Comparative Life Histories of *Sennius* (Coleoptera: Bruchidae)[1]

TED D. CENTER[2] AND CLARENCE D. JOHNSON[3]

Department of Biological Sciences, Northern Arizona University, Flagstaff 86001

ABSTRACT

Studies were made of the behavior of *Sennius morosus* (Sharp), *S. simulans* (Schaeffer), *S. medialis* (Sharp), and *S. fallax* (Boheman). The behavior of these closely related seed beetles was modified greatly because of the nature of the pods and seeds of their host plants. All five host plants had dehiscent pods. Those plants with many small seeds were attacked before the fruits matured; a beetle larva consumed several seeds and pupated inside the fruit. The plants with larger seeds were attacked at or near maturity; the beetle larva fed and pupated inside one seed. Those species of seed beetles that oviposited on immature, still expanding pods, produced eggs with strands which attached them to the substrate. Presumably these strands are a modification to allow eggs to adhere to an expanding pod.

Seeds of the genus *Cassia* (Leguminosae) are fed upon by several species of seed beetles, most of which are in the genus *Sennius*. We have noted variations in the breeding behavior in species of several other genera of the Bruchidae and have recently been trying to interpret this behavior. Here we report the results of a study of the breeding behavior of 4 closely related species of beetles that attack 5 species of closely related plants. Before our study, it was our hypothesis that these seed beetles would be related not only in their morphology but in their habits. The results of our study refute this hypothesis. The study of *Sennius* was feasible because studies of the beetles have recently been published (Johnson and Kingsolver 1973), and host data are available.

Methods

Fourteen lots of seeds of 5 species of *Cassia* (Table 1) were collected from Mexico and Arizona from 1968 to 1972. The seed beetles were reared, and as many aspects as possible of their ovipositional, feeding, and pupational behavior were observed.

Results

Sennius morosus *(Sharp) in Seeds of* Cassia bauhinioides

Seeds were collected 2 mi. SW Beaver Creek Ranger Station, Yavapai County, Ariz. in 1970 on June 22 and 27; July 8, 26, and 30; Aug. 6; Sept. 26; and Jan. 10, 1971.

Eggs and Larvae.—One side of the egg is cemented to the immature pod parallel to the grooves along the line of dehiscence. Each egg is surrounded by numerous anchoring strands similar to those described for *Merobruchus julianus* (Horn) on *Acacia greggii* by Forister and Johnson (1970).

After burrowing from the egg and through the wall of the pod, the small larva attacks a single seed but, unlike most bruchids, after it has almost devoured the 1st seed it burrows directly into an adjacent seed. Up to 8 seeds may be fed upon by one larva, although the usual number is 3 or 4. Again, unlike most bruchids, *morosus* glues together the seeds it has partially consumed (Fig. 1, 2). There is a feeding cavity within the seeds which is made by the larva. The glue which holds the seeds together is very hard when dry and appears to contain masticated parts of the seed.

In these clusters of seeds there is a gradation of seed size from the first seed attacked to the last (Fig. 1a) because the fruit is apparently not mature when the larvae first start to feed upon seeds. The seeds in which the entry holes were situated were less mature when they were entered than were the adjacent seeds.

The pods of *C. bauhinioides* normally remain attached to the plant for some time, and when the pods dehisce the seeds fall out. The seeds aggregated by *S. morosus*, however, remain inside the pod (Fig. 2). Johnson (1968) investigated a similar phenomenon in *Acacia berlandieri* seeds fed upon by *M. julianus*. He found that the larvae glue the seeds to the pod valve. When the seeds are attached to one another by the larva of *morosus*, the pod septa are held in between the seeds by the same substance that holds the seeds together, which thus prevents the seeds from falling from the pod. Because Janzen (1971) reported that palm seeds on the ground beneath the parent tree contained bruchids that had been killed by a microbial disease and that the litter beneath the tree probably harbors this pathogen, we feel that one of the possible favorable effects of retaining the seeds in the fruit for the larvae and pupae of *morosus* would be to keep them away from the detrimental effects of pathogens on the ground. As for the plants, selection would undoubtedly favor those whose pods dehisced immediately after the seeds were mature and before they were all infested. This would allow at least some of the seeds to be dispersed, and probably only those that fell to the ground would be free of bruchids.

Pupation and Emergence.—The seed cluster consists of a series of seed coats stuck together, with a large central chamber which eventually becomes the pupal chamber. A pupal cocoon is not spun by *morosus*.

