195
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SEEDS IN TAPIR DUNG IN SANTA ROSA NATIONAL PARK, COSTA RICA

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ABSTRACT

In Santa Rosa National Park in the deciduous forests of northwestern Costa Rica, tapir (*Tapirus bairdii*) dung contains seeds and seed fragments. Large seeds such as those of *Mastichodendron capriri, Manilkara zapota* and *Quercus oleoides* are invariably crushed by the molar mill. Large hard seeds such as those of *Enterolobium cyclocarpum* and *Pithecellobium saman* are not crushed by the mollar mill but may scarified sufficiently that they begin to germinate in the tapir gut and are therefore killed; however, some survive the trip as well. At least some of the small seeds that are normally dispersed via vertebrate guts survive the trip through the tapir, but the wind-dispersed seeds of *Cochlospermum vitifolium* are killed by the digestive process. Whether the tapir should be viewed as a seed predator or dispersal agent, or some combination of the two, depends on the species of plant.

Baird's tapir (*Tapirus bairdii*) is the largest of the few large mammals that escaped the Pleistocene extinctions in Central America about 10,000 years ago (Janzen and Martin 1982). This animal is a browser (e.g., Terwilliger 1980, Janzen 1982a) and also consumes numerous species of fallen large fruits from the forest floor. The seeds in these fruits were very likely in great part dispersed by the Central American Pleistocene megafauna. Considering that the megafauna was extinguished and that not all trees whose fruits were dispersed by it also disappeared, there is the puzzle of what did disperse the seeds of these trees during the last 10,000 years. The remaining large contemporary herbivores are obvious candidates. The tapir is the largest of these potential seed dispersers. However, when the seeds from a native fruit were fed to a Baird's tapir, a substantial fraction of the large hard seeds were digested by the animal (Janzen 1981a) just as they were by horses (Janzen 1981b). As I no longer have a Baird's tapir for controlled feedings, I report below the condition of various seeds of large wild fruits in the dung of wild tapirs in the deciduous forests of Santa Rosa National Park.

Study area

Santa Rosa National Park (10,800 ha) liest at 0–350 m elevation on the plateau, slopes and narrow coastal plain between the old Pan-American Highway (Costa Rica Route 1) and the Pacific Ocean, in extreme northwestern Guanacaste Province, about 25 km south of La Cruz, Costa Rica. The area was covered with decidous forest containing narrow strips and small patches of evergreen forest. Over the past 200–300 years the area has been subjected to light selective logging, some clearing for small farms, and conversion of about 60 percent of the upland forest to cattle pasture. In 1977–1978 the last cattle were removed and the succession of grasslands to forest is proceeding rapidly where fires do not occur annually.

The mosaic of habitat types and disturbance histories at Santa Rosa contains 600–700 species of broadleafed plants (Janzen and Liesner 1981). Of these, about 400 species are trees, treelets, vines, shrubs, and other life forms of perennial large plants. Many of these species have foliage and/or fruits that are potentially available as food to an animal the size of a tapir. A study in progress on Santa Rosa tapir diets (K. Williams, personal communication) will tell us the array of species eaten (and see Janzen 1982a). Here I focus instead on those species whose seeds appear in tapir dung.

Seeds in dung

Seeds are present in tapir dung as fragments, whole but dead seeds, and living dormant seeds.

Seed fragments: Seed fragments are most dramatically represented by species with large seeds. Tapirs readily eat the large-seeded fruits of *Mastichodendron capiri* (Sapotaceae), *Manilkara zapota* (Sapotaceae), and *Quercus oleoides* (Fagaceae). I have found four different piles of tapir dung (one pile = a single defecation) left by an animal that had been eating *M. capiri* fruits. By counting the distinctive grooved area on the seed coats (one per seed), I found fragments of a minimum of 12, 16, 43 and 53 *M. capriri* seeds in the four dung piles. All seeds had been broken by chewing and were dead. Only seed coat fragments persisted. *M. capirri* seeds are nearly spherical, 1–2 cm diameter, very smooth and not firmly attached to the sweet pulp of the indehiscent gray plum-like fruit in which they are imbedded. When a tapir eats one of these fruits, it simply chews up the entire fruit, seed and all. The seed coat is hard and tough, but weak enough that I can break it with my teeth. The seed contents are soft and easily chewed up.

I have found five tapir dung piles containing *Manilkara zapota* seed parts. All seeds were dead and represented only by seed coat fragments. *M. zapota* seeds are flattened smooth ovals 11–15 mm long, 6–10 mm wide and 3–5 mm thick. There are 1–5 seeds imbedded in a sweet and juicy plum-like fruit 2–3 cm in diameter. The seeds do not adhere tightly to the fruit tissue. The seed coat is brittle and I can easily crack it between my teeth. The seed contents are soft and easily chewed up.

I was not able to count exactly the minimum number of *M. zapota* seeds in the five dung piles in which they were found, but I estimated that at least 10, 40, 40, 50 and 100 seeds were represented by the seed coat fragments.

