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SELECTIVE POD ABORTION BY *BAPTISIA LEUCANTHA* (FABACEAE)  
AS AFFECTED BY A CURCULIONID SEED PREDATOR,  
*APION ROSTRUM* (COLEOPTERA)

Chris E. Petersen<sup>1</sup> and Jo Ann Sleboda

ABSTRACT

The effect of a seed predator, *Apion rostrum* (Coleoptera: Curculionidae), on selective pod abortion from *Baptisia leucantha* (Fabaceae) was investigated in a restored tallgrass prairie plot. Weevil densities in and undamaged seed contents of attached and detached pods were compared over four occasions during the summer of 1993. Detached pods had similar to lower counts of weevils/pod and fewer seeds/pod than attached pods. Weevil density in pods appears only important in promoting pod abortion through effects on seed number/pod as pods having fewer seeds are selectively aborted.

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Selective abortion of damaged fruits has been explained as a mechanism by which a plant can cease investment in fruits that are unlikely to contribute to plant fitness (Janzen 1969, Stephenson 1981). Fruits possessing fewer seeds or which are infested by predator-transmitted fungi are those abscised (Janzen 1969, Sallabanks and Courtney 1992). Thus, predispersal seed predation can lead to additional seed mortality through effects on fruit abortion (Boucher and Sork 1979, Janzen 1969, Phillips 1941). In the following study, pod abortion by the legume *Baptisia leucantha* as affected by the seed predator *Apion rostrum* Say (Coleoptera: Curculionidae) was examined in a restored tallgrass prairie located in northeastern Illinois. *Baptisia leucantha* is known to suffer higher rates of pod abortion when infested by *A. rostrum* (Petersen 1990). However, it has not been shown how the presence of the weevil causes abortion and if pod abortion is selective. The objective of this study was to test the prediction that *A. rostrum* affects selective abortion of pods.

*B. leucantha* is a widely distributed prairie native of the Midwest (Larisey 1940). The species, like other members of the lupine genus, contains a number of alkaloids (Cranmer and Turner 1967) which have been used to explain the lack of consumers feeding on it (Frost 1945). *A. rostrum* is the only known consumer of the wild indigo's tissues in the prairie plot under study. In northeastern Illinois, a seasonal cycle of growth by the perennial begins with new above-ground emergence as the ground thaws during spring. Flowering occurs from May to June with *Bombus fervidus* and *B. bimaculatus* being the major pollinators. New flowers appear as indeterminate racemes elongate. Racemes usually number one or two per plant, but may number as high as fourteen. By late June, flowering has ceased and pollinated flowers have transformed into inflated pods. Pods typically initiate 30 to 38 seeds. Many of the pods are aborted as they ripen with rates of pod loss greater among plants infested by

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*A. rostrum*. Racemes may bear over 200 mature pods. Seeds are dispersed as the ripened pods dehisce during autumn.

Over-wintering weevils oviposit into sealed developing pods during June (Petersen 1989). Eggs are inserted individually, although as many as twelve eggs have been found within a pod. A single weevil may consume over five seeds as it develops, and in pods with four or more weevils, it is not uncommon for all of the seeds to have been eaten. Pupation occurs during July as surviving seeds begin to harden and turn from green to a golden color. Adults disperse as the ripened pods dehisce.

## MATERIALS AND METHODS

The study site was the 0.06 ha restored tallgrass prairie located on the northeastern corner of the College of DuPage campus. The college is located in largely residential DuPage County, Illinois. Restoration of the plot began in the early 1970s. Big bluestem (*Andropogon gerardi*) and Indian grass (*Sorghastrum nutans*) dominate the site which is burned annually, usually in the fall. Approximately 150 *B. leucantha* populate the site.

Eighty *B. leucantha* were randomly selected for study as pods began to form during June, 1993. These plants were further randomly subdivided into four groups of 20 plants each. The four groups were sampled sequentially during the summer to examine how sampling time could effect measured outcomes. The first group was sampled on 24 June as pods began to inflate and with the appearance of *A. rostrum* eggs and larvae. The second group was sampled on 11 July as pods fully inflated and when larval weevils composed the majority life stage. Sampling on 28 July coincided with the maturation of the weevils. The final sampling was conducted on 17 August as pods ripened.

