IMPACTS OF POLLEN-DONOR DISTANCE AND NUTRIENT AVAILABILITY ON

REPRODUCTIVE SUCCESS IN A CARNIVOROUS PLANT

By

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Introduction

Genetic diversity has important consequences for the survival of plant populations after natural or human disturbance. Disturbances such as reduction of contiguous habitat, overcollection and fire suppression lead to smaller and/or spatially isolated populations, which in turn can affect the genetic variation of populations (Young et al. 1996; Ouborg & Van Treuren 1995). Decreases in population size and increasing interpopulation isolation, may lead to a genetic bottleneck that can affect genetic variation and pollination success (Cunningham 2000; Young et al. 1996). The direct relationship between genetic variation and population size has been observed in both woody and herbaceous plant species (Aguilar et al. 2008; González et al. 2019; Wilson & Provan 2003; Vranckx et al. 2012; Honnay & Jacquemyn 2012). Sexual reproduction helps maintain genetic variation and can make populations more resilient by increasing the likelihood of inheriting traits that improve survival (Madsen 1991). The success of sexual reproduction can be affected by pollination success and resource availability, which can affect both the quantity and quality of the offspring produced (Casper & Niesenbaum 1993).

Inbreeding, from a plant mating with itself (selfing) or a close relative (biparental inbreeding), decreases genetic variation. This results in an increased probability that recessive traits will be expressed and negatively affect the fitness of offspring, called inbreeding depression (Hereford 2010). Alternatively, outbreeding depression can occur with matings between two genetically distant plant populations which may produce offspring lacking benefits of localized adaptations or fewer offspring overall. Due to the sedentary nature of plants, the magnitude of a variability of a fitness trait can be partially attributed to spatial separation between pollen donor and pollen recipient (Souto et al. 2002, Aizen & Harder 2007, Waser &

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Price 1991). Ongoing habitat fragmentation and destruction directly affect pollen-donor distance which in turn might lead to inbreeding or outbreeding depression in affected populations.

Nutrient resources (e.g., nitrogen and phosphorus) are required to produce plant tissues, including seeds. Resource limitation can lead to reduced seed production (Doust 1989; Campbell & Halama 1993). There are many causes of resource limitation including herbivory, insufficient light, and nutrient-poor environments. Mother plants with limited nutrients may fill fewer seeds, produce lower quality seed, or abort seeds/fruit (Helenurm & Schaal 1996). The effects of nutrient availability on seed production are well understood in many species (Zhang et al. 2007; Butler & Ellison 2007).

The effects of nutrient limitation and pollen quality on reproduction are relatively well known. However, their combined effect is a new area of investigation. Due to environmental stochasticity, nutrient limitation often increases inbreeding depression, but the magnitude can vary by year and other confounding factors (Sandner 2021; Leimu 2008; Armbruster & Reed 2005; Keller et al. 2007). While nutrients are important to the development of high-quality seeds, an abundance of nutrients might not fully overcome the consequences of poor genetics and deleterious recessive alleles.

Sarracenia alata is a carnivorous pitcher plant found in nutrient-poor pine savannahs and seepage bogs from eastern Texas to southwestern Alabama. While *S. alata* populations are locally abundant and expanding east of the Mississippi River; western populations are contracting with the loss of pine savannah habitat and historic fire regimes (Koopman & Carstens 2009). The implications of continued habitat loss and degradation are important to the conservation of endemic species like *Sarracenia alata*.

There is more genetic variation within remnant western populations of *Sarracenia alata* than there is between extant populations (Horner et al. 2014). Without structures to enable long-distance travel, *Sarracenia* seeds have a short-dispersal distance from the parent plant (mean 12.8 cm) (Ellison & Parker 2002). While individuals are self-compatible, pollen transfer within a flower in the absence of an animal vector (known as autogamy) seems to occur by accident. Pollination of *Sarracenia* is dependent primarily on bees from the genus *Bombus*, which have an average foraging range under 2 km (Knight et al. 2005; Kreyer et al. 2004). The limited gene flow among extant populations (Horner et al. 2014) compels us to examine other factors which might reduce genetic variation within peripheral populations. Understanding the variance in pollen quality within populations is important for restoration and management of small and/or isolated populations.

Nutrients from digestion of insect prey significantly influence vegetative growth (Butler & Ellison 2007) and seed production (Ne'eman et al. 2006) in *Sarracenia purpurea*. However, the effects of nutrient availability in combination with pollen-donor distance on reproductive success has not been studied in *S. alata*. In this study, we examined the effects of pollen-donor distance, prey capture, and their interaction in the production of seeds and germination success in *Sarracenia alata*.

