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Spondias mombin is culturally deprived in megafauna-free forest

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ABSTRACT. In the semi-deciduous forests of Santa Rosa National Park in the Pacific coastal lowlands of northwestern Costa Rica, the large and fast-growing tree *Spondias mombin* (Anacardiaceae) experiences greater than 95% post-dispersal seed predation by a bruchid beetle (*Amblycerus spondiae*) on its nuts that have been dispersed to any part of pristine or secondary successional forest. Nuts dispersed (by white-tailed deer) to abandoned pastures immediately adjacent to the forest suffer less than 20% post-dispersal seed predation but seedlings are killed by frequent grass fires. *S. mombin* displays significant recruitment of saplings and young trees only on forest edges free of fire for long intervals. The very high percent seed predation in the forest and the failure of many nuts to ever be dispersed away from the parent tree is attributed directly and indirectly to the absence of a herbivorous (frugivorous) megafauna that would have been part of the habitat of *S. mombin* through most of its evolutionary history. These large animals would have consumed large numbers of *S. mombin* fruits and thereby dispersed the nuts in such a manner as to have both led to more escape from bruchids and an overall reduction in the bruchid population density. By their defecation patterns, these mammals would also have defecated more nuts in sites of high quality for *S. mombin* sapling survival than is the case at present. In contemporary habitats, *S. mombin* is culturally deprived in that it can no longer interact with the habitats, animals and densities of animals whose selective pressures were a major force in the evolution of the tree's traits.

KEY WORDS: bruchid, Costa Rica, frugivory, herbivory, nut, Pleistocene megafauna, seed dispersal, seed predation, tropical deciduous forest.

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INTRODUCTION

It is commonplace for a fleshy-fruited tropical tree species to have its fruits eaten by many species of vertebrates (e.g. Bonaccorso *et al.* 1980, Cruz 1981, Howe 1977, Howe & Vande Kerckhove 1981, Howe *et al.* 1985, Janzen 1979, Leighton & Leighton 1982, Scott & Martin 1984). Its seed shadow is then

generated by a multiple-species disperser coterie that is a subset of these vertebrates. The fitness-enhancement of each member of the disperser coterie will not be proportional to the numbers of fruits or seeds that each member eats. Why not? What matters in evaluating a disperser is how many viable seeds are carried where and when (e.g. Augspurger 1984; Augspurger & Kelly 1984; Howe *et al.* 1985; Janzen 1970, 1982b; Sork 1983). Furthermore, the proportion of a tree's seed crop that is dispersed by a particular disperser will have a non-random relationship to the quality of the deposition sites only to the degree that there has been ecological or evolutionary moulding of the tree-disperser interaction in that direction. Since there are many pathways whereby the disperser coterie obtains its dependencies on, and use of, a fruit crop, it is likely that many members of the disperser coterie will not obtain or release seeds in direct proportion to the value of the animals' dispersal activities to the plant. This logic is especially pertinent if a major portion of a plant's disperser coterie has been recently extinguished.

Spondias mombin, a common and widespread Neotropical tree, appears to be such a plant. In this paper I describe the short-term fate of the seeds in its nuts (endocarps) after they have been dispersed by a multiple-species disperser coterie in a mosaic of semi-deciduous forest and abandoned pasture in the Pacific coastal lowlands of Costa Rica. My goal is a descriptive example of the complex relation of disperser activities to the value of different parts of a seed shadow. I also examine how ecological shaping of the disperser coterie of a particular habitat and tree influences a tree's reproduction. In short, *S. mombin* nuts are dispersed within forest and to adjacent abandoned pasture undergoing woody secondary succession. There are quite different intensities of post-dispersal seed predation in the two habitats, as well as the expected great differences in seedling survival. Since different species of animals produce different parts of the *S. mombin* seed shadow, the habitat-specific seed predation changes the relative significance of members of the disperser coterie from that expected solely from a consideration of the number of fruits eaten per animal or species. My observation of tropical seed dispersal systems leads me to feel that for many species of plants this kind of complication needs to be added to the more generally appreciated habitat-specific seedling mortality and density-specific seedling mortality when considering why a tree such as *S. mombin* is what it is and where it is. Furthermore, this kind of detailed examination of plant demography must recognize that a plant is seriously culturally deprived if it abruptly loses a major portion of the disperser coterie with which it has evolved for millions of years. A major portion of its phenotype has been deleted through the loss of the consequences of only a small part of its genetic program, the part that places a tough nut and juicy fruit bait around its seeds.

The significance of the plant-animal interactions reported here can only be understood in the context of the details of the biologies of the participants. Since the relevant natural histories of the participants have never been treated in the literature, and since they will be directly unfamiliar to many readers, I provide substantial descriptive information in the following sections.

NATURAL HISTORY BACKGROUND

Spondias mombin. This large tree is in the mango, sumac and cashew family (Anacardiaceae). It is native from tropical Mexico (Pennington & Sarukhan 1968, Standley 1920) through Central America (Blackwell 1968, Croat 1978, Hartshorn & Poveda 1983, Holdridge & Poveda 1975, Witsberger *et al.* 1982) and into tropical South America. It is a lowland plant, usually occurring below 1000 m elevation. Its fruits are frequently mentioned as food for primates (Croat 1974b, Estrada 1984, Estrada & Estrada 1984, Freese 1983, Hladik & Hladik 1969), bats (Gardner 1977, Morrison 1983, Vasquez-Yanes *et al.* 1975), and rodents (Glanz 1984, Glanz *et al.* 1982, Smythe 1970). At Santa Rosa, the nuts are often found below feeding roosts of frugivorous bats, mixed with seeds of *Ficus*.

S. mombin become fruit-bearing trees as young as 20 years of age, range from 5–30 m in height when fruit-bearing, and are most frequently noticed as pioneer members of primary and secondary succession in old fields and roadsides. They are members of the canopy through all stages of succession and I suspect that most adults die of senescence before their 200th birthday. In large expanses of Costa Rican pristine forest, *S. mombin* is usually a rare tree in major disturbance habitats such as river banks and on steep contours. Very rarely it is encountered in the regeneration in natural tree falls. With anthropogenic disturbance (especially selective logging and the introduction of cattle) it may become very common. For example, the high density of *S. mombin* in the old secondary succession forest on Barro Colorado Island, Panama, is probably due to massive seeding into, and survival in the insolation of, the old field environment that once covered half the island. In Costa Rica, the drier the habitat the more likely *S. mombin* is to appear to be a member of the pristine high forest canopy. However, if the forested site is so dry that the mature pristine canopy is only 2–4 m in height, then *S. mombin* is absent.

At the study site, Santa Rosa National Park, *S. mombin* flowers while leafless and during the last month (late April to early May) of the six month dry season (December to May). It may still be bearing flowers during the first several weeks of the rainy season. The fruits (jobo, jobo jocote) mature from mid-August through October. Different individuals vary by as much as 2 months in the initiation of fruit ripening, and a large *S. mombin* crown bears ripe fruits for about one month. The glabrous yellow plum-like juicy fruits (Figure 1b) taste sweet and lightly acidic with an overlain slightly resinous to pungent flavour. Once ripe, the fruits hang for 1–2 weeks and then drop. The fruits weigh 6–15 g each and fall directly below the branch bearing them. A large tree with a full-sized crown may bear as many as 10,000 fruits in one crop (or as few as several hundred, owing to a dry year or defoliation by caterpillars). *S. mombin* is in full leaf when bearing fruits of all ages; the fruits are pendant on long peduncles and hang throughout the crown outside the large tufts of leaves on the widely spaced thick branchlets.



