

THE INTERACTION OF SEED PREDATORS AND SEED CHEMISTRY

by D.H. JANZEN

Résumé

La distribution des produits toxiques des arbres caduques d'une forêt tropicale et son influence sur l'organisation de la communauté animale.

Les différentes espèces de plantes renferment dans le même organe divers produits toxiques. Dans la forêt tropicale caduque de Costa-Rica, la plupart des graines d'arbres contiennent différents produits toxiques. Dans un tel habitat les animaux qui consomment ces graines ont subi une sélection naturelle en relation avec la diversité de composition chimique de ces graines. Cette diversité, réciproquement, influe puissamment sur la détermination des espèces qui peuvent consommer de tels types de graines. La plupart des animaux qui consomment des graines ne peuvent utiliser qu'une espèce de graines. La plupart des espèces de graines n'ont qu'une ou deux espèces de consommateurs. Par conséquent, le nombre d'espèces d'arbres dans l'habitat correspond, pour une grande part, au nombre d'espèces animales qui consomment les graines. Une autre conséquence en est qu'une espèce déterminée qui consomme des graines dans l'habitat ne peut excéder le nombre de graines produites par l'espèce d'arbre utilisée. Une troisième conséquence en est que les consommateurs de graines n'entrent pas en concurrence sinon à l'échelle de l'évolution.

The plant world is not colored green. The world is colored tannin, morphine, caffeine, L-dopa, L-canavanine, cyclopropane fatty acid, oxalic acid, turpentine, lectins, cardiac glycosides, etc. These secondary compounds and their concentrations are not distributed at random among the parts, individuals and species of plants in a habitat. The pattern of their distribution is on the one hand a major cause of the feeding patterns of herbivores, and on the other hand largely generated by herbivores over evolutionary time. The relationship of secondary

compounds and herbivores is the most complex and grandiose example of coevolution on the planet. In this presentation, I will not attempt an overview of all patterns of interactions of animals and secondary compounds in plants. Rather, I will focus on the interaction between beetles that are seed predators, and the seeds they prey on.

The study area is the deciduous forest (and riparian evergreen forest) of Guanacaste Province on the Pacific coastal plain of northwestern Costa Rica. About 12,000 km² in area, the study area has a six-month dry season and annual rainfall of about 1600-2000 mm. Much of my data has been gathered in Santa Rosa National Park, which is about 100 km² in area and near the Nicaraguan border. The study area contains about 2000 species of angiosperms. My work has been very strongly aided by taxonomists (most notably J.M. Kingsolver, D.R. Whitehead, V. Rudd, R. Liesner) and natural-products chemists (most notably E.A. Bell, I.E. Liener, G.A. Rosenthal), and supported by the National Science Foundation (BMS-75-14268).

Host specificity of Guanacaste seed predators

As I have noted before (Janzen 1973a, 1973b, 1974, 1975, 1976), Guanacaste seed predators are extremely host-specific. The data in Table 1 are the most up-to-date for three families of beetles (Bruchidae, Curculionidae and Cerambycidae) and take priority over all previous summaries. In the next two years more records will be added to this data, but I do not expect the general picture to change. To date, 95 species of beetles have been reared from lowland Guanacaste seeds; 82% are bruchids, 14% are curculionids and 4% are cerambycids. All the species of curculionids and cerambycids have only one species of seed as prey. Of the 78 species of bruchids, 57 (73%) have only 1 species of seed as prey, 12 have 2, 5 have 3, 3 have 4, and 1 (*Stator limbatus*) has 6. Lest the beetle with six prey species be viewed as a generalist, bear in mind that there are 2000 species of plants within its range in Guanacaste and at least half of them have a seed large enough to feed one larva of *S. limbatus* throughout its development.

Among them, the 95 species of coleopteran seed predators prey on 88 species of plants (slightly less than 5% of the flora). However, the prey list contains about 30% of the large woody plants. Why do the 95 species of beetles restrict themselves to only 88 species of plants, and why does each species restrict itself to only a few of the 88 species of plants? In Table 2 I have listed some of the more conspicuous

TABLE 1

Hosts of seed predators in Guanacaste Province, Costa Rica.

BRUCHIDAE.

