

The Fate of *Scheelea rostrata* Fruits Beneath the Parent Tree: Predispersal Attack by Bruchids

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Scheelea palms are common in some Central American lowland forests with a mild dry season, and occasionally are common in swamps and riparian sites experiencing a severe dry season. In Costa Rica, the seeds of these large trees are subject to intense predation by two species of bruchid beetles and several species of terrestrial rodents. Predation beneath the parent tree by bruchids is described here as the first step in an examination of the effect of seed predation on the population dynamics of *Scheelea rostrata* (Fig. 1a).

General Interaction

An individual tree of *Scheelea rostrata* usually produces one or none (maximum of two) fruit-bearing inflorescences (Fig. 1a) each year. Fruit maturation requires at least six months and about 1400 large yellow fruits fall from one inflorescence over a month-long period. In moderately undisturbed forests, terrestrial rodents then chew the rind and mildly sweet pulp (exocarp and mesocarp) from the fruit, leaving the bony endocarp which is indehiscent and contains one to four seeds. Newly cleaned endocarps are often discarded within 3 m. of the tree trunk. Some intact fruits and clean endocarps are carried away by rodents and scatter- or cache-hoarded. Since individual clean endocarps that have been dispersed by rodents probably have a much lower probability of being found by bruchids than those clumped beneath the tree, they are probably es-

sential to the survival of the *S. rostrata* population. The fate of such dispersed endocarps is the subject of a study in progress (Janzen and Wilson, 1971).

Endocarps remaining beneath the tree are highly susceptible to oviposition by bruchids almost immediately after being partially cleaned of pulp. Since very newly cleaned endocarps have only one egg on them, a bruchid probably lays only one egg (Fig. 1b) per endocarp per encounter. However, there are enough encounters so that most endocarps receive two to five eggs (Fig. 1c) with extremes at 15 to 20 eggs. Endocarps are susceptible to oviposition for at least one month, or at least until the taste and odor of fermentation are gone from their surface. Oviposition occurs even when the endocarp is covered by the light litter of fruit rinds, old flowers, and frond fragments beneath the parent palm.

The first instar bruchid larva bores directly through the endocarp into the endosperm of the seed. More than one larva usually enters the endosperm, but only one matures, probably because the largest larva cannibalizes the smaller ones. There may be up to three seeds per endocarp and very rarely four, and occasionally a bruchid matures in each; more usually, one larva eats all the seeds in an endocarp. A larva consumes all of each seed available to it. Just before pupating (Fig. 1d), the larva cuts an exit tunnel almost all the way through

TABLE 1. Percent of seed mortality in 10,925 endocarps collected below 118 *Scheelea rostrata* in different habitats and at different endocarp ages in five Costa Rican sites. Approximately 100 endocarps were collected from beneath each of the parent palms. Status of endocarp determined by dissection, and at this level of discrimination, all seeds in an attacked endocarp are regarded as dead.

	Percent apparently viable	Percent containing bruchid larvae	Percent dead for unknown reasons	Examined:	
				Total endocarps	Total trees
<i>Forest</i>					
Newly fallen endocarps	89.6	9.7	0.7	888	9
Medium age endocarps	14.9	77.0	8.1	6219	67
Old and rotting endocarps	10.2	18.1	70.7	1056	12
<i>Pasture</i>					
Medium age, all endocarps	63.9	19.3	16.8	2707	30
Stream or pond edge only	4.0	65.1	30.9	571	7
Open grass only	81.3	7.0	11.7	2136	23

the endocarp wall; the emerging adult finishes the job (Fig. 1e).

