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INTENSITY OF PREDATION ON *PITHECELLOBIUM SAMAN* (LEGUMINOSAE) SEEDS BY *MEROBRUCHUS COLUMBINUS* AND *STATOR LIMBATUS* (BRUCHIDAE) IN COSTA RICAN DECIDUOUS FOREST

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INTRODUCTION

The rain tree, or "genizaro" ("cenizaro") (*Pithecellobium saman* (Jacq.) Benth. = *Samanea saman* (Jacq.) Merrill) is common throughout the lowlands of Central America and much of South America, and has been introduced throughout the lowland tropics. This mimosaceous legume is indigenous to the Pacific coastal lowland deciduous and riparian forests of Guanacaste Province, Costa Rica, where I have been studying its natural history since 1963. In this paper I describe the intensity of seed predation by two species of bruchid beetles in the seed crops of 81 large adult trees growing in 6 different habitats. I intend this data to augment the slowly growing body of information on the pattern and intensity of seed predation in Costa Rican tropical forests (Janzen 1969, 1970a, 1971a, 1971b, 1971c, 1972, 1974, 1975a, 1975b, 1975c, 1976a, 1977a, 1977b, 1977c; Wilson and Janzen 1972; Hatheway and Baker 1970) and thereby to be of use in understanding the potential impact of seed predation on tropical forest structure.

THE TREE

In Guanacaste, an adult *P. saman* may be as much as 1.5 m DBH and attain a height of 40 m in dense riparian or otherwise well-watered soil. It is common in open pastures where it develops a broadly spreading crown and rarely grows more than 20 m tall (Fig. 1a); in closed tall forest it takes on the more elongate life-form of any other tall canopy-member tree. Flowering (and fruit bearing) occurs over the entire upper surface of the crown except where shaded by other crowns. Flowers (Fig. 1b) are produced during the last half of the dry season (late March through May; the drier the site, the later the flowering period). At this time the fruits from the previous year have just fallen or are falling and the new leaf crop has been produced. I do not know at what size *P. saman* starts flowering (or fruit bearing), but 100% of 86 large trees examined in the last two weeks of May 1976 in Santa Rosa National Park (northern Guanacaste Province) were just finishing bearing a heavy flower crop that had begun during the first two weeks of March 1976. To date, there is no indication that *P. saman* adults with insulated crowns fail to fruit in normal years, although following a severe drought in southern Guanacaste in June-July of 1971, numerous *P. saman* aborted their entire crop of immature fruits.

The fruits do not mature until late in the first half of the dry season (February-

March) a year after the dry season in which the flowers were produced. The fruits remain only 2-3 cm in length until the end of the rainy season (Fig. 1c); for example on May 15, 1976, 20 pods from one branch had a mean length of 24 mm (s. d.=3 mm) and an average dry weight of 0.08 g; on 1 December of the same year, 35 pods from the same branch had increased to only an average length of 34 mm (s.d.=7 mm) and an average dry weight of 0.10 g. The mature pods on a neighbouring branch, on 26 February 1977, were 121 mm in length ($n=30$, s.d.=48) and their average dry weight was 3.89 g (including dry seeds).



Fig. 1. (a) An adult *Pithecellobium saman* that has grown free of crown competition for all of its life; this tree can bear as many as 30,000 fruits (Rosa National Park, Guanacaste Province, Costa Rica). (b) Inflorescence of *P. saman*. (c) Infructescence of *P. saman* with small fruits as they will appear for the next 7 months. (All photographs May 15, 1976).

Upon maturing, the indehiscent walls of the pods contain a chocolate-brown molasses-like sweet goo; this sticky material is not, however, in the dry cavities containing the clean dry seeds (Fig. 2). The pods fall when ripe and are eaten entire by cattle in contemporary pastures. The seeds apparently pass through the gut unharmed. The seeds that I have picked out of cattle dung usually germinate as soon as they are placed in moist soil. Seeds taken from the pods and placed in moist soil may not germinate for at least three months and often wait much longer. Small



Fig. 2. Upper—fruit (pod) of *Pithecellobium saman* split open to show filled seeds and full-sized aborted seeds *in situ*. Lower—intact indehiscent fruit of *P. saman* with exit holes of adult *Merobruchus columbinus* (ruler in mm).

rodents also carry off the fallen pods and eat off the outer material; they discard the core, which contains the seeds. Presumably, the original large dispersal agents were Baird's tapir (*Tapirus bairdi*), the two species of peccaries (*Tayassu tajacu*, *T. pecari*), and white-tailed deer (*Odocoileus virginianus*). In captivity all four will chew up entire pods of *P. saman* and swallow the seeds along with the masticated pod.

