross-pollination in seed production. We haphazardly selected 14 *Y. xanthocephalus* plants at the Cedar Rim population and 20 plants at the Sand Draw population to estimate the degree to which these plants were pollen-limited. Plants were selected before flowers bloomed in mid-June 2018. Three inflorescence branches were selected on each plant to receive one of each treatment. Bagged treatments restricted pollinator access and measured the degree to which flowers can self-pollinate and self-fertilize. Open treatments left capitula accessible for local pollinators to visit and measured the number of seeds produced under ambient conditions. The hand-pollinated treatment added excess pollen in addition to local pollinators to measure seed production when

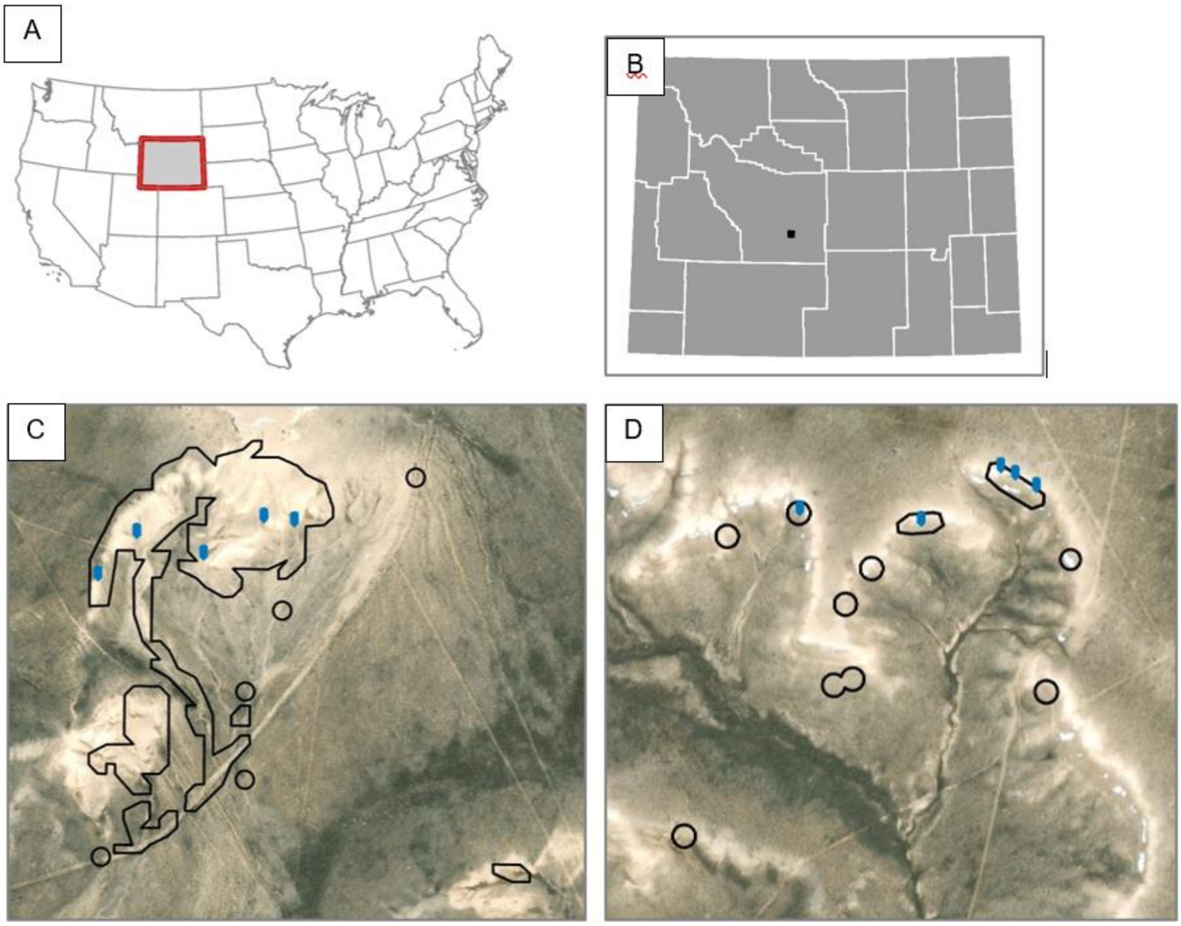

**Figure 1. A.) Map of the United States showing the location of Wyoming and B.) the location of *Yermo xanthocephalus* in central Wyoming. The location of pollinator sampling stations (blue darts) in the *Yermo xanthocephalus* populations (black outlines) at C.) Sand Draw (~0.5 km east to west) and D.) Cedar Rim (~0.35 km east to west) (ESRI 2011).**