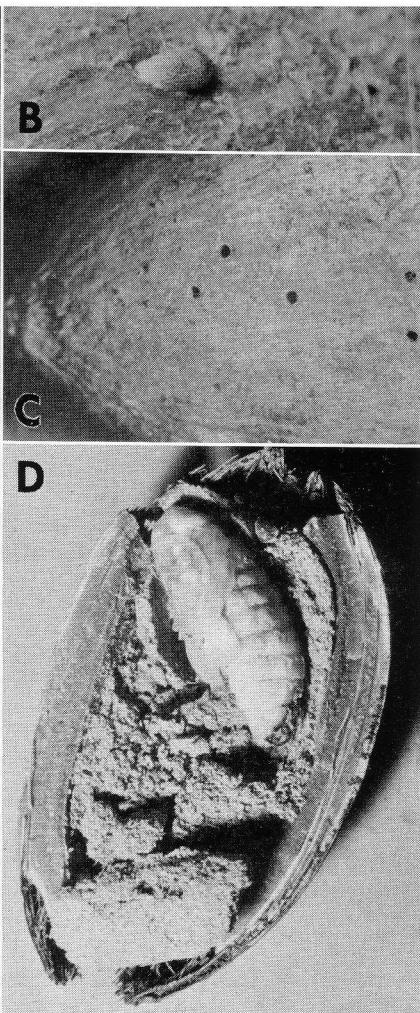
No arthropod parasites of the bruchid have been found in the 10,925 endocarps opened in this study (Table 1). However, an unidentified microbial disease kills a highly variable number of pupae, full-sized larvae, and adults before they complete development. The litter beneath the parent palm is probably thoroughly contaminated by this pathogen, owing to the disintegration of endocarps containing the remains of diseased bruchids.

The moderate synchrony of fruit fall from one palm results in some synchrony of the bruchid life stages under a given adult tree. However, in any local palm population, fruit crops of all ages are present (though their relative frequency varies). Bruchids of all ages are there-

fore present in a pooled sample of endocarps from below several trees; susceptible endocarps are oviposited on at all times of year.

At unknown times of year (neither mid rainy season—September, nor mid dry season—February, March), at least two species of terrestrial rodents chew open large numbers of medium aged endocarps (Fig. 1e) beneath the parent tree. They are in search of either mature bruchid larvae or palm seeds. The hypothesis that the rodents are in search of bruchid larvae is supported by the observation that the rodent only chews until the cavity containing the seed is opened (Fig. 1e); through this small access hole the bruchid larva could be removed but the tight-fitting, intact seed could not be pulled or chewed out. In

1. Bruchid predation in *Scheelea rostrata*. a, Reproductive adult *Scheelea rostrata*, Barranca Site, February, 1970. Note cluster of fruits at arrow. b, Freshly laid egg of *Caryobruchus buscki* (1.8 mm long). c, Entrance holes of first instar larvae of *C. buscki* in endocarp. d, Pupa of *C. buscki* with head in exit tunnel through stony endocarp; entire endosperm replaced by powdery frass from feeding by bruchid larva. e, Left to right: endocarp chewed open laterally by rodent, apparently to prey on bruchid larva; two endocarps with *C. buscki* exit holes; double-seeded endocarps with end cut off by rodent, apparently to eat bruchid larvae; ditto, single-seeded endocarp.



addition, most superficially intact endocarps at this time in the history of the crop are medium-aged and contain bruchid larvae (Table 1, column 2). Further, it is probable that the metabolically active larva contains a wider variety of nutrients than the oil-rich endosperm and quiescent embryo.

The few unattacked seeds beneath the parent germinate at least during the first four months of the rainy season (May–September). Whether the young plants survive the following dry season appears related to factors such as herbivore damage, moistness of the site, and the amount of sunlight received during the year. Beneath adult *S. rostrata* that are left in pastures after clearing the forest, there is no seedling survival.

Materials and Methods

This report is restricted to five somewhat separate populations of *S. rostrata* in the northwestern part of Costa Rica.

1) Barranca site—intensive endocarp collecting (February, July, September, 1970) was done in the local population on the hills and bottom-lands of the small river drainage that crosses the Pan-American highway, 5.6 to 8.5 miles northwest of the turn-off into the city of Puntarenas from this same highway. This site is centered on Orian's (1969) "Barranca site." The original areal extent of this population is unknown owing to extensive clearing, but the absence of *S. rostrata* in riparian vegetation to the north and south of the Barranca site suggests that it was not continuous with any of the other local populations in the dry northwestern lowlands of Costa Rica. I estimate that there are at least 1000, and not over 2000, adult *S. rostrata* growing in habitats where they can reproduce at the Barranca site.