<i>Pachymerus</i> sp. 1	<i>Scheelea rostrata</i> Burret
<i>Caryobruchus buski</i> Bridwell	<i>Scheelea rostrata</i> Burret
<i>Megacerus leucospilus</i> Sharp	<i>Ipomoea pes-caprae</i> (L.) Roth
	<i>Ipomoea carnea</i> Jacq.
	<i>Ipomoea</i> 1 (Palo Verde)
<i>Megacerus flabelliger</i> Fahraeus	<i>Merremia umbellata</i> (L.) Hall. f.
<i>Megacerus porosus</i> Sharp	<i>Merremia aegyptia</i> (L.) Urban
<i>Megacerus maculiventris</i> Pic	<i>Ipomoea hederacea</i> Jacq.
<i>Megacerus cubiculus</i> Motsch.	<i>Ipomoea hederacea</i> Jacq.
	<i>Ipomoea meyeri</i> (Spreng.) G. Don
<i>Megacerus cubicus</i> Motsch.	Convolvulaceae VI-20-1972-XXVII
<i>Megacerus biflocosus</i> Motsch.	<i>Merremia umbellata</i> (L.) Hall. f.
<i>Pygiopachymerus lineola</i> Chevrolat	<i>Cassia grandis</i> L.
<i>Ctenocolum acapulcensis</i> Kingsolver	<i>Lonchocarpus eriocarinalis</i> Micheli
<i>Ctenocolum biolleyi</i> K. and W.	<i>Lonchocarpus eriocarinalis</i> Micheli
<i>Ctenocolum janzeni</i> K. and W.	<i>Piscidia carthagenensis</i> Jacq.
<i>Ctenocolum tuberculatum</i> Motsch.	<i>Lonchocarpus minimiflorus</i> D. Smith
	<i>Lonchocarpus costaricensis</i> D. Smith
	<i>Lonchocarpus rugosus</i> Benth.
<i>Ctenocolum crotonae</i> Fähr.	<i>Lonchocarpus minimiflorus</i> D. Smith
	<i>Lonchocarpus costaricensis</i> D. Smith
	<i>Lonchocarpus rugosus</i> Benth.
	<i>Piscidia carthagenensis</i> Jacq.
<i>Gibbibruchus guanacaste</i> W. and K.	<i>Bauhinia pauletia</i> Pers.
	<i>Bauhinia unguolata</i> L.
	<i>Bauhinia glabra</i> Jacq. (one record)
	<i>Bauhinia pauletia</i> Pers.
<i>Gibbibruchus cristicollis</i> Sharp	<i>Dioclea megacarpa</i> Rolfe
<i>Caryedes brasiliensis</i> Thunberg	<i>Centrosema pubescens</i> Benth.
<i>Caryedes helvius</i> Motsch.	<i>Centrosema pubescens</i> Benth.
<i>Caryedes incensus</i> Sharp	<i>Centrosema plumieri</i> (Turp.) Benth.
<i>Caryedes quadridens</i> Jeckel	<i>Calopogonium caeruleum</i> (Benth.)
<i>Caryedes paradisensis</i> K. and W.	Hemsl.
	<i>Galactia striata</i> (Jacq.) Urban
<i>Caryedes juno</i> Sharp	<i>Bauhinia glabra</i> Jacq.
<i>Caryedes cavatus</i> K. and W.	<i>Bauhinia glabra</i> Jacq.
<i>Caryedes x-liturus</i> Sharp	<i>Cassia grandis</i> L.
<i>Megasennius muricatus</i> Sharp	<i>Cassia bacillaris</i> L.
<i>Sennius breveapicalis</i> Pic	<i>Cassia obtusifolia</i> L.
<i>Sennius instabilis</i> Sharp	<i>Cassia alata</i> L. (introduced)
	<i>Cassia obtusifolia</i> L.
<i>Sennius morosus</i> Sharp	<i>Cassia leptocarpa</i> Benth.
<i>Sennius celatus</i> Sharp	<i>Cassia biflora</i> L.
<i>Sennius auricomus</i> J. and K.	<i>Cassia leptocarpa</i> Benth.
	<i>Cassia biflora</i> L.
<i>Sennius biflorae</i> W. and K.	<i>Cassia grandis</i> L.
<i>Zabrotes interstitialis</i> Chevrolat	<i>Phaseolus lunatus</i> L.
<i>Zabrotes subfasciatus</i> Boh.	<i>Cassia leptocarpa</i> Benth.
<i>Zabrotes</i> sp. 1	<i>Pithecellobium saman</i> (Jacq.) Benth.
<i>Merobruchus columbinus</i> Sharp	

