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SEED-EATERS VERSUS SEED SIZE, NUMBER, TOXICITY AND DISPERSAL[1]

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"Many legumes contain poisonous principles, particularly alkaloids and glucosides, and we should expect Bruchids to be affected by some of these." With this statement, Bridwell (1918) anticipated the subject of this discussion: what traits of seeds may be the result of selective pressure by insects and other seed-eaters? In this discussion of the escape of the offspring of a large sessile organism from predators and parasites, Leguminosae (the bean family) and the bruchid beetles that attack their seeds are used as an empirical example. In a subsequent paper (Janzen, 1968*b*), a model of seed dispersal is developed as background for discussion of the relevance of seed dispersal and mortality to the density and presence of a species of plant in a community.

I intend the data presented here to support the arguments advanced by Stebbins (1967) and Harper (1967) against the philosophy, explicit or implicit in much of the literature on the reproductive biology of plants, that "a plant produces so much seed that variation in seed mortality is unimportant, since only one seed has to survive to produce another plant" (which might be termed the "prodigal parent theory"). The time is also ripe for examination of this problem in other organisms that produce very large numbers of relatively helpless offspring (e.g., fish, Toetz, 1967; *Conus*, Kohn, 1961). This discussion is also pertinent to the polemic on the regulation of plant density by herbivores (recently generated by Hairston et al., 1960; Murdoch, 1966; Ehrlich and Birch, 1967; and Slobodkin et al., 1967), in light of the fact that herbivores do kill large numbers of juvenile plants.

Nearly all studies in wild plant biology have regarded the traits of seeds and seed crops as the direct result of physiological processes that are in turn correlated with the immediate environment. When selection is considered, it is associated with interplant competition, seed longevity, seed dispersal to better germination sites, or seedling survival (Salisbury, 1942; Carlquist, 1966*a*, *b*, *c*; Sharp and Sprague, 1967; Palmblad, 1968; Trevis, 1958; Janzen, 1967*a*; Baker, 1967). The selection

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produced by predators on seeds and its consequences in the communities of mature plants have been largely ignored with the exception of Gillett's (1962) brief discussion of the positive impact of seed-eating insects on plant community complexity and adaptive radiation. The term "predator" is here used to emphasize the process and deemphasize the taxonomic affiliation and trophic level of the organisms involved.

While the "prodigal parent theory" has undoubtedly contributed to the failure to discuss the evolutionary consequences of seed mortality, the implications, recently expressed by Slobodkin et al. (1967), that seeds are "plant products" has also had a detrimental effect. Seeds are clearly juvenile plants, not products. To place flower nectar and seeds in the same functional category (Slobodkin et al., 1967), is like placing human sweat and children in the same functional category. To dismiss a priori the destruction of seeds as unimportant in regulation or limitation of adult plant population density is to regard the mortality of young animals as unimportant in density regulation of adult animals. Mature seeds are functionaly identical to eggs and juveniles of vertebrates and invertebrates.

Parental care of eggs, young, and seeds obviously varies among groups or organisms, but these are, however, quantitative differences, not qualitative ones. That the relative importance and prominence of the three functions of propagules (escape, genetic recombination, dispersal for colonization) differ strongly is unfortunate in that it has led to the idea that population recruitment by animals is somehow functionally different from that by plants. That adult plants are generally close to being immune to mortality until they senesce, and constitute the obvious part of the plant community, has also added to the erroneous feeling that plants are for the most part not killed by predators. It is generally not recognized, for example, that in many areas where squirrels, acorn weevils, and other predators occur, over 90% of oaks are killed by predators (Watt, 1919; Janzen, unpublished).

The major studies of insect destruction of wild plant seeds are reported in the biological control literature and are summarized by Huffaker (1959), Wilson (1964), and DeBach (1964). These studies are concerned with "weeds" (ruderals) in fields and pastures and therefore with how the plant population density and/or biomass is reduced by insects, rather than with evolution of seed and seed crop traits as a result of the selective pressures of predators. They cite numerous examples where the density of a plant species could be influenced (usually negatively) by seed-eating insects. The literature of economic entomology abounds with data on seed and fruit destruction by insects. These reports show that insects are capable of destroying large parts of a seed crop, but are only indirectly helpful in understanding the selective pressures that seed-eating insects bring to bear on wild plants in natural communities.

MORPHOLOGICAL AND CHEMICAL TRAITS OF SEEDS AND SEED CROPS

Have morphological and chemical traits of seeds been selected for by animals that eat (and sometimes disperse) seeds? The trivial answer is clearly "yes" but more testable (detailed) hypotheses rest primarily on circumstantial evidence.

Evidence is rapidly accumulating to support the idea that the primary role of so-called "secondary plant substances" or "waste products" is in influencing intra- and interspecific encounters between the plant and other organisms (e.g., natural herbicides—allelopathy, natural insecticides or repellents, natural fungicides; Muller, 1966; Janzen, 1969; Fraenkel, 1959; Brower et al., 1964, 1967; Kaplanis et al., 1967; Ben-Aziz, 1967; Farnsworth, 1968; Feeny, 1968; Feeny and Bostock, 1968; Beck, 1965; Stark, 1965; Applebaum, 1964; Applebaum et al., 1965; Cranmer and Turner, 1967; Brown, 1967, etc.), despite comments to the effect that they "appear to have no biological role in the plants which produce them" (Leete, 1965). These compounds are, by analogy, the tools that the plant uses in its competitive and protective encounters. It is significant that virtually all the pharmacologically useful compounds extracted from plants are "secondary substances" rather than identifiable as part of the machinery common to most cells or plant species, and that these compounds are much less well represented in animals. While most animals rely heavily on behavioral as well as chemical traits, plants interact with their zoological environment almost entirely in a chemical manner. As Bu'lock (1965) put it, secondary compounds "express the individuality of [plant] species in chemical terms."

The evolution of morphological and phenological defense mechanisms of plants have received much less attention than the chemically oriented studies cited above. Exceptions are Salisbury's (1942) and Baker's (1967) monographic examinations of seed weights and other traits of the British Isles and California, respectively, and Janzen's (1967*a*) discussion of the negative relationship between sexual reproduction of tropical trees and intra-tree competition.

Seeds and sexual reproductive behavior of adult plants are expected to display chemical, morphological, and phenological defensive mechanisms and strategies. These defenses should not necessarily be the same (in kind or proportion) as in the vegetative portions of the plant, since different herbivores usually affect these two stages. Further, the results of the interaction are different (e.g., colonization, survival of a juvenile) and the traits are "budgeted" from different portions of the energy budget.

The production of these traits should be related in an important way, through the total energy budget of the plant, to such seed crop traits as the mean seed weight (size), the mean weight and seed number per unit of photosynthetic ability. The partitioning of the total energy budget among reproductive, defensive and maintenance components (Cody, 1966; Williams, 1966; Smith, 1968, 1969; Harper, 1967) is treated in this study as an integral part of the evolutionary response to predators on juvenile plants.

Leguminosae and Bruchidae

These statements could be evaluated for any large plant family, but woody perennial Central American Leguminosae were chosen for the following reasons: (1) They constitute a major part of lowland New World tropical vegetation and have high morphological, ecological, and species diversity. (2) The Bruchidae or "pea weevils," with at least 400 species in Central America are the major predators on their seeds; however, not all species are attacked. (3) A number of seed and seed crop traits appear to have been selected for by this seed mortality. (4) Not being wind dispersed for the most part, seed crops of individual plants are easily collected and the bruchids reared from them. (5) There are taxonomists able and willing to aid with the determinations of the specimens (Bruchidae: Dr. J. M. Kingsolver; and Leguminosae: Dr. V. E. Rudd, both at the U. S. National Museum). (6) I am somewhat familiar with their biology.

This is not a unique system. The first three reasons apply equally well to sucking Hemiptera (primarily Lygaeidae, Pyrrhocoridae and Coreidae) versus Asclepiadaceae and Apocynaceae, and Malvaceae, Sterculiaceae and Bombacaceae, indicating that these two groups would be amenable to similar analyses.

The Bruchidae represent an adaptive radiation of a chrysomeloid group onto the seeds of Leguminosae (Kingsolver, pers. comm.; Bridwell, 1918). They feed on the seeds of a large majority of legume species with medium-sized hard seeds. The female beetle lays her eggs (50–150) on or in the seed pod, or directly on the seed(s). The generation time ranges from 6–15 weeks in non-diapausing species. The larva may burrow through the green pod, eating an undetermined number of embryos before settling in one large seed, or it may penetrate

TABLE 1. *Seed mortality and other related parameters of seed crops of those species of Central American Leguminosae that are attacked by Bruchidae. All weights are based on apparently viable seeds, not those from which bruchids have emerged, except number 22 and 38 where volumetric estimates were used.*