2) Taboga site—intensive sampling (July, September, 1970) was done in

the river bottoms along the Rio Higuerón on Finca Taboga (south of Cañas, Guanacaste Province) in the southeastern portion of the Costa Rican M.A.G. Field Station. The reproducing portion of this very local population is now restricted to the narrow strip of forest remaining along the river ("Area III" in Janzen and Schoener, 1968) and the contiguous palm forest (*palmar*) of about 10 acres extent that is occasionally flooded. A few adult trees remain in the pastures cleared in 1963–1965 on the flood plain of the Rio Higuerón. I estimate that there are about 200 reproducing adult *S. rostrata* at the Taboga site.

3) Colorado site—a few collections were made from the 13 adult *S. rostrata* remaining in pastures along the creek network about halfway between the Barranca and Taboga sites (6.6 miles from the Pan-American highway on the road from that highway to Colorado on the Gulf of Nicoya; September, 1970). Since there is total seedling mortality during the dry season in the pastures around these palms, they are only a small and non-reproducing remnant of what probably was a population equivalent to that at the Barranca or Taboga sites; they appear to be the only adult *S. rostrata* between the two sites.

4) Esparta site—the palms (September, 1970) are scattered among hillside pastures and clumped in some creek bottoms from about 50 to 200 m. elevation along the Puntarenas—San Ramon highway (Puntarenas Province, 3 to 6 miles northeast of Esparta). This population, containing at least a thousand widely spaced adults, probably represents what used to be the northernmost extension of the large *S. rostrata* population that currently extends along the Pacific coastal foothills south of Puntarenas at least as far south as Palmar Sur and the Golfito region of Costa Rica.

The Esparta population might at one time have been continuous with the Barranca population, but the pastures and deciduous forest between them now give no hint of it.

5) Peñas Blancas site—separated from the Taboga site by at least 90 miles of forest subjected to a very severe dry season, this population extends along the Pan American highway from the Costa Rican—Nicaraguan border to 10 miles south (September, 1970); this population extends north into Nicaragua for an unknown distance along rivers draining into Lake Nicaragua. At present, it probably contains less than 200 adults in habitats where they can reproduce south of the Nicaraguan border. This population may, however, extend eastward and thus be continuous with a large population on the Atlantic coastal plain.

The taxonomy of the genus *Scheelea* is somewhat muddled, but two things are clear. There is no indication that the large palm at the five sites listed above represents more than one morphospecies; *coyol* (*Acrocomia vinifera* Oerst.) is the only other large palm in the vicinity of the five sites, and it reproduces in drier sites than *S. rostrata*. The three species of *Scheelea* listed by Standley (1937) for this part of Costa Rica [*S. costaricensis* Burret, *S. gomphococca* (Mart.) Burret, *S. rostrata* (Oerst.) Burret] are either described from one of the five populations listed above or were described from cultivated plants (Moore, pers. comm.); Standley's claim that *Scheelea* is widespread in the lowlands of northwestern Costa Rica was not based on personal observation and is unlikely ever to have been true under contemporary weather regimes. I have applied the name *S. rostrata* (cf. Burret, 1929) to the palms examined in this study on the advice of Dr. H. E. Moore, Jr.

Caryobruchus buscki Bridwell is one of the world's largest bruchids (Bridwell 1929) and ranges from Costa Rica to Venezuela (Kingsolver, in lit.). It is responsible for almost all the mortality by bruchids at the four southernmost sites (1-4). The slightly smaller *Pachymerus cardo* (Fahraeus) (Kingsolver, in lit.) had only occasionally been encountered there. At the Peñas Blancas site, *P. cardo* appears to be responsible for as high as 50 percent of the bruchid predation on some seeds. The damage by these two beetles has not been recorded separately in this study, but differences between them are probably responsible for a small amount of the intercrop and inter-habitat variance in seed mortality recorded in Table 1. Numerous other species of palm bruchids are briefly discussed by Bridwell (1929) and Paxson (1961).

