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Coevolution, Guilds and Ecology of some New World Non-Economic Bruchid Beetles

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Beetles in the family Bruchidae feed the seeds of about 33 families of plants, but most feed in the Fabaceae (Johnson 1981a, 1989). The reasons for host specificity to any family and especially to the Fabaceae are not readily ascertained, but some possible reasons are discussed below. All known seed beetles feed on and usually live in seeds.

The family Bruchidae consists of about 1300 described species and about 56 genera grouped in the subfamilies Amblycerinae, Bruchinae, Eubaptinae, Kytorhininae, Pachymerinae and Rhaebinae (Southgate, 1979). About 80% of bruchid species are in the Bruchinae, 10% in the Amblycerinae, 9% in the Pachymerinae, with the other 1% assigned to the other three subfamilies.

The life histories of bruchids vary considerably in oviposition, larval entry and larval feeding behaviour. The general life cycle is that the adult lays an egg on a pod or seed and the first stage (instar) larva bores through the pod and/or seed coat and enters the seed. The first stage larva is highly modified to enter seeds and has many spines and often well-developed legs for this purpose (Kunhikannan 1923, Pfaffenberger and Johnson, 1976). Once it has entered a seed, it mouts into a legless grub and commences to feed. A larva usually mouts three more times as it continues to feed inside the seed; usually only one, but sometimes several seeds are eaten. Bruchids usually pupate inside the seed that the larva has fed upon, but those that feed on several seeds may build a pupal chamber by gluing several seeds together or some may leave the seeds and spin a cocoon in which they pupate. The larva starts and usually the adult finishes making a round exit hole in the seed and/or pod and the adult exits. Adult bruchids feed on pollen and nectar and are not known to feed on seeds or pods. In the laboratory or in stored seeds, bruchids may complete many generations without the adults feeding; however, it has been shown that adult bruchids will lay more eggs, if provided with ample food and water, and they are suspected to feed on flowers, pollen and nectar in the field.

According to Johnson (1981a), it is likely that the chrysomeloid ancestors of bruchids radiated onto the seeds of the Fabaceae (or possibly its ancestors) shortly after it arose and then later evolved the ability to feed in seeds of other families.

About 84% of the hosts of bruchids are in the Fabaceae (Johnson, 1970) Most of the other hosts are in the families Convolvulaceae (4.5%), Palmae (4.5%) and Malvaceae (2%) The other 5% are in 29 other families. Of these 5%, the Combretaceae, Rhamnaceae, Sterculiaceae, and especially the Tiliaceae host more bruchids than the other families. Johnson (1981a) listed host families and discussed bruchid host preferences. He also stressed that many more hosts for bruchids remain to be found, especially in tropical America, Africa, Asia and possibly much of Australia. He also found in an analysis of the host preferences of bruchids in the legumes that these are primarily specific to taxa of legumes from the generic to the family level, but are usually not specific to particular species of hosts over the entire range of the bruchids.

Johnson (1981a) discussed the distribution, ecology, and economic importance of bruchids. He pointed out that bruchids and their relationships with their hosts make them especially good organisms for studies of plant-animal interactions and briefly discussed these interactions as they relate to coevolution.

For economic reasons, most of the research on the bionomics of bruchid beetles has been conducted on those species that feed on seeds that are used by man. Conversely relatively few species of non-economic bruchids have been studied intensively. Economic reasons are a factor, but the availability of food (*i.e.*, that used by man for insects in the laboratory) is another. To conduct experiments on non-economic species, the seeds they feed upon in nature must be collected and brought to the laboratory, not purchased at a grocery store. Since Janzen (1969) discussed the coevolution of non-economic bruchid beetles, numerous articles have been published regarding the coevolution, ecology and behaviour of non-economic bruchid beetles (*e.g.*, Center and Johnson, 1974; Fox and Mousseau, 1995; Fox *et al.*, 1995, 1996; Janzen, 1971, 1975a, b, 1977; Johnson, 1981a, b,c,d, 1983, 1987, 1990b, 1994; Johnson and Janzen, 1982; Johnson and Kistler, 1987; Johnson and Siemens, 1991, 1995, 1996; 1997a,b; Johnson *et al.*, 1995; Kingsolver *et al.*, 1977; Mitchell 1977; Nelson and Johnson, 1983; Rosenthal, 1990; Siemens and Johnson, 1990, 1992, 1996; Siemens *et al.*, 1991, 1992, 1994; Traveset 1990, 1991, 1992; Wilson and Janzen, 1972). A brief summary of selected articles on bruchid coevolution, guilds and ecology follows.