A large *P. saman* produces several thousand pods (70,000 is the maximum I have counted, Janzen 1969) and each pod normally contains 5 to 20 filled seeds. When the pods fall, they often break into pieces 5 to 15 cm in length. If not eaten by animals, the pod walls rot away during the rainy season, and most of the seeds are liberated into the seed bank directly below the parent. With trees in pasture this rarely occurs, as cattle are avid consumers of *P. saman* pods.

When collected in the field, less than one percent of the mature fruit contain microlepidopteran larvae that eat the region between the epidermis and the wall of the cavity containing the seed; on rare occasions the larvae also consume an intact seed, but the more usual case is that they feed on seed fragments left after the bruchids have left the seeds.

Aside from digestion of intact mature seeds as they pass through a large mammal, the known seed predators of *P. saman* seeds are an unidentified galling insect in pods a few weeks old, parrots that split the full-sized green pod and eat parts of the still soft seeds, and two species of bruchid beetles. In this paper I will deal only with the latter two pre-dispersal seed predators.

THE BRUCHIDS

Merobruchus columbinus (Sharp) (see Kingsolver 1975). This large bruchid (Fig. 1) has never been reared from any other seed than those of *Pithecellobium saman* (records in the United States National Museum of Natural History) and has been collected in Honduras, El Salvador, Nicaragua, Costa Rica, Trinidad, Venezuela

and Colombia (records in the U.S.N.M.N.H.). I have not found it in any other seed crops than those of *P. saman*, and have reared the insects (if any be) from at least one large seed sample of all Guanacaste species of plants with seeds large enough to support a larva of *M. columbinus*.

The female beetles appear at the fruits when they are full-sized and contain full-sized seeds. The seed coats are still soft at this time. Single eggs are glued to the surface of the pod, and the first instar larvae hatch within two weeks. They drill through the fruit wall and into a seed. Many larvae may enter a single seed, but only one emerges as an adult (larval losses are presumably due to cannibalism). The larva cuts a circular groove in the seed coat before it pupates, and the newly emerged adult cuts/pushes out this escape hatch. It then cuts an exit hole directly through the wall of the ripe fruit. Many adults emerge while the pod is still on the tree, but only slightly before the pods are ready to fall. A sample collected just after the pods have fallen still generates many beetles. This sloppiness in the timing of emergence suggests that in natural circumstances, the pods were not eaten immediately upon falling but may have remained on the ground for weeks before taken by a dispersal agent.

The newly emerged adults leave the immediate vicinity of the tree and I have collected them in sweepnet samples, Malaise traps and at sugar baits sprayed on leaves in May, June, July, September and November. They are presumably passing the time until the next pod crop ripens, and probably visit flowers for nectar and pollen when possible. There is no reason to believe that an adult lives more than one year. They fly well, and can live in the laboratory for at least 7 months with no more than dilute honey for sustenance. Normally there is only one generation per year.

No parasite has ever been reared from *M. columbinus* larvae or adults, but I have not searched for egg parasites. There are occasional braconid parasites in the fruit samples, but in all cases to date, the parasite cocoons have been found associated with microlepidopteran frass and the characteristic microlepidopteran fruit damage.

Stator limbatus Horn. This small black bruchid is the most omnivorous of the Guanacaste bruchids. It is the sole bruchid seed predator of the undescribed "mimosa big leaf" (known only from Santa Rosa National Park) and *Pithecellobium oblongum* Benth., and shares seed predation with other bruchids at least in *Acacia tenuifolia* (L.) Willd., *Albizia caribaea* (Urb.) Britt. and Rose, *Albizia adinocephala* (Donn. Smith) Britt. and Rose, and *Lysiloma* spp. In the driest parts of Guanacaste (Santa Rosa National Park and vicinity), it occurs as a rare animal in most *P. saman* fruit crops, often killing some number less than 5% of the seeds by the time the fruits have been on the ground for several weeks to a month.

S. limbatus is a specialist on seeds free of the fruit (as often are other members of its genus). In *P. saman*, it lays eggs on seeds that have been exposed by pod breakage, mining of microlepidoptera larvae, and *M. columbinus* exit holes in the pod wall. A seed previously occupied by *M. columbinus* does not contain edibles but by entering the cavity it occupies, the *S. limbatus* can sometimes squeeze or chew its way into adjacent seed cavities. The eggs are glued directly to the seed coat; the larva drills through the bottom of the egg and the seed coat directly below the egg. The full-grown larva cuts a circular groove in the seed coat before pupating, and the newly

emerged adult completes the job. As many as six adults have been recorded to emerge from one seed, but the more usual number is 1-2. I doubt that the adult ever cuts an exit hole through the fruit wall; if the female can get to the seed to lay an egg, it is likely that the newly emerging adult can leave by the same route. Presumably the newly emerged adult can mate and then oviposit on seeds remaining in the fruit from which she emerged; multiple generations within the year should occur until the seed crop is exhausted.