Methods

Study Species

Sarracenia alata is a terrestrial carnivorous plant native to nutrient-poor bogs across southern Alabama, Mississippi, Louisiana, and eastern Texas. This perennial, rhizomatous plant

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produces modified leaves fused into hollow tubes creating a pitfall trap called a pitcher. Although *S. alata* usually produces one flower per genet in late March to early April, robust plants can produce up to three flowers (Bodri & Gaspard 2006). The yellow-green flower, positioned atop a 30-40 cm peduncle, typically blooms prior to the opening of carnivorous traps on the same genet (Horner 2014), although a small percentage of genets have concurrently active pitchers and flowers. Due to the temporal avoidance of flowers and carnivorous traps, where they are rarely active at the same time (Juniper et al. 1989; Horner 2014), we are able to manipulate pollination and/or feeding independently.

Nodding perfect flowers have a calyx composed of three green to reddish bracts and five persistent yellow-green sepals (Figure 1). Five pendulous petals interdigitate with the five lobes of the umbrella-like style; a stigma on the notched tip of each lobe becomes receptive when the flower is fully opened. Deciduous petals fall 10-14 days after the flower opens, which corresponds with a decrease in stigma receptivity (Bodri & Gaspard 2006). The uniquely shaped floral structures create a chamber which allows collection of pollen in the style after dehiscence of the anthers. The size of the chamber allows for effective pollination by large-bodied insects, primarily *Bombus ssp*. Foraging bumblebees access the chamber by crawling under a style ray and between overlapping petal margins. The bumblebees contact the stigma, while entering the corolla chamber (Schnell 1983, Horner observations). Fruit mature and dehisce in the late summer to early fall and produce over 1000 small (mean 1.99 mm) seeds (Ellison 2001).

Pitchers photosynthesize and capture insect prey to acquire nutrients. During late April to early May, pitcher leaves arise in a rosette and reach maximum height before opening (Green & Horner 2007). Production of new pitchers continues throughout the

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season, decreasing in frequency in mid to late summer. The slender pitcher terminates in a

rolled lip called a peristome and a hood that covers but does not obstruct the pitcher opening.

Extrafloral nectaries are found on the entirety of the pitcher but are concentrated along the

peristome and immediately within the opening. Nectar production is variable throughout the

day and season, reaching a peak approximately three weeks after pitchers open (Green &

Horner 2007; Deppe et al. 2000). Pitcher traps lure insect prey with a combination of

volatiles, nectar and visual nectar guides and capture a large diversity of species (Bhattarai &

Horner 2009, Green & Horner 2007, Horner et al. 2012, Horner et al. 2018).

a.   *b.*
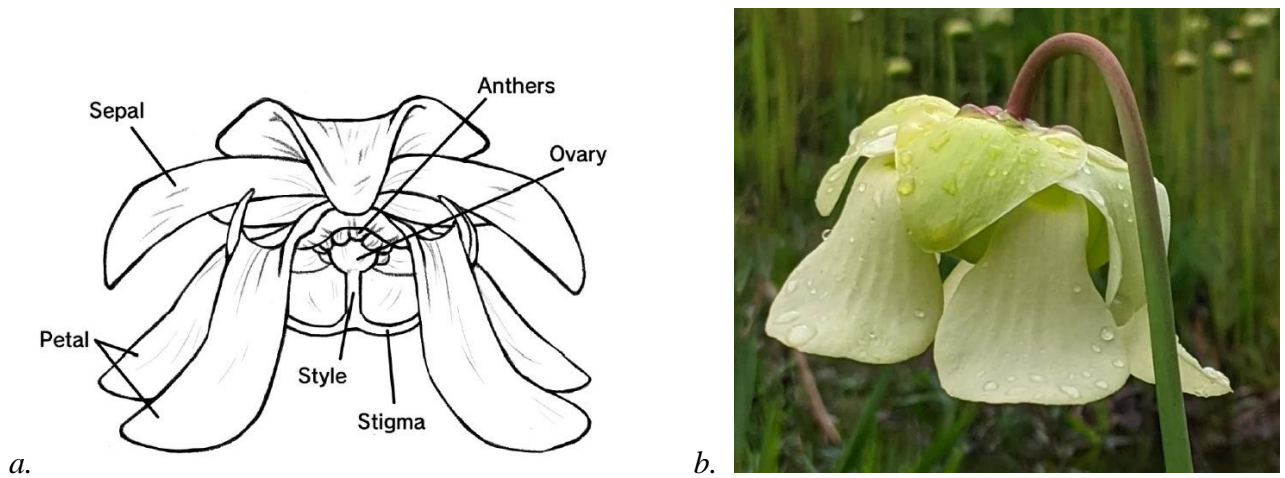
Figure 1. *Sarracenia alata* flowers a.) Cross section illustration of flower structure by K.Kang b.) Photograph

by H. Eastburn

Study Site

This study was conducted at a hillside seepage bog on private property in Leon

County, Texas (~31.54ºN – 95.91ºW). The bog is dominated by loblolly pine (*Pinus taeda*),

