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Daniel H. Janzen

Ecology, Vol. 62, No. 3. (Jun., 1981), pp. 593-601.

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ENTEROLOBIUM CYCLOCARPUM SEED PASSAGE RATE AND SURVIVAL IN HORSES, COSTA RICAN PLEISTOCENE SEED DISPERSAL AGENTS¹

DANIEL H. JANZEN

Department of Biology, University of Pennsylvania,
Philadelphia, Pennsylvania 19104 USA

Abstract Costa Rican horses ranging free in deciduous forest-grassland habitats swallow about half of the seeds in the *Enterolobium cyclocarpum* fruits that they eat, and six such horses defecated at least 9-56% of the seeds alive. While about three-quarters of the surviving seeds appeared by the 14th d after ingestion, about a quarter of the surviving seeds emerged 15-60 d after ingestion. The horse kills *Enterolobium* seeds by digestive processes shortly after the seed germinates in response to the moisture of the intestinal tract. More than 90% of the seeds that survived the trip did so as hard dormant seeds. They showed no indication that they would germinate more rapidly (break dormancy more rapidly) than seeds planted directly from the fruits. The horse-seed interaction suggests that Pleistocene horses may have contributed to both local and long-distance population recruitment by *Enterolobium cyclocarpum*, and contemporary horses certainly have the potential to do so.

Key words: Costa Rica; *Enterolobium cyclocarpum*; *Equus caballus*; *guanacaste tree*; *Leguminosae*; seed digestion; seed dispersal; seed predation.

INTRODUCTION

Enterolobium cyclocarpum is a native neotropical mimosaceous legume tree of deciduous lowlands forests, and its fruits are avidly eaten by free-ranging horses (*Equus caballus*). The huge trees are rare but very conspicuous and bear the Indian name of "guanacaste" or "conocaste" in Spanish-speaking countries. *E. cyclocarpum* has large, indehiscent, dry and sweet fruits that fall to the ground when ripe. The large, hard and ovoid seeds (Fig. 1) require scarification to germinate and have all the traits of a species that is dispersed via the gut of a large mammal. However, the natural Costa Rican habitat of guanacaste trees lacks native contemporary large mammals that perform this service with high fidelity. Horses swallow 25-62% of the seeds in the guanacaste fruits that they eat (Janzen 1981a) and the seeds are commonly encountered in horse dung in pastures cut out of the deciduous lowland forests of the Pacific northwestern coastal plain of Costa Rica. Since introduced horses and cattle eagerly eat the fruits and disperse the seeds, I hypothesize that the native Pleistocene horse (*Equus fraternus*) was once an important disperser of *E. cyclocarpum* seeds (D. H. Janzen and P. S. Martin, personal communication). However, feeding *E. cyclocarpum* seeds to another Costa Rican perissodactyl, Baird's tapir (*Tapirus bairdii*), demonstrated intense digestive seed predation (Janzen 1981b) and raised the possibility that an animal such as a horse may be an intense seed predator as well as a dispersal agent.

Here I report the results of experiments with *E.*

cyclocarpum seed passage through six Costa Rican range horses. Four questions were addressed. What fraction of the seeds swallowed survive passage through a horse? What is the distribution of transit times of surviving seeds from a cohort of swallowed seeds? When the horse is swallowing a large and relatively constant daily dose of seeds, how many living seeds are defecated daily? Are the dormant seeds that survive the trip scarified, and do they germinate at a different time than they would if they had not made the trip?

MATERIALS AND METHODS

Animals

Six healthy full-grown gelding range horses were selected by availability from the large herd maintained as riding stock for the park guards in Parque Nacional Santa Rosa, northwestern lowland Guanacaste Province, Costa Rica. Their normal diet is grass, pasture forbs, and browse, supplemented with ripe fallen fruits of deciduous forest trees growing in and around the brushy pastures (e.g., *Enterolobium cyclocarpum*, *Pithecellobium saman*, *Guazuma ulmifolia*, *Prosopis juliflora*, *Crescentia alata*). While it was not possible to weigh any of them, these horses are about half the mass of an adult thoroughbred racehorse and are about the size of the smallest western cow ponies. The horses were tethered on ropes 7-10 m long, and tied far enough apart that dung origin was unambiguous. They were moved to new pasture daily. Free-ranging animals visited waterholes once or twice per day, and the tethered animals were allowed to drink ad libitum from large water pails one or more times per day. Throughout the experiments the horses were healthy,

¹ Manuscript received 21 April 1980; revised 24 September 1980; accepted 4 October 1980.

