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## **Lepidopteran Granivory Reduces Seed Counts in a Rare Species of Riparian Scour Prairies**

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# Lepidopteran Granivory Reduces Seed Counts in a Rare Species of Riparian Scour Prairies

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## ABSTRACT

In Pennsylvania *Baptisia australis* var. *australis* is found along only four waterways: the Allegheny River, Youghiogheny River, Clarion River, and Red Bank Creek. Because of its limited distribution and small number of extant populations, the species is considered state-threatened in Pennsylvania. In addition, the riparian prairie habitat that Pennsylvania *Baptisia australis* var. *australis* is restricted to is also in decline and considered vulnerable. Because of these conservation concerns, insights into the natural history of the taxon in the state is valuable and will inform conservation efforts. Field surveys and fruit collections along the Allegheny River and herbarium collections were used to investigate and document granivory in Pennsylvania *Baptisia australis* var. *australis*, a phenomenon recorded in other parts of the species' range, but not previously reported on in Pennsylvania. Using a model of best fit, the number of seeds found in fruit was found to be significantly impacted by the presence of granivores. We also report that visual surveys of fruits in the field are found to be accurate assessments of the presence and potential impact of granivores. In turn, our results will inform the conservation and management of *Baptisia australis* var. *australis* populations in Pennsylvania and highlight the importance of field surveys in protecting threatened taxa.

*Index terms:* *Baptisia*; *Grapholita*; natural history; prairie; seed bank

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## INTRODUCTION

While plant–herbivore interactions are a critical component of many ecosystems, these relationships rarely influence conservation decisions unless the interactions result in significant loss of adult individuals (PA DCNR 2017) or population size has already decreased (Bevill et al. 1999). Likewise, insect impacts on seed production are also well studied, but are not often a factor in assessments of conservation risk and population management because only current population size is considered (e.g., NatureServe Conservation Rank Calculator). Evidence varies regarding whether herbivory and granivory impact plant growth, abundance, and distribution and may be system specific (Andersen 1989; Crawley 1992; Maron and Gardner 2000). Ultimately, impacts of granivory on plant populations appear to depend upon habitat and life history strategies of the species in question. In particular, plants with seed banks, those that are disturbance dependent, and those with the ability to reproduce via both seeds and clonally (e.g., via rhizomes) present additional challenges to deciphering the true impacts of granivores. While some studies propose that the number of sites appropriate for colonization (i.e., “safe sites”) is the primary factor in limiting plant numbers, and not herbivory (Andersen 1989; Maron and Simms 1997), others seem to indicate that the notion of “safe site” limited plant dispersal should not be ubiquitously applied. Application of the concept may be appropriate for taxa with healthy, stable populations, but in species or populations of concern it may be appropriate to place

greater weight on the impacts of granivory. Small and/or fragmented populations are often already susceptible to genetic drift (Frankham 2010) and thus loss of seed further endangers genetic diversity within these populations.

The perennial wildflower *Baptisia australis* (L.) R. Br. (Fabaceae) meets many of the aforementioned criteria related to potential granivory-dependent limitation. The species occurs almost exclusively in grasslands, its populations are often fragmented, and reproduction occurs via both seed and rhizome (Broyles 2006). The genus is known to maintain a seed bank by which new individuals are recruited (Young et al. 2007). Like many legumes, *Baptisia* is generally well protected from most insect herbivory by means of chemical defenses including glycosides, alkaloids, and saponins (Frost 1945; Cranmer and Mabry 1966; Cranmer and Turner 1967; Markham et al. 1968; Udayama et al. 1998). Multiple studies have focused on the impacts of insect herbivory on midwestern *Baptisia* populations (Petersen and Sleboda 1994; Petersen et al. 1998; Petersen and Wang 2006), as well as the secondary defense compounds present in the genus (Frost 1945; Cranmer and Mabry 1966; Cranmer and Turner 1967; Markham et al. 1968; Udayama et al. 1998). Although *Baptisia* species are well defended via secondary defense compounds, a suite of specialist insects including weevils, blister beetles, and lepidopterans still impact members of the genus (Frost 1945; Cranmer and Mabry 1966; Cranmer and Turner 1967; Markham et al. 1968; Udayama et al. 1998).