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post oak (*Quercus stellate*), maples (*Acer spp*.), bog laurel (*Kalmia polifolia*) and non-carnivorous herbaceous plants. The sandy saturated soils are also inhabited by a variety of carnivorous plants, including *Utricularia gibba*, *U. cornuta*, *Drosera capillaris*, and *Sarracenia alata*, which is the only species of *Sarracenia* present at this location. The landowner conducts a prescribed burn at this site every 2-3 years, the most recent burn occurred in February 2021. The bog is bisected by a tree line and dense vegetation which divides the pitcher plant population into two large fragments separated by approximately 100 m. We identified two patches of pitcher plants to receive pollen (named North and South) and four donor patches: self-fertilization (A) and increased distances from each patch (B-D).

Experimental Design

 We used a two-factor cross-classified design with distance to pollen source as one factor with four levels and resource availability as the other factor with two levels. We randomly selected plants in the North patch to receive donor pollen from self-fertilization (0 m) and donor patches B, C and D (35, 90, and 190 m, respectively). Randomly selected plants in the South patch received donor pollen from self-fertilization (0 m) and donor patches B, C, and D (60, 90, and 125 m respectively). Pollen recipients were also assigned a resource treatment: either natural prey capture (control) or all pitchers occluded with loosely packed cotton to prevent prey capture. There were 26 replicates at pollen-donor distances of 0 and 90 meters and 13 replicates at all other distances for a total of 208 plants manipulated.

 A single flower on each focal plant was covered with a pollinator exclusion bag (10 x 15 cm bags of translucent, nonwoven, polypropylene) and closed with thread approximately

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2 weeks before the onset of blooming. Bags were secured to wire survey flags with metal clips, which was effective at preventing flowers from falling over during spring storms. Hand pollination commenced as flowers began to release pollen and became receptive to pollination (approximately the first week of April). Pollen was collected from 7-10 randomly chosen donors from each donor distance, except "selfing", on the same day pollination treatments occurred. The stylar umbrella was removed from each donor, and pollen was emptied into vials, mixed, and labeled for each corresponding distance. Pollinator exclusion bags were removed and all five stigmas on a flower were pollinated using a Q-tip; for each intrapopulation distance the same Q-tip was used, while a clean Q-tip was used for each selfed flower. Focal plants were labeled with assigned pollen and pitcher treatments and bags were replaced and secured for the remainder of the growing season. Pitchers selected for occlusion treatment were loosely packed with cotton in the mouth of all pitchers of a genet. Repeat trips were made every 2-4 weeks for the entirety of the growing season to plug newly opened pitchers and to check the integrity of the pollinator exclusion bags and flag supports.

Ovaries were collected in mid-October and stored at room temperature in paper bags. Seeds and ovules were extracted, counted, and weighed. Inbreeding depression may be indicated through a reduction in seed set, total mass of seeds, average seed mass, and percentage of germination (Lande & Schemske 1985). The number of seeds, mass per seed, average seed mass, and the proportion ovules fertilized were used as an indicator of reproductive success (Wiens 1984; Larson & Barrett 2000). We excluded ovaries that were damaged through herbivory or extensive fungal growth. Major outliers calculated using the Inter-Quartile Range (IQR) were also excluded because the ovaries had fully desiccated prior to dissection.

Germination Trials

Twenty randomly selected seeds from each replicate (n=168) were soaked for 24h in distilled water, surface sterilized with a 10% bleach solution for 60 seconds, and then triple washed with distilled water. Seeds were sown onto sterile filter paper in a 9-cm petri dish and moistened with 2 mL of distilled water. Dishes were covered, the overlapping edge was wrapped with parafilm to reduce desiccation, and stratified in a dark refrigerator at 3C for 4 weeks. After cold-wet stratification, plates were placed under 80W SuncoGrow Full Spectrum LED Grow Lights at 22.8 C in a climate-controlled incubator and given a 14-hr photoperiod for 34 days. Germination plates were examined daily for radicle emergence and 1 mL of distilled water was added as needed to prevent desiccation. After 34 days, plates were removed from the incubator and ungerminated seeds in every plate were scored and soaked in 1% tetrazolium chloride for 48 hours without light exposure. Ungerminated seeds were dissected, and viability was determined by the presence of a stained embryo. We excluded plates with fungus that affected more than 60% of seeds.

