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ABSTRACT

Canada milk-vetch (*Astragalus canadensis* L.), North America's most widespread species of *Astragalus*, is important for herbivores and granivores in natural ecosystems but suffers heavy seed losses to bruchids and curculionids. Our objectives were: (1) compile a species inventory and describe life histories of insects associated with seed production in Canada milk-vetch, and (2) determine frequencies of pod predation and primary parasitism in Canada milk-vetch. The seed predators were *Acanthoscelides perforatus* (Horn) and *Tychius liljebladi* Blatchley. Frequency of pod predation varied between two plant populations (46 and 70%) and between *A. perforatus* (37 %) and *T. liljebladi* (21 %). The primary parasitoids were two exotics [*Dinarmus acutus* Thomson and *Eupelmus vesicularis* (Retzius)] and two natives [*Eurytoma tylodermatis* Ashmead and an unidentified chalcid (Pteromalidae)]. Parasitism rates were 10% for *T. liljebladi* and 22% for *A. perforatus*. The seed predators had similar niches. Larvae of both species fed on the same food source (occasionally inside the same pod), and adults of both species were active on the plants concurrently. However, *A. perforatus* overwintered as full-grown larvae inside the pods, whereas larvae of *T. liljebladi* exited pods in late July and overwintered as pupae in the soil. This research identified a unique community of insects composed, in part, of two seed predators that utilized the same food source and two exotic and two native parasitoids. More research is needed to determine the stability of this insect community in response to variation in production at the first trophic level.

Keywords

Bruchid beetles, chalcids, parasitization, niche overlap

INTRODUCTION

Canada milk-vetch is the New World's most widely dispersed species of *Astragalus*. It is found in a variety of habitats across all but the extreme southeastern and southwestern United States (Barneby 1964) and has potential for forage, wildlife habitat, and conservation (Boe and Fluharty 1993). The bruchid beetle *Acanthosecelides perforatus* (Horn) infested 70% of the pods and destroyed nearly 50% of the seed crop of Canada milk-vetch growing in nurseries in eastern South Dakota (Boe et al. 1988). Boe et al. (1988) reported larvae of *A. perforatus* parasitized by larvae of *Dinarmus acutus* Thomson (Pteromalidae) consumed fewer seeds of Canada milk-vetch than un-parasitized larvae, thus having a direct effect on the size of the seed crop.

The snout weevil *Tychius liljebladi* Blatchley was collected on flowers of Canada milk-vetch in eastern South Dakota (Kirk and Balsbaugh 1975). However, no reports have been made of its impact on seed production.

Objectives of this research were: (1) obtain an inventory of seed predators of Canada milk-vetch and their parasitoids in eastern South Dakota, (2) determine host-parasitoid associations, (3) discern general life histories and determine frequencies of pod predation for seed predators, and (4) estimate levels of parasitization of the seed predators.

METHODS

Pods of Canada milk-vetch were collected from two populations in eastern South Dakota during July and November of 1999. The populations were located at South Dakota State University's Oak Lake Field Station near Astoria, SD and on the campus of South Dakota State University at Brookings, SD. The Oak Lake population contained several hundred individuals spread over about 2000 m2, whereas the Brookings population was less than 100 individuals spread over about 150 m2. The primary species of the associated vegetation were smooth bromegrass (*Bromus inermis* Leyss.) at Oak Lake and sweetgrass [*Hierochloe hirta* (Schrank) Borbás ssp. *arctica* (J. Presl) G. Weim.] at Brookings.

Canada milk-vetch began flowering during late June. Pod collection during July was when valves of the pods and seeds were well developed but still green. Observations during previous years indicated emergence of insects from pods began during late July.

Several inflorescences collected during July 1999 were placed in covered petri dishes in an air-conditioned laboratory and monitored daily for emergence of immature and adult insects. Larvae of *T. liljebladi* that exited by chewing holes in immature pods were placed on loose moist soil in petri dishes in the laboratory. Adults of *T. liljebladi* were collected as they emerged from the soil about 40 days later. To insure accurate determination of host-parasitiod associations, several parasitoid larvae and their hosts extracted from dissected pods were placed in small vials until parasitoids reached adulthood. Emergent adults and a sample of *T. liljebladi* larvae were collected and preserved in 80 % ethyl alcohol. Careful attention was paid to feeding damage characteristics inside the pods and of the exit holes made by seed predators and parasitoids so that symptoms of insect activity on mature pods collected during November could be accurately attributed to earlier activity of the appropriate species.

