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CONGENER HOST SELECTION BY THE PRE-DISPERSAL SEED PREDATOR, APION ROSTRUM (COLEOPTERA: APIONIDAE)Chris E. Petersen¹ and Weien Wang¹

ABSTRACT

Apion rostrum Say (Coleoptera: Apionidae) is the major seed predator of the wild indigo congeners, *Baptisia alba* and *B. bracteata* in the Russell Kirt Tallgrass Prairie, a reconstructed prairie located at College of DuPage, Illinois. This study, conducted during 2006, investigated factors attracting *A. rostrum* to each congener. The two *Baptisia* differ in developmental period, stature, and patterns of dispersion. *B. bracteata* flowers and initiates pods usually along a single raceme during late spring, and is a shorter plant that grows in clusters. In contrast, *B. alba* flowers and initiates pods beginning a month after *B. bracteata*, produces a tall central raceme with often several satellite racemes, and does not grow in dense clusters. Mating and ovipositing *A. rostrum* were observed on *B. bracteata* during the first half of June, and with greater abundance on *B. alba* from early June through mid July. Results of stepwise multiple regression showed a positive relationship of weevil counts per plant to raceme counts per cluster for *B. bracteata* and to inflated pod counts per plant for *B. alba*. The developmental synchrony between *A. rostrum* and pods of *B. alba* is evidence of a closer evolutionary relationship than the seed predator has with *B. bracteata*. This can explain the greater number of reproductive weevils seen on *B. alba* as well as the higher levels of pod infestations.

Insects are major pre-dispersal seed predators, affecting the distribution and abundance of plants as a selective force on developmental characteristics (Norambuena and Piper 2000, Cariveau et al. 2004, Nakagawa et al. 2005, Orrock et al. 2006, Whiles and Charlton 2006). Factors attracting seed depredate insects to plants include the availability of seeds as determined by the timing of reproduction, abundance of seeds and fruits, plant height, and plant density (Evans et al. 1989, Molau et al. 1989, Siemens and Johnson 1995, Cariveau et al. 2004, Fenner and Thompson 2005, Tipping and Center 2005).

Apion rostrum Say (Coleoptera: Apionidae) is the major pre-dispersal seed predator of the congeners *Baptisia alba* (L.) Vent (White wild indigo) and *B. bracteata* Muhl. ex. Ell. (Cream wild indigo) in a reconstructed prairie located in northeastern Illinois. The two legumes are native to tallgrass prairie that once covered much of the Midwest, with *B. bracteata* preferring mesic prairie and *B. alba* having a wider distribution extending from sandy marshes to dry clay hills and open woods (Rickett 1963, Swink and Wilhelm 1994). The congeners partly overlap in flowering period and share common pollinators, but differ in the primary time of flowering and patterns of growth (Haddock and Chaplin 1982, Petersen et al. 2000). *B. bracteata* blooms in May and grows in dense clusters of a dozen or more individuals. The slender shoot of the plant emerges from the ground during early April to form usually only a single raceme. A cluster consists of individual shoots located within 15-cm proximity of other shoots. The arching racemes of up to 0.5-m height radiate outward from clusters. In contrast, the shoot of the *B. alba* emerges from the ground about two to three weeks after *B. bracteata*, producing a central raceme of over 1 m in height and usually several smaller satellite racemes which bloom from late May through

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June. Plant counts of pods can be over 5× greater for *B. alba* than *B. bracteata*, and pod counts of ovules and seeds 10× greater (Haddock and Chaplin 1982, Petersen et al. 2006).

Pod infestation by *A. rostrum* is similar for both species of *Baptisia*. After overwintering, adult weevils emerge by late spring to mate. Females then insert eggs into the soft inflating pods with often several eggs inserted per pod. Successful pollination is indicated by pod inflation (Haddock and Chaplin 1982). Emerging larvae consume the seeds as their only source of nutrition. Seed predation is a cause of pod abortion for both *B. bracteata* and *B. alba*, but particularly for the latter (Petersen 1990, Petersen et al. 2000). The adult stage is reached by August with adults leaving pods as pods dehisce.