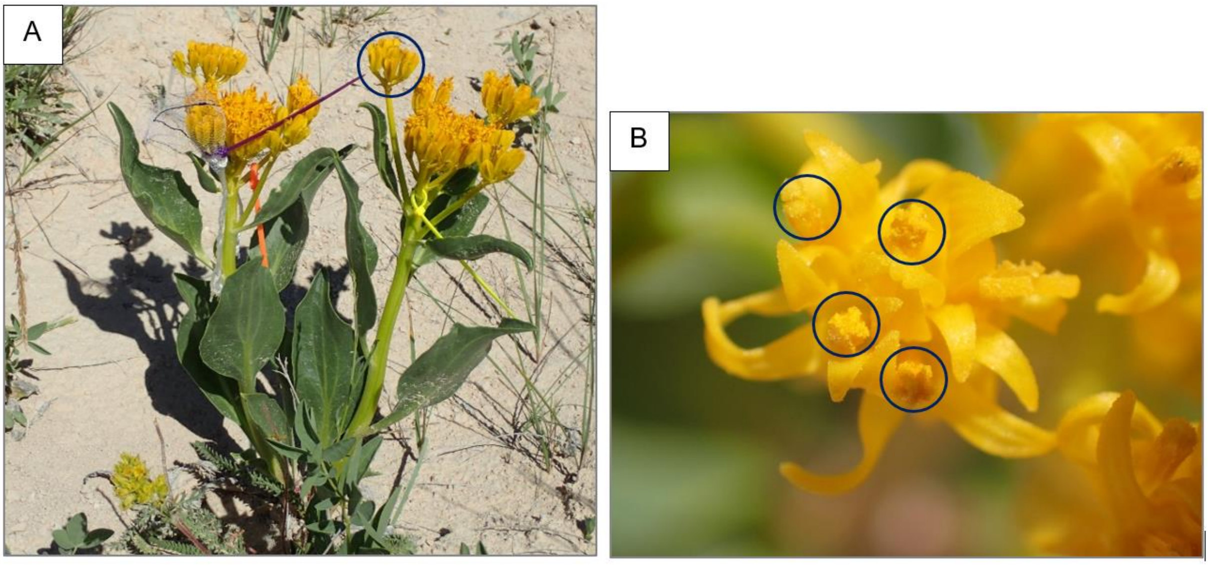

**Figure 2. A) A *Yermo xanthocephalus* plant with a mesh bag over the bagged treatment, and the hand-pollinated and open treatments marked with yellow and orange zip ties, respectively. Circled is one flowering branch. B) *Yermo xanthocephalus* flowerhead with four florets indicated by the circles.**

pollen was not limiting. Pollen came from plants >50 m away; we delicately brushed collected anthers on the stigma of the treatment capitulum within a few minutes to few hours due to travel constraints. Pollen from Sand Draw was used in both populations due to few blooming plants at Cedar Rim. Capitula were covered with mesh bags before (bagged treatment; Fig. 2A) or after (open and hand-pollinated treatments) flowers bloomed to contain the developing seeds. We recorded the number of flowerheads pollinated and marked the flowerheads not ready for pollination in the hand-pollinated treatment so we only analysed capitula that received excess pollen. We monitored treatments and collected fruits when flowerheads were ripe, mid-July through early September. Flowerheads were placed in paper bags, returned to the laboratory and dried at room ambient temperature.

We cleaned, counted, and weighed all the seeds to estimate the degree to which *Y. xanthocephalus* self-pollinated or depended on pollinators. Each *Y. xanthocephalus* flowerhead had one to seven florets, each of which had the potential to produce one seed (Fig. 2B), and there were multiple flowerheads per inflorescence branch (Fig. 2A). We counted the number of flowerheads per inflorescence branch and the number of seeds per flowerhead. We noted seeds that appeared viable (size and mass) and we used Tetrazolium staining to test for viability. Tetrazolium measures the germinative potential of seeds by turning red to indicate cellular respiration (Lindenbein 1964). We placed the seeds between moistened paper towels for 24 hours, cut them to expose the endosperm, and immersed them in tetrazolium solution for 24 hours. The endosperm of viable seeds turned pink or red and the endosperm of non-viable seeds remained white.