During late November 1999, 25 inflorescences were collected at random across each population to determine pod predation and parasitism frequencies for *T. liljebladi* and *A. perforatus*. Ten to 15 pods from each inflorescence were examined for exit holes and dissected to count the number of *A. perforatus* and parasitoid larvae overwintering in the pods. As was done for parasitized larvae of *T. liljebladi* collected during July, several parasitized *A. perforatus* larvae were placed in vials to rear the parasitoid to adulthood for identification. The remaining pods were placed in Whirl Paks and examined during spring 2000 for emergent insects, which were identified, counted, and stored in 80 % ethyl alcohol. In addition, frequency of parasitism of *A. perforatus* larvae was also estimated from bulk pod samples collected from the Brookings population in November 1999 and October 1998. Those samples were placed in rearing containers, and adults were identified and counted as they emerged.

Beginning during early April of 1999 and 2000 and continuing weekly until emergence was complete, we collected samples of the previous growing season's inflorescences to monitor developmental patterns of seed predators that overwintered in the pods. For each collection date, at least 25 pods that contained insects were dissected and the developmental stages of the insects noted. When adult seed predators began to appear on young inflorescences in the field, we initiated periodic observations of their activities on the host plants.

Chi squared analyses were used to test the hypotheses of independence of insect species and location on frequencies of pod predation and parasitization. Indices of dispersion (Ludwig and Reynolds 1988) were calculated and subjected to chi-squared tests to determine if number of seed predators 15 pods-1 inflorescence-1 followed a Poisson distribution (i.e., randomly patterned) in each population.

RESULTS AND DISCUSSION

General aspects of the life histories of seed predators

The seed predators encountered in this study were *A. perforatus* and *T. liljebladi*. *A. perforatus* overwinters as full-grown larvae in cocoons inside pods. *Acanthoscelides perforatus* was previously reported as a seed predator of Canada milk-vetch, but this is the first report of that behavior in *T. liljebladi.*

Larvae of *A. perforatus* were active inside their cocoons by early April. If disturbed, they struck the intruder with their mandibles. Pupation began during early May, and by early June about 50 % of the adults had chewed their way out of their cocoons and were active inside and outside the partially dehisced pods. By mid June all adults had emerged and were active on the flowers of Canada milk-vetch as it came into full bloom during early July. Eggs were generally laid under the calyx of developing pods and were frequently glued to the base of the column of the nine fused stamens in the flower. Larvae typically travelled horizontally under the surface of the pod for a distance of 1-3 mm before boring into the locule and beginning to feed on the seeds. At Brookings we observed several green immature pods that contained 3-4 early instar *A. perforatus* larvae in the same locule and several other pods with two larvae, one usually substantially larger than the other. However in nearly 800 pods examined, we observed only two cases of two full-grown active larvae and only one instance of two cocooned larvae in the same locule. About 6 % of the pods had both locules infested with similar numbers of *T. liljebladi/A. perforatus* and *A. perforatus/A. perforatus* combinations.

Larval development in *A. perforatus* was usually completed by mid August. Larvae generally fed on most or all of the seeds in one locule and frequently bored through the septum and fed on several seeds in the second locule. However, if both locules were occupied by larvae, each fed only in one locule. Larvae completed feeding and enclosed themselves in cocoons by late August. In early maturing ecotypes of Canada milk-vetch, cocoon making began in mid July (Boe, unpublished data).

We are less familiar with various aspects of the life history of *T. liljebladi,* but we observed some general aspects of larval and adult behavior. Adults of *T. liljebladi* were active on flowers at the same time as adults of *A. perforatus*. They often occurred as copulating pairs on the inflorescences in early July. Larvae of *T. liljebladi* grew and developed rapidly. They generally fed in only one locule and exited pods during late July as full-grown larvae by chewing a hole in the immature pod before it dried and dehisced. We observed the behavior of the larvae as they exited pods and dropped on to loose soil in petri dishes in the laboratory. As soon as they contacted the soil, they aggressively used lunging movements to penetrate the soil. On average, it took less than two minutes for them to become buried at a depth of 1.5 cm on the bottom of the petri dish.

General aspects of life histories of parasitoids

All of the parasitioids encountered during this study were ectoparasites belonging to the Chalcidoidea (Hymenoptera). *Tychius liljebladi* was parasitized primarily by *Eurytoma tylodermatis* Ashmead (Eurytomidae) and an unidentified chalcid (Pteromalidae). We reared adults of both species of parasitoids in the laboratory during mid August from pods collected 10 to14 days prior. They exited by chewing holes in the pod wall. All that remained of parasitized *T. liljebladi* larvae was the head capsule and small remnants of the larval skin.