Two tapir dung piles were encountered that were nearly pure hulls of *Quercus oleoides.* The hulls of a least 500 acorns were present in each dung pile. The fruits (acorns) of *Q. oleoides* are 15–20 mm long smooth ovoids (10–15 mm diameter). No hull fragment was any larger than about one quarter of an acorn hull, and most were chips with maximum dimensions of 2–4 mm.

In addition to the three large and relatively soft or brittle seeds mentioned above, tapir dung piles contained seed remains of *Enterolobium cyclocarpum,* a large mimosaceous legume tree. The fruits of *E. cyclocarpum* are eagerly eaten by cattle and horses (Janzen 1982b) and a captive tapir ate them sparingly. This tapir also digested about 70 percent of the *E. cyclocarpum* seeds it swallowed in seed passage rate trials (Janzen 1981a). One tapir dung in Santa Rosa contained one and another three seed coats of *E. cyclocarpum,* with the seed contents throughly digested.

Intact seeds: Intact seeds in tapir dung are either dead or alive. Common intact but dead seeds in three dung piles were those of *Cochlospermum vitifolium* (Cochlospermaceae) and *Caesalpinia coriari* (Leguminosae). The same dung also contained living dormant (hard) seeds of *Caesalpinia coriari.* This dung also contained numerous living seeds of *Guazuma ulmifolia* (Sterculiaceae); this fruit is avidly eaten by horses and livestock (Janzen 1982c).

However, the most dramatic examples of living and dead intact seeds were offered by two dung piles from a tapir that had been eating fruits of *Pithecellobium saman,* a large mimosaceous legume tree that is common in Santa Rosa in old pasture areas and in riparian vegetation. One dung pile contained 154 intact dormant *P. saman* seeds, 16 living germinating *P. saman* seeds and 97 seed coats of seeds with their contents digested out (Figure 1). Another contained 243, 2 and 204 seeds, respectively, in the above condition. The fate of the digested seeds is self-evident. The germinating seeds were ill-fated since the dung was in a dry river bed and they would have been washed away by the first rains. The dormant seeds, however, would appear to have the greatest chance of survival because they would be washed downstream by rainy season floods, and some deposited high on exposed banks by stream action. In short, if the seed germinates in the tapir, digestive fluids kill it; if it germinates in the dung, dung beetles, rain, erosion, fungi, bacteria and seed predator mice are likely to kill it. However, if the seed remains dormant it is likely to be secondarily moved into the litter or other microhabitat where, as a single germinating seed, it has a chance to develop to maturity.

In addition to the seeds mentioned above, seed fragments (SF) or intact living seeds (LS) have been encountered in Santa Rosa tapir dung: *Karwinskia calderoni* (LS, SF), *Cassia emarginata* (LS), *Crescentia alata* (LS), *Ardisia revoluta* (SF), *Bauhinia ungulata* (LS), and *Alibertia edulis* (LS).

Discussion

It is evident that large seeds are crushed when a tapir eates them unless they are exceptionally hard, such as those of *Enterolobium cyclocarpum.* However, even some of these may be killed by scarification of the seed coat, which leads to initiation of germination which in turn makes the seed susceptible to digestion (Janzen 1981a, b). Small seeds may pass through the molar mill without damage but be later killed by digestive processes if they do not have a seed coat that was evolved to withstand gut fluids, such as those of *Cochlospermum vitifolium*; all the *C. vitifolium* seeds in the tapir dung were intact but dead. This plant is normally wind-dispersed and the tapir was consuming the fruits along with the foliage, as an herbivore rather than as a frugivore in the usual sense.

The large sweet indehiscent fruits of *Guazuma ulmifolia, Pithecellobium saman, Enterolobium cyclocarpum, Caesalpinia coriari, Crescentia alata, Manilkara zapota* and *Mastochodendron capriri* all appear to have evolved in response to large mammals as seed dispersal agents. However, the latter two species have seeds that are too large and too weak to withstand the molar mill of a tapir, and their seeds were probably originally dispersed by larger mammals that chewed their food even less throughly, or at least chewed fruits even less throughly. In addition, their disperser coterie has probably alway contained an array of small mammals as well, and it was probably these animals that kept these trees in the game after the Pleistocene extinction (assuming that some dispersal is necessary for a population to persist). The other five species of trees listed have small enough and/or hard enough seeds that they can survive the molar mill of a tapir at least part of the time. Collared peccaries are also major fruit eaters in the Santa Rosa forest and they eat all of the above listed species of trees. They kill all of the seeds by grinding, except those of *Guazuma ulmifolia.* Additionally, they do not appear to be able to break open *Crescentia alata* fruits because they cannot get their jaws open far enough to encompass the large spherical fruits. Peccaries also fail to grind up a fair number of *Crescentia alata* seeds when feeding on fruits that I have broken open for them. The tapir dung contained seeds of two species with small sweet fruits that are classically thought of as containing bird-dispersed seeds: *Ardisia* revoluta and *Karwinskia calderoni.* I suspect that the tapir picked these fruits from among the foliage, though it could also have been browsing the foliage and eaten the fruits quite by accident. The fruits of *Alibertia edulis* are eaten by almost every herbivorous or frugivorous vertebrate in the Santa Rosa forest and it is not surprising that the tapir sought out some fruits of this shrub; however, a captive tapir also avidly consumed the foliage of this evergreen shrub and it could well have eaten fruits along with the foliage or encountered the fruits only because it was in search of *A. edulis* foliage.