- Merobruchus* sp. 1
- Merobruchus cordifer* Sharp
- Stator pruininus* Horn
- Stator championi* Sharp
Stator vittatithorax Pic
- Stator limbatus* Horn
- Amblycerus perfectus* Sharp
Amblycerus sp. 1
Amblycerus geminatus Sharp
Amblycerus cistelinus Gyll.
Amblycerus biolleyi Pic
- Amblycerus* sp. 2
- Amblycerus* sp. 3
Amblycerus sp. 4
Amblycerus sp. 5
Amblycerus sp. 6
Amblycerus sp. 7
- Amblycerus* sp. 8
- Amblycerus* sp. 9
Amblycerus championi Sharp
Algarobius 1
Mimosestes sallaei Sharp
- Mimosestes dominicanus* Jeckel
- Mimosestes amicus* Horn
- Mimosestes viduatus* Sharp
- Acanthoscelides quadridentatus*
Schaeffer
- Acanthoscelides* sp. 1
- Pithecellobium mangense* (Jacq.) Standl.
Mimosa guanacastensis Standl.
Mimosa albida Hum. and Bonpl. ex Willd.
- Sesbania emerus* (Aubl.) Urban
Mimosa quadrivalis L.
Mimosa guanacastensis Standl.
Bixa orellana L.
Acacia tenuifolia (L.) Willd.
Acacia retusa (Jacq.) R.A. Howard
Acacia tenuifolia (L.) Willd.
Pithecellobium saman (Jacq.) Benth.
Pithecellobium oblongum Benth.
Pithecellobium vine 10365
Albizzia caribaea (Urb.) Britt and Rose
- Albizzia adinocephala* (Donn. Smith) Britt. and Rose
Combretum farinosum HBK
Malpighiaceae vine (SRNP)
Malpighiaceae vine (FLP)
Guazuma ulmifolia Lam.
Cordia alliodora (Ruiz and Pavan) Cham.
Cassia leptocarpa Benth.
Cassia obtusifolia L.
Cassia uniflora Mill.
Cassia alata L. (introduced)
Combretum farinosum HBK
Cassia emarginata L.
Propopis juliflora (Sw) DC
Cissus aff. *rhombifolia* Vahl.
Spondias mombin L.
Hippomane mancinella L.
Cordia alliodora (Ruiz and Pavan) Cham.
Cordia gerascanthus L.
Cordia panamensis Riley
Prosopis juliflora (Sw) DC
Acacia farnesiana (L.) Willd.
Acacia 1
Acacia farnesiana (L.) Willd.
Acacia 1
Parkinsonia aculeata
Caesalpinia coriari (Jacq.) Willd.
Parkinsonia aculeata
Prosopis juliflora (Sw) DC
Acacia collinsii Safford
Acacia cornigera (L.) Willd.
Mimosa pigra L.
- Mimosa pigra* L.

Acanthoscelides sp. 2
Acanthoscelides kingsolveri Johnson

Acanthoscelides guazumae J. and K.
Acanthoscelides obrienorum Johnson

Acanthoscelides griseolus Fall
Acanthoscelides puellus Sharp
Acanthoscelides argillaceus Sharp
Acanthoscelides sp. 3

Acanthoscelides flavescens Fähr.
Acanthoscelides apicalis Sharp
Acanthoscelides brevipes Sharp

Acanthoscelides difficilis Sharp

Acanthoscelides sp. 4
Acanthoscelides pertinax Sharp
Acanthoscelides sp. 5

CURCULIONIDAE.

Cleogonus armatus Champ.
Cleogonus rubetra Fabr.
Cleogonus nr. *conicollis* Fabr.
Apion samson Sharp
Rhinochenus transversalis Chevrolat
Rhinochenus stigma L.
Conotrachelus 1
Apion 1
Phymatophosus 1
Phymatophosus 2

Chrysapion chrysocomum Gerstaecker
Apion 3
Apion 4
Apion sublaterale Kissinger

CERAMBYCIDAE.

