

Patterns of American licorice seed predation by *Acanthoscelides aureolus* (Horn) (Coleoptera: Bruchidae) in South Dakota

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Abstract

The bruchid beetle *Acanthoscelides aureolus* (Horn) is a major seed predator on American licorice (*Glycyrrhiza lepidota* Pursh) and other legumes in North America. Mature pods of American licorice from eastern South Dakota populations were examined for seed predation by *A. aureolus* over a 2-year period from 1985-1986. Frequency of seed predation varied significantly between years. Percent seed predation was similar for 2-, 3-, 4-, 5-, and 6-seeded pods, indicating pods were attacked in proportion to number of seeds in the pod. Highest predation frequencies were found for seeds at the rachis end of the pod, regardless of pod size (seeds/pod). The largest seeds in pods with 4 or more seeds were from central positions while the smallest were from proximal and distal positions, suggesting beetle larvae did not select seeds on the basis of large size. When predation levels were low, seed position in the pod was more important than pod or seed size in determining frequency of seed predation by *A. aureolus*.

Key Words: *Glycyrrhiza lepidota* Pursh, *Acanthoscelides aureolus*, seed predation

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In North America, noneconomic native legumes offer a reservoir from which useful cultivars for forage and soil conservation purposes may someday be extracted (Davis 1982). Southgate (1979) pointed out that many species of Bruchidae have economic importance because they breed on grain legumes and consume valuable proteins. He also emphasized that seeds of many non-economic, leguminous species are destroyed by bruchids, and he encouraged research to gain a greater understanding of Bruchidae ecology.

Lists of North American Bruchidae and their host plants have been compiled (Cushman 1911; Center and Johnson 1974, 1976) and estimates of seed destruction by bruchid beetles have been reported for native populations of *Glycyrrhiza lepidota* (Boe and Wynia 1985), *Astragalus cibarius* and *A. utahensis* (Green and Palmbald 1975), *Nissolia schottii* (Johnson 1977), and *Amorpha fruticosa* (Rogers and Garrison 1975).

The loss of seeds as a result of insect predation is a potential threat to the maintenance and expansion of plant populations. Louda (1982) found recruitment and abundance of the shrub *Haplopappus squarrosus* were limited by a high rate of seed loss caused by flower- and seed-feeding insects, and concluded insect predation can be important to the dynamics of indigenous plants in temperate climates.

Recent studies indicated no relationship between plant fecundity

and seed predation by a geometrid moth on *Hamamelis virginiana* (De Steven 1983), or fruit cluster size and seed predation by a weevil on *Actae rubra* (Willson 1983). However, Bradford and Smith (1977) found bruchid beetles concentrated predation on a particular fruit size (1-seeded) in *Scheelea* palm. Number and size of seeds in a legume pod varies widely within species (Mitchell 1977), and few researchers (Mitchell 1975) have studied intraspecific variation in seeds as it relates to differential predation by bruchid beetles.

The objectives of this study were to determine if seed predation by *Acanthoscelides aureolus* on *Glycyrrhiza lepidota* was related to pod and/or seed characteristics, specifically pod size (seeds/pod), seed position in the pod, or seed size. Quantification of seed predation patterns by bruchid beetles is critical to understanding the reproduction ecology and population dynamics of native legumes.

Materials and Methods

In September 1985, mature pods of *G. lepidota* were collected from large populations in ungrazed areas near Lake Norden and Brookings, South Dakota. Pods were stripped from stems at random and bulked in large paper bags. The Lake Norden population was sampled similarly again in September, 1986. For the Brookings population, 150 each of 2-, 3-, 4-, and 5-seeded pods were examined for presence of beetle larvae. For the Lake Norden population, 61 2-seeded, 106 3-seeded, and 150 each of 4-, 5-, and 6-seeded pods were examined in 1985; 150 each of 2-through 6-seeded pods were examined in 1986. In the lab, intact pods were carefully split along the sutures with a scalpel so that natural position of the seeds was not disturbed. Seeds containing larvae usually appeared swollen, were duller in color than noninfested seeds, and were easily crushed by light pressure from a fine-pointed forceps. The inner surfaces of the valves of 50 random pods from each of the 1985 and 1986 collections from the Lake Norden population were examined carefully with a binocular microscope at 30X magnification. The number and locations of entrance holes were determined for each pod. Individual seeds from 50 each of uninfested 3-through 6-seeded and 3-through 5-seeded mature pods were weighed on an analytical balance for 1985 and 1986 collections from the Lake Norden population, respectively. One hundred random pods from each collection were examined for