The genus *Baptisia* is composed of roughly 50 species with numerous papers published on widespread taxa such as *B.*

*australis* and *B. alba* (L.) Vent. Whereas the bulk of this research has been done in the Konza Prairie Biological Station (Kansas, USA; e.g., Evans et al. 1989; Evans 1990) and the College of DuPage reconstructed prairie (Illinois, USA; e.g., Petersen and Sleboda 1994; Petersen et al. 1998; Petersen and Wang 2006) where species are largely secure, studies on populations at the edges-of-range for those species, where populations are often smaller and fragmented, have not been conducted. *Baptisia australis*, in particular *B. australis* var. *australis*, reaches the northeastern extent of its range in Pennsylvania, USA, where it is presently known to occur along only four waterways (Broyles 2006; NatureServe 2018). This variety of the species has the most northeastern distribution of the currently recognized varieties and primarily inhabits riparian prairie systems (or “scour prairies”) of the Ohio and Potomac River Basins, which are created and maintained by annual scouring by river ice. The riparian scours where *Baptisia australis* var. *australis* occurs are increasingly threatened by invasive species encroachment and loss of habitat due to human-mediated impacts such as damming (NatureServe 2018; Perles 2019). Climate change has also altered the dynamics of these systems, with reduced ice scour in the winter and increased rainfall and flooding during the spring and summer seasons (Arnell and Gosling 2016; Perles 2019). In Pennsylvania, the edge of range status and notable habitat risk factors give *B. australis* var. *australis* a state conservation status of threatened (PA DCNR 2017) and a NatureServe conservation status rank of G5T3/S2-imperiled (NatureServe 2018). As part of recent fieldwork aimed at reassessing the conservation status of *Baptisia australis* var. *australis* in Pennsylvania, significant insect damage on some plants and fruit was observed, suggesting potential declines in seed production.

In many other parts of its range *B. australis* sensu lato maintains what appears to be healthy population sizes. These populations, largely found in prairies and savannas, have been studied to better understand the reproductive biology of *Baptisia* species as well as to assess seed predation. Work in Kansas and elsewhere indicates that several insect species impact *B. australis* populations, with common pest insects including the ash-gray blister beetle *Epicauta fabricci* LeConte (Meloidae) (Evans 1990), the lepidopteran *Grapholita tristegana* Clemens (Olethreutidae), the legume specialist weevil *Tychius sordidus* LeConte (Curculionidae) (Evans et al. 1989), and the specialist weevil *Apion rostrum* Say (Apionidae) (Frost 1945). Evans et al. (1989) found that *Grapholita tristegana* and *Tychius sordidus* can infest up to 80–100% of fruits in a population. If insects are not present the yield of seed production can increase 50-fold (Evans et al. 1989). Unaffected *Baptisia australis* fruits yield around 25 seeds but only 3 or 4 seeds often survive in fruits that have experienced granivory (Evans et al. 1989). Among insect seed predators, *Apion rostrum* is particularly well studied, showing significant impacts on seed survival through both direct consumption and whole-fruit abortion (Petersen and Sleboda 1994; Petersen et al. 1998; Petersen and Wang 2006; Petersen et al. 2010).

Despite thorough research of the pests in the main distribution of the species, there has been no research on the presence of insect pests impacting *B. australis* var. *australis* in

**Table 1.**—Sites along the Allegheny River where *Baptisia australis* var. *australis* fruits were collected. Site numbers correspond to CLM’s collection numbers.

Site	Site name	County	Estimated population size (number of individuals)
1	Wood Hill	Venango Co.	50
9	Mill Creek	Venango Co.	1500+
14	Meadowsweet Run	Venango Co.	150
21	Butler County	Butler Co.	1000+
26	Clarion Island	Clarion Co.	60

Pennsylvania. While Frost (1945) did not study *Baptisia australis*, he did find that insect herbivores negatively impacted one of its congeners in Pennsylvania, *Baptisia tinctoria* (L.) R. Br.

