

## COEVOLUTION OF SOME SEED BEETLES (COLEOPTERA: BRUCHIDAE) AND THEIR HOSTS<sup>1</sup>

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*Abstract.* Original observations and a review of the literature revealed many adaptations evolved in seed beetles (Bruchidae) to circumvent the defenses of leguminous plants against seed-feeding insects. Analysis was based on 38 bruchid species and 44 species of host plant. In response to seed toxicity the beetles either avoid the toxins or develop a resistance to them. If the plant produces a greater number of seeds a beetle is apt to feed on several seeds during its life. Other defenses such as rapid dehiscence of the pod, special characteristics of the husk, synchronization of seed set, and special characteristics of the seeds are also circumvented by the Bruchidae. This pattern of coevolution probably rarely allows the host plant to entirely exclude the seed predators.

*Key words:* Bruchidae; coevolution; feeding behavior; host plants; legume seeds; Leguminosae; life histories; seed beetles; seed predators.

### INTRODUCTION

The seed beetles (Bruchidae) are best known for their habits of attacking the seeds of cultivated legumes. Several species, however, feed in the seeds of wild Leguminosae and about 30 other families of plants. Females oviposit on fruits (pods) or seeds. The larvae feed inside a seed or seeds, and then pupate inside one seed or in a protected place. These insects are, for the most part, highly host-specific.

In several recent papers Janzen (1969, 1971a, b, c, 1972) discussed some possible evolutionary responses of plants to seed predation by seed beetles. Janzen's emphasis was on the development of protective devices by the host plants but he stated (1969:18) that "virtually all [defensive traits] seem effective against at least one species of bruchid but only rarely against all bruchids." This phenomenon is our concern here. We give examples of some bruchid traits that have apparently evolved in counteracting the defensive mechanisms of plants.

### METHODS

From 1968 to 1972 we collected 58 lots of seeds of 19 species of plants from California, Arizona, and northern Mexico, from which we reared 13 species of bruchids. We isolated a sampling of seeds from each lot by placing individual seeds, pods, or seed clusters in gelatin capsules. After emergence of the adult bruchid we dissected the seed and pod to determine the location of the pupal chamber, the path of the larva through the seed, the number of seeds fed upon, the point of entry through the pod and seed coat, the oviposition site, and the mode of egg

attachment. Characteristics of the seeds and pods were also examined. Our findings from 13 species of bruchids were compared with similar information published on other species of Bruchidae (Table 1). In all, we compared traits from 38 species of bruchids and 44 species of host plants.

### RESULTS AND DISCUSSION

Our study showed that (1) the substrate on which oviposition occurred was more often the pod than the seed; (2) although about two-thirds of the bruchids fed hidden inside a single seed then pupated there, about one-third consumed one seed almost completely or fed on several seeds, then pupated outside of a seed; (3) 75% of the host plants had indehiscent or tardily dehiscent pods and 25% had dehiscent pods; and (4) 11% of the plants had only one-seeded pods while the remainder had an average of more than one seed per pod. Table 1 summarizes these traits of the bruchids and their host plants.

#### *Seed toxicity*

Janzen (1969) found that of the 36 species of plants he studied, those that were free from bruchid infestation had toxic deterrents in their seeds. The one plant he cited without toxins and not fed upon, *Indigofera suffruticosa*, has since been found to have its seeds eaten by bruchids (Table 1, No. 6; Johnson 1973).

Several species of toxic seeds are attacked by bruchids. Trelease and Trelease (1937) and Johnson (1970) cite collectively numerous examples of species of *Astragalus* which have poisonous seeds and are fed upon quite commonly by several species of the seed beetle genus *Acanthoscelides*. Seeds of species in the genera *Erythrina*, *Abrus*, *Dioclea*, and *Sarothamnus* which are known to contain toxins are

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TABLE 1. Traits of some Bruchidae and their host plants