Owing to its manner of finding seeds, *S. limbatus* has a potential direct but one-way interaction with the dispersal agents of *P. saman*. I doubt that the vertebrates would notice the presence of *S. limbatus* larvae or adults, but once the fruit is consumed the seeds are no longer available to *S. limbatus* unless it will oviposit on them in dung. On the other hand, it is quite possible that a *S. limbatus* larva would be killed by passage of its seed through the gut of a vertebrate. (cf. Lar. prey *et al.* 1974).

The longer the dry season, the more seeds *S. limbatus* may kill. A long dry season may mean that mammals are at a lower density and thus slower to get the *P. saman* fruits. A long dry season is generally associated with a greater proportion of wind-dispersed fruits (species and individuals) in the habitat, and those of these that *S. limbatus* can attack will increase its total available food. Finally, the longer the dry season the longer the seeds are on the ground before the rains moisten the habitat and take them away from *S. limbatus* by germination and burial in moist litter. *S. limbatus* is one of the bruchids that might display a rise in population density with increased human use of the habitat, except that humans usually mean cows, loss of its other seed prey species, and (perhaps) removal of the adults' nectar and pollen hosts.

METHODS

Large adult trees were located visually from a distance, and all trees so found were sampled. At a distance there is no way to know the intensity of seed predation, so the data cannot be biased through tree selection. However, such a method does bias toward large trees and thus large fruit crops, which in turn may have different degrees of seed predation than small trees.

Samples were taken by standing in one place and picking up all the pod fragments visible on the ground. The herbaceous vegetation was largely dead, leafless and beige in colour at this time of year, so the chocolate-brown pods were easy to see. However, fragments less than 2-3 cm in length are sometimes missed by this method. In short, the pod collector was getting about what a large mammal, such as a cow or tapir, would get if it searched only visually. An intact pod is 15-20 cm in length, but many break in half or into quarter-sized lengths in the tree or after falling. The collectors were instructed to pick up about 2 litres of pods below each tree. This quantity usually means about 100 pod fragments.

When a sample was brought in from the field, it was tied compactly and tightly in a plastic bag. This closed bag was then hung inside a larger inflated plastic bag, and the whole contraption hung from a ceiling for at least three months. The beetles emerged from the pods, cut a hole through the first plastic bag, and spent the rest of their lives walking about the inside of the second plastic bag. Since *Merobruchus columbinus* oviposits in nature on the pods while they are green and just beginning

to mature, it did not re-oviposit on the pods it emerged from, even if it did not leave the inner plastic bag. *Stator limbatus* in nature oviposits on mature seeds that have been exposed by breakage of mature fruits. Under appropriate culture conditions, it will probably re-cycle through fruits until all available seeds have been destroyed. However, under the rearing conditions described above, it exited through the first plastic bag and did not continue to breed. There were occasional larvae of small moths in the fruits at the time of collection; they confined their feeding largely to the fruit wall, but on rare occasions ate seeds. In no sample did they kill more than 0.5% of the seeds, so I have not included their presence in Table 1 or other records of the sample. At times they confused the picture by eating the remains of a seed after a bruchid had left it. Again, under appropriate breeding conditions, the moths might well consume many seeds as they run out of fruit in continuous culture, but they did not do this in the double-bagged samples.

Though slightly moist at the time of collection, naturally fallen (mature) *Pithecellobium saman* fruits do not rot even if placed in closed plastic bags during the dry season in Guanacaste. The oldest samples were in bags for four years and seemed as moist, fresh and odoriferous as the day they were collected. This suggests powerful but unknown anti-fungal and anti-bacterial traits of the fruit wall and its thick molasses-like fluid.