In the endocarp samples recorded in Table 1, only superficially intact endocarps were collected. Samples of about 100 endocarps each were collected from beneath the following number of palms at each site: Barranca 88, Taboga 23, Peñas Blancas 4, Colorado 2, Esparta 1. Endocarps chewed upon by rodents, endocarps with bruchid exit holes, and endocarps with germinating pores rotted open were not included. When encountered, endocarps with germinated seeds were also discarded, but this did not normally enter into the decision-making process as the actual number of living and newly germinated seedlings below most forest palms sampled was far less than 1 percent of the total number of intact endocarps. The age of the endocarps beneath the tree was subjectively estimated, based on such things as their degree of decomposition and amount and age of litter that had fallen on them. The total number of endocarps of all ages beneath a palm usually ranged from 1000 to 5000 (e.g., Table 2). Endocarps

TABLE 2. *Fate of seeds in 1385 endocarps of all ages (about ¼ of total) below a large adult S. rostrata (forest, Barranca site, 12 September 1970).*

Percent endocarps with at least one viable seed	1.8
percent of these endocarps double-seeded with one seed dead, and dead bruchid larva in other seed	36.0
Percent endocarps with all seeds killed by bruchid	80.4
Percent of these with:	
one seed, killed by now dead larva	46.8
two seeds, both killed by now dead larva	7.3
one seed, dead pupa	0.4
two seeds, dead adult and dead larva	0.1
one seed, dead adult	2.3
one seed, live larva	16.8
two seeds, live larvae	0.8
one seed, live pupa	0.1
adult burchid exits (17% of these had 2 exits)	25.1
Percent endocarps with only aborted seeds or other non-predator mortality	7.5
Percent endocarps killed by rodent chewing in the middle	10.2

were inspected by breaking them with a hammer.

parent plant (*cf.* Janzen and Wilson, 1971).

Seed Mortality

The variation in seed mortality beneath the parent tree can be most profitably discussed in the context of the age of the endocarp after falling, the fate of the bruchid and palm seeds in the endocarp, and the habitat of the parent palm. This should be regarded as pre-dispersal mortality (Janzen, 1970) for the following reason. Judging from the enclosure of the well-armored seed(s) in the sweet exocarp, release of the fruit by the parent (so-called "gravity dispersal") should be regarded as a behavioral trait analogous to the various morphological traits of many tropical plants that increase fruit availability to the dispersal agents. In this case, then, the drupe is not dispersed until it has been carried away from beneath the

Age of drupes and degree of predation by bruchids.

As an endocarp ages, it becomes increasingly difficult to ascertain exactly why its seed(s) died. Further, a live seed in an old endocarp has a very different probability of being killed by a bruchid than one in an endocarp newly cleaned of exocarp and mesocarp. For these reasons, seed mortality is discussed separately for different age classes whenever possible.

Newly fallen endocarps. Endocarps newly cleaned of exocarp and mesocarp characteristically have a low percent of infestation by bruchids and a high percent of apparently viable seeds (Table 1) (Jordan, 1970, records 61 percent germination for seeds in endocarps of this age from a Peruvian *Scheelea*,

though the reason for failure of 39 percent was not given). Such endocarps have been on the ground up to a month, are beige to white, are extremely hard, have the fibrous cap over the germinating pores firmly in place, have numerous pulp fibers attached to the surface, often smell or taste slightly fermented, and often have the remains of bruchid eggs cemented firmly to their upper surface. These endocarps often have new fruit rinds prominently mixed with them and are quite distinct from older endocarps from previous inflorescences. First or second (or rarely third) instar bruchid larvae are found in the seeds in freshly cleaned endocarps; these young larvae have usually eaten up to 30 percent of the endosperm. By the time the larva has reached the second instar, it has almost always eaten the embryo. It should be noted that first instar larvae and small second instar larvae are difficult to locate in the remains of a seed after smashing the bony endocarp open, and despite careful searching for larvae, the figure of 89.6 percent seed viability in Table 1 is probably a five to ten percent over-estimate. For the purposes of this sample, if at least one seed is attacked by a bruchid, it is considered that all seeds in that endocarp will die (see later discussion of multiple-seeded endocarps).

When the endocarps have been on the ground beneath the parent palm one to four months, the highest percent mortality unquestionably due to bruchids is recorded (Table 1). Of the 67 crops examined, 64 percent had bruchids in more than 85 percent of their superficially intact endocarps beneath the parent. That only 77 percent of the total endocarps examined in this age class had bruchids is partly due to the presence of a number of endocarp crops of about one month age. Characteristically, only 40 to 70 percent of these

endocarps contain bruchid larvae since bruchid attack of the crop is not yet complete. There are also some crops in this sample that are old enough that 10 to 30 percent of the bruchids have died in the endocarp, causing it to be classified as "dead for unknown reasons." Microhabitat differences within the forest also lead to lower percentages of unquestionable seed mortality by bruchids, and will be discussed in a later section.