Our primary aim was to assess whether granivores are present in Pennsylvania populations of *Baptisia australis* var. *australis* and if there is past evidence of granivory. Historical specimens from the region were examined to determine the historical context of granivore presence. In addition, analyses were conducted using field-collected data to examine if insect damage is correlated with seed loss or other factors that may help in predicting insect herbivory. A generalized linear mixed model was used to determine if the number of seeds was correlated with the presence of insects or factors other than insects such as sampling site. The following hypotheses were tested: (1) the number of seeds generated in a population that might contribute to future generations is impacted by herbivore/granivore presence, and (2) the damage, such as seed loss, is correlated with factors that help predict what plants may be susceptible to granivores such as particular sites or visual cues noticeable in the field.

## MATERIALS AND METHODS

### Sampling

Five sites or subpopulations along the Allegheny River (Table 1, Figure 1) were surveyed in mid-July 2018. These sites vary in size, species composition, and other factors. For the purposes of this study, “site” refers to geographically distinct subpopulations. In Pennsylvania, peak bloom for *B. australis* var. *australis* occurs from late May to late June (Rhoads and Block 2007), thus surveys occurred after seeds were set and before fruits dehisced. At each site fruits were collected from 15 plants. The third fruit from the top of the tallest raceme was collected in a 50 mL conical centrifuge tube of 70% ethanol. Plants from which fruits were removed were also sampled for leaf tissue for use in a population genomics project (Moore et al. in prep.). Sampled plants were phenotypically representative of populations and were greater than 1 m apart in an effort to reduce sampling within a genet. If a plant sampled for tissue did not have fruit, a fruit from the nearest fruiting plant not already sampled was collected. At the time of collection height of plant, number of racemes, number of fruits, and approximate distance to the Allegheny River were recorded. Any evidence of insect presence was also noted (e.g., holes in fruits, leaf or flower herbivory; Figure 2). Fruits were preserved in 70% ethanol until the time of dissection.