Statistical Analysis

Multiple measurements can be used to quantify the same aspect of fitness. We performed a correlation analysis of measures (total seed number and mass, total ovule number and mass, mass per seed, mass per ovule, the proportion of total ovules producing seeds, and the proportion of viable seeds germinated) to identify highly correlated measurements ($r > \pm 0.700$) (Table 1). We reduced the number of dependent variables analyzed based on the correlation analysis. The effects of pollen-donor distance, prey capture, recipient patch, and the interaction

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of donor distance and prey capture on measures of fitness (total seed number, total ovule number, the proportion of total ovules producing seeds, and the proportion of viable seeds germinated) were analyzed by separate General Linear Models (GLM). The main effects were prey capture (two levels) and recipient patch (two levels), with pollen-donor distance as a covariate. There is controversy around the appropriate analysis of proportion data (Warton and Hui 2011; Lin and Xu 2020). Therefore, we performed analyses on both untransformed and arcsine-transformed proportional data. Although transformation changed the values of the GLM, it did not change the overall results on traits. Therefore, we present results with the untransformed data for ease of interpretation. All analyses performed on SPSS Software (version 27) and Microsoft Excel 365.

Results

There was a significant positive correlation between seed number and both seed mass and the proportion of total ovules producing seeds (Table 1) . Ovule number was significantly inversely correlated with the proportion of total ovules producing seeds. We excluded highly correlated variables from the GLM. Distance to pollen-donor had a significant effect on seed number (Figure 2), ovule number and the proportion of total ovules producing seeds (Table 2). There were no significant effects of prey capture or recipient patch on seed number or ovule number, total proportion of ovules producing seeds, or the proportion of viable seeds that germination. Nor was there an interaction between prey capture and pollen-donor distance on any measure of seed production or germination. The mean proportion of viable seeds that germinated was 0.92 ± 0.01 (mean $\pm$ SE) and there was no significant effect by any of the independent variables.   9

Table 1. Correlation analysis of seed production and germination data in *Sarracenia alata*. Pearson's correlation coefficient (r) shown in the white cells and p-values are in the shaded cells.

	seed number	seed mass (mg)	mass per seed (g)	ovule number	ovule mass (mg)	mass per ovule (g)	prop total ovules producing seeds	prop of viable seeds germinated
seed number	■	0.809	0.197	-0.658	-0.243	0.387	0.780	-0.221
seed mass (mg)	0.000	■	0.581	-0.524	-0.187	0.303	0.606	-0.262
mass per seed (g)	0.015	0.000	■	-0.123	-0.023	-0.043	0.110	-0.135
ovule number	0.000	0.000	0.138	■	0.631	-0.445	-0.958	0.068
ovule mass (mg)	0.003	0.021	0.780	0.000	■	0.133	-0.558	0.021
mass per ovule (g)	0.000	0.000	0.604	0.000	0.108	■	0.427	0.036
prop total ovules producing seeds	0.000	0.000	0.184	0.000	0.000	0.000	■	-0.108
prop of viable seeds germinated	0.006	0.001	0.097	0.410	0.793	0.662	0.193	■

Table 2. Summary statistics of the GLM analysis of the effects of pollen-donor distance, prey capture, recipient patch and the interaction of distance and prey capture on total seed number, total ovule number, the proportion of total ovules producing seeds and the proportion of viable seeds that germinated in *Sarracenia alata* in 2021. N = 35-40 for seed production measurements, N = 168 for germinability.

Trait	Source of Variation	df	MS	F	p
total seed number	Distance (covariate)	1	1056305	9.491	0.002
	Prey Capture	1	7237	0.065	0.799
	Patch	1	55379	0.498	0.482
	Distance*Feeding	1	3418	0.031	0.861
	Error	147	111293		
total ovule number	Distance (covariate)	1	746928	13.6	0.000
	Feeding	1	16814	0.306	0.581
	Patch	1	41200	0.765	0.383
	Distance*Feeding	1	14717	0.268	0.696