Species	Tree number	Est. tot. seed crop this tree	Est. tot. canopy vol. this tree m^3	Dry wt. tot. seed crop (g)	$\bar{X}$ ind. see wt. (g)	Grams seed/m^3 of canopy	% seed crop dest. by bruchids	$\bar{X}$ number of seed/m^3 of canopy
Acacia farnesiana	(1)	83	14.10	6.03	0.0726	0.43	22	5.9
	(2)	262	1.75	35.89	0.1370	20.51	0	149.7
	(3)	2500	179.00	203.25	0.0813	1.14	72	14.0
	(4)	281	4.20	15.32	0.0545	3.65	82	66.9
	(5)	1004	113.00	60.14	0.0599	0.53	48	8.9
	(6)	3820	0.52	205.90	0.0539	395.94	77	7346.1
	(7)	6647	4.20	326.37	0.0491	77.71	85	1582.6
	(8)	4701	4.20	252.45	0.0537	60.11	85	1119.3
	(9)	1757	14.10	161.82	0.0921	11.56	36	124.6
Acaicia cornigera	(10)	974	0.52	56.01	0.0575	107.69	80	1873.0
	(11)	84	0.52	7.72	0.0919	14.85	21	161.5
Mimosa pigra	(32)	6000	0.52	60.00	0.0100	114.22	49	11538.4
	(36)	2242	0.52	38.34	0.0171	73.71	20	4311.5
Cassia biflora	(33)	2968	0.52	10.09	0.0034	19.40	27	5707.6
Mimosa sp. 1	(34)	3200	0.52	42.88	0.0134	82.46	34	6153.8
Canavalia sp .1	(35)	414	4.20	9.20	0.0222	2.19	8	98.6
Pithecellobium saman	(37)	650,000	4176.00	81,640.00	0.1256	19.55	46	155.6
Dioclea reflexa	(38)	150	112.00	600.00	5.0000	5.36	100	1.4
Rhynchosia pyramidalis	(39)	1212	4.20	72.24	0.0596	17.20	42	288.6
Phaseolus lunatus	(40)	847	0.52	50.91	0.0601	97.89	52	1628.8
Leucaena shannonii	(22)	2000	65.00	122.80	0.0614	1.89	100	30.8
Acacia sp. 1	(24)	166	0.52	9.60	0.0578	18.45	19	319.2
Acacia collinsii	(25)	3000	1.75	100.50	0.0335	57.43	27	1714.2
Acacia sp. 2	(26)	1500	1.75	129.00	0.0860	73.71	83	857.1
Lysiloma bahamensis	(27)	2000	14.10	37.80	0.0189	26.81	56	141.8
Pithecellobium albicans	(28)	270	33.00	18.28	0.0677	0.55	76	8.2
Leucaena leucocephala	(29)	466	0.52	18.83	0.0404	36.19	18	896.1
	(30)	5000	14.10	248.00	0.0496	17.59	64	354.6
	(31)	210	4.20	7.12	0.0339	1.70	57	5.0
	(23)	2189	0.52	106.60	0.0487	205.00	10	4209.6
	(12)	1269	4.20	65.35	0.0515	15.56	92	302.1
	(18)	730	0.52	51.83	0.0710	99.67	99	1403.8
Acacia gaumeri	(13)	400	33.00	14.24	0.0356	0.43	74	12.0
Acacia gentlei	(14)	1954	4.20	119.00	0.0609	28.34	84	465.2
	(15)	2500	4.20	130.25	0.0521	31.02	76	595.2
Acacia hindsii	(16)	600	1.75	23.10	0.0385	13.20	90	342.8
Acacia cochliacantha	(17)	563	1.75	13.63	0.0242	7.78	71	321.7
Acacia rigidula	(19)	4516	4.20	116.51	0.0258	27.74	87	1075.2
	(20)	3913	0.52	88.43	0.0226	170.07	81	7525.0
Acacia macracantha	(21)	1600	266.00	76.48	0.0478	0.29	46	6.0

a seed directly. It develops in the seed, eating the cotyledons and other parts; in many species, there is one bruchid per seed, but some large-seeded legumes have 2–25 beetles per seed and in others a single larva eats several mature seeds (Johnson, 1967; Howe and Currie, 1964; Vaurie, 1950; Larson and Fisher, 1924; Bridwell, 1918, 1920). Bruchids are not restricted to Leguminosae, but most species use these seeds and up to ten species of bruchids may feed on one species of legume (Bridwell, 1918;

TABLE 2. *Parameters of seed crops of Central American Leguminosae that are not attacked by bruchid beetles. All weights are based on apparently viable seeds, oven dried to constant weight.*

Species	Tree number	Est. tot. seed crop this tree	Est. tot. canopy vol. this tree m^3	Dry wt. tot. seed crop (g)	$\bar{X}$ ind. seed wt. (g)	Grams seed/m^3 of canopy	$\bar{X}$ number seed/m^3 of canopy
Mucuna mutisiana	(1)	500	34.00	3,977.95	7.9559	116.97	14.7
Canavalia sp. 1	(2)	50	4.20	21.06	0.4212	5.01	11.9
Entada polystachia	(3)	80	266.00	1,925.73	24.0716	7.24	0.3
Hymenaea courbaril	(4)	650	1,761.00	2,284.23	3.5142	1.30	0.4
Canavalia sp. 2	(5)	321	8.20	130.36	0.4061	15.90	39.2
Gliricidia sepium	(6)	183	22.30	14.44	0.0789	0.65	8.2
Leguminosae sp. 1	(7)	4,000	65.00	250.40	0.0626	3.85	615.4
Indigofera suffruticosa	(8)	7,622	0.52	22.87	0.0030	42.86	14,657.6
	(9)	19,000	0.52	49.40	0.0026	95.00	36,538.4
Erythrina standleyana	(10)	141	4.20	31.51	0.2235	7.50	33.6
	(11)	37	4.20	13.15	0.3555	3.14	8.8
Erythrina macrophylla	(12)	203	65.00	28.89	0.1423	0.44	3.1
	(13)	52	14.10	8.55	0.1645	0.61	3.7
Erythrina sp. 1	(14)	94	179.00	25.72	0.2736	0.14	0.5
	(15)	339	4.20	82.00	0.2419	19.52	80.7
Schizolobium parahybum	(16)	3,020	2,293.00	2,396.67	0.7936	1.05	1.3
Enterolobium cyclocarpum	(17)	11,200	4,698.00	12,055.68	1.0764	2.57	2.4

Zacher, 1951, 1952; Cushman, 1911; J. M. Kingsolver, pers. comm.). Bruchids have long been recognized as serious pests of stored peas, beans, etc. (Howe and Currie, 1964), but their importance to wild legumes is only vaguely indicated by comments such as that of Bews (1917) about *Acacia arabica* (= *A. nilotica*): "Insects sometimes enter the pods and destroy the majority of the seeds."

Materials and methods.—From 1965 to 1967, seed crops of 36 species of wild native lowland Central American (9 to 21 degrees N. latitude) woody Leguminosae were analyzed in respect to numbers of seeds in a single seed crop, total grams dry weight of this crop, canopy volume, grams and numbers of seeds per m^3 of canopy, mean dry weight of individual seeds, and percentage of the crop destroyed by Bruchidae (Tables 1 and 2). These are not simple parameters to interpret and require the following qualifications.

A seed crop is defined as the total number of mature seeds produced by a single plant following a single period of continuous flowering. The dry season in lowland Central America usually leads to distinct, and generally non-overlapping seed crops (Fournier and Salas, 1966; Janzen, 1967*a*) by a given species of woody wild Leguminosae (though seed crop maturation is sometimes drawn out over a period of one to several months). At a given site, there are often a few individuals of a single species that are out of phase. These plants can be used to assess insect damage to seeds but interpretation is more complicated. Ovipositing adults of the host-specific bruchid species may be active only during the usual fruiting period (e.g., Miller, in Huffaker, 1959) and therefore such asynchronized plants were avoided. The actual tree sampled was based on its ease of access and presence at sites chosen for other reasons. The crop was usually collected directly from the tree and from the ground (rarely) only if the pods were indehiscent. Plants were chosen whose canopies were separate from those of other members of the same species. Samples were sometimes taken from trees with abnormally high exposure to insolation and thus their seed set may have been exceptionally high (see discussion in Sharp and Sprague, 1967). The extreme and skewed intraspecific variation in legume seed crop size is fully recognized (cf., Harper, 1967), but these species of legumes do have consistent interspecific differences in respect to seed crop size. I am familiar with large populations of nearly all of the species in Tables 1 and 2 and feel that the numbers are representative of individuals with the canopy sizes recorded.

The m^3 of space occupied by the canopy was adopted as a simple index of photosynthetic ability of the plant. It was estimated based on canopy depth and maximum diameter, taking the general canopy shape into consideration when it deviated greatly from a hemisphere or spheroid. This weighted estimate of tree size is necessary to compare seed crop sizes and weight among the species of different sizes, and individuals of different age and stature. This measure is very difficult to obtain for the vines (e.g., *Mucuna, Canavalia, Rhynchosia*) and a more refined study should use leaf surface area or weight.

Intact seeds were oven-dried to constant weight 1–2 years after collection. Only apparently viable seeds were used in weight determinations and means are based on five or more seeds.

To determine seed mortality, the bruchids were allowed to complete development and emerge. They were usually captured very shortly after emergence, and reinfestation was certain only for *Acacia farnesiana*. While the intent was to determine mortality at the time of collection, it is known that many species of bruchids reinfest the indehiscent pods of many species of legumes in the field (Cushman, 1911; Bridwell, 1918, 1920; Janzen, 1967*b*) and thus the figures are probably low for the final natural seed mortality of many of the species in Table 1. Crops were collected in the dry season or early part of the rainy season (January–July) and had been mature for 0.5–2 months; those on the tree for long periods probably had more than one generation of bruchids pass through them. Only seeds with bruchid emergence holes were counted as dead; this also leads to low mortality estimates because many bruchid immatures die at a stage sufficiently advanced to have killed the seed. Thorough examination of the seeds of some species indicates that the actual seed mortality attributable to bruchids, from the infestation at the date of seed collection, ranges from 5–50% higher than that recorded in Table 1. Examination of seeds by soft X-ray is a much better technique to determine mortality but was not available. The mortality from bruchid larvae that kill green seeds by eating them entirely or disrupting development in part of the pod (Bridwell, 1918; J. E. Mathwig, pers. comm.) is not considered in Table 1.

This study is not representative of Leguminosae as a family. Introduced or cultivated species (e.g., *Delonix regia*) were ignored since here the absence of bruchids may have nothing to do with the traits of the seeds or seed crop. Fleshy seeds (usually large), characteristic of Leguminosae of lowland wet sites, were erroneously excluded from the original sample program (e.g., *Mora oleifera, Pentaclethra* sp., *Pithecellobium arboreum*, *Inga* spp.). They clearly would have strengthened the dichotomy between Table 1 and 2 since they have large seeds unattacked by bruchids. Herbaceous annuals were not examined because at the time seeds were collected, nearly all had their seeds dispersed. Finally, 36 species are only a small part of the Central American Leguminosae—Standley (1922) lists at least 750 native legume trees and shrubs in Mexico alone.