### POLLINATORS

We collected potential pollinators at the same locations as the seed-set experiments to estimate which insects pollinated this Threatened plant. Pollinator stations were used to estimate the abundance and diversity of pollinators within the *Y. xanthocephalus* populations, and to assess which pollinators collect *Y. xanthocephalus* pollen. We deployed five pollinator stations in each population for 24-48 hours eight times between 12 June and 6 July 2018, and four times between 19 June and 17 July 2019. Preservation techniques did not allow us to examine pollen on bees in the 2018 collections. Pollinator stations consisted of one blue vane trap (vane trap hereafter; ~0.5 m above ground) and three pan traps (yellow, blue and white; ~10 cm above ground) filled with soapy water (Fig. 3A). We recorded the location, dates and times we deployed and retrieved stations, and only collected pollinators during fair weather. Pollinators collected with vane traps were used to assess pollen, because these traps were dry and minimally altered pollen loads. We also netted

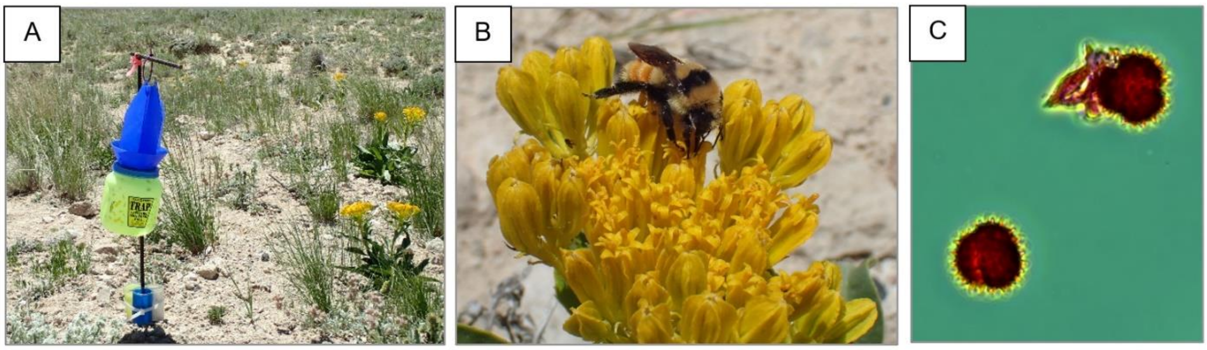

**Figure 3. A.) We collected pollinators using pollinator sampling stations with vane traps (top) and pan traps (bottom). B.) *Bombus huntii* visiting *Yermo xanthocephalus* flowerheads and a C.) stained *Yermo xanthocephalus* pollen grains.**

pollinators opportunistically when we saw them visiting *Y. xanthocephalus* flowers (Fig. 3B); however, we did not assess capture via netting because we did not have dedicated transects for recorded time periods. Bees were identified to genus (Michener 1994) and other insects were generally identified at coarser taxonomic levels (e.g., family). We removed the portion of the bee's body with scopae that carried pollen, which was typically a hind leg, except Megachilidae, who carry pollen on the underside of the abdomen. A recent analysis discovered that the richness of plant pollen was higher in bee scopae compared to on their body (Tourbez et al. 2023) and we were interested in quantifying the visitors of this rare plant. We performed acetolysis on the removed portion to strip pollen grains of lipids, proteins, and carbohydrates, making pollen easier to identify, and stained the pollen with Safranin O (Jones 2014; Fig. 3C). The resulting pollen was slide mounted and identified under a compound microscope at 200x. Pollen was compared to a library made from pollen of *Y. xanthocephalus* and other plants collected in the area, usually identified to genus. We counted the number of pollen grains of each plant taxon on individual bees to estimate pollen loads and which species collected pollen from *Y. xanthocephalus*.

### Analyses

We estimated how precipitation, air temperature, and the number, mass and viability of seeds differed through time or between populations. We used time series analysis to estimate how air temperatures and precipitation varied through time (prais; Franz 2021). We measured how seed characteristics differed between populations and among treatments using linear mixed-effect models (lmer) where treatment and population were a fixed effect and plant was a random effect. The number of seeds met statistical assumptions and we analysed using a normal distribution. Seed mass and viability had non-constant variance. We natural log transformed seed mass and used a gamma distribution to analyse the transformed seed mass and seed viability. We chose the distribution that best fit the data using the fitdistrplus package (Delignette-Muller and Dutang 2015) and by examining histograms. We used a general linear model (glm) to assess differences in pollinators between populations. We calculated differences among treatments using estimated marginal means using the emmeans package (Lenth 2022). Data analysis occurred in Program R (R Core Team 2017) and we used the plyr package (Wickham 2011) to sort, summarize and compute data.

## RESULTS

### CLIMATE

Precipitation and temperature varied among the years that we monitored the plant and among months. The most precipitation fell during spring and October (April through June; prais, $t > 2.6$, $P < 0.001$) although the amount did not vary among years (prais, $t = 0.27$, $P = 0.78$). When we considered only spring precipitation (April – June), May received the most moisture (prais, $t = 5.0$, $P < 0.0001$), but spring precipitation did not vary among years (prais, $t = 0.4$, $P = 0.69$; a). Spring mean temperatures varied among years (prais, $t = 2.8$, $P = 0.006$; b) and among months, with June having the highest temperatures (prais, $t > 9.7$, $P < 0.0001$).