Over a period of 4 years I dissected the samples one by one. Without knowing the source of the bag, I blindly selected handfuls of fruit for dissection from each bag. I stopped once I had dissected 30 pod fragments. It can be seen from Table 1 that these fragments averaged 3.9 to 7.0 filled seeds each, which is about half the number to be found in an intact pod. About half the seed cavities contained only a tiny shrivelled remnant of a seed. These were not counted. All seeds large enough to have an approximately full-sized seed coat were saved. If very flat or distorted, they were discarded as aborted. All remaining seeds from the 30 pod fragments were pooled and sorted into four categories: those with *Merobruchus columbinus* exit holes, those with *Stator limbatus* exit holes, those chewed into by moth larvae, and those apparently intact. The apparently intact seeds were then X-rayed (using mammography RPL X-ray film, Radelin HR screens, filter removed, 35KV, 0.6 mm focal spot, 1/360 sec., at 40 inch distance; also, see Kamra 1976) in the hospitals of the University of Michigan and University of Pennsylvania. In an X-ray photograph, the intact (solid white), aborted (white irregular centre surrounded by black, or dull gray) and attacked (white with round to oval dark cavities) seeds were easily identified. In an early sample these determinations were verified by opening the seeds as well. There are two reasons why the pods cannot be easily X-rayed directly. First, they are strongly curved and would have to be broken into pieces to lay flat. Second, one cannot distinguish in an X-ray between a seed from which the beetle has exited, and a seed in which the beetle died.

The question of how many seeds to examine per sample is difficult. If many seeds or fruit fragments are examined, then few samples can be examined. The goal of the present study was to understand the intensity and variation of seed predation over a wide geographic and habitat range, and among the members of the *P. saman* population. In two preliminary samples, where several hundred fruits were dissected, I was left with the impression that after about 20 fruit fragments, the

percent seed mortality in the sample was not changing. I arbitrarily chose 30 fruit fragments as a sample size that would optimize the compromise between number of samples and sample size. To quantify the above impressions, for one tree a bushel of fruits was collected and the fruits sampled cumulatively in groups of 30. The cumulative percent of the filled seeds that were killed by *Merobruchus columbinus* was the following: 26, 24, 25, 25, . . . 9 more times. For 14 individual 30-fruit samples, the mean was 25% (s.d.=3.7). Given the small variation among the 14 30-fruit samples from one tree, and given the subjective impression that this homogeneity of damage among fruits is representative of the other trees sampled, I am willing to accept a 30-fruit sample as representative of the entire fruit crop from a tree, at the level of questions asked in this paper.

All statistical comparisons of percentages are based on arc-sin transformations of the raw percentages (Sokal and Rohlf 1969).

The following habitats were sampled; all are in the lowlands of Guanacaste Province, Costa Rica.

Taboga Riparian: *P. saman* growing in closed-canopy forest along the south-east edge of the riparian forest bordering the Rio Higueron on the property of the experiment station of the Ministerio de Agricultura y Ganaderia in Finca Taboga. This site is about 10 km south and 10 km west of Cañas. The exact site is area II described in Janzen and Schoener 19 and immediately to the northwest of the Taboga Forest Site described in Janzen (1973). The forest is evergreen to semi-evergreen, with a heavily shaded understory during most of the year.

Taboga Pasture: *P. saman* growing as isolated and fully-isolated individuals in moderately grazed grass pastures (cut from deciduous forest) along the dirt road from the Pan American Highway (about 10 km south of Cañas) to the government experiment station mentioned above. These trees are 1 to 8 km from those growing in the Taboga Riparian habitat. They are exposed to strong and continuous dry season winds, and the grass and dicot herbs below them are parched and dry for at least 5 months of the year. This site is the same as that described as Taboga Pasture in Janzen (1973).

Finca La Pacifica Woods: *P. saman* growing in fully closed canopy deciduous forest on low hills in the northern portion of Finca La Pacifica and about 9 km north of Cañas along the Pan American Highway. The forest in this area has now been cut and converted to grain fields and pasture. At the time of collection, some of the trees were in the forest edge near, but not in, pastures. This forest is like that described by Fleming (1974), and Janzen (1970b) but several kilometers away from it.

Palo Verde Forest: *P. saman* growing in fully closed canopy deciduous forest on low hilly terrain along the "Beehive Road" from Palo Verde to El Colmenar along the edge of the Tempisque river basin in the western end of the COMELCO ranch (15 km SW of Bagaces). This forest seems to be about as dry as that in the Finca La Pacifica Woods habitat. It is described in Frankie *et al.* (1974). Some trees were in the forest edge near, but not in, a 3 ha pasture cut out of the forest.

Palo Verde Creek: *P. saman* growing along the permanent creek about 3 km east of the Organization for Tropical Studies field station at Palo Verde in the west end of the COMELCO ranch. These trees are surrounded by brushy pasture but within 100 m of permanent water and 200 m of a closed canopy swamp forest. The site

should be viewed as generally more moist than either the Finca La Pacifica Woods or Palo Verde Forest habitats.