determining frequencies of pod sizes (seeds/pod).

Predation frequency by seed position in the pod and pod size were analyzed by Chi-square. Subdivision of total Chi-squares into linear and deviation from linear regression components was accomplished using methods described by Cochran (1954). Seed weight by seed position data were subjected to analyses of variance.

Results and Discussion

Chi-square analyses of the 1985 data indicated larvae of *Acanthoscelides aureolus* were not randomly distributed among seeds within pods (Table 1). In general, significant positive linear relationships were observed between predation frequency and seed position from distal to proximal ends of pods of both populations. In all cases, highest predation frequencies were found for seeds closest to the rachis. In pods with only 1 larva, there was a strong tendency for the infested seed to be from the proximal position. For the Lake Norden population in 1985, 63, 42, 33, and 53% of 3-, 4-, 5-, and 6-seeded pods containing 1 larva harbored it in the proximal seed, respectively.

Little is known about oviposition site selection in the Bruchidae (Southgate 1979). Nelson and Johnson (1983) reported oviposition on pods of *Astragalus praelongus* by 3 species of *Acanthoscelides*, including *A. aureolus*, often occurred on the pod surface beneath the calyx and suggested this position protected eggs from the sun, parasites, and predators. Mitchell (1975) reported that females of *Callosobruchus maculatus* avoided adding eggs to mung bean seeds with 1 or more eggs when unused seeds were available. He also observed that females oviposited on largest seeds first. We did not study oviposition behavior of *A. aureolus* in the field, but we have observed greater numbers of hatched eggs on calyxes and proximal ends of pods than any other regions of mature inflorescences.

Bruchid larvae of species that oviposit on external pod surfaces generally burrow through the pod in close proximity to the egg and enter the first available seed. Larvae of some species appear to be more selective and will crawl past several seeds before infesting one, but the basis of choice is not known (Southgate 1979). Number of beetle-infested seeds equaled number of entrance holes in 98 of the 100 pods examined, and locations of entrance holes were generally closely aligned with infested seeds. In several

Table 1. Seed predation frequencies of *Acanthoscelides aureolus* by seed position in pods of two *Glycyrrhiza lepidota* populations from eastern South Dakota, and chi-square analysis of the relationship between predation frequency and seed position.

Seeds Per Pod	Population		Seed Position ¹					Chi-square			
			Proximal 1	2	3	4	5	Distal 6	Total	Linear	Deviation
Number of seeds infested/150 seeds											
2	Brookings	1985	28	22					0.51		
	Lake Norden	1985 ²	16	4					8.60**		
	Lake Norden	1986	49	50					0.01		
3	Brookings	1985	40	32	16				12.67**		
	Lake Norden	1985 ³	26	13	12				8.57**		
	Lake Norden	1986	42	37	47				1.65		
4	Brookings	1985	32	27	17	17			8.59*	7.70**	0.89
	Lake Norden	1985	34	19	20	20			7.87*	4.28*	3.59
	Lake Norden	1986	63	48	54	47			4.72		
5	Brookings	1985	33	27	22	16	14		12.89*	12.62***	0.27
	Lake Norden	1985	45	22	31	21	14		26.01***	10.37**	15.64**
	Lake Norden	1986	53	39	36	49	38		7.45		
6	Lake Norden	1985	42	33	33	24	23	14	21.12***	18.81***	2.31
	Lake Norden	1986	63	56	65	55	61	44	8.13		

***, **Significant at 0.05, 0.01, and 0.001 levels, respectively.

¹Data are from a 150-pod sample for each pod size (seeds/pod) within each population unless indicated otherwise.