Results.—Nonparametric tests (Table 3; Wilcoxon's, see Sokal and Rohlf, 1968) show that the three statistical populations of seed traits determined from attacked species (Table 1) are significantly different from those determined from unattacked species. The means reflect this and attacked species have significantly smaller seeds, more seeds per m^3 of canopy, and more grams of seed per m^3 of canopy, than do unattacked species. Table 1 is represen-

TABLE 3. *Contrasts of seed parameters from woody Central American Leguminosae grouped on the basis of their seeds being attacked (23 species) or not (13 species) by bruchid beetle larvae, and extracted from data in Tables 1 and 2; where several samples of a species were collected, these were pooled and their means treated as exemplars. The* A *column lists the percent level of significant difference between the relative locations of the statistical populations by the Wilcoxon signed rank test.*

		Attacked		Unattacked	
	A	Average	*S.D.*	Average	*S.D.*
$\bar{X}$ g dry weight of individual seeds	0.02	0.2623	1.0330	3.0065	6.7076
$\bar{X}$ g of seed per m^3 of canopy	3.14	37.18	35.00	18.40	34.78
$\bar{X}$ number of seeds per m^3 of canopy	0.06	1020.00	2218.00	13.89*	18.84*

* Based on the sample after *Indigofera suffruticosa* (number 8,9) was removed since this species probably represents a strategy of escape from bruchids characterized by seeds too small to be attacked by bruchids, and therefore different from the other unattacked species.

tative of data reported for legume crop plants in the field (Prevett, 1961; Peake, 1952; Middlekauf, 1951; Shevchenko, 1958; Hinckley, 1960), but low for the total damage done over the year.

A nonparametric test was used because the populations have unknown distributions, and only in the case of grams of seed per m^3 of canopy do they have similar variances. The presence of highly deviant members in two samples also distorts the variance greatly; the very large seeds of *Dioclea reflexa* (number 38) are unrepresentative of species attacked by bruchids, just as the very small seeds of *Indigofera suffruticosa* are unrepresentative of unattacked woody Central American legumes.

Discussion.—To understand the relationship between attack by bruchids and (1) smaller seeds, (2) higher weight of seed per unit of canopy, and (3) higher number of seeds per unit of canopy, it is instructive first to examine a pair of species representative of these three differences between Tables 1 and 2. *Pithecellobium saman* (*Samanea saman*) and *Enterolobium cyclocarpum* are similar large trees (up to 60 m tall, umbrella-shaped life form, and often emergent) in the subfamily Mimosoideae. They grow side by side in primary and degraded forest in lowland Central America, with the latter species extending onto drier hillsides than the former. Where the seed samples were taken (near Canas, Guanacaste Prov., Costa Rica), the average density of adult plants in river bottoms is about one per 4 hectares for each species and in undisturbed forest they constitute about as much of the canopy volume as any other large tree species (2–5%). Seeds of *P. saman* are attacked by at least three species of bruchids, whereas those of *E. cyclocarpum* are not attacked by any bruchid.

Both species produce mature fruits during the dry season, usually from flowers of the previous year's dry season. The large indehiscent fruits fall to the ground where they are eaten and carried about by a variety of large and small herbivorous mammals, apparently attracted to the sweet flavor of the valves (pod). Normal seed dispersal is thus via the intestinal tract of large vertebrates and mechanical transport by squirrels and other small vertebrates. Seeds of both species recovered from deer, pig, and cow droppings have been germinated. Parrots commonly eat the immature seeds of *P. saman* but not those of *E. cyclocarpum*.

In Table 1 is described a representative, freshly fallen seed crop for *P. saman* (number 37): 650,000 seeds (about 81 kg with a mean dry weight of 0.1256 gm per seed). A minimum of 46% of these had been destroyed by several species of Bruchidae at the time of collection and as high as 99% would have been destroyed before the end of the dry season (based on examination of older seed crops). In Table 2 is described a representative seed crop for a mature *E. cyclocarpum* (number 17) of the same age (50–100 years), size, and exposure: 11,200 seeds (12.05 kg with a mean dry weight of about 1.076 gm per seed), none of which have been or would have been attacked by Bruchidae. (From many seed crops of this species, only one individual of a tineid moth was reared.) The *P. saman* produced 19.55 grams and 155.6 seeds per m^3 of canopy while the *E. cyclocarpum* produced 2.57 grams and 2.4 seeds per m^3 of canopy.

The *E. cyclocarpum* has placed 11,200 viable seeds in the environment. The *P. saman* will have placed 6,500 or less by the time the bruchids have undergone several generations and achieved their usual 99% or better seed mortality. Therefore, *P. saman* had to produce nearly 60 times as many seeds as *E. cyclocarpum* to attain half the viable seed yield.

P. saman and *E. cyclocarpum* are examples of two hypothesized adaptive strategies which probably include most woody hard-seeded Leguminosae in Central America (and probably elsewhere).

I) In the strategy represented by *P. saman*, the evolutionary consequences of the shift of several bruchid species to *P. saman* has apparently been the selection for (1) larger numbers of seeds per unit of photosynthetic ability (yielding a higher absolute number of surviving seeds), (2) smaller seeds (allowing the production of more seeds), (3) more grams of seed per unit of photosynthetic ability (yielding a higher absolute weight of surviving seeds), and (4) reduction of chemical defensive compounds (or other defenses) present in the seeds, which may in part make the first three points possible.

Of utmost importance is that most seeds produced are dead before they are dispersed. Dispersal agents have no chance to selectively remove live seeds, since the beetles oviposit before the pods are mature and virtually all pods have some eggs laid on them in the first generation of bruchids.

II) In the strategy represented by *E. cyclocarpum*, either the original absence or later removal of seed-destroying bruchids (point 4 below) has led to selection for evolutionary shifts in the direction of (1) smaller numbers of seeds per unit of photosynthetic ability (allowing the storage of more and higher quality reserves for the seedling) (2) larger seeds (made possible by the reduction in seed number), (3) fewer grams of seed per unit of photosynthetic ability (necessary to support the production of bruchid deterrent traits and perhaps higher seed quality not reflected in seed weight, or more vegetative activity by the plant), and (4) maintenance of chemical (and other) defenses in the seeds.

Of utmost importance is that virtually every seed dispersed from the parent tree is living. Probably almost none of the hard seeds of these legumes are destroyed by passing through a vertebrate dispersal agent.

A very similar example from northern latitudes is that of the honey-locust (*Gleditsia triacanthos*) and the Kentucky coffee bean (*Gymnocladis dioeca*) in eastern Kansas. A honey-locust tree 8 m tall has about 10,000 seeds in the crop weighing about 1.3 kg (mean seed dry weight is about 0.133 gm); between 30 and 50% of these seeds are destroyed in the first bruchid generation (*Amblycerus robiniae*). In eastern Kansas the indehiscent seed pods are removed from the area of the parent tree by fox squirrels (*Sciurus niger*). The squirrels eat the sweet upper edge of the valves, not the mature seeds. These pods that remain under the tree suffer 90–100% seed destruction by successive generations of the bruchid (J. E. Mathwig, pers. comm). A Kentucky coffee bean tree of the same size and age has about 400 seeds in the crop weighing about 0.8 kg (mean seed dry weight is about 2.035 gm). Seeds of *G. dioeca* are not attacked by bruchids; in addition to having an exceedingly hard seed coat, they contain at least 5% dry weight of an undescribed free amino acid (E. A. Bell, pers. comm.) which may be a bruchid toxicant.

It should be stressed that not all woody legumes will follow one or the other of these two strategies, but it appears that many do. The two unrepresentative legumes mentioned earlier, *Dioclea reflexa* and *Indigofera suffruticosa*, are representative exceptions.

This brief discussion of the sexual subsystem of the total plant system and energy budget requires considerable qualification. In the following discussion of seed number, size, and toxicity, the total photosynthate output of an individual in an evolving population is treated as constant; complications in direction of evolution produced by changes in photosynthetic ability are explicitly identified. It is assumed that the energy required for the sexual reproduction of a plant (flowers, seeds, fruits, and supporting stems) is not a trivial portion of the energy budget (cf., Harper, 1967). This energy expenditure complements the other major energy expenditure of maintaining vegetative status in respect to neighboring plants (competition and protection). The selective pressure for traits maintaining this status is derived from the loss of materials for reproduction that accompanies loss in status (shading, defoliation, desiccation, inorganic nutrient starvation, etc.).

Seed number.—Salisbury (1942) was well aware that the number of juveniles produced by a plant is related to juvenile mortality when he asked "is the larger number of potential offspring a necessity imposed by an increased susceptibility to the natural causes of mortality?" and followed with the statement that "the potential reproductive capacity of a species is a measure of its susceptibility to natural mortality."

In addition to the smaller seed size that accompanies increased subdivision of the sexual reproductive component of the energy budget, the subdivision influences the "support" activities of the parent plant. The smaller the seed (the more there are), the higher the ratio of seed coat (useless to the seedling) to seed content. Each seed requires an embryo irrespective of how much storage material is in the seed (most of the seed weight); it is doubtful if the content of the embryo aside from the cotyledons can be subdivided with the same freedom as the content of the storage organs. It would be of interest to contrast the ratio of embryo size (minus cotyledons) in attacked versus unattacked legumes with the ratio of their seed weights. A flower plus vegetative support structure must be produced for each seed pod, and their size is not likely correlated with seed size in woody legumes. To the degree that seed number is increased by increasing seed pod number, the cost of these support structures per unit weight of seed will stay the same or become proportionately higher as seed number increases. Some species of legumes, however, appear to have increased the seed crop by increasing the number of ovules per pod (see Stebbins, 1967, for further discussion of this general problem). In some cases, decrease in size (increase in number) of seeds may be countered by increased susceptibility to seed-eating birds (cf. Kendeigh and West, 1965). The above selective pressures countering reduction in seed size will be further augmented by the decrease in quantity and quality of storage products.