Larvae of *Acanthoscelides perforatus* were parasitized by *Dinarmus acutus* and *Eupelmus vesicularis.* Both parasitioids attacked primarily full-grown larvae in cocoons. In this study, we observed only several instances of *D.acutus* parasitizing larvae of *A. perforatus* that were not in cocoons. However, *D. acutus* has been reported to attack well-developed larvae of *A. perforatus* before they constructed cocoons (Boe et al. 1989). The last (4th) instar of the bruchid *Callosobruchus chinensis* L. was the preferred host stage of *Dinarmus basalis* (Rond.) (Islam 1997). Host age of larvae of *C. chinensis* was shown to affect offspring number and size in *D. basalis* (Islam 1995).

Both *D. acutus* and *E. vesicularis* overwintered as larvae inside the cocoons of *A. perforatus*. Adults of these two parasitoids usually emerged before adults of *A. perforatus* from pods collected in the field and brought into room temperature conditions in the laboratory during the winter. *Dinarmus acutus* and *E. vesicu-*

laris are exotic species (Burks 1979). *Dinarmus acutus* was introduced to control the vetch bruchid (Leong and Dickason 1975). *Eupelmus vesicularis* is one of the most polyphagous of all parasitic chalcids (Burks 1979) and is often hyperparasitic.

We reared a few adults of *E. tylodermatis* and the unidentified pteromalid from cocoons of parasitized *A. perforatus* larvae. However, these species parasitized *A. perforatus* much less frequently than *T. liljebladi.* Examination of remnants of hosts in cocoons indicated *E. tylodermatis* and the pteromalid were primary parasites of *A. perforatus* larvae.

Pod predation and parasitization rates

Total frequency of pod predation was not independent (P<0.001) of population (Table 1). Pod predation frequencies were 42% for the Oak Lake population and 68% for the Brookings population. Pod predation frequencies of individual species were also not independent (P<0.001) of location. At Brookings, 54% of the pods were infested by *A. perforatus,* whereas at Oak Lake the infestation rate was 20%. The opposite pattern was observed for *T. liljebladi*. It infested 17 % of the pods at Brookings compared with 26% at Oak Lake (Table 1). Three percent of the pods were infested with both species at Brookings compared with 4% double occupancy at Oak Lake. In an earlier study at Brookings, Boe et al. (1989) reported a slightly higher level (i.e., 77%) of pod predation by *A. perforatus.*

Table 1. Pod predation frequencies by two seed beetles from two populations of Canada milkvetch in eastern South Dakota during 1999. Frequencies of occurrence of both seed predators in the same pod were 3 % at Brookings and 4 % at Oak Lake.

Population	Uninfested pods (no.)	Pods infested by *T. liljebladi* (no.)	Pods infested by *A. perforatus* (no.)	Total (no.)
Brookings	115	61	194	359
Oak Lake	240	111	83	424

The two species of beetles had similar niches, with the same stage of the life cycle feeding on the same food supply concurrently. There was no indication of strong spatial separation as 4 % of the infested pods contained individuals of both species, albeit usually in separate locules. In one instance we observed a larva of *A. perforatus* feeding on the few seeds that remained after a larva of *T. liljebladi* had completed development and exited the pod. Since 30% of the pods at Brookings and nearly 60% of the pods at Oak Lake were uninfested, an abundance of food may have reduced competition between the two species. Although the two species coexisted in both plant populations, numbers of individuals of each species varied considerably between locations. The Brookings population produced 3.2 times as many *A. perforatus* as *T. liljebladi* larvae. On the other hand, the Oak Lake population had 30% more *T. liljebladi* than *A. perforatus* larvae.

Based on examination of the contents of nearly 800 pods collected during Nov. 1999, we estimated parasitism rates to be significantly (P<0.01) higher for *A. perforatus* than *T. liljebladi* and higher for both species at Brookings (Table 2). However, we determined parasitism frequency of *T. liljebladi* from exit-hole characteristics and larval remnants inside the pod and did not attempt to identify the larvae parasitizing *A. perforatus*. Therefore, those data represent frequencies of parasitism for all parasitoids. For *A. perforatus*, we estimated frequency of parasitism for individual parasitoid species by rearing adult beetles and chalcids from the 25-pod samples collected from both populations during November 1999 and from bulk pod samples collected at Brookings during autumn1998 and 1999 (Table 3). Frequency of parasitism of *A. perforatus* by *D. acutus* and *E. vesicularis* combined was relatively consistent at about 27% for both years. *Dinarmus acutus* and *Eupelmus vesicularis* had the highest parasitism rates, but a few *Eurytoma tylodermatis* and unidentified pteromalid adults were also reared from *A. perforatus* larvae.