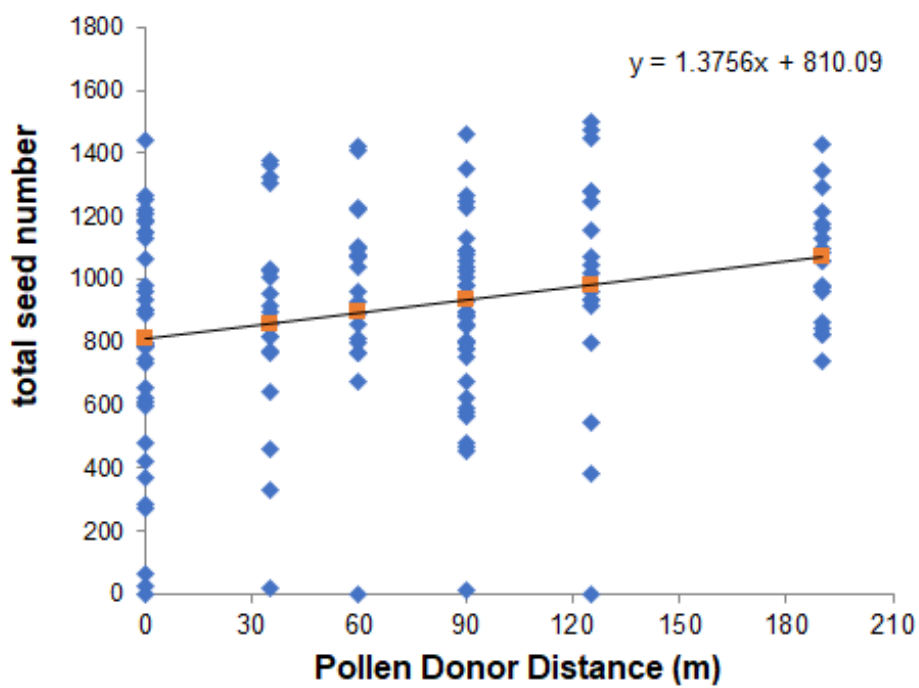|				
	Error	142	54923		
Proportion of total ovules producing seeds	Distance (covariate)	1	0.83	13	0.000
	Feeding	1	0.078	1.225	0.270
	Patch	1	0.007	0.104	0.747
	Distance*Feeding	1	0.033	0.524	0.470
	Error	141	0.039		
Proportion of viable seeds germinated	Distance (covariate)	1	6.82E-05	0.001	0.976
	Feeding	1	0.147	1.896	0.171
	Patch	1	0.193	2.492	0.116
	Distance*Feeding	1	0.219	2.835	0.094
	Error	141	0.064		

Figure 2. Seed production as a function of pollen-donor distance in *Sarracenia alata* harvested in October 2021 from Leon County, TX

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Discussion

We found that seed production increased significantly with increased distance between pollen donor and recipient. We did not observe any indication of inbreeding or outbreeding depression. However, a similar study in *Sarracenia flava* did not demonstrate outbreeding depression even with pollen donors sourced from populations several kilometers away (Sheridan & Karowe 2000). While pollen-donor distance only had marginal effects on viable seeds germinated, it is important to examine indices of offspring fitness which have indicated inbreeding depression in full grown offspring in other *Sarracenia* studies (Sheridan & Karowe 2000). The distances we tested were also not close enough to detect any possible biparental inbreeding effects. We noticed that bees would spend up to a minute in each flower and the next flower they visited would be within a couple meters. Based on these observations of bumblebee movement in the bog, we hypothesize that bumblebees transport pollen from donors within several meters more often than they do from opposite sides of the bog. Future studies should examine the effects of pollen donated from within 35 m and from more distant populations of *S. alata* to look for possible effects of biparental inbreeding or outbreeding depression, respectively. This would further refine our idea of which plants are suitable for transplant should the need arise for conservation of plant fragments or establishment of new populations.

While *Sarracenia spp.* are known to be nutrient limited, we found no significant effects of prey exclusion on seed production or germination in this population. There was no effect of either prey capture or the interaction between prey capture and pollen-donor distance on seed production or germination. A similar study in *Sarracenia purpurea* also found that restricting prey capture alone had no effect on seed production (Ne'eman et al. 2006). We originally

hypothesized there would be an effect of current season prey capture because seed filling continues throughout the growing season and late season pitchers are known to contribute to current season growth of pitchers (Butler and Ellison 2007). However, nutrient allocation and storage strategies might be dependent on the number of pitchers or a predisposition to store nutrients before aiding growth. During 2021 we did not observe any of our study plants with more than three pitchers per genet, but genets have been recorded with as many as twenty pitchers in previous years. It is possible that the small number of pitchers did not allow for current season nutrient transfer to filling seeds, so that plants had to rely only on stored resources.

The proportion of seed production at our study site was 0.74 in 2015 and 0.69 in 2016 (Brilleslyper 2019) and 0.79 in 2021. However, in 2019 and 2020 the average proportion of seeds produced was significantly lower (0.11 and 0.07 respectively) (Kang 2020, unpublished data), which might be an effect of decreased pollinator availability. While we did not see an effect of prey capture in 2021, our understanding of nutrient storage and transport in *Sarracenia spp.* leads us to hypothesize that this decrease in seed production could also be an effect of decreases in prey capture over multiple years. Application of chemical pesticides in the surrounding agricultural areas would likely affect both pollinating and prey insects. This has made us curious about quantifying the natural variation of prey capture in this population. Our prey exclusion experiment was conducted only in a single season and the substantial translocation of stored nutrients likely overcame deficits from one season of prey reduction. Understanding the source-sink relationships between prey capture, stored nutrients, and the production of leaves, flowers, and seeds would be an interesting avenue to explore. Tracking the

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growth and allocation of nutrients in individual plants over multiple seasons is extremely difficult *in situ* because pitchers do not always arise from the same position on the rhizome each season. These studies might be best conducted in a greenhouse environment where genets can be monitored with greater confidence and control.