Leptostylus spermovoratis Chemsak
Leptostylus gibbulosus Bates
 Cerambycidae 1

Triumfetta lappula L.
Indigofera suffruticosa Mill.
Indigofera costaricensis Benth.
Guazuma ulmifolia Lam.
Cassia skinneri Benth.
Cassia biflora L.
Sesbania emerus (Aubl.) Urban
Calopogonium mucunoides Desv.
Phaseolus lunatus L.
Calopogonium caeruleum (Benth.)
 Hemsl.

Rhynchosia minima (L.) DC
 Malvaceae (Herb, Bagaces)
Sida 1
Sida 2
Mimosa pudica L.
Mimosa albida Humb. and Bonpl. ex
 Willd.
Mimosa guanacastensis Standl.
Aeschynomene americana L.
Aeschynomene americana L.
Mimosa dormiens Humb. and Bonpl.

Andira inermis (W. Wright) DC
Hymenaea courbaril L.
Hymenaea courbaril L.
Caearia corymbosa HBK
Pterocarpus rohrii Vahl
Cayaponia racemosa (Sw.) Cogn.
Cayaponia attenuata (Hook. and Arn.)
 Cogn.
Aeschynomene americana L.
Aeschynomene americana L.
Ateleia herbert-smithii Pittier
Lonchocarpus 1 (Boucher 544)

Diospyros nicaraguensis Standl.
Sapindus saponaria L.
Manilkara zapota (L.) v. Royen

TABLE 2

Some of the seed traits of importance in defense of the individual seed.

SEED DEFENSES.

<i>Chemical</i>	<i>Behavioral</i>
Fruit chemistry (green + ripe)	Length of development of fruit and seed
Fruit thickness	
Fruit hardness	Timing of seed production within the year
Seed coat hardness	Timing of seed production among years
Seed coat thickness	
Seed coat odor	
Seed coat chemistry	Location of seeds in fruit
Seed size	
Seed contents chemistry	Location of fruits in plant crown
Kinds	Number of seeds per fruit
Concentrations	Number of fruits per crop
Combinations	Rate of dispersal
Location (vacuoles, embryo, endosperm)	Thoroughness of dispersal
Lectins (phytohemagglutinins)	
Proteinase inhibitors	
Alkaloids	
Polyphenols (tannins, etc.)	
Non-protein amino acids	
Protein amino acids	
Cyanogenic glycosides	
Cyclopropane fatty acids	
Heteropolysaccharides	
Saponins	
Miscellaneous carcinogens	

defenses of individual seeds. In addition, the absence of a beetle from the seeds of a particular species of plant can be due to competitors (e.g., moth larvae, bugs, rodents), predators (e.g., parasitic Hymenoptera), habitat inhospitality, low density of prey seeds, and failure of the beetle to try.

A primary way to understand the host-specificity of the beetles is to isolate the traits of the seeds and test them on the beetles. Which traits do you choose? I feel that the seed contents should receive primary attention for the following reasons. First, I consider the cues that the beetles use to locate the seeds, and use to decide to oviposit on them, are generally evolved in response to the suitability of the host, rather than being what controls the suitability of the host. Second, the fruit and seed coat walls may be hard or toxic, and thus

an important barrier, but if the beetle larvae can mechanically penetrate them, they should be relatively easy defenses to overcome. In addition, if a larva can get through seed coat defenses of one species of seed, it is likely to be able to do it to other species of seed. Third, the larva has to more than just get into the seed contents. It has to live there and derive enough nutrients to survive. To do this, it is maximally exposed to any toxic compounds in the seed contents. Since there are many kinds of toxic compounds found in seeds, and since the possible combinations are almost infinitely varied, it appears that only the seed contents are sufficiently important and sufficiently variable among species to lead to great host-specificity by the beetles.

