Digestive Seed Predation by a Costa Rican Baird's Tapir

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ABSTRACT

The large ungerminated seeds of guanacaste (*Enterolobium cyclocarpum*) and carao trees (*Cassia grandis*), and plastic buttons, were fed to a captive adult male Costa Rican Baird's tapir (*Tapirus bairdi*) in artificial fruits. Seed survival during gastrointestinal passage and seed passage rate was studied. The tapir's digestive processes killed 78 percent of the guanacaste seeds and all of the carao seeds, despite their hard seed coats, apparently because they germinated and thereby become suspectible to digestive fluids. Guanacaste seeds that survived required an average of 15.3 days to make the trip through the tapir; the dead carao seeds required an average of 10.3 days and the two sizes of buttons required an average of 8.1 days (730 mg) and 10.3 days (360 mg) to make the passage. The tapir is clearly a seed predator of guanacaste seeds as well as a potential dispersal agent. Which of these functions is more important depends on the unknown behavioral interaction between the tree and the tapir.

VERTEBRATE SEED PREDATORS KILL SEEDS by chipping them with a beak or incisors, breaking and grinding them with molars or a gizzard, and by direct chemical digestion. Very hard seeds and nuts, and especially legume seeds, are generally viewed as immune to chemical digestion. Hard seeds and nuts which are dispersed by complete passage through the digestive tract are often encountered in the dung of large herbivorous mammals. It is commonplace to assume that the number found in the dung approximate the number of intact seeds that were swallowed. This assumption may be reasonable for certain species of seeds and animals, but here I show that it is not valid for Baird's tapir (*Tapirus bairdi*) and the large hard seeds of two legumes, guanacaste (*Enterolobium cyclocarpum*) and carao (*Cassia grandis*).

MATERIALS AND METHODS

I used the captive adult male Baird's tapir at Finca La Pacifica (7 km north of Cañas, Guanacaste Province, Costa Rica) for experiments. Born in late 1970 and acquired by Finca La Pacifica a few months later, it ranged free around the ranch house, eating milk, table scraps, and wild vegetation. At about two years of age, it was placed in a wood-fenced corral approximately 20 by 20 m in area. It was seven years old at the time of the experiments and suffered only occasional indispositions with tick infestations and foot fungal attacks, both of which were cleared up by treating with the chemicals used to cure horses and cows of the same diseases. It seemed well adjusted to corral life and did not display pacing or other behaviors associated with neurotic caged animals. Its diet, on which it appeared quite healthy, was kitchen refuse, table scraps, and copious supplies of weedy vegetation offered twice a day. It took food readily from the hand and was an eager participant in the feeding experiments described here which were conducted in the same period as were choice tests with foliage (Janzen 1981a); the regular diet was therefore supplemented with a greater species richness of foliage than usual, but not greater bulk or roughage.

I have found that wild Baird's tapirs in Santa Rosa National Park (northwestern Guanacaste) defecate in water wherever possible, and the captive tapir did the same (and see Young 1906). The stream that flowed through its corral was diverted into a concrete-lined pool 20-40 cm deep with a plugged drain. Dung floated in the pool for a short time and then disintegrated through soaking and trampling. The seeds and buttons used in the experiments are all denser than water, with the result that they collected in the pool bottom. Once a day the plug was pulled and the pool contents passed through a 3 mm mesh screen that removed all particles large enough to be a button or seed fragment.

The particular species of seeds used in the experiments (fig. 1) were chosen because 1) they were large enough to locate easily after passage through the animal but small enough to be swallowed readily, 2) they were hard enough to escape digestion, 3) one seed type (guanacaste) is found in livestock dung and is believed to have been dispersed this way by Pleistocene mammals (Janzen and Martin 1981), and 4) they are potentially dispersed by tapirs in the wild since the captive tapir would eat the fruit of both species and both species occur in tapir habitat. The guanacaste seeds (*Enterolobium cyclocarpum*) weighed between 450 and 650 mg (specific gravity 1.34) and came from a single crop collected in March 1977 from below tree number 34 in Santa Rosa National Park. They were shelled by hand out of naturally fallen mature fruits and not touched by