Medium aged endocarps. Endocarps of this age are beige to dark brown, are moderately hard, have a disintegrating fibrous cap over the germinating pores, have no remains of pulp fibers, smell and taste like litter composed of leaves and branches, and are often partially or totally buried in litter. If washed, these endocarps display various numbers of 0.4 mm. diameter entrance holes made by first instar bruchid larvae. The fourth and last instar bruchid larvae have usually eaten all of one or more seeds in the endocarp and have sometimes cut the first part of an exit hole. Occasionally, larvae or pupae killed by disease are encountered in medium-aged endocarps. This is the age at which endocarps are normally chewed open by rodents.

Old endocarps. Once the endocarp crop has been on the ground more than about five months, the percent bruchid infestation of superficially intact endocarps is again low (forest palms, Table 1). This is due for the most part to two causes. 1) Part of the endocarps have bruchid exit holes or have been chewed open by a rodent (Fig. 1e). The opened endocarps are not included in the sample. 2) Part of the bruchids have died of disease and the endocarps containing these are pooled under "dead for unknown reasons." Since it is very difficult to determine the upper age limit of old endocarps, these samples very likely contain endocarps from two or three

inflorescences, and these endocarps range from five to eighteen months in age. Bruchids appear to have a short life span in the endocarp as compared to live seeds, which can live at least one year. Therefore, the percent viability of seeds in old endocarps is probably biased upwards and the percent of endocarps with bruchids biased downwards, if the data from forest palms in Table 1 are treated as representative of a crop from one palm, followed through time. On the other hand, some viable seeds will also have germinated; this will bias the percent of viable seeds slightly downwards.

Characteristically, old endocarps are very dark brown, weigh less than younger ones, have a surface easily gouged with the thumbnail, are easily broken with a hammer, and have the germinating pores partially exposed. The few bruchids found in these endocarps are full grown larvae, pupae or adults. Many are dead from disease, their bodies turgid with milky fluid. At a slightly later stage, only the bruchid's body fragments remain. When care is taken to distinguish seeds that rotted internally from those with endosperm eaten by a bruchid which later died, it is clear that 80 percent or better of the seeds in the "dead for unknown reasons" endocarps in Table 1 were killed by bruchid larvae (and see later detailed crop analysis in Table 2). Further, it is impossible to know what percent of apparently rotted seeds were killed by a first instar larva that died after entering the seed endosperm.

In summary, as a given crop of endocarps ages on the ground below forest palms, the number of endocarps containing viable seeds declines rapidly, and after about one month reaches a low level of 5 to 20 percent which then continues to gradually decline. The percent of superficially intact endocarps

containing live bruchids climbs rapidly during the first month, and then slowly declines. The percent of endocarps "dead for unknown reasons" remains small until the crop is three to five months old. After this, bruchids begin to die or emerge.

These changes with age of the endocarp crop are also reflected in the content of a sample of endocarps of all ages collected below one parent tree (Table 2). All endocarps were gathered from approximately one quarter of the area within 2 m. of the base of a fully reproductive *S. rostrata* (12 September 1970, Barranca site). This tree was in old secondary forest and evidence of rodent activity was less than usual near its base. The endocarps below the tree ranged from medium-aged (fallen two to three months before) to an age where the endocarp was beginning to disintegrate; endocarps so old that they could be broken between the fingers were not collected. There was the exceptional number of about 200, two- to five-month-old seedlings beneath the palm (about 50 in the area from which drupes were collected). The exceptional number of seedlings beneath this palm was probably due to the unusual dryness (for *Scheelea* habitat) of this hilltop forest being inimical to the bruchid population. Taking these seedlings into account, and adding in the endocarps probably removed by rodents, there appears to have been the remains of the endocarps from four to five inflorescences beneath the tree. In this sample, care was taken to distinguish between those seeds killed by bruchids that later died in the endocarp, and those that aborted or rotted following germination; the high figure of bruchid mortality (46.8%, Table 2) shows clearly that the high percent of "dead from unknown causes" (70.7%) recorded in Table 1 is primarily due to bruchids.