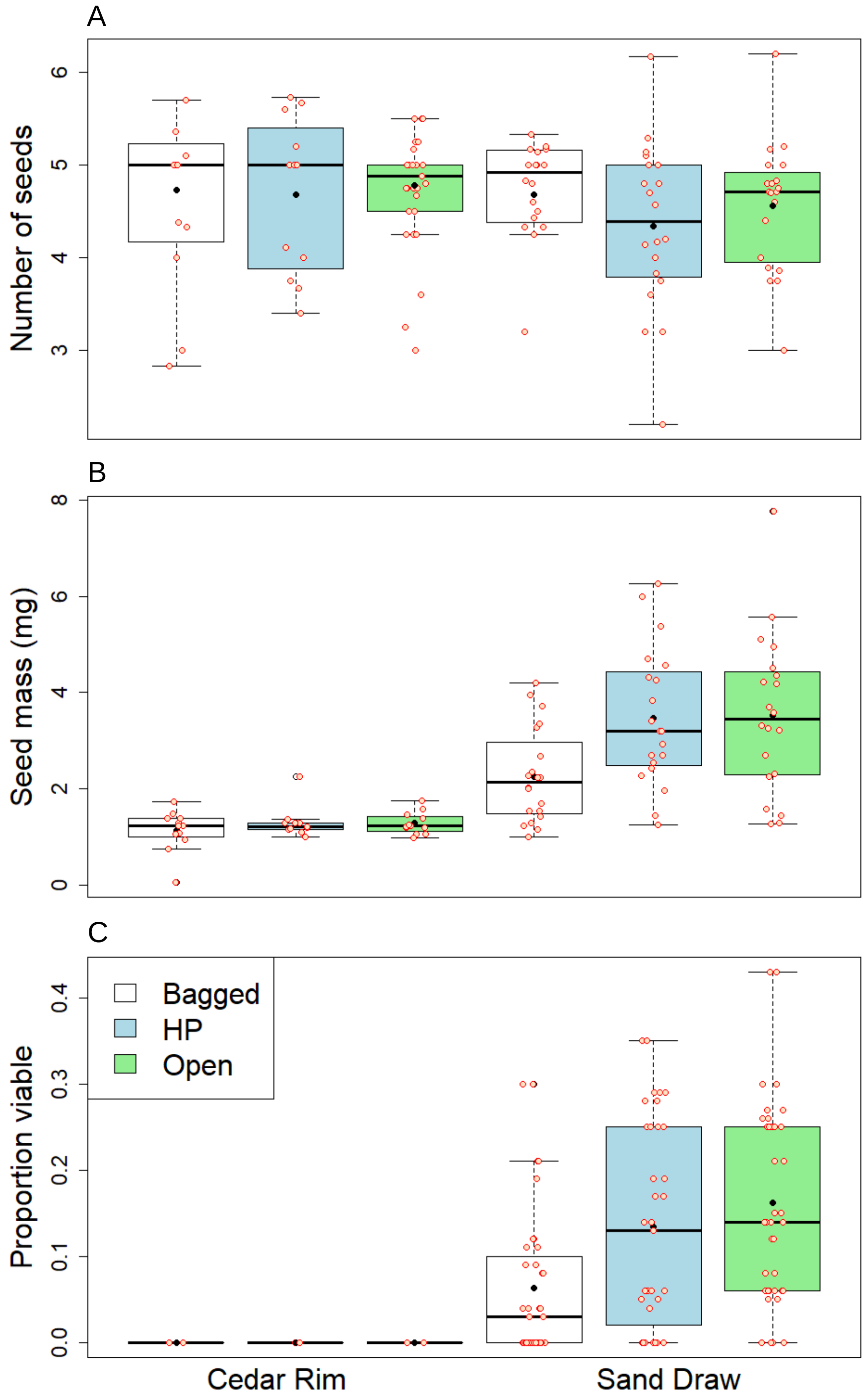

**Figure 4. A.) The number, B.) mass and C.) viability of seeds produced by *Yermo xanthocephalus* in the Cedar Rim and Sand Draw populations in three treatments. The bagged treatment tested the plant's ability to self-pollinate, the hand-pollinated (HP) treatment measured seed production with excess pollen and the open treatment estimated seed production under ambient conditions. The bold line is the median, the black circle is the mean, the lower and upper limits of the box is the 25th and 75th percentile, whiskers are the upper and lower limits of the data excluding outliers and the open circles are data points.**