In increasing the absolute number of escaping seeds by increasing the number of seeds per crop, the plant is in part using the strategy termed "predator foolhardiness" by Lloyd and Dybas when discussing cicadas (1966). This appears to be a common phenomenon where the prey, such as legume seeds, have no active defense mechanisms. Here, the predators are satiated in respect to such things as hunger, time of prey capture, time of prey handling, etc., and since there is not time for a numerical response, prey individuals above a certain number go free. This is accompanied by a lack of selection for individual escape mechanisms because these are antagonistic to effective mating behavior and other components of the life history. In the legume-bruchid system, an example of this may be selection against the presence of those chemical defenses broached by the bruchid species that attack the seed, since these chemicals are a cost that may be converted into more seeds; this reduction in defense, however, may make the tree susceptible to more species of bruchids (nearly all the species in Table 1 are attacked by two or more bruchid species), leading to the need for even more seeds to accomplish bruchid satiation. This will be discussed in detail below.

Predator satiation in the bruchid-legume system works in the following manner. When a legume tree matures a fruit crop, the first "wave" of bruchid females to find it is unable to kill every seed owing to various shortcomings, such as the following: (1) a low number of eggs per female (50–150; Bridwell, 1918; Howe and Currie, 1964; Cushman, 1911); (2) a low number of females being in the area and finding the tree; (3) the seed pods dehiscing before all eggs have been laid (Bridwell, 1918); (4) lack of care in choice of oviposition sites pattern exhibited by some bruchid species (Bridwell, 1918); and of very great importance (5) the removal of seeds by active dispersal agents before the bruchids find them. In essence the legume "surprises" the bruchids by fruiting in a manner spatially and temporally unpredictable such that all the available bruchids cannot kill all the seeds before some escape. As successive generations of bruchids pass through the seed crops on or below the tree, a progressively higher percentage of the seeds removed by any dispersal agent are dead. This should clearly lead to selection for traits favoring those dispersal agents that remove the seeds immediately after maturation (throughout the discussion, it is arbitrarily assumed that a seed has not been "produced" until it leaves the plant).

This dispersal probably does not, however, usually lead to bruchid dispersal. Bruchid-occupied seeds of *Acacia cornigera* fed to a tame brown-tailed jay (*Psilorhinus morio*) were broken up as they passed through the bird, and only viable seeds of *A. cornigera* have been recovered from bird, deer, and cattle droppings. That the seeds disintegrate in the soil very rapidly after bruchid emergence may account for the absence of legume seed in Barbour and Lange's (1967) soil samples directly under Australian acacias that had only recently been in seed.

My observations and collections of maturing seed crops of various mimosaceous legumes in Mexico indicate that a survivorship curve for the seeds on the trees drops steeply downward with the first group of female bruchids, decreases at a lower rate as occasional females later find the tree, and then drops very steeply downward as second, third, etc. generations emerge and re-oviposit in the seed crop. As the density of bruchids at the site builds up from newly emerging individuals, the number of new individuals finding the tree and the egg-laying ability per female should become relatively less important. This may be in part offset by the adults of many species of bruchids having to seek nectar and/or pollen before ovipositing (Waloff, 1968; Howe and Currie, 1964), and thus having to find an oviposition host tree again after feeding. The more discontinuous the bruchid-legume interaction, the less expensive will be predator satiation. If the adult bruchid is using the larval host plant as a food source, selection should favor asynchrony of flowering with the time of major bruchid emergence from the pods.

On the average, increasing the number of species of bruchids using a single species of legume will increase the difficulty of predator (bruchid) satiation, since this will increase the probability that maximal oviposition is attained for trees growing under a variety of physical and biotic circumstances. The degree to which the beetles compete for seeds is not known, but it is improbable that competition lowers the *total* seed mortality, averaged over many seed crops.

This system has been observed in some detail with *Acacia cornigera* in lowland Veracruz, Tamaulipas, and Oaxaca, Mexico (Janzen, 1967*a*, *b*, 1968*a*, and unpublished field notes) and with other swollen-thorn acacias. The bruchids (*Acanthoscelides oblongoguttatus*, *Mimosestes* sp., and *Stator subaeneus*) achieve 20 to 80% destruction of the seeds in the indehiscent pods on a given plant in the first generation. This destruction is greater the closer other seed-bearing *A. cornigera* are, and the more similar the age of the general vegetation is to that in which seed-bearing *A. cornigera* are normally found (3 to 8 years of undisturbed regeneration, Janzen, unpublished). Percent seed destruction is lowest during the later part of the rainy season, but trees bearing seeds at this time are also out of synchrony with the remainder of the population (and therefore "far" from other seed-bearing individuals). The emerging females plus those that have found the tree in the meantime oviposit so thoroughly that I have never found a viable seed in a crop that has hung on the acacia over 2 months. A representative *A. cornigera* produces 60,000 seeds in its lifetime and it is doubtful if more than 600 escape from the parent tree. However, during the period between initial and later bruchid oviposition, the pods are split and seeds eaten by characteristic birds of second growth (e.g., *Saltator atriceps*, *S. coerulescens*, and *Psilorhinus morio*). These birds are responsible for nearly all the survival of *A. cornigera* seeds; the seeds lacking bruchids pass through the gut unharmed (100% germination in several hundred collected from feces of *P. morio*). Other birds such as orioles split the pods for the pulp but do not eat the seeds. These seeds fall to the ground. Such seeds, plus those defecated, are responsible for the very rare seedlings found near the parent acacia.

In short, when a seed crop matures, "all the eggs have been put in one basket" and the question is how to get some out before the bruchids get all. Dispersal seems to be the major solution.

Therefore, the selective pressures associated with seed escape must be added to those associated with passage of inimical seasons and dispersal to sites with higher survival probabilities. This escape is an essential component of dispersal of all Leguminosae attacked by bruchids (just as seed protection is a component of the energy budget of all Leguminosae, attacked or not), and for that matter for all species of plants where dispersal lowers the probability of seed predation by animals or fungus (probably most angiosperms and gymnosperms). The number of seeds that survive the bruchids must be sufficient to produce the density of adult plants observed at present. For the plant population to survive at its present density on this number of seeds, or fewer, requires some device to totally deter the bruchids, as will be discussed at a later point. This escape function should constitute an increasing proportion of the selection for dispersal, the less of a colonizer the species is.

There is at least one circumstance where bruchid predation may select for a crop of a few giant seeds. In some forest habitats a very large seed may be essential, with any surviving seed having a very high chance of maturation (as perhaps with seedlings of the tropical primary forest vines, *Entada, Mucuna*, and *Dioclea*). In this case, reduction in seed size (to yield more seeds and thereby increase the number of seeds escaping from the bruchid) may lead to a very rapid reduction of the probability of maturation. Bruchid attack might therefore lead to selection for even bigger seeds with a very high probability of maturation of the few that escape. While compensating for seed mortality, this might make dispersal more difficult and the seed more attractive to large vertebrate predators.

Selection for more seeds for predator satiation is clearly complicated by complementary selection for increased seed yield to rapidly exploit an area and yield a high rate of discovery of new sites to colonize. Adding to the confusion, once a plant has become established, its seed crop may seem absurdly large to replace the small adult population (Harper, in lit.). Insects may then eat much of this seed crop with little or no influence on the density of adult plants. However, even in this case, there should be strong selection favoring the genotype that contributes the highest proportion of new plants to later generations. This contribution may be maximized through selection for seed predator satiation even though the density of the plant population never changes.

Seed size.—"Considered individually, without regard for their numbers, the chances of survival must increase with the increase of reserve food material in the seed" (Salisbury, 1942). Exceptions to this statement are clear (e.g., when the increased seed weight lowers the probability of dispersal for escape or other reasons), but it is nevertheless useful. Seed size is obviously related to seed number, but is clearly not a simple dependent outcome of subdivision of the reproductive output. I wish to stress that the reduction in seed size discussed here is not on the basis of some reproductive energy being diverted for physical or chemical defenses (Smith, 1968, 1969), but rather that it is a consequence of increased seed number.

Species having seeds so small that bruchids cannot develop in them (Bridwell, 1918) are not well represented among the legumes listed in Table 2; *Indigofera suffruticosa* is the only possible example of those collected (Bridwell records that a very few dwarfed bruchids emerged from seeds of *Indigofera*). Since *I. suffruticosa* probably represents this other strategy, it does not belong in Table 2 and was removed before the mean number of seeds per m^3 of canopy was calculated. If Table 2 contained an equal representation of herbaceous and woody legumes, it is doubtful that the means of seed weight (and seed number per m^3) between Table 1 and 2 would have been much different. This is because Table 2 would then have been a composite of the population of very small and very large-seeded legumes.

Small seeds are usually associated with the general strategy and requirements of a herbaceous plant (which is very often a colonizing plant), as opposed to a woody one (Baker, 1967; Salisbury, 1942). On the other hand, among Central American Leguminosae the minimal-sized seeds required by the smallest bruchids are not much larger than many unattacked herbaceous legume seeds. This suggests that a bruchid's shift onto a legume as a new host plant could easily reverse a selection for increased seed size. It is also likely that there has been selection for reduction in size of some species of bruchid to counter a reduction in seed size. Bridwell (1918) has pointed out that seed dimensions such as thinness may exclude bruchids in some cases (e.g., *Cassia* spp.).

Selection for large legume seeds may be regarded as "allowed" by freedom from seed predation by bruchids, since this permits partioning of the seed reproductive output into a few large units, each producing a seedling with higher quality and quantity food reserves. In those rare cases where a large seeded legume is attacked, such as *Dioclea reflexa* (Table 1, number 38), *D. marginata* (Bondar, 1931), and *Mucuna rostrata* (Vaurie, 1950), one of three circumstances may be causal. (1) As described above, large seeds may be *very* important to seedling survival; however, it is more likely the plant has not yet evolutionarily responded to the presence of the bruchid. (2) Such a response may never occur, but the contrast of seed weights in Tables 1 and 2 suggests that it usually does, and this is why *D. reflexa* may not properly belong in Table 1. A failure in response by a rare plant should generally be reflected in a change in density, most likely downward (Gillett, 1962). If the seed destruction found in *Dioclea reflexa* (100% by the first bruchid generation in the sample collected) is representative, it is easy to envision pathways by which the density of *D. reflexa* may have been reduced when the bruchid (*Caryedes* sp.) shifted onto it. (3) Another failure in response (very unlikely for a rare plant) could be associated with the case where the number of surviving seeds is irrelevant to the density of adult plants (the "prodigal parent theory").