Laboratory tests of seed chemicals

It is my general hypothesis that a major cause of the high host specificity of Guanacaste coleopteran seed predators is that each species of seed has a different set of chemical defenses, and that the specialists on the seeds of one species of plant cannot deal with the combination of chemicals in the seeds of other species. I had hoped to be able to tell you the seed chemistry of the species in table 1; this work goes slowly and all I can say is that for the plant species we have examined to date, it appears that every one has different combination of secondary compounds in its seeds.

While this is underway, I need also to show that the secondary compounds in seeds are toxic to most seed-eating beetles. Again this goes slow owing to the difficulty of getting wild beetles into culture. However, I have been able to obtain striking results with the southern cowpea bruchid (*Callosobruchus maculatus*). The methods have been described in Janzen, 1975; Janzen *et al.*, 1976, 1977 a. In short, the pure secondary compounds are added at approximately natural concentrations to cowpea flour (*Vigna unguiculata*) and the flour pressed into artificial seeds. The southern cowpea bruchid oviposits normally on these artificial seeds.

Table 3 summarizes the results of testing 87 different secondary compounds (including 20 protein amino acids) at 0.1, 1 and 5 percent concentrations (see Janzen *et al.*, 1977, for details). Alkaloids were the most toxic compounds tested. It is probably not a coincidence that alkaloids commonly occur in seeds at concentrations of 1% or less. Greater quantities would probably represent defensive overkill, except against vertebrates that might dilute the toxin with other foods.

TABLE 3

Toxicity of various kinds of seed constituents when added to the diets of the larvae of *Callosobruchus maculatus*.

	Percent lethal at the following concentrations		
	0.1 %	1 %	5 %
Alkaloids ($n = 11$)	82 %	100 %	100 %
Non-protein amino acids ($n = 24$)	28 %	41 %	90 %
Protein amino acids ($n = 20$)	0 %	0 %	32 %
	(by implication)		
Miscellaneous ($n = 32$)	10 %	36 %	55 %

The non-protein amino acids (e.g., L-canavanine, L-dopa, albizzine, Djenkolic acid, azetidine-2-carboxylic acid) are more toxic than protein amino acids. Non-protein amino acids are toxic to a variety of other organisms (e.g., Fowden *et al.*, 1967), but since legume seeds are rich in non-protein amino acids and bruchids feed on these seeds, one might expect bruchids as a group to be resistant to them. Non-protein amino acids are certainly toxic to larvae of *C. maculatus*. It was surprising that some protein amino acids could be toxic to a bruchid larva. However, some of the toxic protein amino acids are not even found in cowpeas and therefore are probably quite novel structures to *C. maculatus*: the toxicity of other protein amino acids is probably due to simple nutrient imbalances.

The miscellaneous compounds mentioned in table 3 are very diverse. Small glass beads and ground cellulose were added up to a concentration of 5% to demonstrate that the detrimental effects of adding secondary compounds was not merely that of dilution of the food. Heat-denatured lectins were added to a level of 5% to demonstrate that it was not simply the proteinaceous material that makes a 5% lectin addition lethal (Janzen *et al.*, 1976 a). In general, phenolics and odd seed oils (cyclopropanoid fatty acids, cyanolipids) were quite toxic, while common spices were variable in their effect.

In several cases it was found that the mixture of two compounds each of which alone was non-toxic, was toxic to the beetle larvae. For example, Djenkolic acid and D, L-pipecolic acid by themselves at 1% concentration had no depressant effect on production of adult beetles. However, when each was present at 1% in the same tablet, there was a highly significant depression of beetle production (Janzen *et al.*, 1977).

Direct tests on seeds

What would happen in nature if *Callosobruchus maculatus* were to oviposit on the various seeds that grow wild in the general vicinity of the areas where it occurs as a stored product of field pest? I have tested the beetle on 74 species of seeds, many of which occur wild in the general vicinity of wild populations of *C. maculatus* (Janzen, 1977). The seeds were cut in half before they were offered to the beetles for oviposition, so that I could test independently the seed coat and the seed contents as a defense.

Against *C. maculatus* the seed coat is clearly a defense. The larvae were able to penetrate the seed coats of only 35% of the species of seeds. However, cowpeas have exceptionally thin seed coats when compared with other legume seeds, and therefore it is not surprising that the larvae are not prepared to drill through a heavy seed coat. For example, in a similar ongoing experiment, the larvae of the bruchid *Mimosestes sallaei* were able to drill through the seed coats of almost all of the 74 species of seeds. The larvae of *M. sallaei* normally develop in the seeds of *Acacia farnesiana*. This legume seed has a very thick and hard seed coat.