In this study, we examine how *A. rostrum* is attracted to the congeners based on reproductive yield, stature, density, and for *B. bracteata*, cluster size. Reproductive yield was quantified by counts of seeds, pods, and racemes per plant, stature by plant height, and density by counts of all *Baptisia* species. Cluster size for *B. bracteata* was characterized by counts of shoots emerging from the ground. Raceme count per cluster provided an additional measure of reproductive yield per cluster.

MATERIALS AND METHODS

Reconstruction of the 7.1-ha study site, the Russell Kirt Tallgrass Prairie, began in 1984 at College of DuPage, Glen Ellyn, Illinois. The prairie is characterized by the grasses, big bluestem (*Andropogon gerardii* Vitman) and prairie dropseed (*Sporobolus heterolepis* Gray) (Poaceae), and some 150 native tallgrass forbs which include *B. alba* and *B. bracteata* (Kirt 1996). The site has been reconstructed to represent the flora of mesic tallgrass prairie that was once found in the local area. The prairie is burned annually and was burned during early spring, 2006, prior to the beginning of this study.

Activity of reproductive adult *A. rostrum* was examined by visually inspecting 40 *Baptisia* of each congener for the presence of weevils beginning in May and ending in August after a 2-week period of not observing adults. Not knowing when weevils are most active, observations of activity were done over the course of a day. Three times a week, either during the morning, afternoon, or evening, plants were randomly inspected for the adult weevils.

Differences in oviposition patterns of *A. rostrum* between the congeners was evaluated by comparing counts of developing weevils per pod, largely eggs, from samples taken on 13 June. Pod inspection through time also permitted observations of weevil development and seed loss. The number of ovules, seeds initiated, seeds surviving, and the developmental stages of *A. rostrum* were observed by sampling pods from 30 randomly selected *Baptisia* of each congener. Sampling of pods which began on 13 June was conducted every other week until the pods ripened and the adult stage of the weevil was reached. The 30 plants sampled across the time interval were not necessarily the same plants, but rather a random selection from hundreds of individuals found in the prairie.

A final tally of seeds surviving and developmental stages of the weevil were taken from 40 plants of each congener that had been randomly selected early in the season as the plants began to flower. These plants were never those sampled for pod content prior to pod ripening and provided additional measures of reproductive yield as well as stature and density. The 40 specimens of *B. bracteata* were selected as they began to bloom during early May. Each specimen came from a different cluster of the plant. Shoot count per cluster and raceme count per cluster from which each sample plant was selected were recorded as measures of density. Similarly, 40 *B. alba* were selected as they flowered during June.

Analyses of all 80 plants involved recording height and counts of racemes, inflated pods, and pods ripened to maturity. Height at the tallest point of a plant was taken at peak flowering. Once pods ripened, five pods were sampled per raceme of all racemes per plant. Sampling involved counts of remaining seeds and weevils. Pods sampled included the most basal pod, the most distal pod, and 3 pods between. If a raceme had fewer than 5 pods, all were sampled. Counts of all *Baptisia* individuals of both congeners within 3-m-distance of each of the 80 tagged plants provided measurement of density. A distance of 3 m was chosen based on the spatial distributions of the *Baptisia* species in the prairie where a greater distance tended to not include additional *Baptisia* individuals.