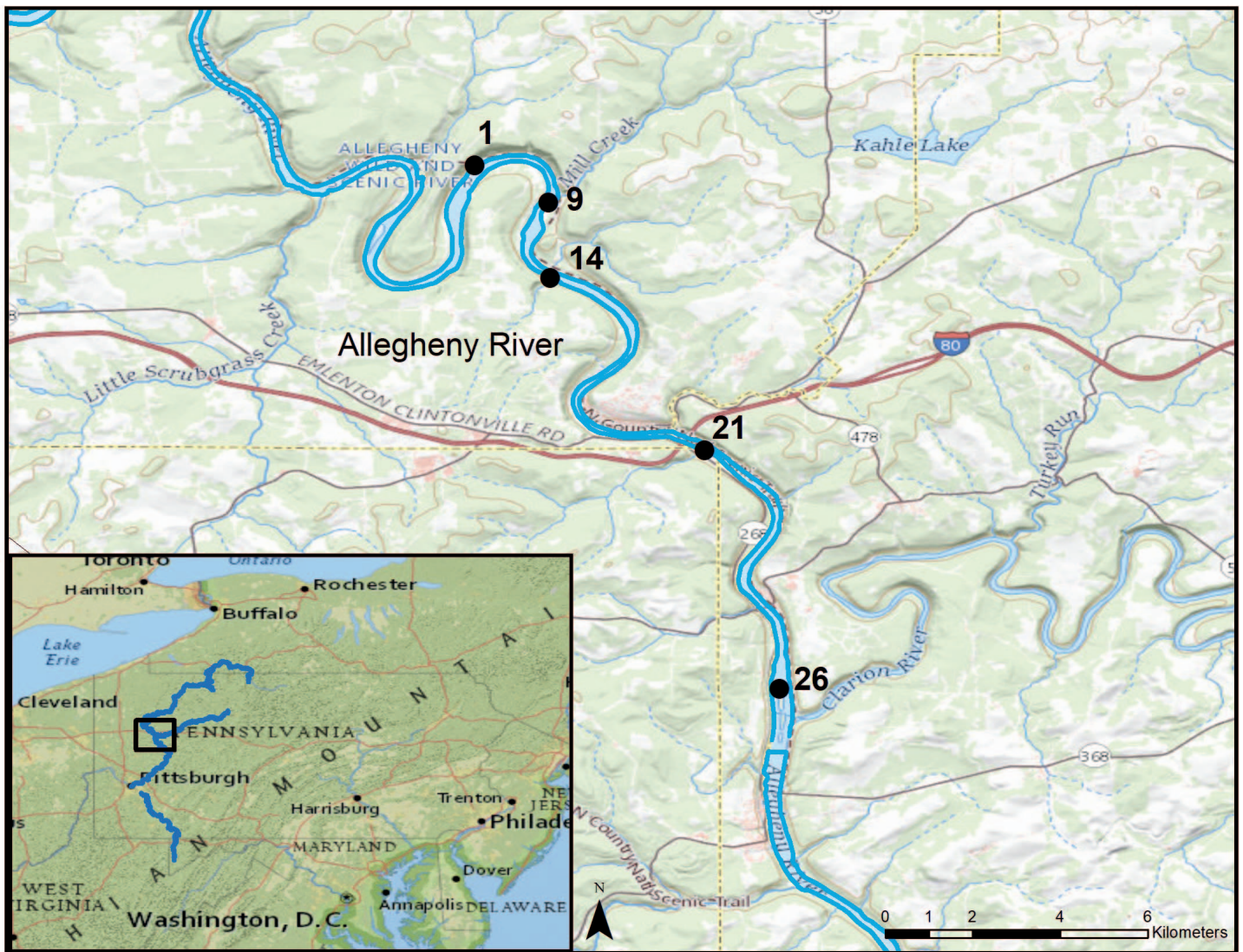


Figure 1.—Map of sampling sites along the Allegheny River in northwestern Pennsylvania. Site labels correspond with Table 1. Map created with ArcGIS (ESRI 2011).

### Sample Processing

In the lab, fruits were examined under a dissecting scope and the number of fully developed and aborted seeds counted. When mature seeds were present, the length of five randomly selected seeds was measured to the nearest 0.1 mm. All evidence of insect presence was recorded, including exoskeleton or frass within fruit (Figure 3). If an entire insect was found it was recorded, measured, and identified to family. For analyses, evidence of insect herbivory was considered to be frass, insect parts, entire insects, or visible fruit damage. These were aggregated into the category of insect presence for a subset of analyses.

### Analyses

All analyses were conducted in R 3.6.2 (R Core Team 2018). The package lme4 (Bates et al. 2015) was used to perform a generalized linear mixed model (GLMM) to assess support for the two main hypotheses (Table 2). Number of mature seeds was selected as the response variable with field and lab measures as

explanatory variables. A Poisson distribution was used, as the response variable is count data. The second model used insect damage as the response variable, again with other field- and lab-collected data as explanatory variables. A full list of explanatory variables used for the full starting models and their correlation coefficients can be found in Supplemental Table 1. The variable of damage was denoted as presence or absence and was determined by considering the presence or absence of frass, insect or insect part, or other evidence of insect granivory found during dissection of fruit. For both models, site of sampling was treated as a random effect. Both models also employed a binomial distribution. Model selection was done based on AIC and BIC scores. This was checked with a stepwise GLMM selection function stepAIC in the package cAIC4 (Saeften et al. 2018). We also ran a one-way analysis of variance (ANOVA) for number of seeds and site as well as damage and site, since site is treated as a random effect in the models. Finally, we used a Student's *t*-test conducted in base R to compare seed counts of





**Figure 2.**—Photos from Allegheny River field work in July 2019 showing insect damage to *Baptisia australis* var. *australis* fruits.

Pennsylvania populations versus average per fruit seed count reported in the literature (Isely 1990, 1998). For all statistical tests an alpha value of 0.05 was used.