²Data are from a 61-pod sample.

³Data are from a 106-pod sample.

instances, we observed entrance holes at extreme distal ends of pods and predation of proximal seeds, indicating larvae would occasionally crawl past several seeds before selecting one to infest.

Under the higher infestation rates that occurred in the Lake Norden population in 1986, there was not a strong trend for predation frequencies to decrease linearly from proximal to distal seed positions (Table 1). However, 46, 42, and 29% of the 4-, 5-, and 6-seeded pods, respectively, containing a single larva harbored it in the proximal seed. Chi-square analyses indicated these observed frequencies were significantly ($P < 0.05$) different than expected for random distributions in 4- and 5-seeded pods. This suggested that when larval competition for seeds within a pod was low there was a tendency for larvae to be located in the proximal seed, as was found in 1985. Preference for proximal seeds was not likely due to intra-pod seed maturity differences, since seeds within a pod mature uniformly. Time of oviposition determines the stage of development at which larvae enter the seed. We have observed entrance holes in developing as well as fully mature seeds.

No incidence of multiple, fully-formed larvae in a single seed was observed over the 2-year study period, during which thousands of seeds were examined. This suggests that infested seeds were recognized and subsequently avoided by other larvae or that competition and/or cannibalism (Pinckney 1937, Bradford and Smith 1977) took place within the seeds. Cannibalism has been observed among larvae of *A. aureolus* in seeds of *A. praelongus* (Pfaffenberger and Johnson 1976). We observed a dead, intact, early-stage larva in several seeds that had 2 entrance holes and contained a healthy fully-formed larva. Larvae consumed both cotyledons and the embryo axis. All that remained of the seed after adult emergence was the testa containing an exit hole and frass packed into one end. Beetles can develop within a range of seed sizes (Boe and Wynia 1985), and the size of emergent adults varies dramatically, but food reserves within a single seed appear adequate for the complete development of only 1 beetle.

Seed position had no influence on mean seed weight in 3-seeded pods. However, seeds from proximal and distal positions were significantly lighter than seeds from at least 1 of the intermediate positions in pods with 4 to 6 seeds (Table 2). These results concur with studies on seed size of other leguminous species such as Palo Verde (Mitchell 1977), pea (*Pisum sativum*) (Linck 1961), and *Lupinus texensis* (Schaal 1980). Since seeds closest to the rachis often exhibited higher predation frequencies, but were significantly smaller than more central seeds in large (4 or more seeds) pods, there is no indication that larvae preferentially infested the largest seeds within a pod. Mitchell (1977) found no relationship between size and seed predation by *Mimosetes amicus* (Bruchidae) on Palo Verde. Conversely, although sizes of proximal and distal seeds were similar (Table 2), generally the highest and lowest infestation frequencies were observed for proximal and distal positions, respectively. Small seed size has been listed as one trait that eliminates or substantially lowers bruchid destruction of seeds of many wild herbaceous legumes, because the insect cannot develop within the seed (Janzen 1969). Boe and Wynia (1985) reported a wide range in mean seed size of approximately 20 populations of *G. lepidota* from the Dakotas, but found no correlation between mean seed size and mean predation by a bruchid. Center and Johnson (1974) found the size of *A. aureolus* depended upon the size of the seed of the species in which it developed, and because of this plasticity, reduced seed size did not preclude bruchid predation.