There is no indication that the large legume seeds with a hard seed coat are physically inimical to bruchid development. *Dioclea reflexa*, and *Mucuna rostrata* (Vaurie, 1950) may have 10 to 25 bruchids per seed, and bruchids often fail to eat all the inside of the seed. Incidentally, where seeds are so small that only one bruchid can mature per seed, there should be selection for the female to lay only as many eggs as can develop in the pod. This pattern has a much higher chance of leading to a numerical mistake by the female with subsequent escape of a seed, than does the case where many eggs are laid on the pod because many bruchids can develop in each seed.

Numerous rain forest legumes in Central America have large and fleshy seeds and no evidence of bruchid damage has been found (e.g., *Pentaclethra* spp., *Prioria copaifera*, *Pithecellobium arboreum*, *Inga* spp., *Cassia* sp.). These seeds germinate or die within several weeks or less (as contrasted with hard seeds that remain dormant for years) and this is not sufficient time for bruchid larvae to complete development. These species characteristically have seed crops with the same numbers of seeds as those of legumes with large and hard seeds.

Seed crop weight.—That more grams of seed per unit of canopy are produced by the attacked species suggests that they have more than just increased the subdivision of the seed reproductive output to accomplish predator satiation. They are apparently putting into seeds some of the material that unattacked species use for vegetative activity (competitive or defensive). This is further suggested by the production of many more seeds per m^3 of canopy of attacked species. This indicates that increase in total seed crop weight did not involve a simple increase in canopy volume (through an increase in competitive ability by the parent). This means that the attacked species of legume may have less vegetative competitive ability than the unattacked species. This obviously can influence the density of the species and its ecological distribution. This point has been lightly explored by Gillett (1962) and Griggs (1940) and is important to the regulation of plant density by seed predators.

The change in seed weight per unit of photosynthetic ability has at least two major selective components. Increasing seed number (holding seed weight constant) by increasing seed crop weight is detrimental to the parent tree. Increasing seed number by decreasing weight of the individual seed is detrimental to the seedling. The outcome should be a balance between these two; the attacked legumes in Table 1 are at a disadvantage to those in Table 2 on both counts.

Seed toxicity and other deterrents.—While various traits of legumes may serve to reduce damage done by bruchids (Table 3), it is doubtful if any except very direct deterrents can confer the apparent total immunity to bruchid attack of those species in Table 2. Chemical traits are the most likely candidates for this role. Bridwell (1918, 1919, 1925, 1938) and Howe and Currie (1964) noted the possible causal relationship between toxins in seeds and the failure of bruchid larvae to develop in them. Applebaum (1964) and Applebaum et al. (1965) have demonstrated this relationship experimentally with both toxins (saponins) and nutrient imbalances with several commercially important legumes. This may be generally expressed as "In most cases the larvae had been able to penetrate through the seed coat into the cotyledon and had perished there as the result of their first meal upon its substrate" (Bridwell, 1919, and a similar statement in Applebaum et al., 1965). The actual cause of death is not as clear as Bridwell indicates; nevertheless the presence of toxins in the cotyledons is strongly suggested.

Many species of bruchids develop normally on a number of species of legumes in nature (Figure 1). These are, however, only a small fraction of the legume species in their respective habitats. Experiments

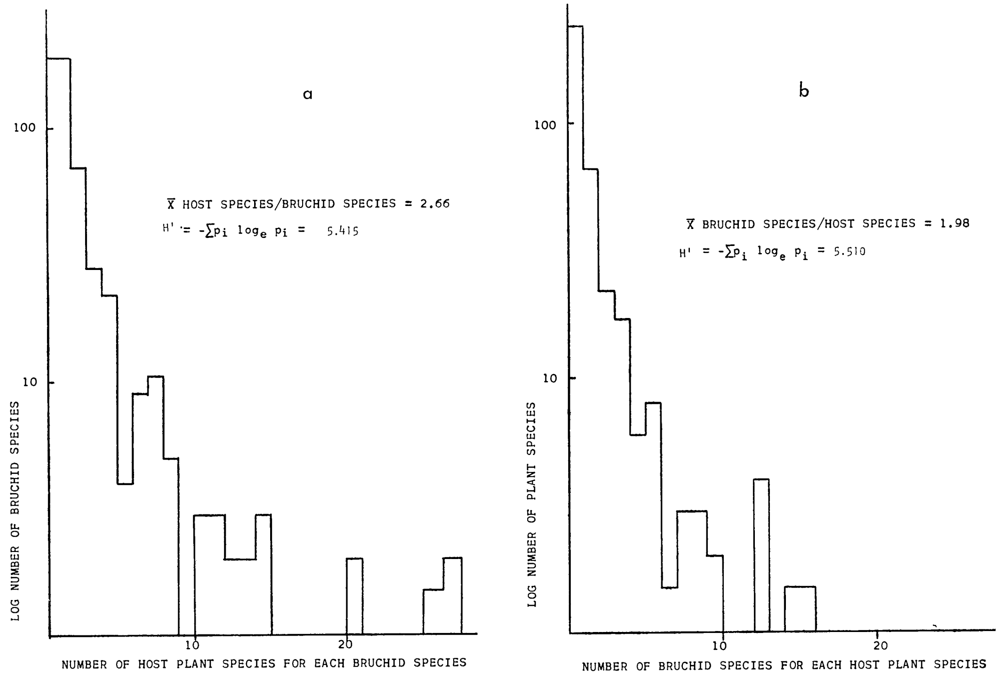
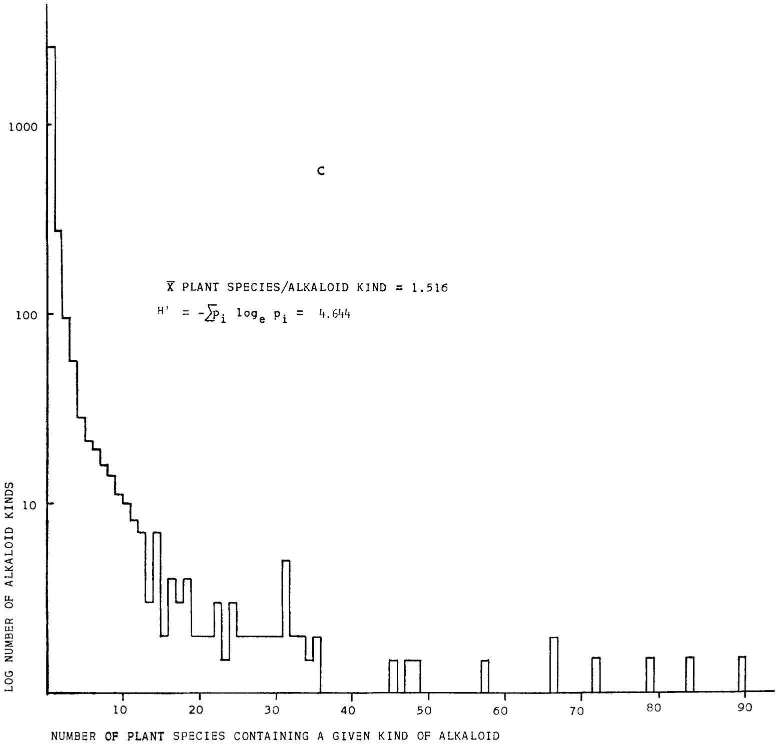


FIG. 1. (a) Distribution of host plant species among the 366 species of bruchids recorded by Zacher (1952). The high diversity of the host plant relationships may only be due to insufficient collection records, but it does agree with the general distribution of legume species among the bruchid species listed in Table 1. (b) Distribution of bruchid species among the 380 host species recorded by Zacher (1952). As with (*a*) above, the high diversity of the host plant relationships may only be due to sampling error, but it does agree with the general distribution of bruchids among the host species in Table 1. (c) Distribution of plant species among the kinds of alkaloids produced by them (all the

conducted by Bridwell (1918) indicate that this specificity may well be due to seed traits as well as inability of the bruchid to locate the host, asynchrony between bruchid and host, etc. He offered seeds of 56 species of Leguminosae to one or more of six species of bruchids and found (a) 48 species of legumes had at least one failure of larvae to survive after eggs were laid on the seed; (b) 25 species had failures of all eggs laid on them; and (c) of the 85 cases of oviposition on the seeds, only 41% resulted in a new generation of bruchids. Specifically, *Stator pruininus* oviposited on 44 species of seeds but developed in only 11 of them while *Callosobruchus chinensis* oviposited on 40 species and developed in eight of them.

This subject was examined more directly by a pilot experiment introducing very small percentages of finely ground seed coats and seed contents of *Erythrina standleyana* (seeds of *Erythrina*—Table 2—have long been known to contain alkaloids toxic to vertebrates) into the flour medium of several laboratory stocks of *Tribolium castaneum*. This caused a highly significant decrease in larval weight and survival to maturity, and increase in larval development period (Y. Chen, unpublished, in the laboratory of R. R. Sokal). *Erythrina* was chosen because the seeds of this large pan-tropical genus are characteristically free from bruchid attack, with one exception (Bridwell, 1938).