Bruchid	Oviposition		Feeding		Pupation		Host plants	Pods		Seeds		References
	On pod	On seed	Eats one seed completely or feeds upon several seeds	Feeds inside one seed only	Outside one seed	Inside one seed		Dehiscent	Tardily dehiscent or indehiscent	One seed/pod	Several seeds/pod (2-90)	
1. <i>Acanthoscelides alboscuteallatus</i>			×		×		<i>Ludwigia alternifolia</i>	?		×		Hamilton 1892.
2. <i>A. collusus</i>	×			×		×	<i>Errazurizia rotundata</i> <i>Parryella filifolia</i>	×		×		
3. <i>A. compressicornis</i>	×		×		×		<i>Desmanthus cooleyi</i> <i>Hoffmanseggia drepanocarpa</i>	×		×		
4. <i>A. fraterculus</i>	×		×		×		<i>Astragalus mollissimus</i> <i>Lotus mearnsii</i>		×		×	
5. <i>A. guazumae</i>				×		×	<i>L. crassifolius</i> <i>Guazuma tomentosa</i>	×		×		Johnson and Kingsolver 1971.
6. <i>A. kingsolveri</i>	×			×		×	<i>Indigofera suffruticosa</i> <i>I. sphaerocarpa</i>	×		×		
7. <i>A. lobatus</i>	×		×		×		<i>Astragalus troglodytus</i>	×		×		
8. <i>A. obtectus</i>		×		×		×	<i>Cajanus</i> sp., <i>Phaseolus</i> sp., and <i>Vigna</i> sp.	×		×		Lukianovich and Ter-Minasian 1957, Skaife 1925, 1926, Teixeira Constantino 1956, Bondar 1937, Larson and Fisher 1938.
9. <i>A. submuticus</i>	×			×		×	<i>Amorpha fruticosa</i>	×		×		
10. <i>Amblycerus guazumicola</i>			×		×		<i>Guazuma tomentosa</i>	×		×		Johnson and Kingsolver 1971.
11. <i>A. nigromarginatus</i>	×		×		×		<i>Cassia</i> spp.			×		Bondar 1931c, 1937.
12. <i>Bruchidius baudoni</i>		×		×		×	<i>Acacia arabica</i> <i>A. nilotica</i>	×		×		Peake 1952. Prevett 1967a,b.
13. <i>B. natalensis</i>	×		×		×		<i>Acacia sieberiana</i>			×		Prevett 1967a,b.
14. <i>B. schoutedeni</i>		×					<i>Sesbania pachycarpa</i>	×		×		Prevett 1967a,b.
15. <i>B. strangulatus</i>	×		×		×		<i>Crotalaria</i> spp.			×		Prevett 1967a,b.
16. <i>Bruchus brachialis</i>	×			×		×	<i>Vicia villosa</i>	×		×		Bridwell and Bottimer 1933.
17. <i>B. pisorum</i>	×			×		×	<i>Pisum</i> sp.	×		×		Skaife 1926, Zacher 1930, Brindley et al., 1946.
18. <i>B. rufimanus</i>	×			×		×	<i>Vicia faba</i>			×		Middlekauff 1951.
19. <i>Callosobruchus chinensis</i>	×	×		×		×	<i>Pisum</i> sp. and <i>Vigna</i> sp.			×		Skaife 1925, 1926, Howe and Currie 1964.
20. <i>C. maculatus</i>	×	×		×		×	<i>Vigna</i> sp., <i>Soja</i> sp., <i>Cajanus</i> sp., <i>Lens</i> sp., <i>Cicer</i> sp., <i>Lathyrus</i> spp., <i>Vicia</i> spp., <i>Pisum</i> spp., <i>Phaseolus</i> spp., and <i>Dolichos</i> sp.			×		Skaife 1926, Bondar 1937, Larson and Fisher 1938, Howe and Currie 1964.

TABLE 1. (Continued)