### SEED-SET EXPERIMENTS

*Yermo xanthocephalus* produced nearly 5 ovules per flowerhead on average (range 2-7) and the number of ovules per flowerhead did not differ between populations (lmer, $t = -1.3$; emmeans, $P = 0.20$) or among treatments ($t = -0.63 – -1.39$; emmeans, $P = 0.35 – 0.80$) Fig. 4A. Seed mass averaged 2.4 mg and ranged between 0.05 (non-viable) and 7.8 mg (viable). Seed mass was higher at Sand Draw than Cedar Rim (lmer, $t = 7.3$; emmeans, $P < 0.0001$; Fig. 4B). The mass of seeds in each treatment was lower at Cedar Rim than Sand Draw (interaction between population and treatment; $t = 1.8$; emmeans < 0.03), including the bagged treatments ($P = 0.002$). Seed mass did not differ among treatments at Cedar Rim (emmeans = 0.94 – 1); however, the mass of seeds in the bagged treatment at Sand Draw was lower than the hand-pollinated and open treatments (emmeans, $P <$

0.01). Therefore, *Y. xanthocephalus* produced few viable seeds through self-pollination. The Cedar Rim population produced zero viable seeds and the Sand Draw population produced 12% viable seeds (interaction between population and treatment; t = 0.59 – 0.81, *P* = 0.03). At Sand Draw, only 6% of seeds in the bagged treatment were viable compared to 15% in the hand-pollinated and open treatments; seeds in the bagged treatment had lower viability than the open (emmeans, *P* = 0.004) and hand-pollinated treatments (emmeans, *P* = 0.10).

### POLLINATORS

We collected a diverse assemblage of insects on or near *Y. xanthocephalus*, and more individuals and genera of insects were found at Sand Draw than the Cedar Rim population. We captured 5 orders of insects including 28 genera of bees, 9 species of bumble bees and 8 species of butterflies when *Y. xanthocephalus* was blooming (Supplementary Tab. 1). The bee genera *Agapostemon* (44% of individuals) and *Lasioglossum* (21%) were the most abundant followed by *Osmia* (12%), *Halictus* (6%), *Ceratina* (5%), and *Bombus* (2%). We captured 40% more bees at Sand Draw than Cedar Rim (glm, t = 2.7, *P* = 0.006; Fig. 5A), and we captured more bees in vane traps than pan traps (glm, t = 3.7, *P* = 0.0002); however, abundance did not differ between years (glm. T = 1.0, p 0.31). We captured 50% more bee genera at Sand Draw compared to Cedar Rim (glm, = 3.5, *P* = 0.0005; Fig. 5B), and we caught 3.5 times more genera in vane traps than pan traps (glm, t = 9.2, *P* < 0.0001); however, the richness of bees did not differ among years (glm, t = 0.6, *P* = 0.56).

### POLLEN ANALYSIS

The pollen of *Y. xanthocephalus* was unique and we were able to distinguish it from other aster species in the area. The pollen from *Y. xanthocephalus* is spherical. Each grain has three deep longitudinal grooves and the surface has spikes. Each pollen grain is 6.9 to 11.9 µm in diameter and the spikes varied between 0.7 and 1.4 µm in length (Fig. 3C). Although several species of Asteraceae have similarly shaped pollen, *Y. xanthocephalus* pollen is larger than most other species in the area, the spike length varied among species and the flowering phenologies differed.

Nine genera of bees carried pollen grains from *Y. xanthocephalus* on their scopae indicating that they actively collected the pollen (Fig. 5C, Supplementary Tab. 1). Of all the *Y. xanthocephalus* pollen we encountered, *Hoplitis* carried the most pollen (25%; mean per individual) followed by *Andrena* (17%), *Bombus* (14%), *Agapostemon* (13%), *Lasioglossum* (11%), *Anthophora* (a digger bee; 8%), *Dufourea* (7%), *Osmia* (4%) and *Ceratina* (1%; Fig. 5C). Of all the pollen grains identified on individual bees, pollen from *Y. xanthocephalus* made up 33% of pollen loads for *Hoplitis*, 26% for *Lasioglossum*, 19% for *Bombus* and *Agapostemon*, 16% for *Ceratina* and *Andrena*, 11% for *Anthophora*, 10% for *Osmia* and 9% for *Dufourea* (Fig. 5D). The most pollen from *Y. xanthocephalus* was found on bees in early July (Fig. 6A). Between 42% and 100% of individuals in each bee genus were carrying pollen from *Y. xanthocephalus*, suggesting that this rare plant is used by many bees (Fig. 6B).