Five chemical traits of seeds are sug-



plants listed in Willaman and Schubert, 1961). The subset of Leguminosae was not easily extractable from the summary data given by these authors. However, by inspection, the distribution of legume species as a whole, and the seeds of legumes specifically, among the alkaloids does not differ from the general distribution. To aid in interpretation of the graph, note that of the 1966 alkaloid kinds, there were only 10 that were found in the biochemical repertoire of as many as 11 plant species, 1262 were found only in a single plant species, and only one alkaloid kind was found in 90 species of plants.

gested by the literature as inimical to bruchid activity. Bridwell (1918) noted that those species that develop in legumes whose seeds contain fatty storage compounds do not survive in those that contain starchy storage compounds and vice versa. Ishii and Urushibara (1951) observed that pentose or methyl-pentose sugars in legume seeds were inimical to development of *Callosobruchus*. The demonstration that the saponins in soybeans are toxic to *Callosobruchus* (Applebaum et al., 1965) and that peptide availability to bruchids may be reduced by the presence of endopeptidase inhibitors in legume seeds (Applebaum, 1964; Borchers et al., 1947) adds further to the diversity of chemical defense. While these four factors are clearly functional in mediating host specificity, they probably do not account for the very high diversity of the legume-bruchid interaction shown in Figure 1a and b.

Nitrogenous compounds, specifically alkaloids and free amino acids, do however, occur with sufficient concentration, frequency, and diversity in legume seeds to lead to this diversity of host specificity. Willaman and Schubert (1961) list at least 135 alkaloids from the seeds of legumes (and 2981 from all plants) and Leete (1965) says that "tens of thousands of new alkaloids remain to be discovered in the vast plant kingdom." Fowden (1964) lists over 100 free amino acids (as distinct from the 21 nontoxic amino acids generally found in organisms), many of which are toxic and have been found in seeds of Leguminosae (Bell, 1964, 1966; Hegarty and Pound, 1968; Bell and O'Donovan, 1966; Bell and Tirimanna, 1965).

Seeds in general, and large hard legume seeds in particular, are well known to contain many nitrogenous compounds that are toxic or at least metabolically disruptive to vertebrates. My hypothesis is that *this toxicity is for the most part accidental to vertebrates but is adaptive by slowing the development of or killing bruchid beetle larvae.* Where not accidental in respect to vertebrates, it is probably functional in reducing seed predation by them as well (see below).

For any compound, toxicity to a vertebrate does not necessarily imply toxicity to an insect (see especially examples in Bridwell, 1938). However, I know of no general class of natural compounds that is generally metabolically disruptive to vertebrates but not to insects, or vice versa. Furthermore, a number of alkaloids are known to function as natural insecticides (cf., Shepard, 1951; Kircher et al., 1967; Metcalfe, 1955; Crosby, 1966). While the only indirect evidence that these compounds may be toxic to bruchids is that of the pilot experiment cited above with *Erythrina standleyana* and *Tribolium*, that they are toxic is strongly suggested circumstantially. Further, either by published reports or Central American local folklore, the seeds of every species of plant in Table 2 are known to have been used as a vertebrate poison. *Mucuna mutisiana* (number 1) has been found to contain at least 5% by weight dihydroxyphenylalanine (E. A. Bell, in litt.) but the others have not been quantitatively analyzed. On the other hand, while alkaloids, free amino acids, and other potentially toxic compounds are undoubtedly present in the attacked species of legumes, at least some species of bruchids are immune (*sensu latu*) to those in each seed.

Alkaloids and amino acids have several properties that make them important in a legume–bruchid interaction. Their high diversity (Figure 1c) indicates a multiplicity of possible precursors (which are at times themselves alkaloids and amino acids; cf., Kirby, 1967; Leete, 1965; Fairbairn and El-Masry, 1967), and therefore every species of legume may be highly preadapted for their use as defensive compounds (in contrast to the use of more novel compounds). Their specificity indicates that they are functional in the kinds of processes that are peculiar to single, or a few, species of plants; removals of particular predators from particular plants are such processes. They are rich in nitrogen, a compound that legumes are generally not short of (Stewart, 1967), as is further evidence by the abundance of protein in legume seeds. They are present at high concentrations rather than traces (Bell, personal communication; Bell, 1966). They may be doubly selected for since they can also serve as nitrogen storage compounds for the seedling (Bell, 1966; Bell and Tirimanna, 1965).

They are highly complex structures requiring many intermediate stages of no known metabolic function (see for example the discussions of alkaloid synthesis in Kirby, 1967 and Leete, 1965). This indicates that they are not waste products, but products of biochemical processes selected for by the function of the product, not the intermediate steps in the process. That they are not waste products is further indicated by Tso and Jeffery's suggestion (in Fairbairn and El-Masry, 1967) that "tobacco alkaloids are in a dynamic state and . . . that when ^{14}C and ^{15}N labelled nicotine were fed to tobacco plants, radioactivity was transferred to amino acids, sugars, pigments, organic acids, and other plant metabolites. Transformations of one tobacco alkaloid to another also occurred." They are in no sense "cheap" compounds to produce in terms of either energy or biochemical machinery required in their synthesis (pers. comm. from numerous biochemists).

The various organic acids and other compounds found occasionally in legume seeds and known to be toxic to vertebrates (e.g., those causing lathyrism, Bell, 1968, Bell and O'Donovan, 1966) should be treated in the same analysis. While compounds such as pacifarins (Schneider, 1967) that occur at very low density will be much more difficult to identify in seeds in relation to insect attack, they clearly have the potential of being insect deterrents through the detrimental effect that they may have on the intestinal flora of the insect.

The ability of legumes to synthesize and concentrate compounds toxic to all bruchids is important to the two adaptive strategies represented by the species in Tables 1 and 2. If a plant can synthesize a compound or combination of compounds sufficiently toxic to bruchids to keep all species from switching onto it, or to remove those already there (more difficult), it has then freed itself from the seed number and weight expenditure associated with predator satiation discussed above. This should be sufficient selective pressure to drive the evolution, provided the appropriate precursors are present. The evolution of such a compound or combination of compounds has been relatively rare; a conservative estimate would place the number of woody Central American legumes free of bruchids at 20%.

Selection probably operates more commonly to evolve a specific compound to remove a single species of bruchid. Simultaneously, selection will favor immunity mechanisms in the bruchid (detoxification by excretion, destruction, chelation, etc., Smith, 1962; Brower et al., 1964; also see Trelease and Trelease, 1937, for avoidance by bruchids of selenium in *Astragalus* seeds). Of the several species of bruchids on the legume, selection should be the strongest against that species that kills the most seeds earliest in the life of the crop, since the longer the seed is free from predation, the greater the chance that a dispersal agent will remove it. Selection will also favor the dispersal agent that removes the seeds fastest. A fluid system may well exist among the legumes in a given vegetation type, in which bruchids shift evolutionarily from one host to another while remaining rather evenly dispersed among most of the host species (just as with animals between islands, cf., Janzen, 1968*c*). The more bruchid species there are on a host, the more difficult it will be to satiate them collectively and the stronger selection should be for traits that will remove some of them.

Occasional evolutionary shifts of legumes from being bruchid-attacked to being bruchid-free should be rare, and the reverse more common. Many bruchids lay eggs on a wide variety of seed pods and other objects in which the larvae do not develop (Bridwell, 1918). Such behavior constitutes a continuous test of the presence of toxic compounds in the seeds of an immune species. Further, if an individual tree in a bruchid-free species lacks immunity it is possible for many generations of bruchids (equal to several multiples of the life of the tree in years) to pass through the seed crops of that tree. If this tree is at all isolated, this is a definite opportunity for the selection of a bruchid genotype that can avoid the toxicity of the other members of the species. Finally, once a plant begins the seed-number and seed-size race with a bruchid, there will probably be stronger selection against the production of metabolically "expensive" toxic compounds. This may open the plant to attack by other species or bruchids. Once three to four species of bruchids are feeding on the plant, it would seem to have little chance to remove all of them at once.

Evolutionary shifts of bruchids away from legumes have apparently occurred infrequently (onto Palmae, Annonaceae, etc., Zacher, 1951, 1952). If the generic taxonomy of Bruchidae reflects the history of the group, these have not resulted in adaptive radiations, unless these genera have subsequently returned to Leguminosae. Kingsolver (in litt.) has pointed out that in most cases the seeds attacked are in a hard capsule or pod; he has also noted that some of these plants (e.g., *Ricinus* and *Hip-*

pomane in the Eurphobiaceae) have compounds toxic to some vertebrates.

The *gradual* removal of a bruchid species by a legume species is probably the clearest way that new toxic compounds are evolved. If some usual metabolite or storage product is marginally toxic to a bruchid species, gradual modification of the compound through selection could easily occur, with the increased toxic effect being through lowered viability or longer development of the bruchid (leading to removal of more seeds by a dispersal agent before they are killed). Once a compound has been produced that is sufficiently toxic to remove one species entirely, it may be a lesser step to modify that compound to a structure toxic to other species. In view of the high mortality of seeds (Table 1), an individual tree that lacks bruchid attack would make a dramatically larger contribution to the next generation compared with those individuals still attacked. Finally, by simply modifying the concentration of a compound, the legume may also prevent a bruchid species from feeding on it; in such a case the compound is more likely to be a usual metabolite or a true "waste product" (though the comparative metabolic costs, of making more toxicant with extant biochemical machinery, or evolving new machinery, are not clear; cf., Pauling, 1968).

A particularly complicating interaction between bruchids and nitrogen containing compounds in the seeds of legumes is suggested by Applebaum's (1964) demonstration of a general absence of proteolytic enzymes in *Callosobruchus* and several other Bruchidae. He concludes that the high level of endopeptidase inhibitors in legume seeds (e.g., trypsin inhibitors, Borchers et al., 1947) may have been evolved as a defense mechanism against all kinds of seed-eating insects, and that the primary adaptive radiation of Bruchidae may have been the evolutionary loss of inhibitable endopeptidases. This even indicates that the major adaptive radiation of the Leguminosae may have been as much freedom of their seeds from general insect attack as their ability to fix nitrogen. Applebaum further notes that legume seeds generally have sufficient free low molecular weight peptides plus enzyme activity of their own to "integrate" with the low enzyme activity of the bruchid to provide sufficient nitrogenous compounds for the bruchid. I would carry this one step further in noting that the other nitrogenous compounds, alkaloids and free amino acids may provide nitrogen to certain bruchids. With this step we are back to the questions: (1) did the bruchid lose its ability to break down proteins because of the availability of low molecular weight nitrogenous compounds, or (2) did the bruchid shift onto legumes because of the availability of these compounds in their seeds, or both? I think that both have occurred. This is even further complicated by the hypothesis that these nitrogenous compounds are present in the seeds as defense mechanisms against Bruchidae. Ironically then, it may be evolution of a particular defense mechanism (a nitrogen containing compound) against a particular bruchid that makes the seed susceptible to another species of bruchid, and vice versa.