Figure 1. A. *Spondias mombin* nuts (endocarps): upper row, cross-sectioned undamaged nuts illustrating viable seeds (five on left to one on right); middle row, centre two nuts have had one seed removed by small rodent through the germination canal; bottom row, on left is *Amblycerus spondiae* exit hole and entire row represents variation in nut size and shape that can occur even within a single tree's fruit crop. B. *Spondias purpurea*: upper row, intact fruit (fruit of *S. mombin* is very similar but slightly larger and more irregular in shape) and nuts; middle row, portion of intact *Ctenosaura similis* faeces with two intact *S. purpurea* nuts in centre (separated by break); bottom row, remainder of *C. similis* faeces with two more *S. purpurea* nuts in centre. April 1984, Santa Rosa National Park, Costa Rica.

If the pulp of the fallen *S. mombin* fruit is not eaten by a vertebrate, it rots off within several weeks or is carved off by leaf-cutter ants (*Atta*). The nut is fibrous, stony, tough and hard-walled (Figure 1a). The 0–5 soft and white seeds are cylindrical and about 10 mm long by 2 mm in diameter. They have a bland, nutty flavour. The living and undried seeds weigh 0.04–0.06 g each. There are five seed cavities in the hardest parts of the indehiscent nut. The nuts weigh 3–10 g when newly cleaned of pulp, have a volume of 2–6 cc and float when newly cleaned as well as after thorough drying by the dry season. The nut is a rounded 2–3 cm long cylinder (1.5–2.5 cm diameter) with variably developed and rounded shoulders at the distal end over each seed cavity. Because the nuts have a very low specific gravity, they probably pass through large herbivores at about the same rate as does vegetative fodder. *S. mombin* nuts are regurgitated or defecated intact, with no suggestion of being digestible. They are too hard or tough to be split or crushed by any extant Costa Rican mammal (including cows and horses), though a rodent could undoubtedly gnaw through one (e.g. Glanz 1984) and a large granivorous bird such as the great curassow *Crax rubra* (Galliformes: Cracidae) may grind one up in its gizzard (unpublished observation, Santa Rosa National Park). Once the fruit pulp has been removed, there is no vertebrate at Santa Rosa that is interested in the nut, except for the unidentified small rodent in abandoned pasture that chews into one end and pulls out some seeds (see below).

At Santa Rosa, the pulp-free nut dries thoroughly in the litter during the dry season, and then leaches and rots during the following rainy season. The seeds in a pile of nuts germinate gradually during the first several months of the rainy season. By the second dry season there are no viable seeds remaining. I do not know if some germination retardant needs to be leached out of the nut wall before germination can occur, but the unleached nut wall is resinous in taste and pungent in odour. The seedling exits through a germination canal at the distal end of the nut.

Throughout the Park, *S. mombin* approximately co-occurs with *Spondias purpurea* (jocote garrobo). The latter is a shrubby treelet of forest edges and is probably introduced since its red and sweet fruits (Figure 1b) are widely eaten by humans, it is often planted as a garden and fencerow tree, and the entire Santa Rosa population occurs along old roads and human trails. Its failure to become naturalized is puzzling since the fruits are eagerly consumed by native animals (Figure 1b) and the small nuts are widely dispersed in the Park. *Spondias radlkoferi*, a large tree quite similar to *S. mombin* (e.g. Croat 1974a, 1978) has been hesitatingly reported from Santa Rosa (Janzen 1980, Janzen & Leisner 1980). However, I cannot locate any tree in the Park that can be unambiguously identified as the green-fruited *S. radlkoferi*. Certainly none of the fruits and nuts discussed in this paper are *S. radlkoferi*.

Since *S. mombin* maintains a breeding population in virtually all deciduous to evergreen lowland non-swamp forest types from tropical Mexico through Central America, I assume that it has occurred at Santa Rosa and in the kinds

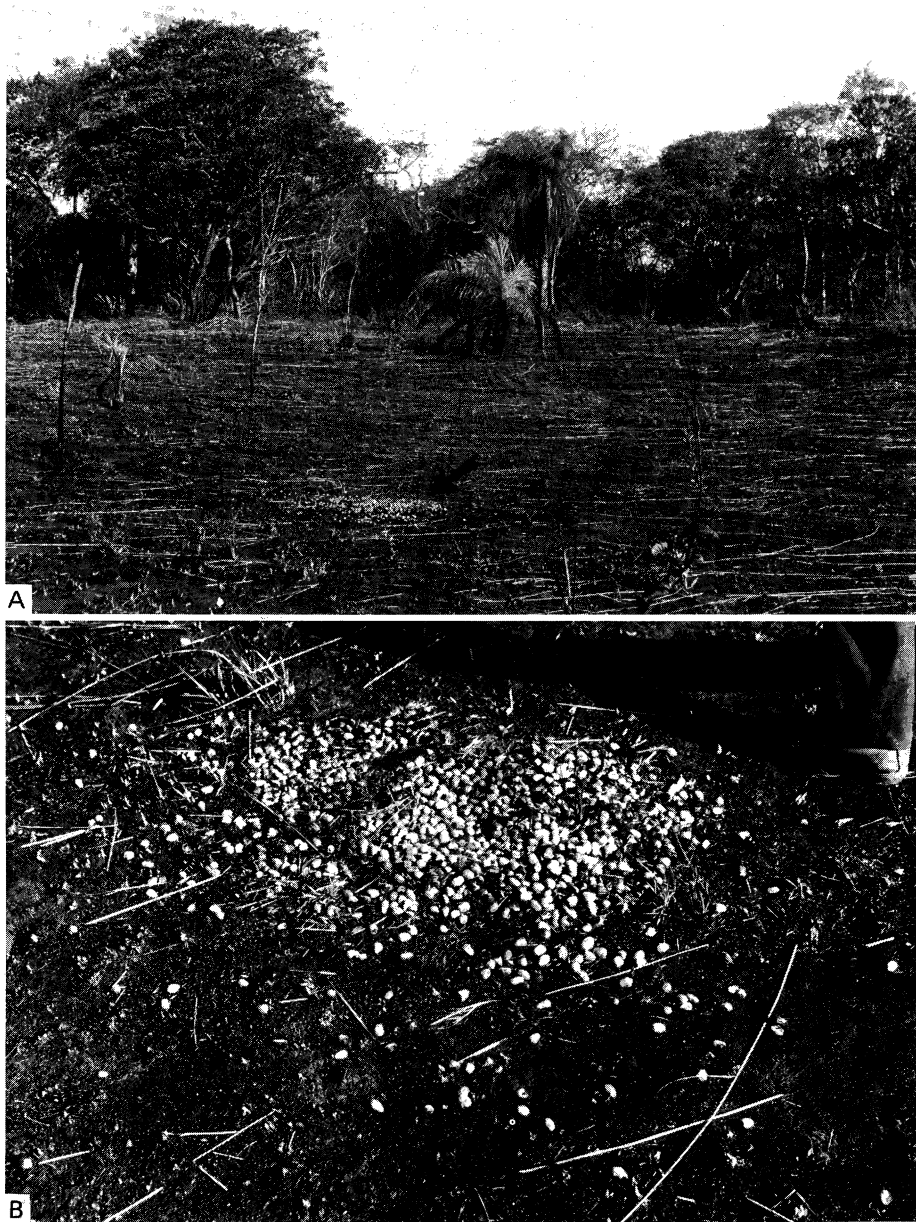


Figure 2. A. Pile of *Spondias mombin* nuts (arrow) regurgitated over many days by a white-tail deer; the nuts have been exposed by a fire that consumed the 1.5 m tall dense stand of *Hypparrhenia rufa* pasture several weeks before the photograph. B. Close view of *S. mombin* nuts in (A) above. May 1984, Santa Rosa National Park, Costa Rica.

of forest at Santa Rosa as long as it has been in Costa Rica (and probably tens of millions of years longer). This assumption suggests that *S. mombin* has been a party to animal-plant interactions in the Park as long as the Park has been above water, and probably much longer elsewhere in the Neotropics.