### Historical Data

To investigate the historical presence of frugivores in Pennsylvania, we examined specimens at the Steere Herbarium at the New York Botanical Gardens (NY) and Carnegie Museum of Natural History (CM) and incorporated evidence from herbarium specimens into our dataset. CM hosts the largest and most comprehensive collection of *Baptisia australis* var. *australis* collected in Pennsylvania and includes 60 specimens from Pennsylvania, all of which were visually inspected. Specimens showing evidence of granivory (e.g., holes in fruits) were photographed and recorded. We did not find any evidence of in situ insect damage. No plant material was taken from specimens for this (e.g., destructive sampling or packet material).

### RESULTS

Overall, the amount of damage present in sites varied. GLMM that best explain fruit damage and number of mature seeds can be seen in Tables 3 and 4. Plant damage noted in the field, length of fruit, and number of racemes were positively correlated with fruit damage. Number of fruits on plants, approximate distance to the Allegheny River, and average seed length were negatively correlated with fruit damage. Correlations among the explana-

tory variables in the final model ranged from  $-0.601$  to  $0.514$  (Supplemental Table 2). The ANOVA results showed no significant effect of site on damage ( $P = 0.0819$ ). The model for number of mature seeds showed that fruit length and number of fruits on plants were positively correlated with number of seeds, indicating that the number of seeds increases with more robust plants. Presence of frass and number of immature seeds were negatively correlated with number of seeds. Correlation values among the explanatory variables in the final model ranged from  $-0.181$  to  $0.187$  (Supplemental Table 3). The ANOVA indicated that there was a significant effect of site on number of seeds ( $P = 0.0192$ ), however a post hoc Tukey test reported no significant relationships.

Significantly fewer seeds were observed in fruits sampled in Pennsylvania populations (overall as well as within each population) than described for typical *Baptisia australis* sensu lato fruits in published keys to the genus (Isely 1990, 1998;  $P < 0.0001$ ). Isely reported 25 or more seeds per fruit while the average number of seeds noted across the five Allegheny River populations was 13.5 seeds. This difference is significant even when only fruits without damage were considered ( $P < 0.0001$ ).

When preserved fruits were opened and insects were found, they were all ( $n = 8$ ) identified as lepidopteran larvae, fitting the description of the genus *Grapholita* (Gilligan and Passoa 2014). In addition, all insect parts found appeared to be from the same genus.

Herbarium specimens examined from CM and NY and were found to have holes in fruits similar to those observed during field work along the Allegheny River. These specimens showed evidence of granivory in Pennsylvania as early as 1868, with continued evidence noted in more recently collected specimens. Of the 39 specimens at CM with fruits, seven had evidence of granivory.

### DISCUSSION

The presence of granivores in Pennsylvania populations of *Baptisia australis* var. *australis* appears to reduce seed count in the populations studied. The generalized linear mixed model of all sites infers that evidence of insect presence significantly correlates with presence of fewer seeds. Other factors that significantly correlate with the number of mature seeds include indicators of plant health such as number of racemes, number of fruits, and size of seeds. Overall, this suggests that larger, healthier plants generally produce more seeds when not impacted by granivores. GLMM results overall indicate that visual assessment could help determine extent of granivore presence; healthy plants that did not have damage indeed had more seeds, and larger plant and fruit size were each positively correlated with damage, perhaps indicating they are preferred by granivores. Number of seeds was found to be significantly negatively correlated with the presence of frass and the number of immature seeds counted in fruits, a relationship supported by previous inference showing that plants often abort developing seeds within *Baptisia* fruits experiencing granivory (Petersen and Sleboda 1994; Petersen et al. 1998).

Several insect taxa have been documented as granivores in *Baptisia*, with common pest insects for this genus including