Up to this point, chemical traits of seeds have been stressed but the morphological and phenological traits can also add considerably to the diversity and complexity of the legume-bruchid interaction. Being more straightforward, they have been listed in Table 4 along with the chemical traits. Perhaps the most spectacular morpho-behavioral escape trait is that of the peanut (*Arachis* spp.). These South American herbaceous legumes have enormous seeds (for their life-form) that are likely quite free from predation by herbivores in general, and bruchids specifically in nature (unless there is an unrecorded burrowing bruchid). However, the bruchid *Caryedon gongora*, is a serious pest of stored peanuts in Africa (Johnson, 1966, Davey, 1958).

In general, chemical, morphological and behavioral defensive traits against bruchid have four important qualifications. First, virtually all seem effective against at least one species of bruchid but only rarely

TABLE 4. *Traits of Leguminosae that may be functional in eliminating or lowering bruchid destruction of seeds. A similar list could be compiled for any large plant group and its predators.*

1) Gum production by seed pods following penetration by first larva from an egg mass; this may push off remaining eggs (Bridwell, 1920, *Prosopis juliflora*) or drown or otherwise obstruct young larvae (Hinckley, 1960) (*Acacia, Pithecolobium, Cassia*).
2) Storage of tannins or other potential toxicants in the walls of seed pods through which the first instar larva must bore.
3) "Copious albumen" on the seed, on which the eggs are laid; the larvae being unable to "penetrate" this, "perish" (Bridwell, 1919 *Cassia nodosa*).
4) A hard and tough layer of "albumen" inside the seed coat that the bruchid larva cannot penetrate even after passing the seed coat (Bridwell, 1918).
5) Dehiscence (*Leucaena*), fragmentation (*Mimosa*) or "explosion" (*Canavalia*) of pods, scattering the seeds to escape from larvae coming through the pod walls and from ovipositing females (Cushman, 1911; Bridwell, 1918).
6) Production of a pod free of surface cracks (*Bruchus prosopis* oviposits only in cracks on *Prosopis juliflora* and cannot glue its eggs to smooth surfaces as do many other Bruchidae, Bridwell, 1918).
7) Pods with walls thin enough such that parasites can oviposit through them onto the bruchid (Bridwell, 1918).
8) Indehiscent pods, excluding those species that deposit only on exposed seeds (*Stator pruinius* on *Prosopis juliflora* when pods opened artificially, Bridwell, 1918).
9) A layer of material on the seed surface that swells when the pod opens and detaches the attached eggs (*Bauhinia monandra*, Bridwell, 1918).
10) Very dense and hard seed coat (Bridwell, 1918; Zacher, 1952; Howe and Currie, 1964).
11) Starch storage products excluding those that feed on oil storage products in the seed, and vice versa (Bridwell, 1918).
12) 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, pers. comm.).
13) Rich in endopeptidase inhibitors, making digestion of the bean by the bruchid very difficult (Applebaum, 1964).
14) Flaking of seed pod surface which may remove eggs laid on that surface (several swollen-thorn acacias).
15) Immature seed remains very small throughout the year and then abruptly grows to maturity just before being dispersed (*Acacia*).
16) Mature seeds so small that the ovipositing female cannot maintain her balance on them to oviposit (Bridwell, 1918).
17) Seeds so thin that bruchid cannot mature in them (*Cassia siamea*, Bridwell, 1918).
18) Seeds so small that bruchids cannot mature in them (many wild herbaceous legumes).
19) Very moist and fleshy seeds that germinate within several weeks or die, and therefore bruchids lack time for development (*Pentaclethra, Inga, Pithecellobium*).
20) More or less smooth or convex seed surfaces correlated with failure to oviposit on different strains of *Phaseolus* (Howe and Currie, 1964).
21) Low nutritional content of the cotyledons or other factors leading to failure of the bruchid larvae to empty the seed, with subsequent pupation in the center of the seed from which the adult cannot escape (Howe and Currie, 1964).
22) Very high asynchrony of seed crops of individuals of a single species, leading to a lower density of females at any one time (advantageous), but a more even distribution in time (disadvantageous).
23) Very low but continuous seed production by widely spaced individuals of the species (*Canavalia, Rhynchosia, Phaseolus*), leading to failure of bruchids to find some crops and a very low bruchid output from any crop found.
24) Asynchrony of seed set of rare species in the community with the common species in which the major part of the bruchid population breeds.
25) Maximal wide spacing of seed bearing trees.
26) Synchrony of seed bearing with that time of year most unfavorable to adult bruchids.
27) Asynchrony of seed bearing with flowering by those species to which adult bruchids go for nectar and pollen.
28) Shedding of green pods that have been oviposited on before the seed matures, resulting in death of bruchids and conservation of the energy that goes into seeds that would have been killed.
29) Synchrony of fruit bearing with those times most favorable to egg and larval parasites.
30) Having a dispersal agent that removed seeds very early after maturation.
31) High synchrony of seed set among individuals of the same species accompanied by long periods with no seed crop.

against all bruchids. Second, most can be countered by evolution of the bruchid. Third, nearly all probably involve other functional systems in the plant relatively independent of direct bruchid attack (except perhaps some chemical defenses). Fourth, and perhaps most important, selection for the defensive properties of a trait will generally *not* proceed to the exclusion of other functions. In other words, while it may be advantageous to mature fruit at the time of year most unfavorable to bruchids, it may be much more advantageous to bear fruit at another time more favorable to the balance between vegetative and sexual productivity (cf., Janzen, 1967*a*); here, the time of fruit maturation will be a compromise.

Other Plants

For many groups of plants, Salisbury's (1942) emphasis was incorrectly placed when he stated that "mortality in plants is mainly a feature of the seedling stage." A steadily growing body of literature documents the high percentages of seed mortality of wild plants by insects (Table 1, and Ollieu and Schenk, 1966; Novak and Foote, 1968; Foote, 1967; Radkyevich, 1963; Barger and Davidson, 1967; Dozier, 1932; Anonymous, 1966; Breedlove and Ehrlich, 1968; Simmonds, 1933; Holloway and Huffaker, 1957; etc.). The tens of thousands of species of seed eating insects must be a very important factor in a plant's biotic environment, both in evolutionary history and present population changes. Further, the death of a mature seed on the parent plant cannot be merely lumped in the same category as the death of a seedling, since the longer the juvenile plant lives, the stronger will be the selection for those traits that keep it alive, as it represents a progressively larger percentage of the next generation. For many plants the seed lives much longer than the seedling.

In addition to the generally unappreciated seed destruction by predators that eat flowers and buds, seeds killed by true bugs are especially hard to recognize since no obvious exit hole is left in the seed (Hemiptera are one of the major general seed eaters and contain several very large groups of almost exclusively seed-eating species). For example, in several occasions, numerous attempts to obtain viable seeds of vines in the Apocynaceae (e.g., *Mandevilla*) from the canopy of Costa Rican and Mexican forests have been unsuccessful because lygaeid bugs feeding through the seed pod wall had killed 100% of the seeds. This cannot be true all the time, but clearly could provide a selective pressure to render these seeds toxic to lygaeids and undoubtedly has influenced the number and sizes of seeds produced. The same is true of vines in the Asclepiadaceae in second growth of the same forests. Bugs in the family Cydnidae are commonly encountered feeding on grass seeds. A sample of seeds of the wild (but introduced from Africa) grass *Panicum maximum* in the dry lowlands of Costa Rica showed 96.6% seed destruction by these bugs (1000 seeds from 21 different plants). This level of damage by bugs to small wild plant seeds is common in the lowland tropics.

An energy conservation mechanism, while as yet undocumented in Leguminosae, is apparently common in other plant species in response to insect seed damage. For example, a representative flower crop (about 1.5 million) of *Ceiba pentandra* (Bombacaceae; near Canas, Guanacaste Prov., Costa Rica; January–February, 1967) set about 11,000 young fruits. During the first two weeks of development, about 90% of these fruits were shed following death of many of the ovules through feeding by lygaeid and coreid bugs. The remaining fruits had little or no feeding damage and developed large pods. It may be that the tree was only balancing the size of the seed crop against the stored energy reserves (which must vary from year to year) available for fruit maturation. Nevertheless, the fruits discarded before much development had occurred were those that would have had few, if any, intact seeds in them.

Circumstantial evidence for the "escape" component of dispersal, described earlier for *Acacia cornigera*, is especially abundant in other groups of plants. Gravity, water, and wind are perhaps the least evolutionarily complex escape mechanisms. They do not themselves usually destroy seeds and little variation in dispersal pattern is available. For example, in Central America Bombacacaeae (e.g., *Bombacopsis*, *Ceiba*, *Bombax*) the small seeds are imbedded in cottony fibers and are blown away from the tree. However, a high percent are released on windless days and fall under the parent. Within several days after pod dehiscence, it is virtually impossible to find a live seed (cotton-stainer bugs are the predators; *Dysdercus* spp. in the Pyrrhocoridae) under the parent tree (see also Myers, 1927), but seeds found 50 m or more from the parent are generally unattacked. Here, the escape component of dispersal could be favored by selection for pods that open only in a high wind. One of the selective forces promoting dry season fruiting in wind dispersed trees (Janzen, 1967*a*) may be the characteristic windiness of dry season days.