Mean percent seed predation, averaged across pod sizes, was significantly higher ($p < 0.01$) for the Lake Norden ($32.6 \pm 1.9\%$) population in 1986, than Lake Norden ($16.7 \pm 0.4\%$) and Brookings ($16.6 \pm 1.0\%$) populations in 1985. Mean percent seed predations, averaged across collections, were similar ($p > 0.05$) for all pod sizes indicating, as in the case of Palo Verde (Mitchell 1977), that *G. lepidota* pods were attacked in proportion to number of seeds/pod. For example, mean numbers of beetles/pod for the Lake Norden population in 1985 ranged from 0.3 to 1.1 for 2- and

6-seeded pods, respectively. Bradford and Smith (1977) found bruchid beetles concentrated predation on 1-seeded fruits of *Scheelea* palm. They reported larval size was a function of endosperm, and larval survivorship was slightly greater in single compared with 2- and 3-seeded fruits. In both 1985 and 1986, percent multiple beetles/pod increased linearly with seeds/pod. Percent multiple occupancy ranged from 42 to 78% for 2- to 6-seeded pods from the Lake Norden population in 1986.

Seeds/pod ranged from 1 to 7 with means of 3.4 ± 0.1 , 3.8 ± 0.1 , and 4.0 ± 0.1 for the 1985 Brookings, 1985 Lake Norden, and 1986 Lake Norden collections, respectively. The Brookings population had 64% 3- and 4-seeded pods compared to 50 and 60% for the Lake Norden population in 1985 and 1986, respectively. No relationship was indicated between frequency of pod size and percent seed predation.

Table 2. Mean weights of individual seeds from each seed position in 50 uninfested pods containing 3, 4, 5, or 6 seeds collected at Lake Norden, South Dakota in 1985 and 1986.

Seed Position	Seeds/pod ¹			
	3	4	5	6
	mg			
	1985			
1	7.96a	7.81b	7.74b	7.06b
2	8.47a	8.74a	8.39a	7.75a
3	7.90a	8.19b	8.36ab	7.51ab
4		7.79b	7.98ab	7.93a
5			7.72b	7.46ab
6				7.09b
	1986			
1	8.50a	6.54b	6.92b	---
2	9.10a	7.34ab	6.70b	---
3	8.54a	7.91a	8.04a	---
4		7.05ab	6.64b	---
5			6.50b	---

¹Means in same column that are followed by a different letter are significantly different by LSD 0.05.

Differences in frequency of seed predation among individual plants have been reported for *Astragalus* spp. (Green and Palm-bald 1975) and *Cassia marilandica* (Baskin and Baskin 1977). We were not able to examine inter-plant differences in *G. lepidota* natural populations because of its aggressive vegetative reproduction. *G. lepidota* plants spread rapidly by rhizomes (Boe and Wynia 1985), making identification of individual genotypes in a natural population extremely difficult. Evaluation of inter-population and/or genotypic variability for seed predation frequency would best be done in a spaced-plant environment where spread of individual plants could be controlled.

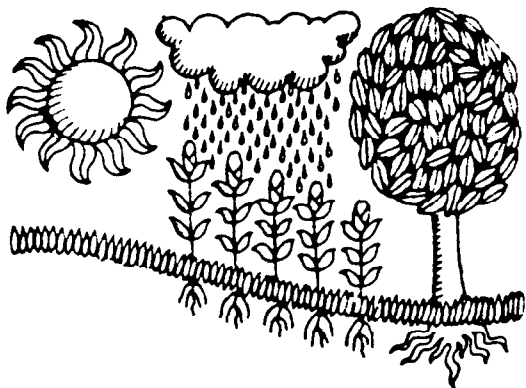
Bruchid beetles undoubtedly play an important role in the population biology of many native legumes, but very little is known about the amount or pattern of seed destruction they cause. Many native legumes, in addition to being important forage-producing and nitrogen-fixing species of rangeland plant communities, have potential as components of seed mixtures for revegetation of disturbed and denuded soils, establishment of wildlife habitats, and beautification of parks and recreation areas. Attempts to increase natural reseeding in populations of native legumes in rangelands and other areas may not be successful due to seed predation by bruchid beetles, and evaluation of native legumes in forage production, soil conservation, and other plantings is dependent upon availability of adequate seed supplies. Identification of seed predators and their parasites, quantification of seed loss to predation, and insights into behavior of seed predators are important prerequisites for systematic collections, seed increases, and experimental evaluations of native legumes.

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