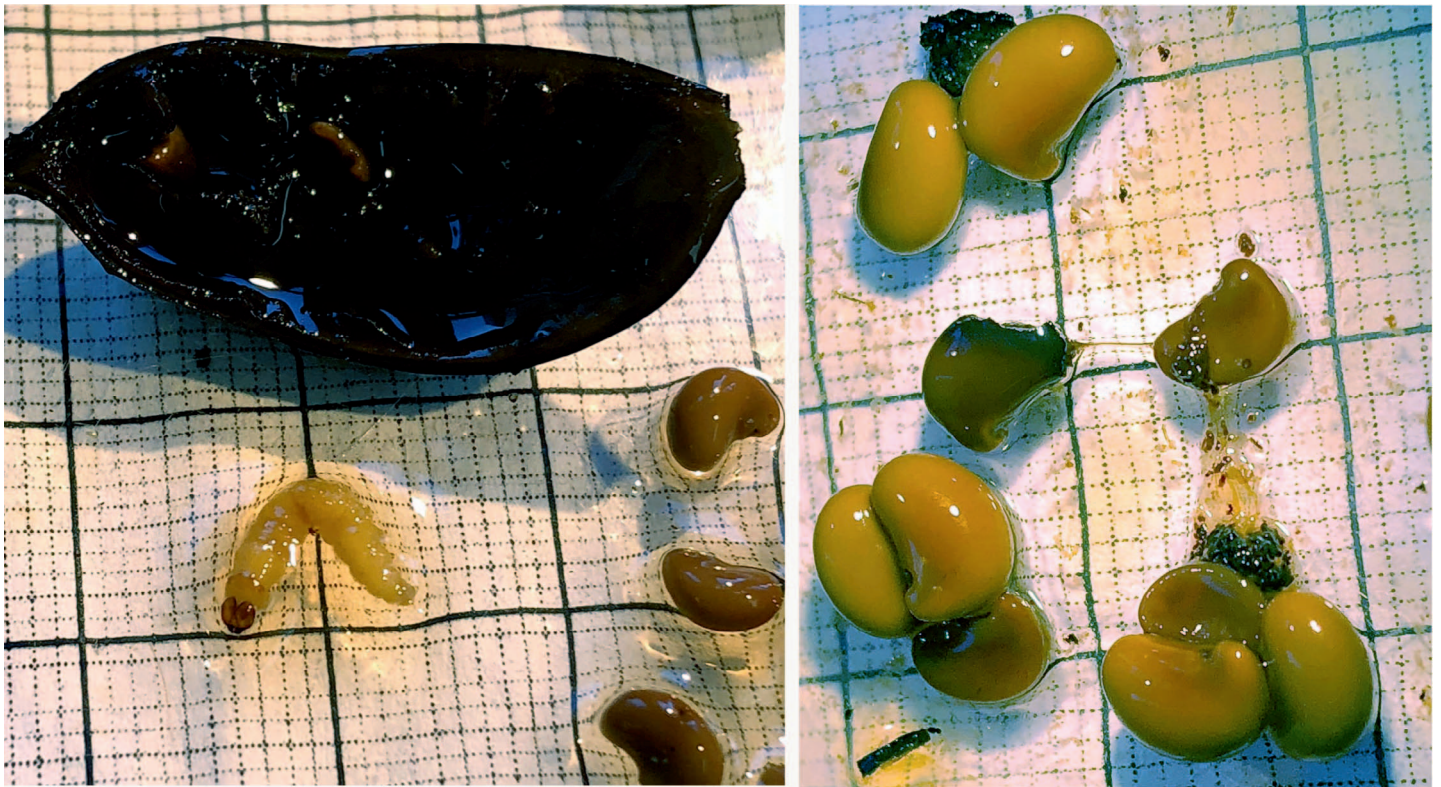


Figure 3.—(Left) *Grapholita* larva found in *Baptisia australis* var. *australis* fruit collected along the Allegheny River. (Right) Partially consumed seed found in *Baptisia australis* var. *australis* fruit and frass. Background for both images is 1 mm grid paper. Photos by Jennifer Davis.

*Epicauta fabricci* (Evans 1990), *Grapholita tristegana*, *Tychius sordidus* (Evans et al. 1989), and *Apion rostrum* (Frost 1945). The only genus we found in our Pennsylvania study populations was *Grapholita*, a lepidopteran larva known to impact *Baptisia australis* sensu lato seed production in the Konza Prairie (Evans et al. 1989). *Grapholita* adults deposit eggs in newly formed fruits, these eggs then hatch, and larvae consume seeds until they mature and emerge from fruits as new adults. This is consistent with what was found in our Pennsylvania study populations (and specimens), as larvae (or exit holes) were often observed within collected fruits accompanied by partially consumed seeds or no seeds at all (Figure 2).