All statistical summarization and analyses were done using Statistica (Statsoft 2001). Mann-Whitney U tests were used to determine statistical differences between *Baptisia* congeners in counts of ovules, seeds, and weevils in developing pods. Forward stepwise regressions were run to test the dependence of counts of *A. rostrum* per plant on counts of pods inflated per plant, counts of racemes per plant, density of all *Baptisia* species per 28.3m², and plant height for both congeners. Cluster size and counts of racemes per cluster were added to the regression model for *B. bracteata*. Variables were only added to regression models where $F > 1.0$. Hence, significant regression models potentially included 1 to 4 or 6 factors, the higher factor number being congener dependent. Counts of *A. rostrum* per plant were computed as the products of counts of pods inflated multiplied by counts of *A. rostrum* per ripened pod. These estimates were believed to most closely predict levels of plant infestation before pod abortion. Prior to regression analyses, counts of *A. rostrum* per plant and pods inflated per plant were $\log_{10}(x + 1)$ transformed, counts of racemes per plant and plant heights were square root transformed, and counts of racemes per cluster of *B. bracteata* were $\log_{10}(x)$ transformed to meet normality.

RESULTS

The first overwintered adult *A. rostrum* was seen climbing a stem of *B. alba* on May 30th when pods of *B. bracteata* were inflating and *B. alba* was blooming. Within the next month, the weevils could be observed mating and ovipositing. Reproductive adults were seen on *B. bracteata* during the first half of June and on *B. alba* from early June to mid July (Fig. 1). The maximum mean count of *A. rostrum* per plant \pm standard error observed during a sampling episode was 0.13 ± 0.05 on 7 June for *B. bracteata* and 0.60 ± 0.11 on 13 July for *B. alba*.

Table 1 summarizes ovule and seed counts as well as counts of the developmental stages of *A. rostrum* through time in pods of each congener. Seed count per pod continually declined through time, presumably due to predation by weevil larvae and newly developed adults. *A. rostrum* showed evidence of mortality within pods of *B. bracteata* with counts decreasing through time. In contrast, counts of weevils per pod showed relatively little change after reaching a high point during late June. Pods of *B. alba* statistically initiated more seeds (13 June counts) and, conceding non-significance for the first sample period, were infested by more weevils throughout the duration of the study period.

Measurements of plant reproductive yield, clustering, and *A. rostrum* counts from the 40 tagged individuals per congener are summarized in Table 2. Stepwise regression analysis for *B. alba* was highly significant ($r^2 = 0.91$, $F_{1,33} = 74.0$, $P < 0.001$), with only inflated pod counts per plant being sufficiently informative as to be included in the model describing weevil attraction to the plant. The regression coefficient for inflated pod counts per plant was positive (Table 3). For *B. bracteata*, the regression analysis was also significant ($r^2 = 0.26$, $F_{2,29} = 5.2$, $P = 0.012$). Raceme count per cluster and cluster size were the two independent factors included in the forward stepwise regression model. However, while each coefficient was positive for these factors, only raceme count per cluster was significant (Table 3).