References

Aguilar, R., Quesada, M., Ashworth, L., Herrerias-Diego, Y. And Lobo, J. (2008), Genetic
consequences of habitat fragmentation in plant populations: Susceptible signals in plant
traits and methodological approaches. *Molecular Ecology, 17*: 5177-
5188. doi.org/10.1111/j.1365-294x.2008.03971.x

Aizen, M. A. and Harder, L. D. (2007). Expanding the Limits of the Pollen-Limitation Concept:
Effects of Pollen Quantity and Quality. *Ecology*, *88*(2), 271–281. Retrieved March 21, 2022
from http://www.jstor.org/stable/27651100

Armbruster, P., Reed, D. (2005). Inbreeding depression in benign and stressful
environments. *Heredity, 95*: 235–242. doi: 10.1038/sj.hdy.6800721

Bhattarai G.P. and Horner J.D. (2009). The importance of pitcher size in prey capture in the
carnivorous plant, *Sarracenia alata* Wood (Sarraceniaceae). *The American Midland
Naturalist, 161*:264–272

Bodri, M., & Gaspard, A. (2006). The Pollination Biology of *Sarracenia alata* Wood (Sarraceniaceae)
in Louisiana. *Bartonia,* (63), 1-9. Retrieved June 17, 2021, from
www.jstor.org/stable/41610117

15

Brilleslyper, E. (2019). Where did all the offspring go? Pollination and pre-dispersal seed predation in a carnivorous plant. Master's Thesis, Texas Christian University, Fort Worth, TX.

Butler, J. L., & A. M. Ellison. (2007). Nitrogen Cycling Dynamics in the Carnivorous Northern Pitcher Plant, Sarracenia Purpurea. *Functional Ecology*, *21*(5), 835–843. Retrieved on March 22, 2022 from http://www.jstor.org/stable/4540091

Campbell, D., & Halama, K. (1993). Resource and Pollen Limitations to Lifetime Seed Production in a Natural Plant Population. *Ecology, 74*(4), 1043-1051. doi:10.2307/1940474

Carmickle, R. N. and J. D. Horner. 2019. Impact of the specialist herbivore Exyra semicrocea on the carnivorous plant Sarracenia alata: a field experiment testing the effects of tissue loss and diminished prey capture on plant growth. *Plant Ecology 220*(6): 553-561. doi: 10.1007/s11258-019-00935-y

Casper, B.B., Niesenbaum, R.A. (1993). Pollen versus resource limitation of seed production: A reconsideration. *Current Science, 65*(3), 210-214. Retrieved November 1, 2020, from http://www.jstor.org/stable/24095117

Cunningham, S.A. (2000), effects of habitat fragmentation on the reproductive ecology of four

    plant species in mallee woodland. *Conservation Biology, 14*:758-768. doi:

    10.1046/j.1523-1739.2000.98609.x

Deppe, J. L., Dress, W. J., Nastase, A. J., Newell, S. J., & Luciano, C. S. (2000). Diel Variation of

    Sugar Amount in Nectar from Pitchers of Sarracenia Purpurea L. with and without Insect

    Visitors. *The American Midland Naturalist*, *144*(1), 123–132.

Doust, J. (1989). Plant reproductive strategies and resource allocation. *Trends in Ecology &*

    Evolution, 4(8), 230-234. doi:10.1016/0169-5347(89)90166-3

Ellison, A.M. (2001). Interspecific and intraspecific variation in seed size and germination

    requirements of *Sarracenia* (Sarraceniaceae). *American Journal of Botany*, *88*(3), 429-

    437. http://www.jstor.org/stable/2657107

Ellison, A. M., Parker, J. N. (2002). Seed dispersal and seedling establishment of *Sarracenia*

    purpurea (Sarraceniaceae). *American Journal of Botany, 89*(6), 1024-1026.

    doi:10.3732/ajb.89.6.1024

González, A., Gómez-Silva, V., Ramírez, M., Fontúrbel, F. (2019), Meta-analysis of the

    differential effects of habitat fragmentation and degradation on plant genetic diversity.