*Baptisia australis* var. *australis* flowers from late May through mid-June and fruits develop from mid- to late June through August, when the legumes begin to dehisce (Broyles 2006; Rhoads and Block 2007; C.L. Moore pers. obs.). Although only one insect taxon was found in our study fruits, it should be noted that fruits were collected in July, early in the fruiting

season. Phenology of *Baptisia* should be considered, such that later in the season, fruits and seeds may be impacted by other pests. Anecdotally, Ernst Seeds in Meadville, Pennsylvania, which grows *Baptisia australis* var. *australis* for seed production, has reported weevil infestations in fruits during August and September, which likely reduces seed set and may also occur in wild Pennsylvania populations. Such weevil presence and impacts could be an avenue for further study in Pennsylvania populations of *B. australis* var. *australis*. In addition, a recent study of various endemic prairie plants used in prairie restorations in Michigan found that insects remove 54% of total seeds in the fall, while only removing 28% of total seeds in the spring in prairie restorations (Linabury et al. 2019).

*Baptisia australis* sensu lato, in its widespread range as a species, is particularly at risk of negative impacts from insect herbivores due to their commonality in grassland habitat types (including riparian scour prairies) where it is typically found. Maron and Crone (2006) documented that grasslands experi-

Table 2.—Variables included in the generalized linear mixed model and hypothesized relationship of dependent variables to the response variable of number of mature seeds.

Response variable	Dependent variables	Expected change in response variable	Explanation
Seed count	Length (mm)	+	Longer fruits will contain more seeds
	Frass present	–	Frass presence indicates granivory, which leads to seed decline
	Number of fruits on plant	+	More fruits indicates a more robust plant, which might have more seeds
	Number of immature seeds	–	Immature seeds indicate herbivory and seed abortion, which would reduce mature seeds
	Number of immature seeds	–	Immature seeds indicate herbivory and seed abortion, which would reduce mature seeds

**Table 3.**—Summary of the effect of independent variables on damage status of fruits based on GLMM of best fit. Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05

	Estimate	Std. error	z value	Pr(> z )
(Intercept)	−4.82612	3.20312	−1.507	0.1319
Length (mm)	0.17681	0.10104	1.750	0.0801
Plant damage present	1.98851	1.09638	1.814	0.0697
Number of racemes	0.19942	0.08311	2.399	0.0164*
Fruits on plant	−0.03414	0.02032	−1.680	0.0929
Approx. dist. to Allegheny (m)	−0.05651	0.03960	−1.427	0.1535
Avg. seed length (mm)	−0.70329	0.43498	−1.617	0.1059

encing regular disturbance show the greatest effect of insect consumers relative to other plant communities. In addition, because *Baptisia australis* is typically found in grasslands, microsite or safe site limitation is less likely to be a factor for the species, as safe site limitation is thought to be more common in closed habitats like forests (Crawley 1992; Maron and Crone 2006). Linabury et al. (2019) also found legume fruits (of *Lespedeza* spp.) were impacted more by insects than other prairie species—especially grasses, the dominant class of taxa co-occurring with *B. australis* var. *australis* in Pennsylvania.

Riparian scour prairie systems like the ones in Pennsylvania face an additional host of unique threats. As a consequence of climate change, flooding events along rivers will likely become more frequent and severe (Arnell and Gosling 2016). Many Allegheny River populations were underwater for most of the month of June in the 2019 field season (USGS 2016; C.L. Moore pers. obs.), when the species normally flowers and begins to set seed (Rhoads and Block 2007). During July 2019 it was observed that the majority of the plants in Allegheny River populations had no fruit, and those that did had fewer than the previous summer (C.L. Moore pers. obs.). If such inundation continues, it could result in a depleted seed bank. Human development also heavily impacts the system in addition to changes caused by climate change. This makes the banks susceptible to erosion and seed bank depletion due to natural flooding as well as boat wakes (Camfield et al. 1980; Nanson et al. 1994).