Nut dispersers. At present, Santa Rosa *S. mombin* have their ripe and ripening fruits plucked directly from the crown by monkeys (white-faced monkey, *Cebus capucinus*; howler monkey, *Alouatta palliata*; spider monkey, *Ateles geoffroyi*), procyonids (coati, *Nasua narica*; kinkajou, *Potos flavus*), frugivorous bats (*Artibeus jamaicensis* and others), variegated squirrels (*Sciurus variegatoides*), and various marsupials. All of these mammals carry fruits as much as 100 m from the tree, chew off the pulp, and drop the nuts. In addition, the non-volant species often swallow the fruits whole and later defecate the nuts intact. All occasionally drop a fruit being carried to a feeding site and all often drop fruits below the parent tree (Figure 3b); such fruits are not recovered and generally retain most of their fruit pulp. The fruit pulp may rot off or the fallen fruit may be harvested by a terrestrial vertebrate. Howler monkeys sometimes defecate small piles of *S. mombin* nuts (2-20 at a site). *Artibeus jamaicensis* may accumulate piles of 5-100 nuts (Figure 3a) directly below temporary feeding roosts (as with *Andira inermis* nuts, Janzen *et al.* 1976). All of these animals occasionally cross non-forested habitats such as abandoned pasture and are therefore potential contributors to the strongly isolated portions of the *S. mombin* seed shadow. However, none of the non-volant species do this regularly, so I suspect their contribution to be small compared to that by other mammals.

The many fruits dropped directly below the parent tree accumulate on the litter in a dense patch (Figure 3b). Some of these fruits are then in turn eaten by more terrestrial mammals. The ripe fruits from the ground are swallowed whole by coatis, white-tail deer (*Odocoileus virginianus*) and ctenosaurs (*Ctenosaurus similis*). Coatis and ctenosaurs defecate (Figure 1b) the nuts on the forest floor (including forest edges). The deer regurgitate the nuts while chewing their cud at resting sites both in the forest (Figure 3b) and in the open grass and forb vegetation of the abandoned pastures (Figure 2). The nuts never pass into the lower digestive tract. The deer are the major contemporary dispersers to the strongly isolated portions of the *S. mombin* seed shadow, at least with respect to the numbers of nuts deposited. Collared peccaries (*Tayassu dicoteles*), agoutis (*Dasyprocta punctata*), pacas (*Aguti paca*), free-ranging horses (*Equus caballus*), and tapirs (*Tapirus bairdii*) chew the fruit pulp off the nut and drop it (spit it) where it was found. Horses rarely also swallow the nuts but tapirs occasionally swallow large numbers of nuts. Agoutis have been reported to disperse and bury *S. mombin* nuts in Panamanian rain forest (Smythe 1970) but they do not do this at Santa Rosa (W. Hallwachs, personal communication). The terrestrial animals that only chew off the pulp and then drop the seed usually do not directly modify the seed shadow of a *S. mombin* tree but they prevent nut dispersal by rendering the nut uninteresting through removal



Figure 3. A. Small pile of *Spondias mombin* nuts in forest floor litter where they were dropped beneath an *Artibeus* or *Phyllostomus* bat feeding-roost eight months previously; all the seeds in these nuts have been killed by *Amblycerus spondiae* larvae. B. A portion of a 2-4-nut-deep layer of *Spondias mombin* nuts on the forest floor beneath a parent tree; this accumulation was produced by fruit drop and regurgitation by white-tail deer eight months previously; 99.2% of the seeds have been killed by *A. spondiae* larvae. May 1984, Santa Rosa National Park, Costa Rica.

of its fruit pulp. Presumably when there was a larger fauna of terrestrial herbivores large enough to frequently swallow *S. mombin* fruits whole (Janzen & Martin 1982), the negative impact of the nut spitters would have been greater than in the contemporary situation where many or most *S. mombin* fruits that fall below the parent in a heavy fruiting year simply rot there (Figure 3b). The fruit droppers, however, would have had less impact because of the terrestrial fauna available to consume the fallen fruits.

There is no suggestion that nuts with their fruit pulp eaten or rotted off, dispersed or otherwise, are secondarily dispersed by any animal at Santa Rosa. However, surface water runoff during heavy rain through a deciduous canopy, as occurs at the beginning of the rainy season, moves some a few decimetres across the soil surface. Furthermore, nuts dropped in water channels may be moved secondarily for hundreds of metres, and even deposited on insulated bare soil in the riverbed.

Until about 9000 years ago, the megafauna of large herbivores (Janzen & Martin 1982) very likely swallowed and defecated a large proportion of the *S. mombin* fruit crop. The fruits would have been obtained both from the tree crowns and the ground below. These animals – ground sloths, proboscidians, equids, glyptodonts – were not ruminants and would therefore have defecated rather than regurgitated nuts in both forest and insulated low vegetation. However, in the northern part of its range, *S. mombin* was undoubtedly also in contact with large ruminants – bovids, cervids, camelids – some of which would have spat out all nuts during rumination as do white-tail deer. Since modern peccaries and rodents show no interest in collecting *S. mombin* nuts from horse dung at Santa Rosa (in contrast to other, more edible seeds, Janzen 1982a, b), I will assume that the *S. mombin* nuts dispersed in extinct megafauna dung stayed where they were defecated.

S. mombin fruits are highly edible to humans (though it is the slightly sweeter and more easily harvested *S. purpurea* that is commonly sold in Neotropical markets). It is certain that they would have been eaten and transported by Costa Rican Indians for at least the past 5000 years. Village sites should have been high density sites of *S. mombin* originating from nuts in trash heaps. It is likely that contemporary *S. mombin* distributions in Costa Rica in general, and in Santa Rosa specifically, still reflect the activities of these human dispersal agents, since they have been extinguished for less than 400 years.

In short, the contemporary seed shadow of *S. mombin* in Santa Rosa is generated by dropping, regurgitating and defecating by monkeys, bats, coatis, deer and ctenosaurs. This is only part of the potential frugivore coterie of this tree species, and only part of the seed disperser coterie that it presumably had during all but a tiny percent of its evolutionary past. As a rough estimate, at present at least half of the nuts in a tree's crop currently remain on the ground directly below the parent in a year of heavy fruiting, and therefore are not part of the dispersed portion of the tree's seed shadow. Monkeys and bats appear to remove at least 95% of the nuts that are removed, with deer removing perhaps

4 of the other 5%. I assume that with an intact fauna of large Pleistocene (or earlier) herbivores, the percent removed by arboreal and volant small mammals would have been somewhat reduced and virtually all the fallen fruits would have had their nuts dispersed.