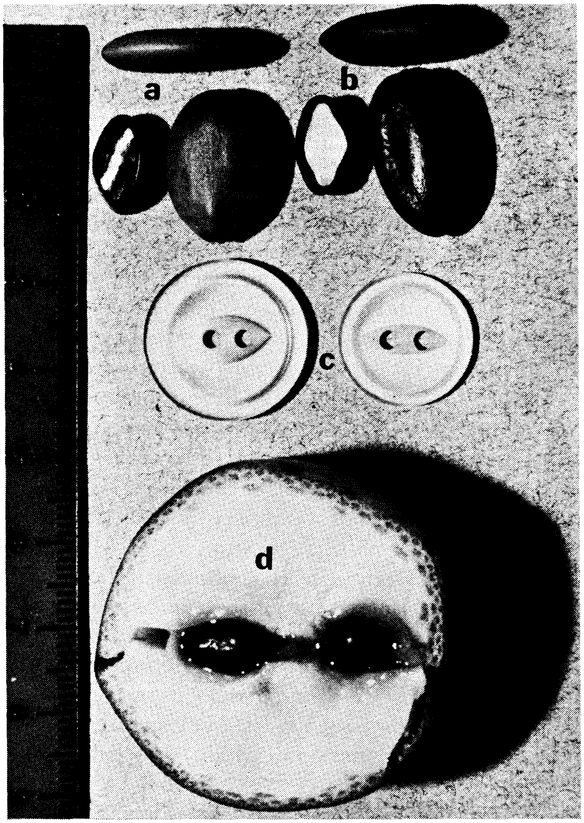

FIGURE 1. a. Flat, edge, and cross-section view of *Cassia grandis seeds.* b. Flat, edge, and cross-section view of *Enterolobium cyclocarpum* seeds. c. 730 and 360 mg white plastic buttons fed as indigestible seed mimics. d. Synthetic fruit—3 cm section of ripe banana containing two seeds of *Enterolobium cyclocarpum.*

metal objects. When a sample of 300 living seeds was placed in water, 3 percent germinated immediately, and the remainder did not take up water for at least two months. When a subset of 100 of the ungerminated seeds was notched with a file and placed in water, all germinated within two days. Guanacaste seeds are hard and smooth and require about 70-200 kg direct pressure to break, depending on the angle of attack (Janzen and Higgins 1979). The carao seeds (*Cassia grandis*) were similar in weight, shape, texture, and appearance to the guanacaste seeds (fig. 1a and Janzen 1977) and were hand-shelled out of freshly fallen mature pods from the tree growing by the carpenter's shop at Finca La Pacifica. When a sample of 100 seeds was placed in water for two months, none germinated. After these seeds were notched with a file, all germinated within two days in water.

If guanacaste fruits were offered to the tapir, it chewed them thoroughly and spat out a variable percent of the seeds, swallowed others, and broke or scarified a few. It would not chew up entire carao fruit in its well-fed state. Therefore, to examine the fate of the seeds in a maximally controlled manner, I used artificial fruits to entice the tapir to swallow large numbers of seeds in one meal. Unpeeled ripe bananas were cut into 3 cm sections, and two seeds (or buttons, see below) were inserted in a slit in the pulp of each section (fig. 1d). Since ripe banana was a favorite food of the tapir, the seeds were always swallowed (though an increase in seed numbers per 'fruit' resulted in seed spitting, Janzen 1981b). Rarely, the seeds were chewed lightly before swallowing, and, on five occasions, a guanacaste seed was broken. When a seed was broken, the break made a very loud noise, and these seeds were not counted in the tabulations reported here. The volume of seeds and buttons fed, about 200 cc, is a trivial portion of the daily diet of the tapir. There is no reason to believe that the seed-passage rate was influenced by the contents of the artificial fruits. It ate several kilos of bananas almost every meal, and the seeds were immediately separated from the slippery banana pulp by tongue, palate, and throat action. The seeds were collected from dung until no more seeds appeared for at least four days.

In order to know if seeds which never reappeared had been digested or were simply delayed in passage, I also fed the tapir indigestible white plastic buttons along with the seeds. Some were broken in chewing, but all fragments of a quarter of a button or better were recovered from the dung. When a button broke, it could be heard distinctly. The particular buttons were chosen because their shape and size were similar to those of the seeds (fig. 1c). They weighed 360 or 730 mg and had a specific gravity of 1.75.

These experiments cannot be repeated exactly because the tapir died of a respiratory disease in August 1978.