Seed coat hardness was not the only trait that deterred the larvae of *C. maculatus*. In the case of seeds of *Erythrina berteroana* from Costa Rica and *Ormosia venezolana* from Venezuela, the larvae died in the eggs without ever starting to penetrate the seed coat. Both of these seeds are rich in alkaloids, and alkaloids have been shown to be very toxic to *C. maculatus* (table 3). Seed coat toxicity, and the general question of the exact location of secondary compounds in seeds, is a topic long overdue for extensive examination.

The fate of the larvae from eggs laid on the cut surface of the seeds tells what would happen were the larvae able to penetrate the seed coat. In 7% of the cases, the larvae survived in the seed contents. As expected, they did fine in seeds of *Vigna unguiculata*. Quite unexpectedly, they developed normally into adults, and emerged, in the seeds of the wild Costa Rican herbaceous vine *Rhynchosia calycosa*. The larvae developed to full-sized adults, pupae or larvae in the embryos of *Delonix regia*, *Parkinsonia aculeata* and *Schizolobium parahybum*. To get to the embryo, the larvae had to drill through the polysaccharide gum endosperm, and this endosperm showed no deterrent effect on the larvae. The development time in the embryos of these caesalpinaceous legumes was at least two months, which is at least a month greater

than in cowpeas. That they could develop at all in the seeds of *Delonix regia* and *Schizolobium parahybum* I find quite amazing. The seeds of both species are rich sources of azetidine-2-carboxylic acid (L. Fowden and E.A. Bell, pers. commun.), and we have shown this non-protein amino acid to be lethal to *C. maculatus* larvae when added to the diet at concentrations as low as 0.1% (Janzen *et al.*, 1977). This brings up the distinct possibility that the azetidine-2-carboxylic acid is concentrated in the endosperm (or even the seed coat?) of these plants. Since endosperm and embryo tissue are generally very different in their nutrient content, it seems reasonable that they would also be very different in their secondary compound contents.

Detoxification of seed defenses by bruchids

It is evident that every bruchid that invades a legume seed has to deal with one or more compounds that are known to be toxic, or likely to be toxic. As Applebaum (1964) pointed out some time ago, legumes seeds in general contain protease inhibitors. The big biochemical breakthrough that set the stage for the radiation of bruchids was probably the avoidance of this defense by having a gut that did not rely on proteases. Applebaum also noted that this meant that the beetle larvae had to depend on short chain peptides and free amino acids in the legume seed for their protein building blocks. The example of canavanine, to be discussed below, show how very correct he was.

My procedure is to start with the easiest system and work toward the harder ones. *Dioclea magacarpa* seeds are the largest legume seeds in Guanacaste (5 to 15 gm) and produce the largest bruchid (*Caryedes brasiliensis*) that preys on a legume seed in Guanacaste. The seeds contain 5 to 10% canavanine in the cotyledons, and therefore the bruchids must be able to deal with this concentration of canavanine in their diet. Dr. Jerry Rosenthal, an active specialist on canavanine biochemistry, agreed to help determine how the beetle larvae do this. Seeds containing live larvae were shipped to Rosenthal, and he has been able to determine several very interesting things about the larvae. First, the arginyl-tRNA synthetase of the bruchid beetle larva discriminates between L-arginine and L-canavanine, and therefore the L-arginine does not get substituted in growing protein chains as is the case in animals susceptible to canavanine; canavanyl proteins do not function properly (Rosenthal *et al.*, 1976). This may be regarded as the first line of defense of *C. brasiliensis* against canavanine. This is

also the way that many plants avoid autotoxicity from the non-protein amino acids that they synthesize (Fowden *et al.*, 1967).

However, the beetle larvae do more than just avoid the canavanine. Canavanine constitutes 55% of the total amino acids in the seed. Its use would probably provide all the protein needs of the bruchid larva. Rosenthal has now shown (Rosenthal *et al.*, 1977) that the larvae degrade about 60% of the canavanine in the seed to canaline and urea. They possess extraordinarily high urease levels, and the urease is used to degrade the urea to ammonia which can then enter the nitrogen pool of the larva.