    Conservation Biology, 34:711-720. doi: 10.1111/cobi.13422

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Green M, Horner J.D. (2007). The relationship between prey capture and characteristics of the carnivorous pitcher plant, *Sarracenia alata* Wood. *The American Midland Naturalist, 158*:424–431. Retrieved on March 22, 2022 from http://www.jstor.org/stable/4500672.

Helenurm, K. and Schaal, B.A. (1996). Genetic load, nutrient limitation and seed production in Lupinus texensis (Fabaceae). *American Journal of Botany. 83(12)*:1585-1595.

Hereford, J. (2010). Does selfing or outcrossing promote local adaptation?. *American Journal of Botany. 97*(2): 298-302. doi:10.3732/ajb.0900224

Honnay, O. and Jacquemyn, H. (2007), Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conservation Biology, 21*: 823-831. doi.org/10.1111/j.1523-1739.2006.00646.x

Horner, J. D., J. Cross Steele, C. Underwood, and D. Lingamfelter. (2012). Age-related changes in characteristics and prey capture of seasonal cohorts of Sarracenia alata pitchers. *American Midland Naturalist 167*: 13-27. Retrieved on March 22, 2022 from http://www.jstor.org/stable/41412517.

Horner, J.D. (2014). Phenology and pollinator-prey conflict in the carnivorous plant, *Sarracenica alata*. *The American Midland Naturalist, 171*(1), 153-156. doi: 10.1674/0003-0031-171.1.153

Horner J.D., Hodcroft E.B., Hale A.M., Williams D.A. (2014). Clonality, genetic variation, and

    the origin of isolated western populations of the carnivorous plant, *Sarracenia alata*.

    Journal of the Torrey Botanical Society 141(4), 326–337. doi: 10.3159/TORREY-D-13-

    00080.1

Horner J.D., Płachno B.J., Bauer U., Di Giusto B. (2018). Attraction of prey. In: Ellison AM,

    Adamec L, editors. *Carnivorous plants: physiology, ecology, and*

    evolution. Oxford: Oxford University Press. p. 157–66.

Juniper, B. E., R. J. Robins and D. M. Joel. 1989. The Carnivorous Plants. Academic Press, Inc.,

    San Diego. p. 353

Kang, K. (2020). Effects of pollen limitation on seed production in the pale pitcher plant

    (Sarracenia alata). Master's thesis, Texas Christian University, Fort Worth, TX

Keller, L.F. and Waller, D.M. (2002). Inbreeding effects in wild populations. *Trends in Ecology*

    & Evolution, 17(5): 230-241. doi:10.1016/S0169-5347(2)02489-8

Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, R.A., and Goulson,

    D. (2005). An interspecific comparison of foraging range and nest density of four

    bumblebee (Bombus) species. *Molecular Ecology, 14*: 1811-1820. doi: 10.1111/j.1365-

    294X.2005.02540.x

Koopman, M.M. and Carstens, B.C. (2010). Conservation genetic inferences in the carnivorous

    pitcher plant Sarracenia alata (Sarraceniaceae). *Conservation Genetics, 11*:2027-2038.

    doi:10.1007/s10592-010-0095-7

Kreyer, D., Oed, A., Walther-Hellwig, K., and Frankl R. (2004). Are forests potential landscape

    barriers for foraging bumblebees? Landscape scale experiments with Bombus terrestris

    agg. And Bombus pascuorum (Hymenoptera, Apidae). *Biological Conservation,*

    116(1):111-118. doi:10.1016/S0006-3207(03)00182-4

Lande, R. and Schemske, D.W. (1985). The evolution of self-fertilization and inbreeding

    depression in plants. I. Genetic models. *Evolution*, 39: 24-40.

Larson, B.M.H. and Barrett, S.C.H. (2000). A comparative analysis of pollen limitation in

    flowering plants. *Biological Journal of the Linnean Society*, *69*(4), 503-520.

    doi:10.1006/bijl.1999.0372

Leimu, R., Kloss, L., and Fischer M. (2008). Effects of experimental inbreeding on herbivore

    resistance and plant fitness: the role of history of inbreeding, herbivory and abiotic

    factors. *Ecology Letter*, *11*(10):1101-10. doi:10.1111/j.1461-0248.2008.01222.x.