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[2] Present address: Department of Entomology, University of Florida, Gainesville.

[3] Coauthors.

Table 1. — Seed and pod characteristics of some species of *Cassia*.

	bauhinioides	*leptadenia*	*leptocarpa*	*occidentalis*	*polyantha*
Length of pod	2–3 cm	1.2–3.9 cm	9.5–23 cm	10.2–11.5 cm	ca. 11 cm
Pods dehiscent	yes	yes	yes	yes	yes
Septa between seeds	yes	yes	yes	yes	no
Pod breaks into numeral-seeded sections	no	no	no	no	yes
No. seeds/pod	20–30	5–11	40–65	49–53	ca. 12
Ca. size of mature seeds	3×2.5×1.5 mm	2×2×1 mm	2.5×3×2.5 mm	4×3.5×1.75 mm	7.5×5×2 mm
Infesting species of *Sennius*	*morosus*	*simulans*	*medialis*	*fallax*	*fallax*

Johnson (1968) mentioned that adults emerging from the seeds through the valves of a dehiscent pod is unusual. Examination of more than 50 infested dehiscent pods of *C. bauhinioides* in nature revealed that more than half of the bruchids emerged through the seed into the pod cavity and then out between the open valves. The others emerged through the seed and directly through a pod valve.

Several authors have noted that seed shape and size are related to the shape and size of the adult bruchid (Bridwell 1931, Johnson 1970). Johnson observed that those bruchids whose larvae infest a single seed and entirely devour its contents are limited in size by the size of the seed. In the case of *S. morosus* the size of the adult seems to be regulated by the number of seeds in which it develops. The maximum size apparently can be reached in a minimum of 3 seeds. The only individual of *morosus* that was observed to develop from a single seed measured 2.8 mm in length (avg size 3.5 mm). No difference in size was noted between those bruchids that emerged from a 3-seed cluster and those that emerged from a cluster of 6 or 7 seeds. The average adult *morosus* which develops in 3 or more seeds is about 3.5 mm long. A cluster of 3 seeds is about 3.8 mm to 4.0 mm long.

Life Cycle.—The life cycle seems to follow a bivoltine pattern. The emergence of the overwintering individuals occurs in mid-July. These mate and lay eggs shortly after. The 1st-generation adults, which must emerge in early to mid-September, mate and lay eggs. Because adults were found inside seed clusters collected Jan. 10, 1971, it is reasonably certain that the 2nd generation is the overwintering generation and overwinters in the adult stage.

Sennius simulans (*Schaeffer*) *in Seeds of* Cassia leptadenia

Seeds were collected in Carr Canyon, Oct. 9, 1971, and Ramsey Canyon, Oct. 6, 1972, Huachuca Mountains, Cochise County, Ariz.

The eggs laid on the green pods by *simulans* have anchoring strands surrounding them that are similar to those of *morosus*. After the larvae burrow through the pod wall, they consume several immature seeds during their development. They then pupate inside the pod among the frass and fragments of the seeds that they have consumed. There is no evidence of a cocoon being produced.

Those pods whose seeds are attacked by *simulans* open only slightly when they dehisce as opposed to most pods, which split open and allow most seeds to fall out. There is no evidence that the insect produces materials to hold either pod valves or seeds together. The adult apparently exits from the pod through the slightly opened valves as there were no exit holes found in the pod valves of these samples. There were 2 exit holes of parasites found in the pod valves. These pods had not dehisced.

Sennius medialis (*Sharp*) *in Seeds of* Cassia leptocarpa

Seeds were collected in Carr Canyon, Huachuca Mountains, Cochise County, Ariz., Oct. 9, 1971, and Oct. 6, 1972.

The eggs of *medialis* are glued singly or in clusters containing up to 6 eggs along the seam between the pod valves. Some of the eggs have 2 elongate anchoring strands at each end. Most of the larvae enter a septum between seeds after passing through the pod walls.

Each larva penetrates a seed, devours it almost entirely, then pupates inside the intact seed coat. Only a small amount of frass remained inside seeds after the adults emerged through a typical round exit hole in the seed. Cocoons were not found inside these seeds. The adults apparently emerged through the open pod valves, since no holes were found in these structures.

Sennius fallax (*Boheman*) *in Seeds of* Cassia occidentalis *and* C. polyantha

Seeds were collected in Mexico: 11 miles SE Huajuapan de Leon, Oaxaca, July 7, 1968 (*polyantha*), and one mile S Rosamorada, Nayarit, July 12, 1968 (*occidentalis*).