Seed predators. There is no pre-dispersal seed predation of *S. mombin* at Santa Rosa (and none has been recorded elsewhere), except that howler monkeys occasionally eat fruits that are too immature to contain mature seeds. However, as many as 30% of the nuts in normal-appearing fruits (full size and tasting like fruits with seed-rich nuts in them) may contain no viable seeds; the potential significance of this extreme level of seed abortion will not be discussed here, but if the absolute amount of fruit reward at a *S. mombin* crown is an important part of disperser attraction, these seed-free normal-appearing fruits may still be functional.

Almost all post-dispersal seed predation on *S. mombin* at Santa Rosa is committed by the larvae of the large grey-brown bruchid beetle *Amblycerus spondiae* (Janzen 1980, Kingsolver 1980). This insect kills more than 90% of all *S. mombin* seeds produced in Santa Rosa. Once the fruit pulp has been removed from the nut, the adult beetle locates the nut in the forest litter. Just as was the case with two other large bruchids that oviposit on *Scheelea* palm nuts in dry forest to the south of Santa Rosa (Janzen 1971), *A. spondiae* apparently does not usually search for nuts in large insolated areas such as open pasutres. It glues single eggs to the nut surface and as many as 40 eggs may accumulate on a single nut. It is commonplace for there to be 5–13 eggs; each egg probably represents an encounter with a female, rather than one female laying many eggs during one encounter with a nut. The larvae mine through the fibrous nut wall and the hard core and consume the 1–5 seeds. If there are no viable seeds, the larva dies. Only one larva matures per nut. The other larvae are consumed by the largest one, or starve. The pre-pupal last instar larva cuts an exit tunnel almost all the way through the nut wall, by way of which the adult exits (Figure 1a) 1–2 months after its egg was laid. As many as half of the attacked nuts fail to produce a beetle (e.g. Table 1) because of larval death through cannibalism and insufficient amounts of food. However, in more than 99% of the times that a larva begins to consume the interior of a nut, all seeds are killed. Adult *A. spondiae* are very variable in size, presumably because the amount of food available ranges from 1–5 seeds. There are no parasitoids of *A. spondiae* larvae or pupae at Santa Rosa (Janzen 1980) and none have been recorded elsewhere.

The newly emerged adults wait approximately 10 months until the next year's crop of nuts is available. Adult *A. spondiae* are found resting (hiding) in rolled leaves and under bark, and visiting flowers, during the dry season and the first half of the rainy season. They are taken as prey from these microhabitats by a wide variety of carnivores, from white-faced monkeys to spiders.

A nut that is unattacked during the several months following dispersal is not then attacked later. I have not determined whether the nuts have lost too much

of their characteristic odour to be located or the adults do not search for them. *A. spondiae* does not have other larval hosts in the inland portions of Santa Rosa, but it does attack the similar-sized nuts of the beach-edge tree *Hippomane mancinella* (Euphorbiaceae) (Janzen 1980). Such attack has not been recorded elsewhere in the range of *H. mancinella* and it is probably a very local phenomenon. The beetle has been reared once from the nuts of *Cordia dodecandra* (Boraginaceae) and *Zizyphus mexicanus* (Rhamnaceae) in Mexico (Kingsolver 1980).

Vertebrates generally show no interest in clean *S. mombin* nuts at Santa Rosa. However, an unidentified small rodent did inflict moderate seed predation on *S. mombin* nuts in one abandoned pasture site (site A, Table 2). I have not found damage done by this animal in any forest habitat.

THE STUDY SITE

This characterization of *S. mombin* and its interaction is intended to apply directly only to the upland forests and their regeneration in Santa Rosa National Park (10,800 ha, 200–350 m elevation; 25 km south of La Cruz, northwestern Guanacaste Province, Costa Rica; Boza & Mendoza 1981, Harts-horn 1983). However, casual observation of *S. mombin* crops in Mexico and Central America over the past 20 years leads me to believe that it applies in general to *S. mombin* in the remainder of its range in the dry coastal lowlands of tropical Mexico and Central America. Santa Rosa receives 900–2500 mm of rain per year, all of it falling between late April and December.

The uplands of the eastern edge of the Park were once covered with evergreen oak forest (*Quercus oleoides*). This forest graded into semi-evergreen forest which in turn became its most deciduous on the west-facing slopes down to the coastal plain. Santa Rosa regenerating forest of 20–250 years of age is much more deciduous than is the pristine forest that once occupied the site, which gives the generally false impression that the original vegetation was deciduous forest. Between about 1600 and 1945, 1–20 ha pastures of irregular shape were cut out of the upland forest. Large areas of forest were selectively logged, some areas were planted as croplands, and all the Park was browsed/grazed by cattle. *S. mombin* occurred and occurs throughout these habitats. Some thoroughly cleared areas were allowed to regenerate to forest. Adult *S. mombin* is today most abundant in this regenerating forest and in the selectively logged forests.

The Santa Rosa pastures were planted with jaragua (*Hyparrhenia rufa*), an introduced grass (cf. Daubenmire 1972), in 1940–60. When heavily grazed, this pasture grass accumulates some fuel but not enough to cause the pasture's dry season fires to eliminate all woody regeneration or to severely carve away at the forest at its margins. The pastureland and forest mosaic therefore existed in a dynamic equilibrium, with more woody invasion of the pastures in wetter

years. *S. mombin* was, and still is, a common member of that invasion. Following conversion to a national park and subsequent removal of the livestock in 1972–78, Santa Rosa's abandoned jaragua pastures generated dense stands of 1–2 m tall grass fuel. Nearly annual fires now severely deplete the woody invaders and carve away at the adjacent forest. *S. mombin* is a commonplace victim of fire in both habitats, but regeneration is still evident in a few sites protected from fire.

Unless otherwise mentioned, the *S. mombin* nut samples collected from forest came from Bosque San Emilio. This forest is 40 to 90-year-old secondary succession lying along the east side of the park entrance road and 0–1.5 km north of the main Park intersection. Within the past 100 years, the site of this highly deciduous 3–20 m tall closed-canopy forest has been open pasture, road- and trail-side, banana plantation, cattle holding area and avenue for driving cattle. It is approximately 450 ha and bounded on three sides by abandoned pasture in various stages of woody regeneration. The aspect of the vegetation and the senescence patterns of the nearly 200 species of woody plants in this forest suggest that it is relatively uniform secondary succession from seed sources that were largely outside the site or left standing but isolated within the site. The low abandoned field and/or pasture aspect of the site, which was the habitat in which the current cohort of adults lived as insulated young juveniles, is no longer present. Most individuals and species of plants are not reproducing themselves on the site as they die of senescence. For example, I have found no surviving sapling *S. mombin* in this forest (away from the roadsides) despite the presence of at least one seed-bearing canopy-level adult per hectare in the forest (and up to 10 per ha in certain sites). In contrast, adjacent more pristine forest (Bosque Humedo, Janzen 1982a) contains less than one large adult *S. mombin* per hectare and a few juvenile *S. mombin* in the treefalls.

The abandoned pasture samples – henceforth referred to as pasture samples – were collected from the open grassland 30–80 m from the Bosque San Emilio western edge (Area A) and 50–110 m into the same grassland alongside the secondary successional forest like Bosque San Emilio but about 2 km to the northwest (Area B). Both pasture sites have been burned almost annually for the past 12 years and probably for long before.