Lin, L. and Xu, C. (2020). Arcsine-based transformations for meta-analysis of proportions: pros,

    cons, and alternatives. *Health Science Reports*, *3*(3), e178. doi:10.1002/hsr2.178

Madsen, J.D. (1991). Resource allocation at the individual plant level. *Aquatic botany, 41*(1-3), 67-86. doi:10.1016/0304-3770(91)90039-8

Ne'eman, G., Ne'eman, R. and Ellison, A. M. (2006). Limits to Reproductive Success of Sarracenia purpurea (Sarraceniaceae). *American Journal of Botany*, *93*(11), 1660–1666. Retrieved on March 21, 2022 from http://www.jstor.org/stable/4123182

Ouborg, N., and Van Treuren, R. (1995). Variation in fitness-related characters among small and large populations of salvia pratensis. *Journal of Ecology, 83*(3), 369-380. doi:10.2307/2261591

Sandner, T.M., Matthies, D., and Waller, D.M. (2021). Stresses affect inbreeding depression in complex ways: disentangling stress-specific genetic effects from effects of initial size in plants. *Heredity, 127*: 347-356.

Schnell, D. E. (1983). Notes on the pollination of Sarracenia flava l. (Sarraceniaceae) in the Piedmont Province of North Carolina. *Rhodora*, *85*(844), 405–420.

Sheridan, P. M., & Karowe, D. N. (2000). Inbreeding, Outbreeding, and Heterosis in the Yellow Pitcher Plant, Sarracenia flava (Sarraceniaceae), in Virginia. *American Journal of Botany*, *87*(11), 1628–1633. doi.org/10.2307/2656739

Souto, C.P., Aizen, M.A., Premoli, A.C. (2002). Effects of crossing distance and genetic
relatedness on pollen performance in *Alstroemeria aurea* (Alstroemeriaceae). *American Journal of Botany, 89*(3), 427-32. doi: 10.3732/ajb.89.3.427

Stephens, J. D., & Folkerts, D. R. (2012). Life History Aspects of Exyra semicrocea (Pitcher Plant
Moth) (Lepidoptera: Noctuidae). *Southeastern Naturalist*, *11*(1), 111–126. Retrieved on
March 21, 2022 from http://www.jstor.org/stable/41475434.

Vranckx, G., Jacquemyn, H., Muys, B. and Honnay, O. (2012), Meta-analysis of susceptibility of
woody plants to loss of genetic diversity through habitat fragmentation. *Conservation Biology, 26*: 228-237. doi: 10.1111/j.1523-1739.2011.01778.x

Warton, D.I. and Hui, F.K.C. (2011). The arcsine is asinine: the analysis of proportions in
ecology. *Ecology, 8*:2993-3001.

Waser, N. M., & Price, M. V. (1991). Outcrossing Distance Effects in Delphinium Nelsonii: Pollen
Loads, Pollen Tubes, and Seed Set. *Ecology*, *72*(1), 171–179. https://doi.org/10.2307/1938912

Wiens, D. (1984). Ovule survivorship, brood size, life history, breeding systems, and
reproductive success in plants. *Oecologia, 64*(1), 47-53. doi:10.1007/bf00377542

Wilson, P. and Provan J. (2003), Effect of habitat fragmentation on levels and patterns of genetic

    diversity in natural populations of the peat moss *Polytrichum commune*. *Proceedings of*

    the Royal Society London B. *270*:881-886. doi: 10.1098/rspb.2002.2324

Young, A., Boyle, T., Brown, T. (1996). The population genetic consequences of habitat

    fragmentation for plants, *Trends in Ecology & Evolution. 11*(10):413-418.

    doi:10.1016/0169-5347(96)10045-8

Zhang, W.H, Zhou, Y., Dibley, K., Tyerman, S.D., Furbank R.T., Patrick, J.W. (2007). Review:

    Nutrient loading of developing seeds. *Functional Plant Biology, 34*:312-331.

    doi:10.1071/FP06271

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Abstract

IMPACTS OF POLLEN-DONOR DISTANCE AND NUTRIENT AVAILABILITY ON

REPRODUCTIVE SUCCESS IN A CARNIVOROUS PLANT

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The maintenance of genetic diversity has important consequences for the survival of plant populations. Because plants are sessile, the distance between plants is often inversely correlated with relatedness. Therefore, the distance between pollen-donor and recipient can determine the level of inbreeding or outbreeding. Both pollen-donor distance and nutrient availability can affect reproductive success in populations of flowering plants. Populations of the carnivorous plant *Sarracenia alata* have dwindled and become extremely fragmented due to human development and agriculture. The purpose of this study was to examine the effects of pollen-donor distance and prey capture on reproductive success in *S. alata*. We hand-pollinated flowers with pollen from varying distances [0 m (self-pollinated) and 35, 60, 90, 125, and 190 m], and we prevented prey capture in half of our study plants. We measured seed production and germination to estimate reproductive success. Pollen-donors from greater distances sired a greater number of seeds but pollen-donor distance did not affect germinability. There was no effect of prey capture alone nor an interaction of pollen-donor and prey capture on seed production or germination. More research is needed to understand nutrient allocation for reproduction over multiple years and natural variance in prey capture which might affect reproductive output in subsequent seasons.