Santa Rosa River Bottom : *P. saman* growing on the banks of the lowland rivers in the western lowlands of Santa Rosa National Park. These trees are part of a deciduous forest along seasonally dry rivers. During the dry season the habitat is as dry as the three deciduous forest sites described above, but is less windy.

Taken as a group, it is my subjective impression that the dryness of these sites, as measured by the difficulty of an insect surviving the dry season, is Taboga Riparian—Palo Verde Creek—Finca La Pacifica Woods—Palo Verde Forest—Santa Rosa River Bottom—Taboga Pasture (wettest to driest).

RESULTS

Abortions : *Pithecellobium saman* fruits regularly contain a large number of seed cavities that contain only a tiny shrivelled remnant of a seed. Often these empty cavities cannot be recognized without fruit dissection, as the fruit develops normally in their vicinity if there were filled seeds in the empty cavities. These abortions were not counted in the present study and their cause is unknown. They could be caused by sucking Hemiptera or galling insects when the pod is young, by total pollination failure, and/or by physiological rejection of seeds pollinated by low quality pollen. In the total of 2430 pod fragments examined, only 14 contained no full-sized seeds. This indicates that the tree does not normally make fruits or long fruit sections with no seeds.

Of the seeds large enough to potentially be filled, the average of their percent abortion per crop ranged from 11 to 31 percent in the 6 habitats (Table 1). The

TABLE 1. *Parameters of seed predation in 81 30-fruit samples of Pithecellobium saman seed crops in 1972 in Guanacaste Province, Costa Rica (see text for details)*

Habitat (number of trees)	Number of filled seeds per fruit fragment			% filled seeds killed by <i>Aferobrachus</i> <i>columbinus</i>		% filled seeds killed by <i>Stator</i> <i>limbatus</i>		% of seeds with <i>M.</i> <i>columbinus</i> that pro- duced brachids	
	\bar{X}	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.
(1) Taboga Riparian .. (11)	3.9	18	14	70	15	1.5	2.0	55	23
(2) Taboga Pasture .. (14)	7.0	11	8	47	18	0.4	0.6	75	21
(3) Finca La Pacifica .. Woods (8)	7.4	16	9	41	27	2.5	5.5	70	21
(4) Palo Verde Forest .. (24)	6.0	31	18	44	15	4.4	5.0	75	19
(5) Palo Verde Creek .. (7)	6.3	17	12	52	12	4.7	6.0	54	24
(6) Santa Rosa River .. Bottom (17)	5.6	18	15	40	17	3.0	2.5	73	14

value of 31% (s.d.=18%) (Palo Verde Forest) is significantly different from any of the other 5 (t test, $p < .01$), but none of the other five differ from each other. Since at least half the seed cavities of most pods do not contain seeds large enough to be counted as potentially filled, the abortion values in Table 1 mean that about 60 to 90% of the ovules in a fruit do not produce filled seeds. For all seeds pooled, 22% were large enough to be filled but were aborted.

The cause of abortions of full-sized (potentially filled) seeds is unknown. The cause may be physiological or due to sucking by Hemiptera at the time when the seed is nearly full-sized but not yet hard enough to resist their penetration. It is also possible that in some cases a *Merobruchus columbinus* larva entered the seed too early, and the plant responded to the damage by cutting off nutrient flow to that seed (thereby aborting the seed and killing the bruchid larva). Such an ability by the plant would quickly select for bruchids that waited until the seed contained enough nutrients for a larva to develop, before it entered the seed.

Bruchids : *Merobruchus columbinus* was present in all 81 samples. However, the percent of the filled seeds in a crop that were killed by this beetle ranged from 5 to 93%. Of the total sample of 14,419 seeds, 43% were killed by *M. columbinus*. However, as noted above, this is probably a low estimate since some of the abortions of full-sized seeds could have been caused by early entry of *M. columbinus* larvae. Only the Taboga Riparian habitat had a percent mortality per sample that is significantly different (greater) from the other five sites (t test, $p < .01$). There is no way that I can suggest what multitude of ecological differences between the Taboga Riparian habitat and the other habitats lead to this difference.