## DISCUSSION

*Yermo xanthocephalus* can self-pollinate; however, the number of viable seeds produced through this process was lower than reported by Scott and Scott (2009) in 1995 when 23.8% of seeds were viable and 10.5% to 13% germinated (Scott & Scott 2009). Additionally, the seed viability is much lower than reported for other rare species of Asteraceae (Colling et al. 2004; Diamond et al. 2006; Masini et al. 2016). The germination rates of the rare aster, *Scorzonera humilis* (Viper's grass), which grows in moist meadows, were up to 97% from four populations (Colling et al. 2004) while another rare aster, *Rudbeckia auriculata* (Eared coneflower), which occurs in wet meadows and bogs, produced ≤31.4% viable seeds in five populations (Diamond et al. 2006). Two species that live in the dry Patagonian steppe, *Gutierrezia solbrigii* (Solbrig's snakeweed) and *Senecio subulatus* (Slender ragwort), produced 82% and 88% viable seeds, respectively (Masini et al. 2016). Thus, another mechanism must limit viable seed production for *Y. xanthocephalus*. *Yermo xanthocephalus* can self-pollinate, is not pollen-limited, does not have a specific pollinator, nor do any flower visitors depend on this plant predominantly. Despite growing in similar conditions ~65 km from *Y. xanthocephalus*, the early blooming *Trifolium barnebyi* (Barneby's clover) is limited by different factors. The first individuals of