Bruchid	Oviposition		Feeding		Pupation		Host plants	Pods		Seeds		References
	On pod	On seed	Eats one seed completely or feeds upon several seeds	Feeds inside one seed only	Outside one seed	Inside one seed		Dehiscent	Tardily dehiscent or indehiscent	One seed/pod	Several seeds/pod (2-90)	
21. <i>Caryedes brasiliensis</i>	×			×		×	<i>Dioclea megacarpa</i>	×		×		Janzen 1971b, Bondar 1931a.
22. <i>C. germaini</i>	×			×		×	<i>Parkinsonia aculeata</i>	×		×		Teran 1962.
23. <i>C. grammica</i>	×			×		×	<i>Canavalia obtusifolia</i>				×	Bondar 1931a.
24. <i>Caryedon gonagra</i>	×	×	×		×		<i>Arachis hypogaea</i>	×		×		Stebbing 1914, Bridwell 1918, Davey 1958, Prevett 1966.
25. <i>Eubaptus rufithorax</i>	×		×		×		<i>Ruellia lorentziana</i>	?			×	Teran 1967.
26. <i>Merobruchus julianus</i>	?		×		×		<i>Acacia berlandieri</i>	×			×	Johnson 1968.
	×			×		×	<i>A. greggii</i>	×			×	Forister and Johnson 1970, Forister 1970.
27. <i>Pseudopachymerina lallemanti</i>	×			×		×	<i>Acacia caven</i>	×			×	Bondar 1937, Teran 1962.
28. <i>Pygiopachymerus lineola</i>	×			×		×	<i>Cassia grandis</i>	×			×	Janzen 1972.
29. <i>Rhaebus mannerheimi</i>	×			×		×	<i>Nitraria schoberi</i>	×	×			Lukianovich and Ter-MinAsian 1957.
30. <i>Sennius fallax</i>		×		×		×	<i>Cassia occidentalis</i>	×			×	
							<i>C. polyantha</i>	×			×	
31. <i>S. medialis</i>	×			×		×	<i>Cassia leptocarpa</i>	×			×	
32. <i>S. morosus</i>	×		×		×		<i>Cassia bauhinioides</i>	×			×	
33. <i>S. simulans</i>			×		×		<i>Cassia leptadenia</i>	×			×	
34. <i>Stator pruininus</i>		×		×		×	<i>Calliandra eriophylla</i>	×			×	
35. <i>S. pygidialis</i>		×		×		×	<i>Calliandra humilis</i>	×			×	
36. <i>Specularius erythrinae</i>		×		×		×	<i>Erythrina abyssinica</i> and <i>E. variegata</i>	×			×	Bridwell 1938.
37. <i>Zabrotes interstitialis</i>		×		×		×	<i>Cassia grandis</i>	×			×	Janzen 1972.
38. <i>Z. subfasciatus</i>		×		×		×	<i>Phaseolus</i> sp.	×			×	Bondar 1931c, Zacher 1930, Howe and Currie 1964.
Total	22 <sup>a</sup>	9 <sup>a</sup>	13	25	13	25		9	27	5	39	
Percent	62 <sup>a</sup>	26 <sup>a</sup>	34	66	34	66		25	75	11	89	

<sup>a</sup> Does not include those bruchids that oviposit on both seeds and pods.

also eaten by bruchids (Janzen 1971c). Rotenone in the seeds of *Cracca virginiana* has no ill effect upon the larvae of *Acanthoscelides obsoletus* (Bridwell 1938).

Brett (1946) reported that the toxin "amorpha,"

which occurs in pods of *Amorpha fruticosa*, acted as both a stomach and contact insecticide. He determined this substance to be much more abundant in glands (or "pustules") scattered over the surface of the fruit. The seeds of the plant apparently con-

tain little or no toxins. The one-seeded, indehiscent fruits of *A. fruticosa* are used as food by at least three species of bruchids. We found that one of these species, *Acanthoscelides submuticus* (Table 1, No. 9), oviposited into the space between the calyx and the pod surface. After eclosion the larvae then emigrated from under the calyx to glands on the pod surface and entered the seed through these glands. Because these seeds are commonly infested by bruchids it is apparent that the bruchids are in some way circumventing "amorpha." Apparently *A. submuticus* has developed a physiological means to resist this toxin because it does contact, and perhaps consume, the toxin.

*Acanthoscelides collusus* (Table 1, No. 2) is known to feed in the seeds of *Amorpha fruticosa* as well as in the two host plants that we studied, *Parryella filifolia* and *Errazurizia rotundata*. The three plants are closely related and have similar pods with many pustules (glands) on their surfaces. All three have a similar aromatic odor and are reported to have insecticidal properties (Kearney and Peebles 1960). It seems probable that *P. filifolia* and *E. rotundata* concentrate toxins in glands on their fruits as does *Amorpha fruticosa*. The eggs of *Acanthoscelides collusus* are glued directly to the pod surface or wedged between the calyx and pod surface. We found that first-instar larvae of *A. collusus*, unlike *A. submuticus*, enter through the pod surfaces rather than through glands of *P. filifolia* and *E. rotundata*. We believe this to be a different kind of evolved mechanism: avoidance of the toxin. Because 62% of the species in Table 1 oviposited on pods rather than seeds, more deterrents to the bruchids might be expected in the pod walls than in the seeds; in this case, however, the bruchids seem to have circumvented the pod toxins.