METHODS

Collecting nuts. Nuts were collected during the second half of the dry season (see Tables for exact dates). This period is well after all bruchids have oviposited and all surviving offspring have emerged from the nuts. Nuts were searched for visually on or in the litter at specific distances from specific adult *S. mombin*, specific habitat types, or proximity to other nuts. *S. mombin* nuts are large enough such that visual inspection of litter scratched through by hand locates all of them. At a collection point, all nuts were collected from a designated area. Nuts more than a year old – those that had lain rotting in the litter

Table 1. Fate of *Spondias mombin* nuts without fruit pulp, on ground in forest

	Number of nuts sampled	<i>Amblycerus</i> exit holes (%)	Externally intact		Percent nuts destroyed by <i>Amblycerus</i>	Number viable seeds per nut	
			Remains of <i>Amblycerus</i> inside (%)	Number of viable seeds			
<i>(a) Scattered single nuts more than 30 m from an adult</i>							
14 March 1981	1016	77	91	33	98	0.0325	
10 May 1982	116	70	91	7	97	0.0603	
12 March 1983	511	53	93	36	97	0.0705	
7 April 1984	430	61	87	36	95	0.0837	
7-10 May 1984	412	45	83	14	91	0.0340	
Σ	2485			126			
\bar{X}		61	89		95.6	0.0562	
SD		12.8	4.0		2.79	0.0225	
<i>(b) Nuts in piles more than 30 m from an adult</i>							
7-10 May 1984							
Pile 1	23	87	67	2	96	0.0870	
2	49	86	100	0	100	0	
3	28	68	100	0	100	0	
4	135	62	100	0	100	0	
5	244	46	99	2	99	0.0082	
6	26	85	100	0	100	0	
7	48	85	100	0	100	0	
8	110	91	99	1	99	0.0091	
9	929	46	100	3	100	0.0032	
Σ	1592			8			
\bar{X}		73	96		99.3	0.0119	
SD		18.0	10.9		1.32	0.0284	
<i>(c) Nuts in high concentrations directly below parent trees</i>							
	Estimated numbers of nuts in area	Number of nuts sampled	<i>Amblycerus</i> exit holes (%)	Externally intact		Percent nuts destroyed by <i>Amblycerus</i>	Number viable seeds per nut
				Remains of <i>Amblycerus</i> inside (%)	Number of viable seeds		
14 May 1981	10,000	2461	73	99	7	99.7	0.0028
10 March 1982	4,000	306	62	95	14	98.0	0.0458
16 March 1983	7,000	1000	39	96	5	99.7	0.0050
26 April 1983	20,000	771	60	98	5	99.1	0.0065
27 April 1983	12,000	523	61	97	12	98.7	0.0229
31 April 1983	10,000	913	49	99	2	99.6	0.0022
7 May 1984	4,000	208	52	97	4	98.6	0.0192
10 May 1984	10,000	600	62	98	4	99.2	0.0067
Σ		6782			53		
\bar{X}			57	97		99.1	0.0139
SD			10.3	1.4		0.61	0.0150

Table 2. Fate of *Spondias mombin* nuts regurgitated by white-tailed deer in abandoned pasture (April-May 1983)

	Number of nuts sampled	<i>Amblycerus</i> exit holes (%)	No visible <i>Amblycerus</i> damage		Percent nuts destroyed by <i>Amblycerus</i>	Number viable seeds per nut	Percent rodent attack	Final viable seeds per fruit
			Remains of <i>Amblycerus</i> inside (%)	Number of viable seeds				
<i>Area A</i>								
Pile 1	1370	5	11	2013	15	1.4693	61	0.8584
2	127	43	52	37	72	0.2756	14	0.1969
3	480	0	0	614	0	1.2792	0	1.2792
4	401	10	17	563	25	1.4040	70	0.5885
5	943	3	9	1539	12	1.6320	72	0.7996
6	1207	0	0	2788	0	2.3099	0	2.3099
7	176	18	12	261	28	1.4830	6	1.4261
8	406	6	7	596	13	1.6932	71	0.7833
9	141	13	8	231	20	1.6383	0	1.6383
10	506	0	0	1189	0	2.3500	0	2.3500
Σ	5757			9831				
\bar{X}		9.80	11.60		18.5	1.5535	29.40	1.2230
SD		13.13	15.30		21.36	0.5756	34.05	0.7172
<i>Area B</i>								
11	55	0	9	84	9	1.5273		
12	59	3	14	117	17	1.9831		
13	99	8	33	40	38	0.4040		
14	119	0	1	188	1	1.5798		
15	60	0	7	62	7	1.0333		
16	22	0	0	39	0	1.7727		
17	24	0	0	51	0	2.1250		
18	92	0	0	122	0	1.3261		
19	59	0	0	110	0	1.8644		
20	20	0	0	40	0	2.0000		
21	58	0	0	65	0	1.1207		
22	15	0	0	29	0	1.9333		
23	17	0	0	34	0	2.0000		
24	157	0	0	238	0	1.5159		
25	99	0	0	158	0	1.5960		
26	122	0	0	226	0	1.8525		
27	48	0	0	96	0	2.1818		
28	32	0	0	47	0	1.4688		
29	89	3	15	101	18	1.3836		
30	35	9	9	54	17	1.8621		
Σ	1281			1901				
\bar{X}	64.05	1.15	4.40	95.05	5.4	1.6274		
SD	40.46	2.68	8.38	63.66	10.01	0.4318		

throughout the previous rainy season - were discarded. Such old nuts are easily recognized by their soft and decomposing nut walls.

Forest sample sites were chosen by either locating adult trees and searching below them (dense patches of nuts) or by walking haphazardly through the forest in search of small piles or single nuts left by dispersers and then deter-

mining the distance to a potential parent by searching in all directions. Whether the adult *S. mombin* that I located were the actual parents is irrelevant for the questions addressed here. Abandoned pasture sample sites were chosen by walking through the habitat, noting piles left by deer (Figure 2), and later returning to collect them. While all nuts were collected from a given concentration (deer resting site), not all piles of nuts left by deer in a given pasture site were located. Area A (e.g. Table 2) was an area where a deer repeatedly returned to the same exact site, resulting in large piles of regurgitated nuts. Area B was an area where a deer tended to use a site once or a few times, resulting in small piles of *S. mombin* nuts.

Seed fate. Nut fate was determined by noting bruchid exit holes and by cutting nuts in half along the equator (right angles to the long axis) with heavy shears. Since the seeds are elongate, any surviving seeds are cross-sectioned with this cut. Seeds with a slightly translucent white, moist and solid interior are alive (Figure 1a). Recently killed, fungus-attacked or bacteria-attacked seeds are either very opaque white or obviously decomposing.

Nuts with internal bruchid damage but no exit hole are evident from the brown powdery frass that fills the cavities where the seeds were and the bruchid(s) mined. Seed fate cannot be scored by counting bruchid eggs on the outside of the nut because sometimes nuts with no evident eggs contain bruchid damage. Bruchid oviposition is often so thorough that all nuts have eggs and the only surviving seeds in a sample are those in nuts in which all of the larvae died. Nuts with bruchid exit holes always have all of their seeds destroyed.

I have encountered no examples in the field or germination in the collection bags that suggest that seeds may germinate in the rainy season during which their nuts are cleaned of fruit pulp. Sampling in the dry season following the rainy season of nut production, therefore, detects all seeds that have survived post-dispersal seed predation by bruchids.