However, a comparison of the Taboga Riparian with the Taboga Pasture makes some biological sense. The Taboga Riparian habitat, forested with largely evergreen trees and containing nearly year-round flowing water, is representative of the moister riparian sites to be found in the Guanacaste lowlands. During the three months of the dry season following emergence from the *Pithecellobium saman* pods, the adult free-living beetles are minimally exposed to desiccation (and food?) problems in such a habitat. Furthermore, *Merobruchus columbinus* adults undoubtedly move into this moist site from nearby deciduous forest, and this may lead to an increase of the general *M. columbinus* density when the pods become available many months later. The Taboga Pasture habitat represents the opposite extreme yet is easily within flight range of the Taboga Riparian habitat. During the dry season, these isolated trees are exposed to the full blast of dry season winds, there is no humid cover in the dried pastures, and it is 2 to 4 kilometers to the nearest moist riverbed. The 11 trees sampled in the Taboga Riparian site averaged 70% mortality to their seeds (s.d.=15) by *M. columbinus* while the 14 Taboga Pasture samples averaged 47% (s.d.=18); these mean values are highly significantly different (t_{23} d.f.=3.45). I suspect the Taboga Pasture and Taboga Riparian beetles are all part of the same large population, and the differences in seed predation reflect how they re-assort themselves during the time between seed crops. However, I should also note that the fruit crops in the open pasture may on the average be larger than those in the forested riparian site (owing to reduced crown competition in the open), and thus the difference be due to greater predator satiation in the pasture than in the forest.

Stator limbatus appears to be a trivial source of *Pithecellobium saman* seed mortality

in the study area. It was present in 79% of the samples, but it only killed 3% of the filled seeds. There are several reasons for believing that any differences in seed predation among the samples by *S. limbatus* are impossible to interpret. First, this bruchid has more species of hosts (8 known) in Guanacaste than any other species of bruchid; therefore its density will be a function of how many individuals of other host species are present. Second, the number of seeds it kills is related to how fractured are the pods; in habitats where pods fall without breaking, there will be little or no infestation by *S. limbatus*; in habitats where the pods are blown violently from and through the tree crowns, or onto hard rocks or dirt, there is much greater opportunity for this beetle to oviposit. Third, the longer the pods are on the ground, the greater the opportunity for oviposition by this beetle. The length of this period is a complex function of frugivore activity in the area and where the samples were taken in the temporal fruiting distribution of individual trees. Since different individuals drop their fruits at different times over a period of several months, at the time of sampling some crops could have had much time for oviposition by *S. limbatus* and others none.

As *P. saman* becomes increasingly a pasture tree, and as natural dispersal agents become very rare, I expect *S. limbatus* to take an increasing percent of the seeds. However, cows are very fond of *P. saman* pods, normally eating them almost as soon as they fall. The cow may be even more effective than wild animal at removing seeds from susceptibility to *Stator limbatus*.

It has been my impression that in southern Guanacaste, *Pithecellobium saman* fruits less frequently have *Stator limbatus* in them than do those in the area from Bagaces to Santa Rosa. Several aspects of these samples are in agreement with this impression. Of the 33 samples from the southern three sites (Taboga Riparian, Taboga Pasture, Finca La Pacifica Woods), only 32% had *S. limbatus* in them; of the 48 samples from the more northern sites, 96% had *S. limbatus* in them. If the percentages attacked by *S. limbatus* are pooled for the 3 southern samples, the mean sample percent is only 1.24 (s.d.=2.96); for the northern 48 samples, the figure is 3.96 (s.d.=4.41). These means are highly significantly different (t_{81} d.f.=6.93, $p<.001$).

As I cannot distinguish in an X-ray (or by dissection) a *Merobruchus columbinus* larva that died while young from a dead larva of the much smaller *Stator limbatus*, I cannot know what fraction of the seeds attacked by *Stator limbatus* generated adult beetles. The picture is further complicated by the fact that several *S. limbatus* may develop in one seed. However, if we count all damaged seeds without exit holes as being due to *M. columbinus*, some idea can be obtained of the success of *M. columbinus* once it has done enough damage to show up in an X-ray (Table 1). Four habitats had indistinguishable fledging success for *M. columbinus*; Palo Verde Forest, Santa Rosa River Bottom, Finca La Pacifica Woods and Taboga Pasture. The two small values (Palo Verde Creek, Taboga Riparian) are likewise indistinguishable from each other; each is significantly lower than the four higher values (t test).

I know nothing of why bruchids such as *M. columbinus* die in seeds. As no arthropod parasite has ever been reared from a larva or adult *M. columbinus*, arthropod parasites are not the cause. When such animals are dissected out of the seed, they do not have the appearance of having been killed by fungus or bacteria.

However, 25 to 46% seems like a rather high rate of developmental failure.