All of these examples we interpret as a specific bruchid's having evolved a resistance to a specific toxin; that is, each bruchid would probably be susceptible to toxins found in seeds of plants other than its hosts.

#### *Predator satiation*

Janzen (1969) suggested that the plants had evolved another strategy, which he termed "predator satiation"; it involves a set of adaptations. By producing smaller seeds the plant is able to produce a greater number of seeds. Hence, seed size and number are complementary phenomena. Synchronization of seed set is another adaptation that may be considered a part of this strategy. The production of many small seeds allows them to be dispersed rapidly before total infestation can occur. Seed mortality is very high and the small seeds with little reserves of

energy have a reduced chance of survival even if they do escape.

The problem for the bruchids, then, was to counter this increase in seed number, gradual reduction in seed size, and rapidity of dispersal with an evolutionary strategy of their own. The bruchids feeding in seeds of plants gradually evolving the strategy of producing more and smaller seeds must either (1) feed on more seeds, (2) become smaller themselves, (3) move to a different host with seeds of a suitable food quality and quantity, or (4) become extinct. We think we have observed several kinds of behavioral responses of alternatives (1) or (2) which the bruchids have probably evolved in response to the strategy of predator satiation.

It is known that the size of many species of bruchids depends on the size of the seed in which it develops (e.g., *Acanthoscelides aureolus* in *Astragalus* spp. is usually much larger than when in the smaller seeds of *Lotus scoparius*, Johnson 1970). Because of this plasticity, a reduction in seed size does not preclude bruchid infestation. *Sennius morosus* normally feeds on a seed cluster. When only one seed is available it still develops fully but does not attain normal adult size. Whether these smaller adults are as fecund and able to compete as the larger individuals is a matter for further investigation. The reduction of adult size in response to food quantity may not be an evolutionary response but this ability certainly enables the species to survive a reduction in seed size (*Acanthoscelides guazumae*, *Sennius medialis*, Table 1, Nos. 5, 31).

Probably a more common bruchid evolutionary reaction to the strategy of predator satiation is that one larva utilizes almost the entire seed instead of only a small portion (e.g., *Acanthoscelides compressicornis*) or that one larva feeds on several seeds. Of the species studied 34% were in one of these categories (Table 1).

Most bruchid larvae that feed on only one seed pass through the seed coat upon entry and exit from the seed leaving a large portion intact. An *Acanthoscelides compressicornis* (Table 1, No. 3) larva, however, devours only one seed almost completely, leaving only bits of the seed coat. The larva then spins a fragile cocoon amongst the remnants of the seed it devoured.

The larvae of four of the species we studied fed upon more than one seed during their development (*Acanthoscelides fraterculus*, *A. lobatus*, *Sennius morosus*, and *S. simulans*) and this behavior has been reported by several other authors in other species of Bruchidae (Table 1, Nos. 4, 7, 32, 33).

If a larva feeds on several seeds then it must build a pupal chamber outside of a single seed. *Caryedon gonagra* (Davey 1958) and *Acanthoscelides*

TABLE 2. Traits of Leguminosae that may be functional in eliminating or lowering bruchid destruction of seeds, and a summary of some corresponding adaptations of bruchids to circumvent these plant defenses