RESULTS

Post-dispersal seed predation by the bruchid *Amblycerus spondiae* was not distributed equally among the three nut groupings in the forest (Table 1) nor between the forest abandoned pasture habitats (Tables 1, 2). The highest percent nuts destroyed by *A. spondiae* occurred in small piles (Figure 3a) scattered in the forest at points more than 30 m from any seed-bearing *S. mombin* crown; 99.7% of 1592 nuts in 9 widely spaced piles were destroyed as compared with 99.4% of 6782 nuts from 8 different high concentrations directly below parent trees (Figure 3b) ($P < 0.05$, one-tailed t test, Sokal & Rohlf 1969:607). By the same test, both of these values are significantly greater than the 95.9% nut destruction of widely scattered single nuts more than 30 m from an adult *S. mombin*. If the samples at different sites and on different dates are treated as the data points, the nuts in small piles do not have nut destruction percentages different from those in high concentration below the parent trees

(99.3 versus 99.1%, respectively, *t* test not significant). However, the 95.6% destruction of single nuts is still significantly less than that of either of the other groupings ($P < 0.01$, *t* test, arcsine transformed percentages). The nuts in isolated small piles differ in another way from those in high concentrations. More than half of the isolated piles had all of their nuts destroyed, while no sample from a high concentration had all of its nuts destroyed. The isolated single nuts could have been dispersed by any of the frugivorous vertebrates in the forest, but most were probably dispersed by bats and monkeys. The widely scattered small piles of nuts were primarily produced by *Artibeus* bats at feeding roosts and by regurgitating deer. The high concentrations beneath parent trees were largely nuts in fruits that fell from the tree and were not removed by dispersal agents (though at the 10 May 1984 sample site a deer had repeatedly regurgitated nuts beneath a heavily fruiting tree (Figure 3b), resulting in a layer 2–4 nuts deep over several square metres).

If the number of surviving viable seeds per nut is treated as the relevant variable, the results are about the same. Pooling all the nuts within a sample type, the widely scattered single nuts yielded 0.0507 viable seeds per nut while the small piles and the high concentrations beneath parents yielded 0.0050 and 0.0078 viable seeds per nut, respectively. All three of these values are different from each other ($P < 0.05$, one-tailed *t* tests, Sokal & Rohlf 1969:607). If the different piles and dates are instead used as the sample points (Table 1), the scattered single nuts (five dates) had an average of 0.0562 surviving viable seeds per nut, which is significantly greater ($P < 0.01$, *t* test) than the values of 0.0119 and 0.0139 surviving seeds per nut for the small piles and the high concentrations, respectively. The latter two values are not significantly different from each other.

The fate of the nuts regurgitated by deer in the abandoned pasture sites (Figure 2) was dramatically different from that of the nuts in the forest (Table 2). Among the 7038 nuts examined in the two pasture sites, the percent nut attack by bruchids was significantly less than in the forest (by inspection, 6.3–11.2% versus 95.9–99.7%). If the separate piles are viewed as the data points, the same general relationship holds (5.4–18.5% nut destruction in the pasture). Likewise, if the number of viable seeds per nut (prior to rodent attack) is the variable of interest, the pasture yielded 1.6–1.7 seeds per nut pooled across all samples, and 1.6 seeds per nut if each pile is viewed as a data point.

In Area A the nuts were also attacked by an unidentified small rodent in six of ten piles (Figure 1a; Table 2). The attack intensity was unrelated to the size of the pile and ranged from 6 to 72%. Summed over all piles in Area A, the rodent reduced the number of viable seeds per nut from 1.7 left by the bruchid to 1.3 (pooled across all samples) or from 1.6 to 1.2 (treating each pile as a sample point). This kind of attack was not seen in either Area B or in the forest, and it has been only very rarely encountered in small regurgitated piles of *S. mombin* in other abandoned pastures in the Park.

Simply scoring nuts for *A. spondiae* exit holes gives a very misleading im-

pression of the intensity of bruchid nut destruction, since well over 70% of the apparently intact nuts in the forest had internal damage. In the abandoned pasture, however, the same figure is much lower.

DISCUSSION

At first glance it appears that to be regurgitated (or otherwise dispersed) into the abandoned pasture is the most desirable fate available to a seed in a fruit from a *Spondias mombin* tree growing in the late secondary succession forest (Bosque San Emilio) in Santa Rosa National Park. There is a nearly twenty-fold greater chance of a nut being destroyed by *Amblycerus spondiae* in the forest than in the abandoned pasture. Equally, the parent gets about 50 times as many surviving seeds per nut produced from the nuts that land in the pasture than from those that land in the forest. The second facile conclusion is that it is slightly better to be left in the dense accumulation below the parent tree than to be dispersed into a small pile of nuts more than 30 m from the parent but still in the forest, but the best of all in the forest is to be in a single (isolated) nut on the litter more than 30 m from a parent. From the parent's viewpoint, the single nuts in the forest also yield about four times as many surviving seeds per nut as do those in either small piles or dense concentrations. Such conclusions appear to give unambiguous numerical values to certain selective pressures relevant to fruit crop sizes and phenology, fruit nutrient traits and nut size, and anti-bruchid traits (to say nothing of the importance of seed predators and dispersers in determining the spatial demography of the *S. mombin* adult population at Santa Rosa). However, all such conclusions need to be dissected because there is far more to tree reproduction than escaping from seed predators, because the Santa Rosa habitats under discussion are very different from those in which *S. mombin* evolved, and because the fate of an individual seed during dispersal (live or die during contact with an animal) does not map readily onto either its fitness or that of its parent. These three caveats are implicit to any study of seed predation; however, they can be explicitly discussed in the case of *S. mombin* because something is known of the remainder of its biology.

What else matters besides escaping from seed predators? Taking into account only the present ecological situation, the seed in a nut that has been swallowed by a deer is not necessarily well on its way to becoming an adult *S. mombin* by virtue of having a high chance of being regurgitated where the only significant post-dispersal seed predator will not find it. First, most of the abandoned pastures at Santa Rosa burn so frequently (about every dry season) and so fiercely (a dense stand of 1–2 m ungrazed dry grass) that there is virtually no chance of a *S. mombin* seedling or sapling surviving to fire-resistant size. In addition to fuelling the fire, the dense grass casts heavy shade and its dense root mat probably offers severe competition to *S. mombin* seedling roots. The only

obvious amelioration of the competitive effect is that some deer beds are located between large grass clumps, and the deer resting sites that are used continually are flattened so that the soil is more insolated than usual. Finally, the pasture is not only drier and hotter throughout the year than is the forest, but it becomes dry and hot sooner than does the forest when the dry season arrives.

By way of comparison, the immediately adjacent Bosque San Emilio is also no seedling's idea of heaven. The dense secondary successional canopy casts heavy shade in the rainy season, and this is not dramatically and clearly interrupted by the large tree falls that occur in more pristine forest. Conditions are ideal for fungal growth and the forest understory is rich in herbivores belonging to species sufficiently generalist to eat young *S. mombin* seedling and sapling foliage.

In short, in Santa Rosa abandoned pastures the nut has about a 90% chance of escaping the bruchid but the seedling has no chance of surviving the physical and biotic challenges of the habitat. In the secondary successional forest the nut has less than a 5% chance of escaping the bruchid, but the seedlings are again confronted by unsurmountable challenges. Leaving aside the pristine forest, where then can *S. mombin* nuts generate new trees at Santa Rosa? Forest edge protected from fire is the obvious site of almost all *S. mombin* regeneration at Santa Rosa at present. Where the edge is a forested roadside - in effect an elongate treefall - all the dispersers mentioned previously are responsible for moving nuts to the site. However, the density of young *S. mombin* is very low - about 1-5 saplings per linear kilometre. I am confident that the primary reason is that the nuts dispersed to this microhabitat are subject to the same very high level of bruchid attack as are those in the immediately adjacent forest. For example, a sample of 500 nuts from small piles in the vicinity of each of three forest roadside *S. mombin* (April 1983) had 99.2, 99.3 and 99.9% of their nuts destroyed by *A. spondiae*.