Table 2. Parasitism rates (%) for **Tychius liljebladi** ***and*** **Acanthoscelides perforatus** ***based on examination of 783 pods collected during November 1999 from two populations of Canada milk-vetch in eastern South Dakota.***

Population	*T. liljebladi*	*A. perforatus*
Brookings	16	25
Oak Lake	4	20

Table 3. Numbers of seed predators and parasitoids obtained from pods of two populations of Canada milk-vetch in eastern South Dakota.

Population	A. perforatus	*D. acutus*	*Eupelmus vesicularis*	*Eurytoma tylodermatis*	Unidentified Pteromalidae
Brookings 1998 Bulk	107	35	4	3	0
Brookings 1999 Bulk	122	41	3	4	4
Brookings 1999	169	41	14	1	2
Oak Lake 1999	72	9	15	0	2

Distribution of *A. perforatus* among inflorescences (Table 4) followed a Poisson distribution at Brookings and a clumped pattern at Oak Lake. This might be expected since numbers of beetles inflorescence-1 was over two times greater at Brookings than Oak Lake. The distribution pattern of *T. liljebladi* among inflorescences was clumped in both populations.

Table 4. Means, variances (Var.), and indices of dispersion (ID) for number pods inflorescence-1 infested by Tychius liljebladi and Acanthoscelides perforatus in two populations of Canada milk-vetch.

Population	*T. lijebladi*			*A. perforatus*		
	Mean	Var.	ID	Mean	Var.	ID
Brookings	2.3	6.6	2.9	7.4	6.4	0.9
Oak Lake	3.7	11.2	3.0	3.2	9.3	2.9

SUMMARY

Several previously unreported host-parasitoid associations were observed. *Eupelmus vesicularis* was a primary parasitoid of *Acanthoscelides perforatus* larvae and *Eurytoma tylodermatis* and an unidentified pteromalid were primary parasitoids of *Tychius liljebladi* larvae in pods of Canada milk-vetch in eastern South Dakota. We also observed low frequency of an unidentified pteromalid parasitizing *A. perforatus.*

New information was obtained for general life history characteristics of *T. liljebladi* and *A. perforatus.* Adults of both species were active on Canada milk-vetch plants from bud through completion of pod set. Larvae of *T. liljeladi* generally fed in only one locule of a pod and exited the pod to pupate in the soil during late July. Larvae of *A. perforatus* fed inside pods until mid to late August and overwintered in cocoons inside pods. Parasitism occurred externally on later instars of *T. liljebladi* and on the last instar of *A. perforatus*.

Total frequency of pod predation was not independent of plant population and ranged from 42 to 68 %. Frequency of pod predation by individual species was also not independent of plant population. *A. perforatus* had a higher rate of pod infestation (54 vs. 20 %) at Brookings, whereas *T. liljebladi* had a higher rate of pod infestation (26 vs. 17 %) at Oak Lake.

Mean parasitism rates, averaged across plant populations, were higher for *A. perforatus* (22 %) compared with *T. liljebladi* (10 %). However, greater variability in frequency of parasitism of *T. liljebladi* was found between plant populations.

Both of the primary parasitoids of *A. perforatus* encountered in this study were exotics. *Dinarmus acutus* was introduced to control other species of Acanthoscelides in introduced legumes (Leong and Dickason 1975) and *Eupelmus vesicularis* is a generalist with a wide range of hosts in the Hymenoptera and Coleoptera (e.g., Burks 1979). Whether or not these exotics are displacing native parasitoids is unknown and worthy of investigation. Most bruchid beetles (Bruchidae) native to North America are parasitized by native parasitoids (Center and Johnson 1976).

Distribution of *T. liljebladi* was clumped in inflorescences of both plant populations. Distribution of *A. perforatus* was clumped at Oak Lake, but random at Brookings. Density of *A. perforatus* larvae was more than two times greater at Brookings compared with Oak Lake.

The two species of beetles appeared to have very similar niches. They fed on the same food supply at the same time, sometimes coexisting in the same pod. However, they were parasitized, for the most part, by different species.

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