Plant defense (after Janzen 1969)	Bruchid adaptation
1. Gum production by seed pods following penetration of first larva from egg mass; this may push off remaining eggs (Bridwell 1920a, <i>Prosopis juliflora</i> ) or drown or otherwise obstruct young larvae (Hinckley 1960) ( <i>Acacia</i> , <i>Pithecolobium</i> , <i>Cassia</i> ).	A period of quiescence in embryonic development in the egg until seed maturation is completed (Pevett 1966, <i>Caryedon albonotatum</i> ). Resistance to these gummy fluids ( <i>Acanthoscelides submuticus</i> , <i>Algarobius prosopis</i> ). Eggs laid singly instead of in clusters (many species).
2. Dehiscence ( <i>Leucaena</i> ), fragmentation ( <i>Mimosa</i> ) or "explosion" ( <i>Canavalia</i> ) of pods, scattering the seeds to escape from larvae coming through the pod walls and from ovipositing females (Cushman 1911, Bridwell 1918).	Oviposition on seeds only after they have been scattered ( <i>Caryobruchus buscki</i> , <i>Pachymerus</i> sp., Janzen 1971a; <i>Acanthoscelides obtectus</i> , <i>Callosobruchus maculatus</i> , Larson and Fisher 1938; <i>Stator pygidialis</i> ). Attachment of seeds to one another or to the pod valve ( <i>Merobruchus julianus</i> , Johnson 1968; <i>Sennius morosus</i> ).
3. Production of a pod free of surface cracks ( <i>Bruchus prosopis</i> oviposits only in cracks on <i>Prosopis juliflora</i> and cannot glue its eggs to smooth surfaces as do many other Bruchidae, Bridwell 1918).	Oviposition into the soft fleshy exocarp ( <i>Acanthoscelides compressicornis</i> ). Chewing holes in the pod walls by the female in which to oviposit ( <i>Acanthoscelides obtectus</i> , <i>Pygiopachymerus lineola</i> , Janzen 1972). Gluing the eggs to the pod surface ( <i>Bruchus</i> , <i>Mimosestes</i> , <i>Caryedon</i> ).
4. Indehiscent pods, excluding those species that deposit only on exposed seeds ( <i>Stator pruininus</i> on <i>Prosopis juliflora</i> when pods opened artificially, Bridwell 1918).	Attachment of the eggs by anchoring strands to allow for substrate expansion ( <i>Merobruchus julianus</i> , Forister and Johnson 1970; <i>Sennius morosus</i> , <i>S. simulans</i> ). Entry of the larva through the pod into the seed before the pod opens (Bridwell 1918).
5. A layer of material on the seed surface that swells when the pod opens and detaches the attached eggs ( <i>Bauhinia monandra</i> , Bridwell 1918).	Mechanisms for avoidance and detoxication. Loss of inhibitable endopeptidases (Applebaum 1964).
6. Poisonous or hallucinogenic compounds such as alkaloids, saponins, pentose sugars, and free amino acids (Bridwell 1918, Farnsworth 1968, Howe and Currie 1964, Applebaum 1964, Applebaum et al. 1965, Ishii and Urushibara 1951, Bell, <i>pers. comm.</i> ).	Oviposition beneath the flaking exocarp ( <i>Acanthoscelides fraterculus</i> ). Rapid embryonic development or feeding on immature seeds to enter the pod before flaking occurs. Oviposition under the calyx away from the pod surface ( <i>Acanthoscelides collus</i> , <i>A. submuticus</i> ).
7. Rich endopeptidase inhibitors, making digestion of the bean by the bruchid very difficult (Applebaum 1964).	Entry and feeding upon immature seeds ( <i>Bruchus</i> , <i>Algarobius</i> , <i>Mimosestes</i> ). Delay of embryonic maturation until seeds are mature ( <i>Caryedon albonotatum</i> , Pevett 1966).
8. Flaking of seed pod surface which may remove eggs laid on that surface (several swollen-thorn acacias).	Utilization of the seed contents more completely ( <i>Acanthoscelides compressicornis</i> ). Feeding on several seeds (several species).
9. Immature seeds remaining very small throughout the year and then abruptly growing to maturity just before being dispersed ( <i>Acacia</i> ).	
10. Seeds so thin that bruchids cannot mature in them ( <i>Cassia siamea</i> , Bridwell 1918).	
11. Seeds so small that bruchids cannot mature in them (many wild herbaceous legumes).	

*fraterculus* (Table 1, Nos. 24, 4) are known to leave the pod to spin a cocoon. More often, however, in most species that consume several seeds, the cocoon is constructed inside the pod. Apparently the reduction in seed size has affected both the larval behavior and pupational behavior.

We have noted a unique behavior that includes feeding on several seeds but appears also to be a response to rapid dehiscence of seed pods. *Sennius morosus* (Table 1, No. 32) larvae glue several seeds to each other and to the pod as they feed upon them. Unattached seeds fall from the dehiscent pod while those glued together remain in the pod and serve as a feeding and pupal chamber. A similar

behavior has been recorded in some species of *Bruchidius* (Pevett 1967a) and *Merobruchus* (Johnson 1968). Possibly these species have responded to an increase in seed number and a reduction in seed size by evolving this method of pupation rather than spinning a cocoon outside seeds.