The seeds attacked by *M. columbinus* are not viable. If the bruchid developed to full size, the seed is devoid of edible contents. Seeds that have half-grown larvae in them germinate only very rarely when planted, and even then I suspect they would have very low fitness in the field owing to depleted reserves and tissue damage (cf. Janzen 1976b).

DISCUSSION

For want of a single figure, 43% may be taken as the *Pithecellobium saman* seed mortality by *Merobruchus columbinus* in 1972 in the lowlands of Guanacaste Province, Costa Rica. While such intense predation is probably not trivial to the parent plant, and certainly not trivial to the seeds killed, its pattern is probably more important than its intensity in its effect on the *P. saman* population. Taken at 10 percentage point intervals (0-10, 11-20, 21-30, etc.), the frequency distribution of percent seed mortality by *M. columbinus* was 1, 3, 13, 18, 13, 12, 10, 7, 3, and 1 (n=81). The mode is therefore 31-40% (below the average) and the median 41-50% (on the average). With respect to percent seed mortality, the intensity of seed predation seems spread fairly well through the population; while certain trees lost a very high fraction or a very low fraction of their seeds to *M. columbinus*, the most common class of damage (31-40%) only involved 22% of the trees. If all seed crops were the same size, it could not be stated that a few trees were contributing most of the viable seeds to the population while the remainder were largely feeding bruchids.

However, not all seed crops are the same size. On *P. saman* they can range from as few as 100 to as many as 70,000 fruits (and probably more). I have no information on the sizes of the seed crops sampled in this study. I therefore cannot reject the hypothesis that the large seed crops are clustered at one end or the other of the frequency distribution on percent seed mortality. I suspect that the large seed crops are at the low end of the frequency distribution (owing to predator satiation with large seed crops), and thus it may be that those few trees with percent seed mortality of 30% or less (21% of the trees) have very large absolute numbers of surviving seeds and thus are contributing disproportionately to the seed pool of the habitat.

The data in Table I leads me to suggest that the riparian *P. saman* adults in undisturbed forest may generally sustain a lower percent seed mortality by *M. columbinus* than those in drier adjacent habitats. However, *P. saman* in riparian sites generally appear larger and more healthy than those in dry sites. It is therefore possible that the portion of the population with the healthiest appearing adults is contributing the smallest amount of genetic information to future generations. However, examination of this possibility will require data on absolute seed crop sizes coupled with percent seed mortality by *M. columbinus*.

I should also note that within one habitat, with two *P. saman* of apparently equal size only 100 m apart, the percent seed mortality can be as much as 80 percentage points apart. While I have no data here to elucidate the causes of such extreme intra-habitat variation, the natural history of the tree and the beetle suggest a number of mutually compatible causes. (1) The fruit crop of one tree may ripen several weeks before the other, resulting in the *M. columbinus* in the immediate vicinity

exhausting their egg supply on the fruit crop of one tree and leaving the other largely unattacked. (2) If the fruit crops are of equal age, and both moderately small, the larger of the two may produce a larger odour cue and result in disproportionately high attack. (3) If the fruit crops are of equal age, and both moderately large, the larger of the two may have disproportionately lower seed damage owing to predator satiation (oviposition satiation). (4) Trees may vary genetically in their sensitivity to abort seeds following entry of beetles first instar larvae, in their seed and pod defensive chemistry, and in the degree of synchronization of the fruit ripening within the crown; variation in all three traits could easily lead to consistent intra-habitat variation in percent seed predation.

Why do *P. saman* trees mature fruits that contain about 22% large yet aborted seeds and have another 50% of the seed cavities with shrivelled ovules (if there is any trace of a seed at all)? Concomitantly, only 0.01% of the pods or pod fragments lacked full-sized seeds (potentially filled seeds). That the fruit wall is often fully developed in the vicinity of seed cavities containing no seed or aborted full-sized seeds suggests that the interaction with dispersal agents is probably important to this question. For a mammal-dispersed seed in an indehiscent fruit or fruit segment, the ratio of seed to reward is undoubtedly important in determining (a) if the fruit will be eaten and (b) if all or some of the seeds will be spit out (directly or when chewing a cud) or cracked with the molars. One way to evolutionarily engineer a higher fruit/seed ratio is to abort seeds. Even potentially filled seeds of *P. saman* are generally much thinner and easily broken when compared with filled seeds. While it might be expected that this would eventually select for a fruit with an initial lower number of ovules, there is the counter selection for a larger number of ovules which allows more freedom in maternal parental choice among zygotes. A second way to evolutionarily engineer a higher fruit/seed ratio is to hold the seed-ovule dynamics constant and increase the fruit pulp amount or quality. Both processes seem likely and cannot be further analyzed with the data at hand.