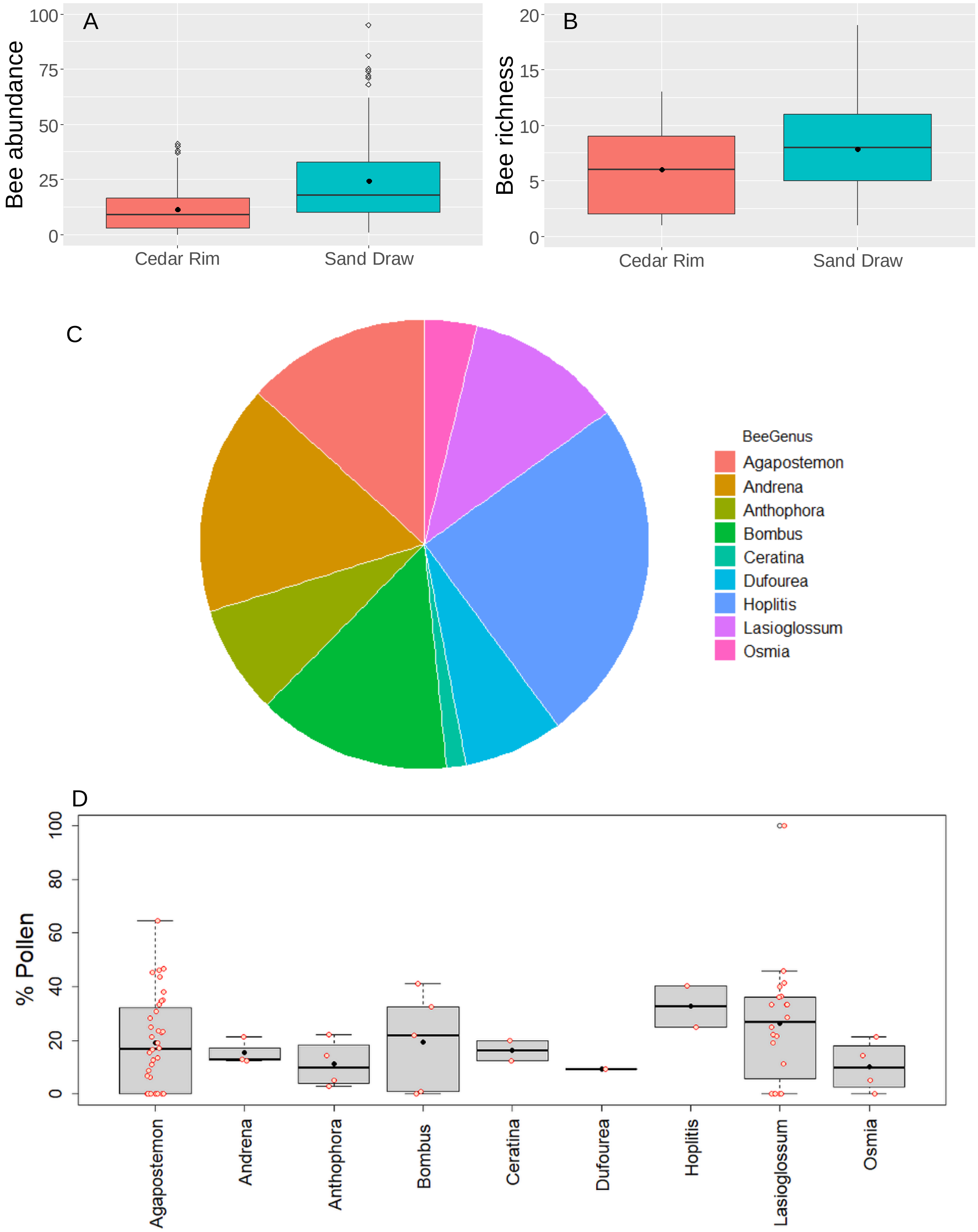

**Figure 5.** **A) The abundance and B) richness of bees collected at Sand Draw and Cedar Rim while *Yermo xanthocephalus* was blooming. C) Mean percent of pollen grains from *Yermo xanthocephalus* carried by nine bee genera. The mason bee, *Hoplitis*, carried the most *Yermo xanthocephalus* pollen. D) The percent of pollen grains from *Yermo xanthocephalus* carried on individual bees by genus compared to all pollen grains counted on a bee. The bold line is the median, the black circle is the mean, the lower and upper limits of the box are the 25th and 75th percentiles, whiskers are the upper and lower limits of the data excluding outliers and the open circles are data points.**

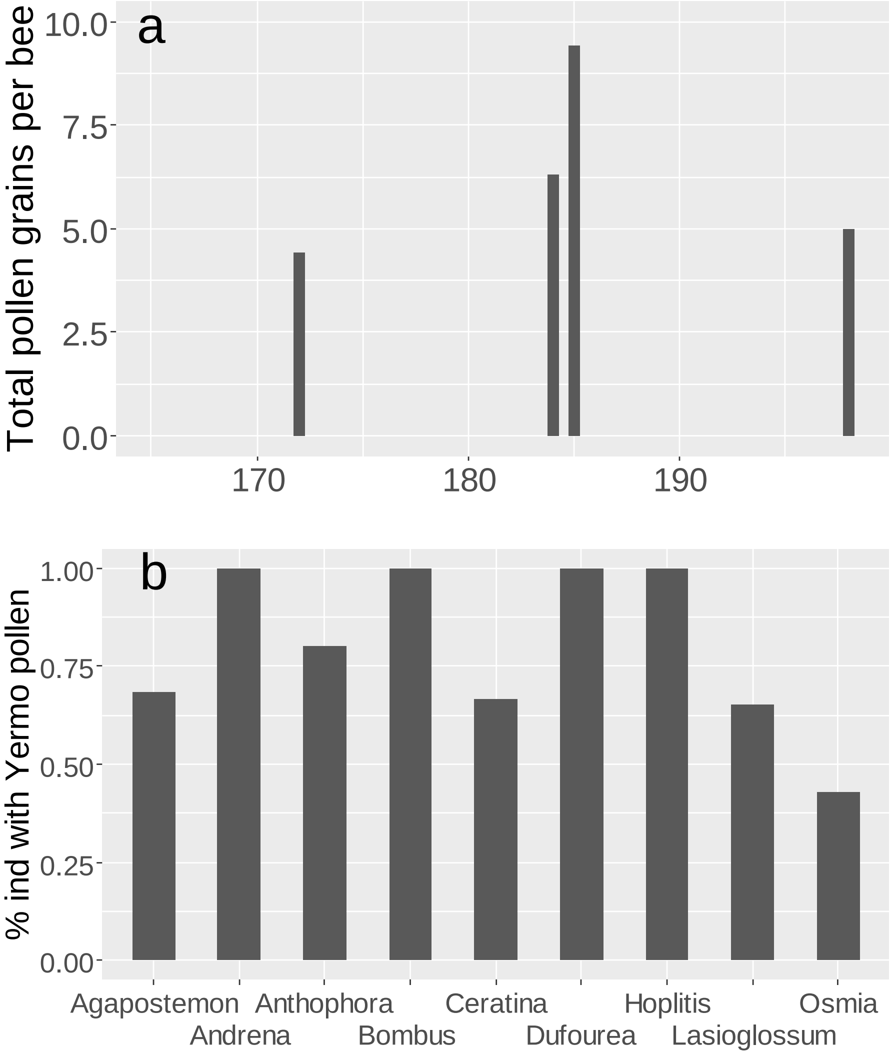

**Figure 6. A) Bees carried the most pollen from *Yermo xanthocephalus* in early July. B) A high percentage of individuals in each bee genus carried pollen from *Yermo xanthocephalus* indicating that many bees collected pollen from this plant while it was blooming.**

*Trifolium barnebyi* to bloom were pollen-limited and relied predominately on one genus of bee (*Andrena*; Handley & Tronstad, 2023). The low seed viability is concerning from a genetic diversity standpoint and for the perpetuation of rare species (Ellstrand & Elam 1993).