There are a few pasture-forest edges at Santa Rosa that erratically burn at 3-6 year intervals. Casual examination of hundreds of piles of *S. mombin* nuts in such areas between 1974 and the present have shown the same variable but usually low intensity of bruchid attack as detailed in Table 2. However, were these edges of pristine forest, with its usual low *S. mombin* density, I suspect that post-dispersal seed predation by bruchids would have been much lower. *S. mombin* saplings are usually 5-20 per ha of pasture in such microhabitats. However, this number is far fewer than would be expected if bruchids were the only source of mortality for juvenile *S. mombin* in such sites (see below for further discussion with reference to crowding).

What does pristine forest at Santa Rosa have to offer in unravelling what else matters to *S. mombin*? There are small patches of semi-deciduous to nearly evergreen forest at Santa Rosa that are either pristine or sufficiently similar to pristine in structure so as to be legitimately viewed as such. I have been able to locate only six *S. mombin* adults in such forest; in contrast to Bosque San Emilio where it is difficult to locate sites more than 30 m from a potentially

seed-bearing adult *S. mombin*, the *S. mombin* in Santa Rosa pristine forest occur at densities of 0.1–0.5 adults per ha and there is often several hundred metres between them. The high concentrations of nuts beneath these six adult trees had 98.3 to 99.7% destruction by *A. spondiae* (n = 504, 600, 401, 567, 903 and 1608 nuts; May 1984). Nearby piles of nuts left by dispersers had the same high levels of attack (casual sampling). I could not locate enough scattered single nuts for a meaningful sample. Until the opportunity arises for experimentally placing *S. mombin* nuts at distances very far removed from bruchid-rich Santa Rosa forest sites, and for the purposes of this discussion, I conclude that *S. mombin* nuts in all kinds of Santa Rosa forest, including tree falls, suffer greater than 95% attack and seed destruction by *A. spondiae*. Pristine forest, therefore, cannot be viewed as a safe haven for *S. mombin*.

However, a cynical caveat is imperative at this point. As recently highlighted for the fauna and flora of pristine forest treefalls at Santa Rosa (Janzen 1983a), I have to consider the impact of the large amount of Santa Rosa secondary successional forest on the small amount of pristine forest. First, in the secondary successional or selectively logged forest making up better than 90% of the forest at Santa Rosa, *S. mombin* is at least 10–50 times more abundant than in pristine forest at the same site. This large population produces an enormous nut crop in most years, which in turn generates an enormous annual crop of *A. spondiae* adults (this species has no larval or pupal parasitoids and therefore is controlled only by nut density and adult mortality). Adult *A. spondiae* are active and mobile, and move about during the ten months between nut crops, rather than merely remain below the parent *S. mombin*. In short, the ocean of adult *S. mombin* in disturbed forest generates an annual wave of bruchids that washes over the nut crops of isolated *S. mombin* in small patches of nearly pristine forest as well as over the more continuously distributed combined seed shadows of all the *S. mombin*. To understand the survival of *S. mombin* nuts dispersed to the various kinds and configurations of microhabitats in pristine forest requires a pristine forest large enough to have portions out of range of the populations of flying bruchids generated by secondary succession. Such forest no longer exists in the dry lowlands of tropical Mexico and Central America.

Second, the ocean of secondary successional forest at Santa Rosa is supporting a high density of dispersers of *S. mombin* nuts. The *S. mombin* fruit crop is one of the ways it does so. The animals, the deer for example, are therefore available to move *S. mombin* nuts into and within the pristine forest patches at a level, pattern and/or intensity quite different from what would be the case were the entire Santa Rosa forest pristine. The forest is pristine with respect to neither its post-dispersal seed predators nor its seed dispersers.

Finally, I need to add that the unburned pasture-forest edge, where *S. mombin* juveniles are surviving and well on their way to producing yet more secondary successional forest rich in adult *S. mombin* such as Bosque San Emilio, is a habitat that is quite artificial. The pastures are virtually pure swards of an

introduced African grass, all the forces that maintained them were anthropogenic, and there is no evidence that there was anything even approximating extensive natural grassland habitats in the lowlands of this area before contemporary agricultural practices.

What was the evolutionary climate for S. mombin? Irrespective of what evolutionary scenario first generated the tree we now call *S. mombin*, until about 9000 years ago this tree evolved for millions of years in habitats containing a large and varied fauna of frugivorous large herbivores (Janzen & Martin 1982). The dispersers that now service it are a coterie reduced both in species richness and, perhaps more importantly, in species with the capacity to consume large amounts of large nuts. Santa Rosa lacks megafaunal herbivores that visit ripe *S. mombin* fruit crops in sufficient numbers to consume much of the fruit from the tree crown and then much of what falls to the ground. A ground sloth standing 5 m tall at the shoulder (e.g. *Eremotherium*), herds of gomphotheres (*Gomphotherium*, Central American ecological equivalents to *Mastodon*), solitary glyptodonts (e.g. *Glyptotherium*, a 1000 kg armadillo-oid), and others were here and would have done quite nicely. The browsing and trampling pressure of such animals, such as is produced by the contemporary megafauna in Africa, would have opened up edges and prolonged succession in treefalls. This action should have produced the equivalent of the contemporary fire-free pasture-forest interfaces where *S. mombin* juvenile survive best at present. These animals would also have defecated *S. mombin* nuts all over such clearings. The defecated nuts would have been at least in part buried in faecal material of sufficient depth and coverage to protect them from *A. spondiae*. This would have been especially true if the dung beetle activity was declining with the oncoming dry season (as is the case with the contemporary dung beetle fauna at Santa Rosa, Janzen 1983b); dung piles would have been left more intact through the time when the nuts are susceptible to oviposition. Such a mammal fauna would also have lowered the *A. spondiae* density in the general site through removing the huge concentrations that offer at least half the contemporary nut crop to the bruchids with minimal searching in the litter.

The details of *S. mombin* fruit and fruiting phenology traits must have evolved and been maintained in the context of a herbivorous megafauna coupled with the smaller animals with which it now interacts. Most of the relevant traits cannot be examined evolutionarily without postulating the reactions of the extinct megafauna to fruits of this type, taste and seasonality. However, one fruit trait is of sufficient importance to the Santa Rosa story that it cannot be left undiscussed. Why does *S. mombin* have 1-5 quite small seeds embedded in a large woody indehiscent nut rather than fewer or even just one larger seed in a nut of the same size? While multiple-seeded large nuts is a *Spondias* generic character, other anacardiaceous genera contain many species with single-seeded fruits (e.g. *Anacardium*, *Mangifera*, *Pistacio*, *Rhus*).

On the one hand, 1-5 small seeds dispersed through a hardy woody nut are probably less weakening to the nut wall than would be a single seed five times

as large. Surviving a gomphothere molar mill should require a container of substance. Equally, one large edible seed would probably be much more attractive to gnawing rodents than are five seeds one-fifth the size and embedded in a very tough matrix. However, 1–5 seeds per nut also gives the maternal parent more abortion options in designing the parentage profile of her fruit crop than would one-fifth as many single-seeded fruits. It is striking in this context that while *S. mombin* nuts sometimes contain five filled seeds and always have five seed cavities, they more commonly contain 0–4 seeds. Finally, 1–5 seeds per nut means more tries per site per dispersed surviving nut. Having many small seeds, despite the large nut, is in keeping with *S. mombin* being a plant of light-rich early succession. But then, why not produce a very large number of small single-seeded fleshy fruits, as do many other tree species of early tropical succession? Here again the megafauna rears its head. Large mammals will seek out and swallow large objects, and large mammals are likely to dump *S. mombin* nuts in favourable sites. The large 1–5 seeded *S. mombin* nut may have its value in being both desired by large mammals and beyond the upper end of the size spectrum of smaller animals that would deposit the nuts in the wrong places (e.g. some forest birds, bats, rodents and peccaries). In other words, if the tree is to present a large crop of seeds to an earthbound disperser coterie of large mammals, traits are functional that minimize the removal of the hanging or fallen fruits by other animals. Large nuts may be such a trait.