Dispersal by vertebrates also has an escape component; even if there is no insect attacking the seeds, escape from the dispersal agent and similar vertebrate predators must be selected for. There will, however, always be some species whose seeds lack predators of all kinds. Reasonable candidates for this rare event are the seeds of understory tropical Rubiaceae which customarily have very few seeds (and in Costa Rica, rarely show evidence of damage by insects; we are probably indebted to the insect community for the caffeine in coffee seeds).

The simplest case of dispersal is when the seed is consumed with the fruit or the fruit is carried about whole. There should be strong selection for traits to withstand the chewing and digestive processes. Seeds are often considered to have to go through the chemical scarification of a vertebrate's intestine to germinate. This may have led to selection for a seed coat hard enough that the seed is undamaged, but soft enough that the coat is broken so that the seed germinates when defecated.

Where the seeds are not destroyed by the dispersal agent, selection associated with dispersal should favor those dispersal agents that remove the seeds before seed destroying animals get them and then carry the seeds to favorable habitats at the right time. If animals are present that destroy seeds over a period of time, dispersal agents that prefer older fruits or seeds will be progressively less selected for. That there is specificity among dispersal agents of tropical trees and other plants is suggested by the very high diversity of fruit flavors found among large groups of bird-dispersed species at the same site (e.g., Palmae, Burseraceae, Vitaceae, Passifloraceae, Melastomataceae, Cucurbitaceae, Solanaceae, etc., on the Osa Peninsula, Costa Rica). A different (and not mutually exclusive) interpretation is that these flavors are functional in protection against a variety of destructive agents and that the birds do not taste them. Specificity by the dispersal agent would then be a result of the fruits' location in the vegetation, size, color, phenology, etc. That a tropical plant species has a large number of species of potential dispersal agents available is suggested by observations such as Land's (1963) of 51 bird species in the canopy and 20 species feeding on the fruit of *Miconia trinerva* (Melastomataceae) in Guatemala. McClure's (1966) descriptions of vertebrates feeding on tree fruits of the Malayan forest indicate differential selectivity by both birds and mammals.

Some dispersal agents kill the seed by chewing or grinding. Here, there should be selection for seed protection through (1) hard seed coats (but soft enough such that the vertebrate can eat some as "bait"), (2) fruits that taste best (or are least toxic), or are tolerated by the least destructive dispersal agent, (e.g., urticating hairs inside pods, *Sterculia apetala*), (3) bad tasting seeds coupled with good tasting fruits (Cacao; *Theobroma*), (4) seeds too large to be eaten so they are carried incidentally with the fruit (e.g., Mango; *Mangifera indica*), (5) very spiny trunks that may deter climbing rodents where the fruits are bird dispersed (Palmae: *Bactris, Acrocomia, Astrocaryum*), etc. Viewed in this manner, it is not surprising that plants with seeds dispersed by vertebrates are highly toxic to some of these, especially those that grind their food. For example, the bright red-orange seeds and fruits of cycads are eaten freely by some wild animals, yet are extremely toxic to man and his domestic animals (Whiting, 1963; Vega and Bell, 1967; Nunn et al., 1967). Since virtually the entire selection for fruit traits has been to attract or use dispersal agents, it is reasonable to expect equally intense selection to keep away detrimental animals.

Selection for dispersal by vertebrates that eat some of the seed may mitigate selection for a natural insecticide in the seed. Furthermore, vertebrate dispersal agents may require a large number of fruits at one time to attract them; this may run counter to selection for a seed crop highly dispersed in time to avoid seed eating insects.

Where the vertebrate seed-eater plays a purely destructive role, selection should be for avoidance traits just as it is with seed destroying insects. Gashwiler (1967) has postulated that the pungent odor of red cedar seeds may prevent birds and small mammals from eating them (while other adjacent conifer seeds are heavily predated), and Smith (1968) notes that even starving mice will not eat balsam fir seeds. West (1967) has cited large size, hardness of seed coat, and unpalatability as reasons why tree sparrows ate seeds of only 41% of the 87 species available to them in nature; further, several of the species eaten by other birds were ignored by tree sparrows. The urticating hairs on the pods of *Mucuna* sp. in Central America may be functional in protecting the developing (and sometimes fleshy when mature) seeds from monkeys or other climbing vertebrates. It is not likely a coincidence that crushed seeds of many fruits are bitter tasting to humans.

Just as flower pollen and nectar have probably been selected for increased nutritional value to the bee population that they support (in addition to the simple attraction function), fruit traits have probably been subject to the same coevolution with their animal dispersal agents. The rather even spread of fruiting periods of bird and vertebrate dispersed plant species across the calendar year (Snow, 1965; Janzen, 1967*a*) is a clear example of this. As the number of species of dispersal agents for a plant species decreases, this coevolution may become progressively tighter. Squirrels and acorns have undoubtedly undergone considerable coevolution, both in relation to the destruction of acorns and the removal of acorns from the site of curculionid weevil infestation under the tree.

Many vertebrates eat seeds while they are still green and soft, and are therefore purely destructive (e.g., Struhsaker, 1967; and unpublished). It is very unlikely a coincidence that fruits turn sweet at the time the seeds mature, and generally not before or after. In this connection it is of interest that as a fruit crop begins to ripen, birds are often seen "tasting" green fruit and rejecting them or unsuccessfully attempting to remove them (particularly noticeable in *Bursera simarouba* in lowland Central America). An extreme case is the fruit of the African cultivated genus ***Blighia*** (Sapindaceae) which is highly poisonous (Persaud, 1968) to humans and rats (and I suspect other vertebrates) until metabolic changes occur concurrent with the fruit opening (seeds are then ripe). Many spiny fruits do not open, and fruits generally do not turn red (witness the stomach-ache produced by green apples), until the seeds are mature. This timing of color change with seed maturation is likewise the case where some other part of the plant is used as a red or orange "flag" to indicate the presence of seeds or fruits (e.g., *Anacardium utilis*, *Pithecellobium arboreum*, Lauaceae, Palmae Annonaceae).

A particularly interesting example of interaction between the dispersal agent in its "proper" role, and as a seed destroyer, is associated with tropical plants with black, brown, or mottled large soft seeds (or fruits over soft seeds) that are easily killed by birds but are also dispersed by birds (e.g., many Lauraceae, Annonaceae, *Pithecellobium arboreum*, small Palmae, etc.). These plants have red or orange peduncles, bracts, receptacles, and/or stems that apparently serve as attractants to the birds that have been observed taking their dark and essentially camouflaged fruits. This suggests the following hypothesis: if the seeds are eaten, they are killed, but if they are dropped they cannot readily be found again by the bird or other frugivores (as they would be if they were red). Thus dispersal of a seed susceptible to predation would be achieved.

Very small insects may be generally free from predation by many insectivorous vertebrates simply because they are too small to be noticed and too small to favor selection for their notice by these vertebrates (Janzen and Schoener, 1968; Schoener and Janzen, 1968; Root, 1968). The evolution of small seed size in plants in general may be in part a similar response. To choose the absurd case, a seed-eating bird would starve to death searching for orchid seeds. Gashwiler (1967) has postulated that one reason why red cedar seeds are avoided and Douglas-fir and hemlock seeds eaten by birds and mammals is their relatively small size (though as mentioned earlier their pungent odor may be equally responsible).

On the other hand, insects undoubtedly find most of their seed prey chemotactically. Dispersal can then be seen as a means of lowering the general chemical signal to a point difficult for an insect to perceive. Further, the smaller the seed in relation to the insect, the less selection value (in terms of insect reproduction) there will be favoring an increase in the ability of the insect to locate its seed prey.

CONCLUSIONS

These ecological observations of seed predators and their hosts allow some concluding suggestions.

1) Based on a sample of 36 species, the woody Central American Leguminosae that are attacked by Bruchidae can be distinguished by their larger seeds, smaller numbers of seeds, and less weight of seeds per seed crop per unit of canopy, from those species that are not attacked. A large variety of morphological, phenological, and chemical traits appear to be responsible for a specific legume's freedom from attack by a specific bruchid. However, alkaloids and free amino acids are the most likely candidates in preventing most or all bruchid attack. This is suggested by a number of traits of these compounds, not the least of which are general toxicity to animals, high specificity to one or a few legume species, high diversity, and potential utility to the seedling as nitrogen sources (multiple selective pressure). There is no evidence that they are of direct metabolic importance to the adult plant.

2) The three major differences between the seed crops of attacked and unattacked species appear to be an evolutionary response to seed predation. If a bruchid species shifts onto a woody legume, either a deterrent mechanism in the seeds is evolved, or the number of seeds is increased to the point of predator satiation. The later strategy probably requires a decrease in seed size, and the diversion from the plant's reserves of materials that could have been used for vegetative growth or defense, or for seeds of higher quality. The former strategy is probably less taxing to the plant's energy budget (smaller total seed crop weight), but requires a more novel biochemical effort.

This would be a coevolutionary system with the bruchids probably shifting among the various legume species in response to changes in the defense system of both parties. It is clear that such evolutionary responses to seed predation by the plant will confound studies attempting correlation of seed weights and behavior with vegetation types, colonization types, life form, insular isolation, etc.

3) Seed-crop traits that yield predator escape and dispersal may be regarded as "fine tuning" to the high diversity of impacts from predators and dispersal needs. These traits can thus be expected to appear repeatedly in unrelated taxonomic groups (e.g., just as with color in mammalian hair and butterfly wing scales), making them very difficult to use in hypothesizing phylogenies. Where these traits are of economic importance (i.e., hallucinogenic drugs, Farnsworth, 1968; natural insecticides), it would seem that the search for them should be not with taxonomic cues, but rather for those plants apparently free of seed predators or adult plant parasites.

4) A very important component of the bruchid-legume interaction, and very likely that of any predator-seed interaction, is the escape component of dispersal. This is expressed most simply by the inability of all seed predators to kill all the seeds before some are removed by dispersal agents. In a more complex manner, this may be done by the selection for phenology, fruit morphology and chemistry, etc. that maximizes seed removal by the dispersal agent most likely to place the seeds in the best sites in time and space for maturation. It is particularly striking that escape may be increased simply by a seed trait that slows development of the predator.

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