Caryedes brasiliensis is thus a canavanine specialist. The interesting question, to which I have no answer, is why it cannot simultaneously be an albizzine specialist and therefore make the same physiological use of the seeds of *Enterolobium cyclocarpum*. The seeds of *E. cyclocarpum* are much more abundant than those of *Dioclea megacarpa* and are not attacked by any bruchid. However, there are other bruchids that prey on Guanacaste seeds rich in albizzine.

It seems a reasonable prediction that many of the Guanacaste bruchids will treat the particular secondary compounds in their diets in a manner analogous to what *Caryedes brasiliensis*, does, but no data is presently available on this point.

Consequences of host specificity of seed predators

The impact of the seed predators on the plants in the habitat is influenced by the extreme host-specificity of the seed predators. However, this is very difficult to demonstrate both because of the time scale involved and the shortage of intact natural forest in which to conduct experiments. There are three major kinds of consequences that are easily postulated.

First, the number of species of seed predators present should be in part determined by the number of plant species present. Even the most common species of plants do not have more than three species of bruchids in their seeds, and there seems to be little relationship between the number of species of bruchids on a plant and its abundance. There are always 1 to 3, if they are there at all. This suggests that they compete strongly for the seeds they occupy (within a species of host), and that the habitat or resource called "seeds of species *n*" is not large enough to support more than 1-3 species of bruchids. If, for example, the ten most common legumes in Guanacaste Province

were replaced by twenty of less common legumes, I suspect that the number of bruchid species present would rise. This statement should be viewed in the context of the hypothesis that if the number of bruchid species in Guanacaste were to rise, some species of plant would probably become scarcer (Janzen 1970) or some other herbivore would become scarcer (Janzen 1973c).

Second, high host-specificity of the beetles means that their welfare depends much on that of the plant whose seeds they prey on. If plant n becomes more abundant, its coleopteran seed predators are likely to do so as well, with the probable outcome that plant n will no longer reproduce as well and therefore become scarcer (Janzen 1970). We thus have a mechanism whereby the beetle as a whole can raise the number of species of trees in the habitat (by preventing the best competitors from occupying all the resource space).

Third, the coleopteran seed predators in a habitat probably compete very little if at all with each other in contemporary time (except, of course, for the few species that attack the same species of plant). However, they undoubtedly compete in evolutionary time. When a new defense appears that removes a bruchid from its regular host seeds, a common consequence is probably for the beetle to move to a new host. However, when it makes such a host switch, if it encounters another species of bruchid already in the seeds, there is likely to be a strong competitive interaction with the result of someone dropping out or moving on. As this process is presumably continually occurring, the beetles are continually competing on an evolutionary time scale. The number of beetles that persist in the community will be a function of how many host plants, and thus other beetles, are present.

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DISCUSSION

Question de L.E. GILBERT :

When I began my experiments on assimilation of amino acids in *Heliconius* I made the mistake of feeding unbuffered. Solutions (pH \cong 3.0) which caused a reverse curl of the proboscis and great fits of kicking by the poor butterfly. Have you buffered the protein amino acids which you added to the "reconstituted" feeds?

Réponse de D.H. JANZEN :

No and yes. At first no, because I wanted to mimic the case of a mutant bean that had an unexpected high concentration of a protein amino acid.

Question de B. NAGY :

Had you found any example, what happens in case of a double infestation of the same seed by two (or three) species. May it occur that larva (species) of quicker larval development may overcome on the other larva (species) ?

Réponse de D.H. JANZEN :

Whichever larva starts to develop first eats the others that enter the seed. It

is possible that the fastest larva wins, but there are too many other aspects to make appreciation.

Question de R. PROKOPY :

With respect to the last *Callosobruchus* species you were speaking of, are there any other herbivores that might feed on this developing seed pods and thus also act as strong selective agents controlling plant density, or is the sole herbivore selective pressure the bean weevil?

Réponse de D.H. JANZEN :

There are numerous other herbivores that feed on developing seeds in young pods and on entire young pods. All of these together are important in lowering plant density.