Fate of the Bruchid and the Palm Seed

To this point, I have treated the endocarp as though its seed was either killed or not. About two out of every five trees, however, have a high frequency of endocarps with two or more seeds (Fig. 2e; seven trees were encountered with a high frequency of triple-seeded endocarps and one with quadruple-seeded endocarps). When multiple-seeded endocarps are subject to a low frequency of oviposition, medium-aged endocarps commonly have a large larva in one or two of the seeds, with the second or third seed still viable. Events may take several courses from this point. Most commonly, a larva chews through the 0.5- to 1 mm.-thick partition between the embryos and eats the other larva or the remaining viable seed. That a larva may eat one to three seeds is probably the proximal cause of the greater than two-fold variation in body weight of newly emerged adults.

Occasionally the larva dies before it cuts into the second seed. The germinating pore of the destroyed seed eventually rots open, admitting the litter fauna and flora. These organisms quickly puncture the thin wall between the seeds and kill the viable seed. In Table 2, 36 percent of the viable seeds were in double-seeded endocarps, each of which contained one bruchid larva that had recently died. These seeds had a much lower chance of producing viable seedlings than did the viable seeds in single-seeded endocarps.

The bruchid may emerge without having chewed into the second seed (or larva). For example, of the 280 endocarps with exit holes in the crop recorded in Table 2, 17 percent had two exit holes. Of the 232 endocarps with single exit holes, 12 percent had been double-seeded endocarps but in no case had the

other seed survived; it was either eaten or rotted.

The death of at least one seed in the endocarp is not insured by a single oviposition on the endocarp. Preliminary surveys of larval success in endocarps newly cleaned of pulp indicate that at least one half of the first instar larvae die while boring through the hard endocarp, or shortly after entering the seed. Their penetration of the endocarp neither leads to germination of the seed nor its immediate death. Fungus or bacterial damage to the seed, however, sometimes begins at this point. If the seed is damaged and then the bruchid larva dies, the endosperm begins to disintegrate quickly in the area of the cavity eaten by the larva. It is likely that bacterial and fungal spores are carried into the seed by the first instar larva, which becomes contaminated when it chews through the egg wall and the outer surface of the endocarp.

A healthy bruchid larva kills the palm seed very quickly. While feeding is initially peripheral, the larva quickly bores into the center of the endosperm. By the third instar it has usually eaten the embryo. Growing larvae that die of disease usually appear to do so after they are full-sized and have consumed all of the seed. I have found only three dead medium-aged larvae among several thousand larvae examined.

Just as oviposition on the endocarp does not guarantee loss of the seed within, the presence of a large larva in a medium-aged endocarp does not insure the production of an adult bruchid. While the frequency of disease was not determined in most samples, diseased larvae were found beneath almost all trees sampled. From the data in Table 2, a rough estimate can be obtained of the number of larval, pupal and adult bruchids that may die of disease. A minimum of 962 bruchids grew to an

age where they either emerged or died in the endocarp; of these bruchids, only 34 percent emerged as adults.

Habitat of the parent palm.

The habitat immediately surrounding the parent palm strongly influences the fate of the endocarp beneath the parent. This is most striking when comparing grassy pasture with adjacent forest (Table 1). A palm need be only a few meters into a grassy pasture for the frequency of bruchids to be drastically reduced. For example, two adults at the Taboga site were 10 and 15 m. from the forest edge, and only 17 and 24 percent of their medium-aged endocarps contained bruchid larvae. This pasture was cleared of forest in 1967. About 2 m. into the adjacent forest, and 20 to 30 m. from the pasture trees, the only other two *S. rostrata* in the area had 72 and 87 percent of their medium-aged endocarps with bruchids in them. If a palm is several hundred meters from forest or a brush-filled watercourse, it usually has no evidence of bruchid damage to endocarps of any age.

Within the grassland there is a significant difference between attack of endocarps under trees in open pasture and those growing within about 5 m. of watercourses (Table 1). The high bruchid damage to *S. rostrata* near watercourses in pastures is probably due to the presence of wet hiding sites for adults during the dry season, rather than due to the brushy vegetation that often grows near water in pastures; palms in pastures on level ground, and accompanied by low brush, have little or no bruchid damage to their endocarps.