We found that pollinators did not limit seed production in *Y. xanthocephalus* because the number of viable seeds produced in the open and hand-pollinated treatments did not differ in 2018. We hypothesize that other climate variables (e.g., precipitation, air temperature) may limit seed viability. Seed production can vary with nutrients, temperature (Young et al. 2004; Bizecki Robson 2010) and water availability (Pol et al. 2010). We predict that seed production for *Y. xanthocephalus* may be higher during wetter years; however, the degree to which precipitation alters seed production is unknown. Precipitation during our study was average compared to recent past records. We do not have an estimate of how many viable seeds are produced over the lifespan of a mature *Y. xanthocephalus* plant, because the longevity of individual *Y. xanthocephalus* plants is unknown as well as the average number of years a plant produces inflorescences. We predict the number of viable seeds produced is low given measured values. Closely monitoring individual plants over time would provide valuable information about this rare plant.

*Yermo xanthocephalus* pollen was found on bees belonging to nine genera. The amount of *Y. xanthocephalus* pollen carried corresponded with the plant's flowering time. *Yermo xanthocephalus* lives in a sparsely vegetated area with a limited number of insect-pollinated flowering plants. Although some studies have noted that bees use pollen from wind-pollinated plants (Saunders 2017), we did not observe this. The bees we collected usually carried pollen from several species including *Y. xanthocephalus*, indicating that bees use as much of the available pollen as possible. Blooming flowers in mid-summer appeared to be scarce, especially during hotter and drier years, likely making *Y. xanthocephalus* a valuable floral resource for many flower visitors. Flowers provide both nectar to fuel adult activities and pollen to feed young (Larson et al. 2018). *Yermo xanthocephalus* was visited by several taxa of common bees, as has been observed for some other rare plant species (e.g., Bascompte et al. 2003). *Yermo xanthocephalus* is an oasis in the semi-arid, unique habitat that this plant calls home.

On-site data loggers recording site conditions would provide a much more accurate portrayal of the weather to estimate how temperature and precipitation alter *Y. xanthocephalus*. We used data from a weather station ~30 km from the sites and 200 m lower in elevation (Jeffrey City weather station; Western Regional Climate Center 2022). Precipitation is often extremely localized and using data from the closest public source may not accurately reflect conditions. Loggers on-site could measure other variables, such as soil moisture which is critical for plant growth (Nyawade et al. 2018; El-Sharnouby et al. 2019). We suggest measuring abiotic conditions within the *Y. xanthocephalus* populations to better understand how climate may alter the number of plants, and sexual and asexual reproduction.

Investigating the mutualisms between plants and their pollinators are crucial, especially for rare plants. Bees are the most prolific pollinators and bees have declined more than most other insect groups (Goulson & Nicholls 2016; Rhodes 2018). Fewer pollinators transporting pollen could lower genetic diversity within rare plant populations reducing their resilience to climate change and other disturbances (Ellstrand & Elam 1993). Understanding the degree to which habitat fragmentation and resource use can influence pollinators and pollination is desperately needed (Xiao et al. 2016). Pollination studies can help clarify the connectivity between plants and their pollinators.

We studied the reproductive ecology of *Y. xanthocephalus* and learned that seed production appeared to limit this rare plant. Pollinators did not limit sexual reproduction the year we measured seed-set, and we hypothesize that climate may play a larger role. The lack of viable seeds produced in one population is especially disturbing and we postulate that this population is a pseudo-sink that depends on the population located upwind. Few viable seeds may constrain the perpetuation of the species and contribute to declining plant numbers. Investigating the genetics of each population may help managers understand the status of the species and how these populations interact.

Our study provides guidance for the conservation of rare plants globally. Investigating seed-set indicates the degree to which a plant self-pollinates, is pollen-limited, or seed production is limited by other factors. Examining pollen from pollinators can reveal which taxa carry pollen from a rare plant species and how common those taxa are in the ecosystem (Popic et al. 2013). We found that *Y. xanthocephalus* produced few viable seeds, but this was not from a lack of suitable pollinators, but instead from other factors, possibly abiotic ones. The populations differed in seed viability suggesting that abiotic factors may differ between these sites despite being located ~8 km apart. Continued research will focus on climatic factors and environmental differences between the populations and compare sexual and asexual reproduction in each population. Investigating species' constraints will inform managers about the abiotic characteristics that limit this rare plant to the largest degree and how the species allocates resources depending on habitat features.

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## AUTHOR CONTRIBUTION

Concept and design LT & JH, data collection JH, data analysis LT, writing JH & LT, edits and approval for publication JH & LT.

## DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

## DATA AVAILABILITY STATEMENT

The data used to write this article are available at the Dryad Digital Repository.

## APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Insects captured in *Yermo xanthocephalus* populations during flowering

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