RESULTS

On 11 August 1977, I fed 96 guanacaste seeds to the tapir in 30 minutes. On 23 August, 12 days later, dung collection for this preliminary experiment was terminated. No entire seeds had passed through the animal, but fragments of at least 24 different guanacaste seed coats were recovered. Simultaneously, 30 carao seeds were fed. None of these were recovered intact, but six seed coats appeared in the dung.

On 5 December 1977, the tapir swallowed 125 guanacaste seeds, 18 small buttons (360 mg), 16 large buttons (730 mg), and 38 button fragments (almost entirely halves and quarters). On 7 December, 53 carao seeds were swallowed. The diary of appearance in dung of these seeds, buttons, and fragments is presented in table 1. By the tenth day after eating the guanacaste seeds, only two intact ungerminated (hard) guanacaste seeds had been passed. Also by this date, six swollen and opened guanacaste seeds with dead and partly digested embryos had appeared, along with 43 large fragments of guanacaste seed coats. Each of these 43 represented one digested seed. On the twenty-third day after feeding, the last intact guanacaste seed appeared in the tapir's dung. The intact seeds required an average of 15.3 days to make the trip (s.d. = 4.0). No passed seed was both germinated and alive. The 27 intact passed guanacaste seeds did not germinate when placed in water for a month. Two months later, all 27 germinated within two days when the seed coat was notched with a file and the seed placed in water. All whole buttons recovered appeared between four and 17 days after feeding. Small buttons averaged 10.3 days (s.d. = 3.9) for the trip, and large buttons averaged 8.1 days (s.d. = 2.9). These averages are not significantly different ($t = 1.31$, d.f. = 32). Eighty-one percent of the carao seeds appeared between four and 17 days after feeding (average transit time was 10.3 days, s.d. = 3.6). All were dead, and I assume that the remaining 19 percent were digested beyond recognition. The carao seeds had the interior permeated with digestive fluids, the embryo-containing end digested out, and were very soft. The average transit time of the carao seeds is highly significantly different from that of guanacaste seeds ($t = 5.32$, $df = 68$, $p < .001$), but the two are not really comparable because the dead and partly digested-out carao seeds have a much reduced specific gravity when compared to ungerminated carao seeds.

DISCUSSION

The tapir unequivocably killed, by digestion, most of the guanacaste seeds it swallowed. Only 22 percent survived passage in the second experiment, and those that did survive did not have their seed coats sufficiently scarified to germinate when placed in water

TABLE 1. *Diary of appearance in dung of intact live* Enterolobium cyclocarpum *seeds, dead* Cassia grandis *seeds, and buttons fed to an adult Baird's tapir.*

Date	*Enterolobium cyclocarpum*	*Cassia grandis*	Whole 360 mg buttons	Whole 730 mg buttons	Button fragments (mostly halves)
5 December	Swallowed 125		Swallowed 18	Swallowed 16	Swallowed 38
7	0	Swallowed 53	0	0	0
8	0	0	0	0	0
9	1	0	1	4	6
10	0	0	0	0	0
11	0	2	2	0	7
12	0	3	2	1	7
13	0	0	2	3	4
14	0	5	2	4	4
15	1	7	1	0	1
16	4	4	2	2	3
17	1	3	0	1	3
18	1	2	3	1	2
19	1	2	0	0	0
20	1	3	0	0	0
21	4	5	1	0	1
22	8	4	2	0	0
23	2	2	0	0	0
24	0	1	0	0	0
25	1	0	0	0	0
26	0	0	0	0	0
27	1	0	0	0	0
28	1	0	0	0	0
29	0	0	0	0	0
30	0	0	0	0	0
31	0	0	0	0	0
1 January	0	0	0	0	0

for two months. Simple immersion in digestive fluids is not adequate to digest the bulk of guanacaste seeds from this tree's crop. I fed myself 20 seeds taken from the sample that was the source of the seeds fed to the tapir. They required 1-2 days to pass through me. I rinsed them and immediately swallowed them again. This procedure was repeated for 30 days, and only one seed started to germinate (day 6). This seed required two more trips through me (four-day passage time) for the seed contents to be digested.