S. rostrata in pastures have greatly reduced rodent activity at their bases. The rind and mesocarp of most fruits rot off in about a month and there is no evidence of rodents chewing into the endocarp. Endocarps with the rinds rotted off are

susceptible to bruchid oviposition. On rare occasions forest fruit crops are free of rodent activity but are heavily attacked by bruchids once the endocarp is exposed.

Despite freedom from bruchid and rodent predation on endocarps, *S. rostrata* in pastures do not reproduce themselves. By the end of the rainy season as many as 500 young seedlings may be found within 3 m. of a pasture tree, provided that cattle have not badly trampled the site. However, these seedlings do not survive the dry season, since seedlings more than a year old are never encountered in pastures in the general study area. Since adult *S. rostrata* are sometimes left standing when the forest is cleared, there is a small fraction of the adult population that appears to be surviving in a pasture habitat. In fact, these trees are as removed from the local gene pool as if they had been cut with the forest, unless they pollinate forest palms or rodents carry their fruits to the forest. However, in southern Costa Rica, where the dry season is less severe (Palmar Sur region, cf. Janzen, 1967), *S. rostrata* seedlings do survive the dry season in pastures.

Within the forest there is one easily recognized large source of variation in seed mortality by bruchids. *S. rostrata* growing such that their endocarps fall where they will be regularly washed well downstream, tend to have substantially reduced bruchid damage. Since no adult bruchids can be emerging from endocarps below such a tree, the low level of infestation is probably due to low rates of movement of adult bruchids between palms. For example, only 1.0, 5.2 and 6.1 percent of the drupes below three palms in stream bottoms at the Barranca site were attacked. There were heavily infested crops within 15 m. of these palms. Interestingly, this low infestation rate is also probably representa-

tive of endocarps from the first inflorescence produced by a palm upon attaining adulthood.

Discussion

These data and anecdotal life histories do not allow a definitive statement as to the impact of the bruchids and rodents on the population dynamics of *S. rostrata*. However, they do suggest a number of readily testable hypotheses that are currently the basis for field experiments in Costa Rica; the hypotheses are outlined here with the hope that they will be applied elsewhere by other workers.

1) If rodents are prevented from removing the endocarps of *S. rostrata* from beneath the parent palm or chewing into the endocarps (in a moderately undisturbed forest), the bruchids should achieve 100 percent predation of the palm seeds. A corollary is that in areas where dispersal agents remove all the palm endocarps rather than discard them beneath the parent, or remove the fruits directly from the parent tree, palm bruchids will not exist.

2) The farther a freshly cleaned palm endocarp is placed from a fruiting parent, the lower will be the probability of the endocarp being attacked by a bruchid.

3) The larger the pile of freshly cleaned endocarps at a site where there is no parent, the more likely that it will be found by bruchids (this experiment mimics the effect of cache-hoarding by rodents).

4) Any distance effects discovered in 2) and 3) above will not be influenced by the proximity of adult *S. rostrata* that have not borne fruit for many years.

The data in this paper, and the apparently very low dispersal ability of the bruchids, suggest an interesting reproductive phenomenon for the palm. For example, let us estimate that a

newly reproductive adult *S. rostrata* palm produces two consecutive inflorescences a year, each bearing 1400 fruits. Assume the bruchids kill 90 percent of each fruit crop left below the parent, once a bruchid sub-population has become established below the palm. If we also assume that the bruchid infestation rate doubles with each inflorescence after the first, and starts at 1.5 percent with the first inflorescence, then the usual high infestation will not be reached until the seventh inflorescence. This means that the first six inflorescences borne by the newly reproductive palm could produce 7187 endocarps free of bruchid attack. It would then take another 25.5 years (51 inflorescences) to subsequently produce as many viable endocarps. Dispersal agents are likely to carry off as many endocarps that have fallen from an inflorescence during the first years as during later years. The palm therefore has a much greater apparent reproductive ability per inflorescence during its first years than during later years. One consequence of this lag in bruchid predation should be strong selection favoring delay of reproduction until the palm has grown to an age when it can produce full-sized inflorescences as rapidly as can an old adult.