Samplings consisted of counting pods along racemes and then removing five pods from each raceme of a plant whenever possible: the most proximal pod, the most distal pod, and three spaced in between. If a raceme had fewer than five pods, then all were sampled. Pods were measured for maximum width between lines of dehiscence and for length. These measurements plus first nodal diameters of plants and racemes provided parameters of pod and plant growth, possible factors useful to understanding the impact of weevil seed predation on pod abortion during a phase of pod development. Counts of weevils and undamaged seeds were taken from each pod.

Detached pods lacking visible damage were assumed to have been aborted. Only those having similar appearance in color and stage of development to and which were still sealed as attached pods were sampled beneath each plant. This discrimination among fallen pods was intended to insure the sampling of newly aborted pods, thus limiting the possibility that decomposition affected outcomes. During the entire sampling period attached pods were green to greenish black. Detached pods turn black within two days.

A distribution-free randomization method (Potvin and Roff 1993) was used where necessary to compare grand mean counts of undamaged seeds/pod and of weevils/pod (counts/pod/plant). The probability (P) of obtaining the observed absolute difference between means among 5000 simulated permutations was used to compute significance. Standard error (SE) measurements of P's were computed as  $\sqrt{P(1-P)/N}$ , where N was the number of permutations (i.e., 5000).

Table 1. Mean counts (mean  $\pm$  s) from *Baptista leucantha* of pods/plant, first nodal diameters of plants, and first nodal diameters of racemes/plant according to sampling date during 1993.

Date	Plant number	Pods/plant	First nodal plant diam.	First nodal raceme diam.
24 June	20	38.9 $\pm$ 31.0	13.8 $\pm$ 3.1	4.9 $\pm$ 0.9
11 July	20	6.8 $\pm$ 7.5	14.5 $\pm$ 2.8	4.7 $\pm$ 0.7
28 July	20	5.1 $\pm$ 7.5	14.7 $\pm$ 3.5	4.4 $\pm$ 0.9
17 August	20	2.0 $\pm$ 4.1	14.3 $\pm$ 2.9	5.2 $\pm$ 1.2

## RESULTS AND DISCUSSION

The mean counts of pods/plant progressively decreased through the study period with a large drop occurring between 24 June and 11 July (Table 1). Grand mean counts of seeds/pod also reflected this decrease through time in both pods still attached and those detached (Table 2). *Baptista leucantha* may be most sensitive to aborting pods during the earlier stages of seed development as younger seeds of plants in general are known to produce auxins, gibberellins, and cytokinins that control the mobilization of nutrients into and the maintenance of fruits (Bidwell 1974, Street and Opik 1984). Except for the 24 June sample, differences in grand mean counts of seeds/pod between attached and detached pods were significant (all  $P < 0.001$ ; all  $SE < 0.001$ ).

Trends in weevil development according to sampling date were similar between attached and detached pods, although lagging in pace among the former (Table 3). The greater preponderance of larvae in detached pods during June may explain the lower grand mean counts of seeds/pod. However for a given sampling date, grand mean counts of *A. rostrum*/pod were always higher for attached pods than detached pods, and significantly so for the 11 July ( $P = 0.021$ ;  $SE < 0.001$ ) and 21 July ( $P = 0.011$ ;  $SE < 0.001$ ) samples. Although additional oviposition in pods having more seeds could be advantageous to the weevil by supporting the development of more offspring, such an ability to distinguish among pods has not been shown in *A. rostrum*. The cause of the difference in grand mean counts of weevils/pod remains unknown. Dispersal from aborted pods cannot explain this difference as aborted pods were sealed. Remnants of dead weevils were not apparent.

First nodal diameters of plants and racemes showed little if any change during the course of the experiment (Table 1). By the middle of July, pods had reached full dimensions (Table 4). Changes in size dimensions of detached pods showed a similar pattern over time and were comparable to those of those attached.

Significantly lower grand mean counts of seeds/pod among detached pods provide evidence of selective pod abortion in *B. leucantha*. The affect of weevil

Table 2. Grand mean counts of seeds/pod and weevils/pod ( $\bar{x}$  counts/pod/plant  $\pm$  s [number of plants]) within attached and detached pods of *Baptista leucantha* according to sampling date during 1993.