It appears that some process in the tapir's gut scarifies the seed coat, the seed starts to germinate, and is digested. To germinate guanacaste or carao seeds in water requires only a shallow cut in the hard seed coat, and it may be that the tapir's molars nicked the seed coat. However, tapir molar edges are rounded, the spat-out seeds did not show nicks, nor did they germinate when placed in water, and at least half of the seeds were swallowed very rapidly and with no apparent molar contact. I suspect that some other process is scarifying the seeds. Soaking guanacaste seeds in strong hydrochloric acid for 30 minutes scarifies them *in vitro*. I hypothesize that gut chemicals are doing the same to the swallowed seeds, especially in view of the long time they are in the tapir's gut.

Why did the guanacaste seeds, carao seeds, and buttons remain so long in the tapir's digestive tract? Well-chewed distinctive foliage types require 1-3 days to pass through the tapir, and small light objects like filters from filter cigarettes and pieces of plastic bag require about the same time. The eddy currents in the tapir's gastro-intestinal tract may be a sufficient impediment to the flow of small hard objects to account for the delay. In other caecal digesters such as rabbits, the sharp flexure at the end of the duodenum is a mechanical barrier to the passage of small hard objects (Hoelzel 1930). Hoelzel also found that the stomach is a site of retention of beads in guinea pigs, and that rabbit, rat, and guinea pig caeca selectively remove small glass, gold, and silver beads from the stream of digesta and retain them for many days. In rabbits (Pickard and Stevens 1972), pigs (Argenzio *et al.* 1974), and horses (Clemens *et al.* 1975), the larger the size of the ingested particles, the longer they are retained in the stomach and colon, but the actual mechanism of retention is unknown. It is a common belief among veterinarians that small hard food items are retained in the horse caecum and later voided at intervals. In the tapir, the stomach, the intestinal loops, and the caecum are all suspect as areas of seed retention, but x-ray analysis with metal seed mimics will be required for analysis.

The situation is the same for carao seeds. The tapir was an even more thorough seed predator to them. As with guanacaste seeds, however, mere exposure to digestive fluids is not adequate to digest carao seeds. I swallowed 20 of them in the same manner as the guanacaste seeds, and none germinated. While the carao seeds passed through faster than did ungerminated guanacaste seeds, they also lost their high specific gravity somewhere along the digestive tract and therefore are not strictly comparable with living ungerminated guanacaste seeds. Seed-digestion ability by the tapir could be a purely fortuitous consequence of a digestive system that is designed for other foods, or it could be that there has been actual selection for traits that maximize the chance that seeds will be digested.

Whether the tapir is a trivial or major seed predator and disperser of guanacaste seeds in nature obviously depends on its response to guanacaste fruit crops, a subject on which there are no data except that they do eat guanacaste fruits. In the corral, it ate only 2-5 guanacaste fruits before rejecting them in each meal, and usually spat out about half of the seeds. At this rate it would take years for armies of tapirs to eat the thousands of fruits that fall below a large adult guanacaste tree. In this case, it appears to be a trivial seed predator, but the chance remains that in a less food-rich environment the tapir might become a heavy consumer of guanacaste fruits. Assuming its fruit consumption to be small, the tapir likewise appears to be a trivial dispersal agent. However, the most is not necessarily the best when it comes to dispersal. In an ongoing study, I am finding that the heteromyid rodent *Liomys salvini* is a very intense seed predator on guanacaste seeds in horse dung left in the forest. With its peculiar habit of defecating in water, the tapir will deposit the few seeds that survive its gut in a habitat that is quite free from rodent seed predation and perhaps good for colonization as well. Whether the tapir is an important dispersal agent will clearly depend on what other animals are moving guanacaste seeds and where they are being abandoned.

The literature is devoid of information on the passage rates of large seeds through the large mammals that disperse them. Certainly the slow rate recorded here means that a tapir could generate a very complex and remote seed shadow, with some seeds being moved many kilometers. This is probably a much greater distance than that travelled by the pollen of a guanacaste tree when attached to small moths and other nocturnal insects. Furthermore, the widely spaced appearance of the seeds in the tapir's dung, even though eaten in one meal, means that the seeds will be maximally scattered in the habitat of deposition and have a maximum chance of being deposited in a dung pile with seeds of other species and trees eaten in different meals. Finally, if the tapir does not defecate in water, as it must do in the peak of the dry season, the few seeds buried in a single dung pile are more likely to be missed by searching seed predators than is the case where there are enough seeds to reward the first casual searcher substantially.

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