These brief descriptions of the seeds in a few piles of wild tapir dung show clearly that a tapir is a seed predator to some trees, a potential good dispersal agent to others, and a mixed blessing to yet others. Which of these categories, or rather, how many of these categories, a tapir falls in with respect to a particular plant prob-

ably has to do with where the tapir defecates as well as how many seeds it crushes in its molars and how many it digests. Certainly the tapir cannot be viewed a priori as a dispersal agent for the seeds in all the fruits that it eats.

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Resumen

En el bosque caducifolio del Parque Nacional Santa Rosa, Costa Rica el estiércol de danta (*Tapirus bairdii*) contiene semillas enteras y fragmentadas de varias especies. Las semillas grandes como las de *Mastichodendron capiri* (tempisque), *Manilkara zapota* (níspero) y *Quercus oleoides* (roble aparecen, sin excepción, trituradas por los molares de la danta. Las semillas grandes pero muy duras, como las de *Enterolobium cyclocarpum* (guanacaste) y *Pithecellobium saman* (cenízaro) no son trituradas por los molares pero algunas sufren escarificación, germinan en el tracto digestivo y no sobreviven hasta la defecación. Las semillas pequeñas, normalmente dispersadas por vertebrados, sobreviven al paso por el tracto digestivo de la danta pero, las semillas normalmente dispersadas por el viento como las de *Cochlospermum vitifolium* (poró) son destruidas por el sistema digestivo de los tapires.

El que una danta sirva como dispersor de semillas o sólo como depredador de propágulos, o funcione como una combinación de ambos, depende en la especie de planta.

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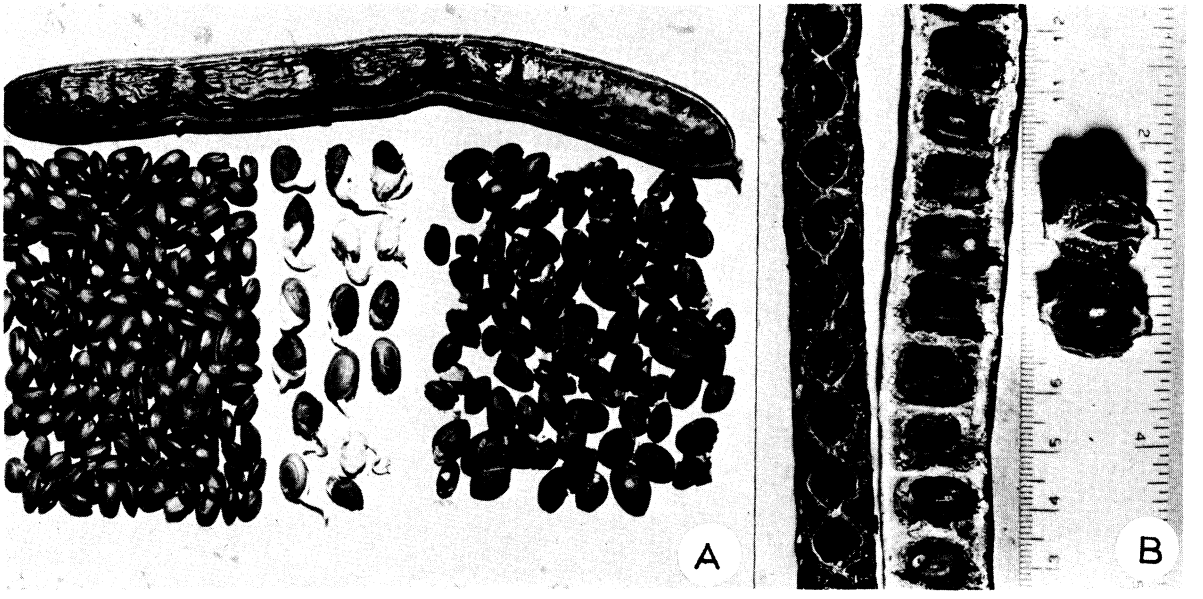

Figure 1. a) Three groups of *Pithecellobium saman* seeds recovered from a single pile of dung from a Baird's tapir in Santa Rosa National Park; those on the left are intact, living, and dormant; those in the center have germinated after being defecated; those on the right are seed coats of seeds whose contents were digested by the tapir; across the top is an intact mature fruit of *P. saman.* b) Two longitudinal sections through a ripe fruit of *P. saman,* and two cross sections of the same fruit; the seeds lie loosely in individual cavities surrounded by a dark brown sweet moist pulp.