COEVOLUTION

The model for studies on coevolution of bruchids was, of course, the paper by Janzen (1969) The interpretations of the results of his research were that in the tropical lowlands of Costa Rica, large seeds were toxic and presumably not fed upon by bruchids. Smaller seeds were less toxic and presumably not fed upon by bruchids. Consequently, seed fitness seems to be determined by seed size and toxicity. Thus, individual large seeds have a better chance of survival than many small seeds. If a plant invests energy in large, toxic seeds, after germination, a seedling has a much better chance of surviving. Conversely, small seeds have less stored energy and toxins are dispersed in great quantities, thus escaping from predators, but after germination, have less chance to develop into viable seedlings. Janzen termed escape from predation by small seeds as predator satiation. Center and Johnson (1974) listed and interpreted examples that presumably showed that bruchids had overcome the defense of predator satiation with counter measures such as evolving the ability to feed in smaller seeds by becoming smaller in body size or feeding in more than one seed during their ontogenetic development. Nelson and Johnson (1983) reported that in some species of *Astragalus*, there was stabilizing selection for an optimal seed size because bruchids in species of *Astragalus* prefer large seeds over smaller ones, but larger seeds had a better chance of germinating and developing into a mature plant. Therefore, because of the opposing processes of predation rates and germination success, the intermediate seed-size classes were most likely to contribute more to the next generation.

Janzen *et al.* (1986) hypothesized that there are five to seven classes "of potentially defensive compounds in a seed (and perhaps there are double that number .... when .... it is common place for a single species of seed to contain several kinds of alkaloids or uncommon amino acids)". Some bruchids have the ability to use chemicals that are toxic to other organisms and metabolize them (*e.g.*, Rosenthal, 1990 and references therein) Seed chemicals undoubtedly play an important role in the host specificity of bruchids and in the evolution of host preferences. Seed chemistry needs to be studied intensively and extensively if the interactions of stepwise coevolution and colonization of bruchids and their hosts are to be understood.

Johnson (1990) cautioned that "coevolution in the Bruchidae is very correlative and thus only presumed to exist. When the contemporary precepts of coevolution were scrutinized and compared with the coevolutionary research on the Bruchidae, it was found that only components of each study of all of the coevolutionary research conducted date to on the Bruchidae was experimental, the balance of each study was correlative. It is suggested that future research on bruchid-plant coevolution uses cladistics and morphometrics in studies of systematics, these can then be used in conjuction with rigorous experimental and manipulative studies of chemistry, biochemistry and detoxification in both plants and herbivores, edaphic factors, primary metabolic requirements, genetics, ecological factors, and variation of these over space and time to conclusively define the process of coevolution".

Guilds Johnson (1981b) analyzed the behaviour and host preferences of many species of bruchids and their hosts and found that there are three guilds of bruchid beetles that attack legume seeds at different times and different ways. There are three patterns of pod dehiscence that correspond to three patterns of seed dispersal; some pods are indehiscent, some are tardily dehiscent, and others are elastically dehiscent. Thus bruchid guild one oviposits on pod surfaces, guild two directly on seeds inside a partially dehiscent pod, and guild three only on seeds that are free of the pod and exposed on the substrate (after dispersal), usually beneath the parent plant. The three guilds of bruchids do not correspond on a one-to-one basis with the three patterns of pod dehiscence, but rather all three bruchid guilds may attack one species of partially dehiscent legume. Thus bruchids feed on seeds of some plants at all stages of their development and even after dispersal (See also Johnson and Siemens, 1995, 1996, 1997a,b).