#### Other seed-protecting traits

Thirty-one "traits of Leguminosae that may be functional in eliminating or lowering bruchid destruction of seeds" were listed by Janzen (1969, Table 2). We have discovered in our own studies, and in the literature, countermechanisms that the bruchids have apparently evolved in response to at

least 11 of these traits (Table 2). Janzen's protective traits are for the most part found in a limited number of species of plants. We will discuss mostly countermechanisms evolved by bruchids that exist in plant species other than those cited by Janzen. Thus, protective traits are apparently functional in some plants but have been overcome by bruchids in others.

A countermechanism to trait 1 (Table 2) may be that which Preveit (1966) reported concerning the eggs of *Caryedon albonotatum* (Pic). It oviposited on the pods of *Acacia nilotica*, which has seeds surrounded "by a gummy fluid." The eggs do not mature for some 2 mo after oviposition. Apparently embryonic development is followed by a period of quiescence. At the end of the 2-mo period "the seeds have enlarged so that, although there is still fluid at the sides of the pod, there is probably little danger to a larva boring straight through to a seed from the region of the septum." Our earlier report of the entry of *Acanthoscelides submuticus* into pods through a gummy material in the surface glands is another example. Larvae of *Algarobius prosopis* are bathed in fluid in *Prosopis* pods and survive (Bridwell 1920b).

One method that bruchids may use to overcome trait 2 is to oviposit on seeds after they have been scattered. Nuts of *Scheelea rostrata* (Palmae) are oviposited upon by *Caryobruchus buscki* and *Pachymerus* sp. after they have fallen to the ground and are cleaned of pulp by rodents (Janzen 1971a, Wilson and Janzen 1972). Beans and cowpeas are oviposited upon while on the ground by *Acanthoscelides obtectus* and *Callosobruchus maculatus* (Table 1, Nos. 8, 20; Larson and Fisher 1938). We have found that *Stator pygidialis* (Table 1, No. 35) oviposits on seeds of *Calliandra humilis* only after they have fallen to the ground. If the pods are more tardily dehiscent, then the attaching of several seeds to one another and to the pod valve by bruchids can keep the seeds from being scattered (i.e., by *Sennius morosus* and *Merobruchus julianus*; Table 1, Nos. 32, 26).

In response to traits 3 and 4, *Acanthoscelides compressicornis* (Table 1, No. 3) is thought to oviposit into the soft, fleshy exocarp of *Desmanthus* spp. Females of *A. obtectus* are known to chew holes in fleshy pods and then oviposit into them, as does *Pygiopachymerus lineola* (Table 1, No. 28) on pods of *Cassia grandis* (Janzen 1972). There are numerous examples of species (*Bruchus*, *Mimosestes*, *Caryedon*) that glue eggs to fleshy pods. All are countermechanisms apparently evolved by bruchids.

Trait 5 is possibly countered by eggs laid with radiating anchoring strands (*Merobruchus julianus*, Table 1, No. 26; Forister and Johnson 1970). We

found that *Sennius morosus* (Table 1, No. 32) also produced eggs with anchoring strands on green pods of *Cassia bauhinioides*, as does *S. simulans* (Table 1, No. 33) on the green pods of *C. leptadenia*. Apparently an egg with anchoring strands will adhere better to a green, still-growing pod. Also if the eggs were laid on the pods and the larvae entered the seeds before the pod dehisced, this plant protective device would not work (Bridwell 1918).

Mechanisms of bruchid avoidance and detoxication of trait 6 were mentioned earlier. Applebaum [1964] states that the presence of endopeptidase inhibitors in many leguminous seeds "could then have been followed in the Bruchidae by the subsequent loss of inhibitable endopeptidases, obligating them to such seeds which contain either a sufficiently high level of initially available peptides or, at the least, containing proteases capable of adding appreciably to this level of integrating with the residual protease activity of the Bruchids." This could be an evolutionary response by the bruchid to trait 7.

Apparently in response to trait 8, *Acanthoscelides fraterculus* (Table 1, No. 4) took advantage of the cracks caused by flaking of the exocarp of pods of *Lotus crassifolius* by ovipositing beneath them. Species of bruchids that have a very rapid embryonic development could enter the pod before flaking occurred. *Acanthoscelides collus* and *A. submuticus* (Table 1, Nos. 2, 9) are known to oviposit beneath the calyx, well away from the surface of the pod. All are possible devices to overcome this strategy of the plant.