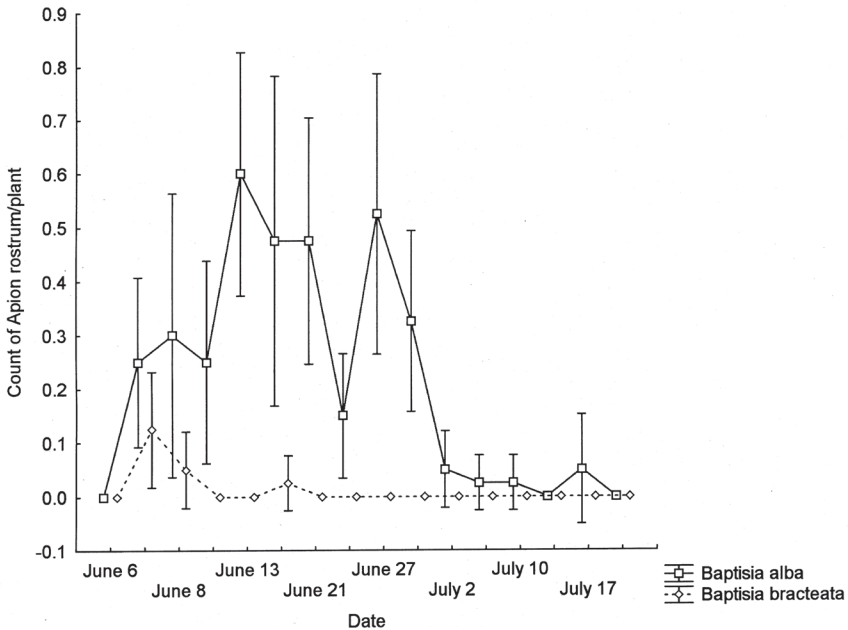


Figure 1. Mean \pm standard error bars of counts of reproductive adult *Apion rostrum* on plants of *Baptisia alba* and *B. bracteata* through time. Each $n = 30$.

DISCUSSION

Pods of *B. alba* produced more ovules and initiated more seeds than *B. bracteata*. They were also more heavily infested by *A. rostrum* than *B. bracteata*. With its activity period timed to when pods of *B. alba* are just inflating and very susceptible to egg insertion, the weevil can maximize its reproductive potential infesting *B. alba*. This synchrony is evidence of a closer evolutionary relationship with *B. alba* than with *B. bracteata*. Factors favoring such a relationship include rewards of higher seed number per pod and per plant that can support a greater number of developing weevils to maturity, and the wider distribution of the legume across habitats. Greater dependence on a host that has a wider distribution may enable weevil persistence when pod yield fails in a particular habitat. The ability to utilize more than one host species should further buffer the seed predator from fluctuations in seed production.

During some years, only a few seeds are matured from the populations of *Baptisia* growing in the study site (Petersen and Sleboda 1994). Weather extremes can lead to pod abortion, leading to the death of weevil larvae within the pods. The host pool is larger when the two congeners are collectively considered, let alone considering that several other species of *Baptisia* are also host to *A. rostrum* in North America (Evans et al. 1989, Horn and Hanula 2004).

The weevil may opportunistically infest *B. bracteata* as influenced by the display of racemes per cluster. Contrarily, the attracting factor may be pods inflated per cluster, a parameter not measured in this study. Discounting counts of inflated pods may explain the low r^2 computed for the analysis and should be included in future studies. The earlier development of pods, fewer seeds per pod and pods, and the reduced visibility of the shorter clumps of *B. bracteata*

Table 1. Mean \pm standard error counts of ovules per pod, seeds per pod, and the various developmental stages of *Apion rostrum* per pod according to congener of *Baptisia* and sampling date. All $n = 30$ unless noted otherwise. *Z* and *P* statistics are from Mann-Whitney comparison of the parameter between congeners. * $n = 32$, ** $n=35$.

Date	Parameter	<i>Baptisia bracteata</i>	<i>Baptisia alba</i>	<i>Z</i>	<i>P</i>
June 13th					
	Ovules/pod	18.13 \pm 0.68	33.80 \pm 0.78	6.60	<0.001
	Seeds/pod	14.63 \pm 0.69	26.53 \pm 1.56	4.97	<0.001
	<i>A. rostrum</i> eggs/pod	0.87 \pm 0.20	1.70 \pm 0.29		
	<i>A. rostrum</i> larvae/pod	0.30 \pm 0.09	0		
	All <i>A. rostrum</i> /pod	1.17 \pm 0.20	1.70 \pm 0.29	1.54	0.124
June 27th					
	Seeds/pod	7.63 \pm 0.79	25.57 \pm 1.30	6.402	<0.001
	<i>A. rostrum</i> eggs/pod	0.20 \pm 0.10	2.60 \pm 0.47		
	<i>A. rostrum</i> larvae/pod	1.43 \pm 0.16	1.80 \pm 0.33		
	All <i>A. rostrum</i> /pod	1.63 \pm 0.19	4.40 \pm 0.39	4.901	<0.001
July 10th					
	Seeds/pod	2.13 \pm 0.42	8.83 \pm 0.92	5.253	<0.001
	<i>A. rostrum</i> larvae/pod	0.43 \pm 0.12	2.13 \pm 0.43		
	<i>A. rostrum</i> pupae/pod	0.83 \pm 0.17	1.53 \pm 0.25		
	<i>A. rostrum</i> adults/pod	0.13 \pm 0.06	0.13 \pm 0.08		
	All <i>A. rostrum</i> /pod	1.40 \pm 0.24	3.80 \pm 0.37	4.517	<0.001
July 24th					
	Seeds/pod	1.90 \pm 0.69	3.30 \pm 1.19	1.937	0.053
	<i>A. rostrum</i> eggs/pod	0	0.07 \pm 0.07		
	<i>A. rostrum</i> larvae/pod	0.07 \pm 0.05	0.10 \pm 0.07		
	<i>A. rostrum</i> pupae/pod	0.07 \pm 0.05	0.37 \pm 0.16		
	<i>A. rostrum</i> adults/pod	0.93 \pm 0.14	3.33 \pm 0.38		
	All <i>A. rostrum</i> /pod	1.07 \pm 0.17	3.87 \pm 0.31	5.877	<0.001
August 2nd					
	Seeds/pod	*0.59 \pm 0.38	**1.58 \pm 0.22	5.561	<0.001
	Adult <i>A. rostrum</i> /pod	*0.85 \pm 0.12	**3.91 \pm 0.16	6.967	<0.001