If in fact there is a very low infestation rate of the endocarps from the first inflorescences produced, there is also strong selection pressure favoring a phenotype that delays fruit production until the bruchids from the endocarps from the previous inflorescence have emerged and died or immigrated. This directional selection is of course countered by the failure of such a palm phenotype to 1) provide food for the local rodents, and 2) place seeds in the habitat while "waiting" for its local bruchid sub-population to decline. Of the total adult-sized palms at the study

sites, those that produce fruits do so almost continually.

If the low infestation of endocarps beneath palms on pasture edges and forest creek-bottoms is due to the bruchids' low dispersal ability between palms, as suggested above, then inter-palm distances probably play a strong role in the variation observed in bruchid infestation in forested sites, where infestation of a particular crop ranges from 60 to 100 percent.

At the study sites, not all adult *S. rostrata* produce large numbers of fruits. The consequence is that some trees are effectively males, while others are male and female. From the bruchid's viewpoint, then, there are fruiting palms (females) and non-fruiting palms (males). If these differences in sexuality are genetically based, and if inter-female distances are correlated with the percent predation on the endocarps below the parent, the bruchids may play an important role in the evolution of the palm's sexuality. A palm genotype that produces only female trees will lower her own reproductive success slightly if she produces an offspring close enough to raise the bruchid infestation of her own future crops. Likewise, she lowers the reproductive success of that offspring by providing a close source of bruchids. A genotype that produces male and female offspring can add one or more male palms in her immediate vicinity without lowering her reproductive output or that of the male. Further, if the female tree produces a reduced number of male flowers (relying on adjacent males for pollination), her total fruit output may be even higher. The outcome of competition between the all female genotype and the male-female genotype should be a progressively more dioecious population the more intensive the bruchid predation. Further, the shift from the first to the second genotype should result in the

total palm density at a site that is progressively closer to the maximum possible were there no drupe predation at all and the palm population density were set by competition alone (*cf.* Janzen, 1970).

The role of the bruchid's disease in this system has not been discussed. It is likely that the pathogenicity of the litter below the palm builds up gradually during the first few years of fruit production. The disease then probably kills a relatively constant percent of each bruchid generation. This constant mortality effectively lowers the carrying capacity of the habitat for bruchids, and should lead to a higher proximity in time and space of the palms than would otherwise be the case. However, it is unlikely that the pathogenicity of the site below the tree is sensitive to slight differences in bruchid density below each palm that may result from differences in distance between adult palms. The disease is therefore likely to influence only the mean density of palms at the site, and not the detailed spatial relationships of the plants.

At the five sites examined in this study, the bruchid-*Scheelea*-rodent interaction is rapidly becoming a historical event. At all sites, more mature forest is being converted to brushy pastures and then to pure grass pasture. Some adult *S. rostrata* are left standing when the forest is cut and it is easy to conclude that they are part of the pasture flora (e.g., Standley, 1937), when in fact they are reproductively dead. One must also be careful not to regard the absence of bruchids in the pasture as normal; the breakdown of the bruchid-palm interaction spells a loud warning to studies attempting to understand the evolution and operation of complex tropical ecosystems in the face of omnipresent agricultural activity.

The large *coyol* palm (*Acrocomia*

vinifera) that replaces *S. rostrata* when the forest is cleared in the vicinity of the five study sites is instructive on this point. *Acrocomia vinifera* is very common and reproduces very well; its fruits are eaten by cattle and the drupes deposited throughout the pasture. In old brushy pastures, there are *A. vinifera* of all ages. It is tempting to regard *coyol* as a native wild palm. However, I have not found any adults in forests more than about 30 years old and they do not occur in natural disturbance sites such as river banks and creek bottoms. *Acrocomia vinifera* also differs from *S. rostrata* in that it has endocarps with single seeds, endocarps about one-third the volume of those of *S. rostrata*, very strongly synchronized fruit maturation (January), two or three synchronized inflorescences per tree, no accumulation of endocarps beneath the tree (owing to cattle eating the fruits), and less than one percent infestation by bruchids. As with any plant that has suddenly become very abundant in a new environment, understanding the evolution and adaptive significance of these traits will be extremely difficult unless its original habitat still exists and can be located.

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