ECOLOGY

Much of the ecological research on non-economic bruchid species has been conducted on *Stator limbatus* (Horn) (Guild 2.) For example Siemens *et al.* (1991) studied many factors to determine the cause of restricted host use by the sympatric *Stator limbatus* and *S. pruininus* (Guild 2.) In north-central Arizona, USA, *S. limbatus* feeds on seeds of *Acacia greggii* (Fabaceae), whereas *S. pruininus* feeds mainly in seeds of *A. constricta* and infrequently in *A. greggii*. Both species of *Stator* are able to complete their life cycle in the seeds of either *Acacia*. The roles of plant microenvironment, interspecific competition and the suitability of seeds for food were assessed experimentally. Of several potential natural enemies, focus was on a very prevalent egg parasite to assess the role of enemy impact. Experiments in which non-host seeds were transferred into host canopies, tested simultaneously the roles of microenvironments and interspecific competition. Oviposition on non-host seeds in host canopies by beetles usually associated with the host was negligible compared to host controls, even though non-host seeds were offered in host microenvironments without potential competitors. Non--host seeds naturally occurring in host canopies because of interdigitating canopies also did not elicit use of non-host seeds by resident beetles. Thus, given a choice, females selectively oviposited on their natural host. Host suitability was determined with split-family experiments for each species of *Stator* when full-siblings on both acacias were compared. *Stator limbatus* performed best on its natural host in all three variables measured, while *S. pruininus* performed best on its natural host in terms of emergence time, but no difference was found in percent emergence or female size. An assessment was made on the impact of an egg parasite, *Uscana semifumipennis* (Trichogrammatidae), on the two species of bruchids when the bruchids occurred in their normal hosts. Thus, the potential for parasite-free space was assessed. *Uscana* attacked both bruchids on their normal hosts at the same level (20% of eggs parasitized) Thus, in this system, the determinant of locally restricted use of hosts is oviposition behaviour.

Oviposition behaviour may determine whether bruchids colonize seeds of non-host plants. Johnson and Siemens (1991) found in a field experiment that non-seed cues such as odours from pod valves of *Acacia flexuosa* on the substrate or in partially digested cow dung are oviposition attractants for *S. vachelliae* (Guild 3) on seeds of this natural host. The close proximity of these seeds and the smooth seeds of *Parkinsonia aculeata* in conjunction with the odours have apparently stimulated *S. vachelliae* to lay eggs on *P. aculeata*. Of 1,118 eggs on *Parkinsonia* seeds, 86% occurred in a narrow zone, where seeds of *Parkinsonia* and *A. flexuosa* were mixed on the ground beneath overlapping canopiesu. *Stator vachelliae* oviposited equally on seeds of both plants. Survivorship on *Parkinsonia* was <0.1% in the field, whereas on *Acacia*, it was 15%. Enemy-free space was available on *Parkinsonia*: only 3% of bruchid eggs on its seeds were parasitized, but on the normal host *Acacia*, 24% were parasitized. They suggested three steps for *S. vachelliae* to include *Parkinsonia* in its host range or for a host shift : (1) oviposition on the potential host in proximity to cues associated with the normal host; (2) larvae of *S. vachelliae* must evolve the ability to complete development in the new host; and (3) the adult beetles must be able to track the new host. Only step 1 has occurred in this system. The results support previous suggestions that the initial colonization of new hosts may be behaviourial. An occasional bruchid survives to adulthood in these latter seeds. Thus, incipient colonization may be occurring.

Incipient colonization may be determined by fitness on different hosts. Siemens and Johnson (1990) conducted experiments with *Stator limbatus* and its hosts in Arizona, USA to determine, if it was substructured into units, each specialized for higher fitness on a specific host species. Results suggest that *S. limbatus* is specialized to certain hosts. On *Cercidium floridum*, beetles originally reared from this host had significantly higher emergence compared to beetles transferred from other hosts. The differences on *C. floridum* were detected from tests between and within beetle populations. Evidence for specialization was not detected on *Cercidium microphyllum* and *Acacia greggii*. On the latter hosts, beetles performed well regardless of their source. Significant differences were detected among individual plants of *C. floridum* as to the suitability of their seeds for development of *S. limbatus*. No such differences were detected among the other host plants. These patterns of conspecific plant variability are opposite of what is expected if plant variability prevents specialization of beetles to particular species of hosts. Thus, the data suggested that seed variability among plants does not prevent specialization to host species in this system. The patterns of host use were discussed in relation to the hypothesis of sympatric host race formation.

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