in an emerging springtime landscape may function to decrease predispersal seed predation by *A. rostrum*. A low count of seeds initiated per pod has been hypothesized to be an evolved response to distracting predispersal seed predators in other legumes (Siemens et al. 1992).

Declines in seed number after the adult stage is reached are evidence that *A. rostrum* continues to feed on seeds beyond the larval stage. We have observed adult weevils that have overwintered in the occasional pod that happened not to detach from a raceme and fragment. However, the importance of seeds as a food resource to these weevils is unknown. The current practice of annual burning removes all remaining pods, yet the weevils reappear every year. Most pods dehisce or fragment, and it is believed that the new generation of adult weevils disperses at this point. Where these weevils overwinter is unknown, but the soil may be the likely reservoir in view of the removal of above-ground vegetation by burning.

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Table 2. Summary (mean \pm sample error; n) of parameters of plant stature, reproductive yield, and infestation by *Apion rostrum* according to congener of *Baptisia*.

Parameter	<i>Baptisia bracteata</i>	<i>Baptisia alba</i>
Flower count/plant	22.13 \pm 1.83; 40	74.73 \pm 6.78; 40
Inflated pod count/plant	10.10 \pm 1.27; 40	39.35 \pm 4.56; 40
Ripened pod count/plant	6.48 \pm 0.83; 40	10.23 \pm 1.52; 40
Racemes/plant	1.23 \pm 0.10; 40	3.43 \pm 0.37; 40
Height (cm)	33.40 \pm 0.88; 40	117.54 \pm 3.42; 40
<i>Apion rostrum</i> count/plant	9.63 \pm 1.37; 32	165.48 \pm 21.34; 35
Cluster size of species		13.53 \pm 1.37; 40
Species density/m ²	4.47 \pm 0.24; 40	0.94 \pm 0.11; 40
Density of all <i>Baptisia</i> /m ²	4.58 \pm 0.26; 40	0.94 \pm 0.11; 40

Table 3. Results of forward stepwise regression according to congener of *Baptisia* in the order factors were added to the model. Factors listed were the only ones included in the model as limited to $F > 1$. Counts of *Apion rostrum* per plant and pods inflated per plant were $\log(x + 1)$ transformed, and counts of racemes per cluster were $\log(x)$ transformed.

Congener	Factor	Regression coefficient	<i>t</i>	<i>P</i>
<i>Baptisia bracteata</i> (n = 32)				
	Racemes/cluster	0.465	2.819	0.009
	Cluster size	0.011	1.458	0.115
<i>Baptisia alba</i> (n = 35)				
	Pods inflated/plant	1.039	17.744	<0.001

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