The interaction with *M. columbinus* may also influence the retention of fruits with a large number of aborted seeds or ovules. If the bruchid cannot determine exactly the location of the filled seeds, owing to a lack of external fruit differentiation in their vicinity, it may have to lay many more eggs per fruit than would be the case if one egg could be placed immediately above each filled seed. Fruits containing aborted seeds and ovules therefore increase the predator satiation capacity of a fruit. This is an advantage that would not be realized were the fruit/seed ratio to be increased by increasing the amount or quality of fruit pulp of a fruit that contained a filled seed in each cavity.

Why does *Merobruchus columbinus* prey only on the seeds of *Pithecellobium saman*, and not also on the equal-sized seeds of many other plants in the habitat (*Acacia* spp., *Pithecellobium* spp., *Calliandra* spp., *Lonchocarpus* spp., *Albizia* spp., *Enterolobium cyclocarpum*, etc.)? Until the chemical analyses are available for all of these seeds, the specifics of the question cannot be dealt with. However, the general answer is probably that (a) the seed contains a number of toxic secondary compounds (protease inhibitors, lectins, non-protein amino acids), the combination of which *M. columbinus* has the biochemistry to deal with, and (b) *M. columbinus* is probably dependent on the constructive use of certain byproducts of the detoxification in its own

catabolism (as has been found with *Caryedes brasiliensis* feeding on the canavanine-rich seeds of *Dioclea megacarpa* in the same habitat, Rosenthal *et al.* (1976, 1977). Here, then, *M. columbinus* is expected to be restricted to *P. saman* because it can detoxify only its seeds and because it can get only from its seeds the nutrients it needs. To date we know that *P. saman* seeds contain 4-8% dry weight albizziine (E. A. Bell, personal communication, Krauss and Reinbothe 1973), and a trace of Djnkolic acid and "moderate" amounts of 4-hydroxypipicollic acid (Krauss and Reinbothe 1973); all three of these non-protein amino acids are toxic to the larvae of at least one species of bruchid beetle (Janzen *et al.* 1977a). However, none of these comments help with the general question of why can't a species of bruchid have the ability to do each of these things to two quite different species of seed, each with quite different seed chemistry?

I should add that by specializing on *P. saman*, *M. columbinus* has a food source that is present every year at a regular time (there is no evidence of supra-annual synchrony of *P. saman* seed crops or sterile years, if indeed they occur at all). Furthermore, *P. saman* is one of the largest trees in the habitat and has a very large seed crop; as deciduous forest trees go, it represents one of the largest seed resources on which a bruchid can specialize (I do not intend to suggest, however, that bruchids do not specialize on scarce seed resources in this habitat).

However, given the previous paragraph, I find it particularly enigmatic that larval *M. columbinus* have no host-specific hymenopterous parasites (though the eggs may). I have only one suggestion. There may be occasional years when many *P. saman* fail to bear mature fruit owing to a generalized early rainy season drought such as occurred in 1971. If the prey (seeds) are very scarce in such years, the "parasitoids" on these prey should be even much scarcer, and therefore "hyper-parasitoids" in the form of specialist parasitic hymenoptera are likely to get pruned off the end of the food chain. This does not help understand why more generalized hymenopterous parasites do not attack *M. columbinus*. The most robust hypothesis at the moment is that the larvae, by virtue of feeding on a food generally toxic to animals are themselves rendered immune to generalists. On the other hand, the high death rates of *M. columbinus* in seeds (32% of all bruchids large enough to consume a large part of the seed did not emerge) suggests that there might be a bacterial or viral disease in the population (as is apparently the case with the hymenopterous parasite-free bruchids of *Scheelea rostrata* palm nuts (Janzen 1951b). If, as seems reasonable, there is a ceiling to the parasite load that a bruchid can carry, then there may not be ecological space for a hymenopterous parasite of *M. columbinus*.

SUMMARY

In samples from 81 fruit crops of *Pithecellobium saman* (a mimosaceous legume) from the Pacific coastal lowlands of Costa Rica in 1972, at least 43% of the seeds were killed by larvae of the bruchid *Merobruchus columbinus* and 1-3% by the larvae of the bruchid *Stator limbatus*. *M. columbinus* was present in all 81 seed crops. The moistest habitat, a riparian one, had the most intense seed predation by *M. columbinus*. About half the ovules (or small zygotes) in the fruits were aborted, and 22% of the full-sized seeds were also aborted. The variation in seed predation between and within habitats, host-specificity of the bruchid, and fruit engineering dynamics were discussed.

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