Trait 9 is probably countered by species of *Bruchus*, *Algarobius*, and *Mimosestes* which enter and feed upon immature seeds. The previously cited case of *Caryedon albonotatum* (Preveit 1966) whose first-instar larva undergoes an apparent quiescent period for some 2 mo before leaving the egg could also be functional in attacking seeds that abruptly grow to maturity. On the other hand, the plant *Amorpha fruticosa* may be favored by delayed seed maturation. Seeds are present on the plant throughout most of the summer but do not mature until mid-August. *Acanthoscelides submuticus* (Table 1, No. 9) feeds only in the mature seeds of this plant; therefore, by the time the first generation of bruchids emerges it is apparently too late in the season for reinfestation, since no second generation appears. Perhaps in this way the plant has evolved a trait that prevents reinfestation of its seeds and allows a maximum period of time for their dispersal.

In response to traits 10 and 11 we cite the very flat and thin seeds of *Hoffmanseggia drepanocarpa*. *Acanthoscelides compressicornis* (Table 1, No. 3) devours almost the entire seed of this plant. The shape seems to have little or no deterrent effect. We

have already cited elsewhere in this paper (and in Table 1) numerous examples of bruchids that feed on several seeds during the course of their development.

A defensive trait cited by Wessling (1958), Marshall and Jain (1970), and Janzen (1971c) was that of hairiness of husk. We found that heavy pubescence sometimes may prevent the first-instar larva from reaching the pod surface (e.g., *Astragalus newberryi* pods are densely pubescent and are not infested by bruchids). However, *Astragalus mollissimus* has a pubescent pod but *Acanthoscelides fraterculus* (Table 1, No. 4) successfully counters this by inserting the ovipositor between the hairs and placing the egg as near as possible to the pod surface. The larva then crawls to the pod surface and enters.

These defense mechanisms of the plant and the corresponding adaptations of the seed predator represent a dynamic balance. The plant probably very seldom completely eliminates the seed predators (Janzen 1969). By the same token, the seed predators are seldom able to utilize the total seed crop. The defensive mechanisms developed by the plant reduce the effect of the infestation to insure the survival of the plant species, which in turn permits the survival of the bruchid.

#### Unexplained phenomena

*Pods with a single seed.*—Eleven percent of the plants in Table 1 have fruits with only one seed. All are of sufficient size for one small bruchid to develop inside them, but only *Errazurizia rotundata* seeds are large enough for development of several bruchids. Some of the fruits have toxic glands on their surfaces but all are fed upon by bruchids. Conceivably the one-seeded pods represent a transitional stage to the ultimate mechanism to exclude seed predators: very small one-seeded pods dispersed over a plant. With seeds so small that one bruchid could not develop in one seed, the larva would have to migrate from one pod to another, a phenomenon not yet observed in the Bruchidae.

*Large nontoxic seeds.*—Large seeds often harbor several bruchid larvae at the same time (*Acanthoscelides obtectus*, species of *Stator*, *Caryedes*, *Pygopachymerus*, *Specularius*, *Callosobruchus* and *Zabrotes*; Table 1). Although some of these large seeds contain toxins and are fed upon (e.g., by *Specularius erythrinae* in *Erythrina*), most are not known to contain toxins. Perhaps predator satiation is functioning here but it seems to us that the production of large seeds that could be destroyed by one small bruchid larva would be an excellent example of prey foolhardiness. Perhaps if this is a seed escape mechanism (predator satiation), then it operates best

when large numbers of eggs are oviposited on single seeds, thereby satiating the female bruchid. For example, many individuals of *Caryedes brasiliensis* (Table 1, No. 21) often emerge from only one of two seeds in a pod, or two of three seeds, etc. (D. H. Janzen, pers. comm.).

*Protective devices in seeds and pods.*—Of the 31 protective traits for seeds (Janzen 1969:19) only 7 are concerned with protective devices in the pods (numbers 1, 2, 5–8, 14) and the remaining 24 have to do with seeds. Because about 75% of plants we studied had indehiscent or tardily dehiscent pods it seems logical that most oviposition—over 62% of the species we studied—is on the pods. It also seems logical that most of the protective devices would be associated with the pod, but this is not the case, if Janzen's citations are indicative of most traits for protecting seeds.

A possible explanation is that, since the seeds are the most important components of a fruit, protective traits have evolved in them rather than in the husk. A more likely explanation is that we have insufficient information at this time about the number of husk protective mechanisms.

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