Although there are arguments proposing that plants such as *Baptisia* may be able to compensate for seed losses via rhizomatous reproduction (Maron and Crone 2006), formation of seed banks (Maron and Simms 1997), and by being safe site limited (Andersen 1989), other factors should be taken into account including various threats to the species and its unusual habitat. The production of seeds via sexual reproduction is important for gene flow, particularly in taxa that can also reproduce via rhizomes, and for seed bank maintenance (Tanksley and McCouch 1997). Seed production is particularly valuable in edge-of-range, fragmented populations such as the one in Pennsylvania that is already susceptible to genetic drift (Frankham et al. 2011; Diekmann and Serrao 2012; Abeli et al. 2014). Edge populations are also often genetically distinct, and thus can be particularly valuable for conservation as a reservoir of genetic diversity (Lesica and Allendorf 1995; Assis et al. 2013). Depending on population size (number of individuals) and genetic health of the population, insect granivores could be significantly impacting reproduction in these edge-of-range demes. In addition, edge-of-range populations often inherently

**Table 4.**—Summary of the effect of independent variables on the number of seeds in fruit based on GLMM of best fit. Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05

	Estimate	Std. error	z value	Pr(> z )
(Intercept)	1.851973	0.209986	8.820	< 2e-16***
Length_(mm)	0.028797	0.005374	5.358	8.40E-08***
Frass_present	−0.439482	0.108806	−4.039	5.36E-05***
Fruits on plant	0.002298	0.001022	2.249	0.0245*
Immature seeds	−0.052868	0.009617	−5.497	3.86E-08***

exhibit reduced seed counts and, at times, reduced overall fitness (Pigott and Huntley 1981; Eckert and Barret 1993; Dorken and Eckert 2001; Jump and Woodward 2003). Smaller populations like the Pennsylvania metapopulation of *B. australis* var. *australis* are thus more susceptible to genetic drift (Frankham et al. 2011). This also applies at the site level; sites with few plants are by definition more susceptible to genetic drift and may be more inbred (Moore et al. in prep.). Reduction of seeds in these populations potentially furthers this loss of genetic diversity.

While questions remain regarding the long-term impact of insect granivores on seed banks, our results indicate that at least one species of lepidopteran is impacting Pennsylvania populations of *Baptisia australis* var. *australis*. Based on generalized linear mixed models of the factors that correlate with evidence of insects, granivores reduce seed counts as early as mid-July. Our examination of herbarium records provides evidence that granivores have been present in these populations for more than 150 y. Although the co-occurrence of *Baptisia australis* var. *australis* and its specialized seed predators may have been a sustainable interaction over some of that period, other synergistic threats have likely exacerbated the consequences of this relationship for populations of this plant in Pennsylvania.

Lindenmayer et al. (2011) proposed “conservation complacency” as the idea that conservation focus is often concentrated on already-rare species, while more research is needed for species that may face rapid decline in the future. *Baptisia australis* var. *australis* is currently a species of concern as state-threatened in Pennsylvania with a NatureServe Rank of S2 indicating the taxon is imperiled with high risk due to restricted range, few populations or occurrences, steep declines, severe threats, or other factors (NatureServe 2018). Although *B. australis* sensu lato is considered stable at the global level with a rank of G5, *B. australis* var. *australis* has a rank of G5T3 and is considered vulnerable for the same reasons it is considered imperiled in Pennsylvania. There are several ways a taxon can become rare (Rabinowitz 1981), but the rarity of *Baptisia australis* var. *australis* in Pennsylvania appears to be related largely to two factors: habitat specificity and local population size. Our research on the impacts of granivory and other threats to these populations suggests that the taxon is in danger of rapid decline and potential loss of genetic diversity, particularly as a disjunct, edge-of-range metapopulation. The species and its habitat should continue to be closely monitored and protected in an effort to avoid the trap of conservation complacency, especially as granivory, a threat not previously considered in Pennsylvania, is shown by this work to impact seed production and, in turn, recruitment. Our observations suggest that visual assessment of



fruits can serve as a proxy for direct measurements of seed loss. This new understanding of threats to the taxon can now inform future inventories through an efficient assessment and improve applied management practices employed by conservation partners to maintain and monitor populations of *Baptisia australis* var. *australis* throughout its range.

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