Date	Seeds/pod		<i>Apion rostrum</i> /pod	
	Attached	Detached	Attached	Detached
24 June	26.4 $\pm$ 6.4(20)	24.4 $\pm$ 4.0(15)	1.6 $\pm$ 1.5(20)	1.5 $\pm$ 1.2(15)
11 July	11.6 $\pm$ 5.3(17)	2.7 $\pm$ 2.1(19)	4.4 $\pm$ 1.8(17)	3.4 $\pm$ 0.9(19)
21 July	4.2 $\pm$ 2.6(15)	0.1 $\pm$ 0.5(19)	3.8 $\pm$ 1.6(15)	2.3 $\pm$ 1.6(19)
17 August	1.1 $\pm$ 0.9 (7)	0 $\pm$ 0 (10)	3.4 $\pm$ 1.7 (7)	2.7 $\pm$ 2.4(10)

Table 3. Frequencies of *Apion rostrum* ( $\bar{x}$  frequency/pod/plant  $\pm$  s) in various life stages according to time of sample and type of pod attachment.

Sampling date and type of pod attachment	<i>Apion rostrum</i> life stage				n
	Egg	Larva	Pupa	Adult	
24 June					
Attached	0.87 $\pm$ 0.12	0.13 $\pm$ 0.12	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	18
Detached	0.63 $\pm$ 0.28	0.37 $\pm$ 0.28	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	13
11 July					
Attached	0.12 $\pm$ 0.33	0.53 $\pm$ 0.32	0.35 $\pm$ 0.28	0.00 $\pm$ 0.01	17
Detached	0.00 $\pm$ 0.01	0.65 $\pm$ 0.16	0.35 $\pm$ 0.16	0.00 $\pm$ 0.01	19
28 July					
Attached	0.0 $\pm$ 0.0	0.03 $\pm$ 0.06	0.28 $\pm$ 0.23	0.69 $\pm$ 0.24	15
Detached	0.0 $\pm$ 0.0	0.09 $\pm$ 0.17	0.14 $\pm$ 0.19	0.77 $\pm$ 0.32	17
17 August					
Attached	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.01 $\pm$ 0.02	0.99 $\pm$ 0.02	7
Detached	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.01	1.0 $\pm$ 0.0	8

seed predation on abortion is less clear as grand mean counts of *A. rostrum*/pod were lower in detached pods. Earlier studies done over multiple years (Petersen 1989, 1990) have consistently found greater pod losses among plants having high pod densities of the weevil in comparison to plants less infested. However, even plants having low weevil densities suffered substantial pod losses leading to the conclusion that predispersal seed predation is only one of a number of factors affecting pod abortion in *B. leucantha*. Selective abortion may thus be a generalized response to the disposal of pods having few seeds. In particular, *A. rostrum* may promote the abortion of pods already having a marginal number of seeds by reducing seed content. *Baptisia leucantha* which have higher pod infestations should be expected to have more of these "marginal" pods to abort. Moreover, if pods are preferentially aborted because of low seed number, then pods with few seeds should be aborted regardless of weevil densities within them. Such a prediction could be tested in future studies among plants where weevil infestations are reduced or absent.

The pollination study of Haddock and Chaplin (1982) provides additional insight into reproductive investment strategies of *B. leucantha*. Haddock and Chaplin concluded that prolific flowering by *B. leucantha* can result in higher rates of pollination success and seed production than the congener, *B. leucophaea*, but at an increased risk of seed loss to seed predators. During years of favorable environmental conditions, including low seed predator activity, *B. leucantha* may gain the benefits of its extent of reproductive investment. Contrarily, during less than favorable years, the species could minimize losses in investments through selective pod abortion. By this means

Table 4. Grand mean pod lengths and widths ( $\bar{x}$  mm/pod/plant  $\pm$  s [number of plants]) for attached and detached pods of *Baptisia leucantha* according to sampling date during 1993.

Date	Length		Width	
	Attached	Detached	Attached	Detached
24 June	15.5 $\pm$ 4.2(20)	16.0 $\pm$ 4.5(15)	5.1 $\pm$ 1.9(20)	5.3 $\pm$ 2.8(15)
11 July	29.5 $\pm$ 3.7(17)	27.0 $\pm$ 2.1(19)	12.5 $\pm$ 2.3(17)	11.7 $\pm$ 1.8(19)
21 July	27.2 $\pm$ 2.5(15)	25.9 $\pm$ 2.9(19)	12.0 $\pm$ 2.5(15)	11.9 $\pm$ 1.8(19)
17 August	28.6 $\pm$ 4.2 (7)	27.7 $\pm$ 3.3(10)	11.0 $\pm$ 1.5 (7)	11.4 $\pm$ 1.9(10)

*B. leucantha* might optimize reproductive effort over its perennial existence. In turn, as a prodispersal seed predator and one of the few consumers of *B. leucantha*, *A. rostrum* would have an exclusive and a fairly productive nutritional resource.

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