There is the question of the evolution of *S. mombin* traits since the neotropical megafauna was extirpated 9000 years ago. One trait is relevant. While a large part of the fruit crop falls below the parent tree, the fruits do hang on the tree for 1–2 weeks after ripening (turning yellow, becoming soft, juicy and sweet). It is quite possible that increased fruit retention is a trait selected for during the recent past by bats and monkeys if they, rather than deer, were most important to the plant in large expanses of pristine forest. *S. mombin* can attain seed-producing size in as little as 20 years. In 450 generations there could easily be realized selection for a trait such as increased fruit retention if virtually all fruits that fall below the parent have their seeds killed *in situ* by the bruchid whereas before, such fallen fruits had their nuts dispersed by large mammals.

The seeds view or the parent's view? All *S. mombin* seeds have 0–4 equal-aged sibs with which to compete irrespective of the nut deposition site. From the viewpoint of the individual seed that has survived post-dispersal seed predation and the rigours of chewing by a disperser, one bigger seed per nut would yield higher seedling fitness than is the present case. However, the parent and sibs are both part of the *S. mombin* morphotype. Highest maternal fitness may well occur through having 1–5 tries with a seedling at the exact site where the unattacked nut lands, with the tries spaced through the first half of the rainy season (the seeds in a *S. mombin* nut do not germinate simultaneously).

There is a second class of seed aggregation in the life cycle of *S. mombin*: that created by the dispersal agents and then non-randomly thinned out by the

bruchids. First, consider the nuts dispersed by deer into the abandoned pasture and its edges. After the small amount of post-dispersal nut attack by the bruchid, a large number of viable seeds – tens to hundreds – remains in an area of 1–2 m². At the best, one *S. mombin* adult can become an adult there. It is not hard to imagine that the fitness of the parent *S. mombin* would be enhanced by a species of deer that dropped a few nuts here and a few there rather than concentrated them. The harder question is whether the bruchids' and rodents' 0–7% thinning of the peaks in the *S. mombin* pasture seed shadow raises the chances that a *S. mombin* adult will appear there. Whether this occurs will depend on the nature of density-dependent seedling competition and herbivore attraction. If it occurs, a mechanism then exists whereby the bruchid could raise the fitness of *S. mombin* in its current ecological circumstance and reproductive phenotype at Santa Rosa. However, considering only the current nut dispersers for *S. mombin*, there is simultaneously strong selection for thinner-walled nuts, larger and fewer seeds, and more delayed germination and other such traits that would lead to more thorough parental probing of the deer's few fire-free regurgitation sites.

Second, consider the *S. mombin* nuts in the Santa Rosa forest. There are three aggregation categories. First, the seeds in nuts deposited singly have fitness demands differing from those of the maternal parent only with respect to the questions raised earlier about the consequences of 1–5 seeds in a nut and of 1–5 sibling seedlings potentially competing for one site. Bruchid attack of the widely scattered single nuts will certainly lower *S. mombin* fitness, provided at least that some nuts land where a tree fall or other opening is or soon occurs. Second, in the large concentrations of nuts directly below the parent, the seeds are probably all best viewed as dead, irrespective of the activities of the bruchids at thinning the crop. Only the nuts deposited there in the one to few years immediately before the death of the parent have any chance of survival; certainly *S. mombin* fruit traits were not selected to place cleaned nuts directly below the parent. Furthermore, the minute *S. mombin* seed size does not appear to be the result of selection for shade-tolerant seedlings. The ecology and fate of the high concentrations directly below the parent should be viewed as an artifact of dispersal failure, whatever its cause. Third, the impact of the bruchids on the fitness of the seeds in the small piles of dispersed nuts on the forest floor (whether in shade or clearings) depends on the same caveats applied to the piles of nuts left by the deer in the abandoned pasture. However, it is doubtful that 95% or better thinning of the seed numbers in small piles in the forest generally enhances parental fitness, especially since all seeds are killed in more than half of the piles. When large herbivores are added back into the system and few nuts remain at the parent tree, it is even easier to imagine that seed predation by the bruchids would not be fitness-enhancing to any adult.

Models. Where does the system described here fit in an attempt to generalize the processes that produce the structure so evident in tropical species-rich

forest? The contemporary animals in Santa Rosa certainly create a heterogeneous seed shadow for *S. mombin*. That heterogeneity bears a predictable relationship to specific habitat types and densities of adult *S. mombin*. The host-specific, dominant post-dispersal seed predator kills seeds in a pattern that is again related to habitat, parent tree location, and detailed pattern of nut dispersal. If the bruchid were to search thoroughly in the abandoned pasture, *S. mombin* recruitment along pasture-forest edges might well be as low as it is inside Bosque San Emilio. On the other hand, the dynamics of seedling competition and herbivory might result in a similar number of surviving adults, if better than 95% of the nuts were attacked in the fire-free open areas (as they are in the forest). Within the forest, a severe reduction in bruchid density would clearly result in many more seedling *S. mombin*. Whether this would result in more saplings or new adults in a late secondary successional forest is uncertain. However, it is unlikely that the minute number of surviving *S. mombin* seeds in the forest represents a complete probe of all the safe sites, and it certainly would not be a complete probe of a pristine forest.

Whatever actual values are to be placed on the variables just mentioned, two caveats are necessary. First, since Bosque San Emilio is in a state of advanced secondary succession over a large area, the dynamics of *S. mombin* with respect to its density, dispersal, spacing and seed predation cannot be tested or modelled in the same context as would be the case were it being examined in a large pristine forest. *S. mombin* seeded into Bosque San Emilio as a heterogeneous invasion from adults outside the area and will go nearly extinct there before the forest is again pristine. The largest adults are already dying of senescence with no sign of replacement. *S. mombin* demise will be caused by the same process: intense competition operating on the very few seedlings left after intense post-dispersal seed predation on the large number of *S. mombin* nuts in the area. The same process prevents a large adult *S. mombin* in Santa Rosa pristine forest from replacing itself when it falls. Just as Sork (1983) found to be the case with hickory trees (*Carya glabra*) in a Michigan forest-field edge, at Santa Rosa it is the fire-free edges where most recruitment is occurring.

Second, *S. mombin* is clearly limping along in a culturally deprived state. Stripping off its megafauna is as damaging as would be excising out the chromosomes that held the program for the traits that would give it back the fitness that it used to buy with a few tens of kilos of fruit pulp and nut walls during most of its evolutionary life span. Contemporary animals give it poor return on its fruit and nut investment in contemporary habitats. *S. mombin* had a close brush with extinction when megafaunal extirpation occurred, but was given part of its reprieve by the human habit of creating forest edges and regenerating patches, patches that are populated by animals that happen to like to eat and move *S. mombin* nuts. It is likewise clear that humans are now extinguishing the tree over most of its range.

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