Unlike *medialis, morosus,* and *simulans,* which attach their eggs to the seed pods, *fallax* glues its eggs directly onto the seeds after the pod had dehisced. No anchoring strands have been observed on these eggs. The 1st-stage larvae burrow directly from the egg into the seed. The entire larval life is spent inside a single seed where it pupates. The adult then emerges through the seed coat. The larva does not spin a cocoon inside the seed. Only one larva develops inside a seed of *occidentalis*. Because the seeds of *polyantha* are larger, a single seed often supports the development of two *fallax* larvae. Sometimes seeds of *polyantha* containing bruchids are glued to the pod valves.

Discussion

It is of interest to compare the seed and pod characteristics of host species of *Cassia* (Table 1) with the modes of life histories evolved by the bruchids that feed upon their seeds (Table 2). We suspect that the characteristics of both plants and insects result from a long coevolution between host and predator, but that is not our primary concern here. We show here how the traits of oviposition, larval feeding behavior, and pupation in 4 species of closely related seed beetles have evolved to fit particular characteristics of 5 species of their host plants.

Oviposition

S. morosus and *S. simulans* both oviposit on green, still growing seed pods of *Cassia bauhinioides* and *C. leptadenia,* respectively. Both bruchids cement eggs to a pod with strands of glue radiating out from each egg. We feel that the strands are an ovipositional modification to prevent the sloughing off of the egg from a green, still growing pod (Forister and Johnson 1970).

Table 2. – Behavioral characteristics of 4 species of *Sennius*.

	morosus	*simulans*	*medialis*	*fallax*
Oviposition				
On pod	x	x	x	
On seed				x
Glued	x	x	x	x
With strands	x	x		
Feeding				
Consumes 1 to several seeds	x	x		
Consumes 1 seed only			x	x
Pupation				
Outside 1 seed	x	x		
Inside 1 seed			x	x

FIG. 1.—Seed cluster made by *S. morosus* in a pod of *C. bauhinioides.* Note the gradation in age and size of seeds. a, entry hole of 1st instar in an immature seed; b, exit hole of an adult in a mature seed (8×).

FIG. 2.—Seed pod of *C. bauhinioides* showing seed clusters attached to pod septa by *S. morosus.* a, pod septum; b, adhesive material between seeds (8×).

S. medialis and *S. fallax* both cement their eggs to the substrate, but their eggs may have only about 4 (*medialis*) or they may completely lack anchoring strands. The apparent reason for the few or lack of anchoring strands seems to be that these species oviposit on well developed pods (*medialis*) and seeds (*fallax*) which are no longer expanding.

It can be seen that 2 kinds of ovipositional behavior have been evolved in closely related bruchids, apparently in response to characteristics peculiar to different host plants.

Larval Feeding Behavior

The relatively small seeds of *C. bauhinioides* and *C. leptadenia* are apparently most often too small for a single bruchid to develop inside them (*S. morosus* in *C. bauhinioides* is an occasional exception) so one bruchid consumes several seeds. Because only green seeds are fed upon by *morosus* and *simulans,* the mature, hard seed coats or some other factor in the mature seeds must deter the bruchids.

S. medialis and *S. fallax* feed upon seeds that are larger and more mature, although the seeds of *C. leptocarpa* are almost too small, as the insides are almost completely consumed by *medialis. S. fallax* can adapt to feeding in only one relatively small seed (*C. occidentalis*), or 2 of its larvae may feed inside the relatively large seeds of *C. polyantha.*

Pupation

An aggregation of seeds glued together makes up the pupal chamber of *S. morosus,* while *S. simulans* pupates among the fragments of seeds left from larval feeding. The pupal chamber of *morosus* is cemented to the inside of the pod. The pods of *C. leptadenia* that have pupae in them do not open widely when the pod dehisces. The end result is the same for both species—individuals of neither species are dropped to the ground. Probably these mechanisms to retain the pupa inside the pods evolved along with the habit of feeding on several small seeds. Other species (e.g., *Caryedon gonagra* (F.) (Davey 1958), have evolved another method of finding a place to pupate. They spin a cocoon outside the pod. Pupating inside one seed is apparently a behavioral mechanism evolved to offset the necessity for spinning a cocoon, as the seeds of *C. leptocarpa, C. occidentalis,* and *C. polyantha,* containing pupae of *S. medialis* and *S. fallax,* fall from the pod soon after dehiscence. These 2 species use their feeding chamber as a pupal chamber but do not spin a cocoon.

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