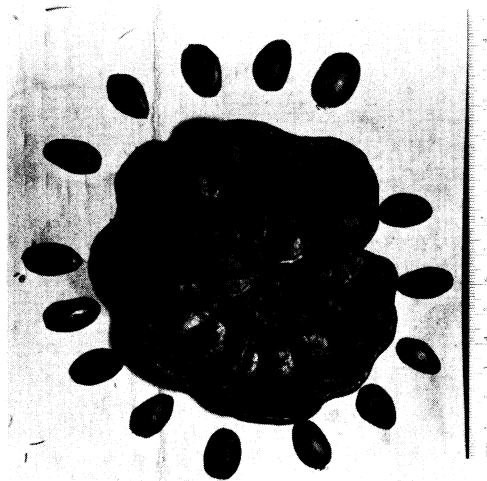


FIG. 1. A 15-seeded fruit of *Enterolobium cyclocarpum* with the hard oval seeds arranged opposite their location in the fruit (Santa Rosa National Park, Guanacaste Province, Costa Rica).

good tempered, and well fed by park standards. Their defecation rates (7–10 times/24 h) and dung piles (1–2 kg per pile) were the same as those of their free-ranging conspecifics in the nearby pastures. The Santa Rosa horses are lethargic and the amount of walking on the tether did not appear to be substantially less than that done by free-ranging horses in nearby pastures. However, the tethered horses did not experience the sudden short bursts of activity associated with fighting among the free-ranging horses.

Three horses from a pasture that does not contain *Enterolobium* trees were fed a daily diet of *Enterolobium* fruits. Although there were no *Enterolobium* seeds in their dung for 3 d before the experiment began, there is a slight chance that the horses were still carrying some *Enterolobium* seeds from fruits eaten 13 mo earlier (when they had access to new-fallen *Enterolobium* crops; *Enterolobium* fruits fall to the ground in April–May at Santa Rosa). The three horses fed a single dose of *Enterolobium* seeds could not have swallowed any of these seeds for at least 170 d before this experiment started (13 November 1979), and their dung was free of *Enterolobium* seeds for 3 d before the experiment began.

Feeding

The three horses (Vallo, Colorado, Negrito) fed a daily diet of *Enterolobium* fruits were simultaneously part of a seed-spitting experiment (Janzen 1981a); the seeds that were swallowed are part of the subject of the present paper. Ripe unrotted fruits from tree number 35 (April 1979 crop) were offered by hand (June 1979) after counting the number of seeds present in the indehiscent fruit. This was done by counting the elongate bumps on the surface of the fruit (the count-

ing error in this method is < 2%, Janzen 1981b). The horse took each entire fruit into its mouth, chewed for ≈ 30 –120 s, and spit or dropped a variable number of seeds out of its mouth. The remainder were swallowed along with the fruit pulp. The seeds were protected in part from direct molar contact by the tough fruit tissue, but some were undoubtedly scarified during chewing (see below). The remainder of the diet was grazed from lush pasture grass.

To eliminate the variable of molar scarification of the seeds and to get a large number of seeds into a horse in one feeding, three horses (Rojo, Blanco, El Tuerto) were thrown and force-fed on 13 November 1979. The seeds were mixed in 50-seed doses with water, sugar, and oatmeal in a one-L wine bottle. With the horse lying on its side but the head held above the ground with the nose upward and the long axis of the head perpendicular to the ground, the bottle was inverted down the horse's throat and shaken so that the solution and the seeds went into the throat simultaneously. This was repeated until it appeared that the horse could accept no more without choking. Blanco swallowed all seeds without any chewing. Rojo and El Tuerto sorted a few seeds out of the mix and sequestered them in the cavity between the molars and cheeks while drinking the bulk of the dose. While massaging the cheeks and throat to induce the horse to swallow these seeds, some seeds were undoubtedly scarified by molar action, but it appeared to be < 10%. Whenever the horse started chewing seeds, it was allowed to stand up, whereupon it spit out all the seeds remaining in its mouth. These seeds were not used again and are not included in any statements about seed fate in this paper. In addition, Rojo and El Tuerto were each fed 20 brass buttons as indigestible seed mimics, mixed in with the seeds. I dropped 20 brass buttons down Blanco's open throat; three were spit back out and 17 swallowed. After this artificial feeding, the horses were immediately put out to graze on high-quality grass. All six horses noticeably gained mass during the experiment.

Seeds and buttons

Full-sized *E. cyclocarpum* seeds from ripe fallen fruit are >99.9% viable, and take up water and begin to germinate immediately if the seed coat is notched with a file (Vasquez-Yanes and Perez-Garcia 1977, D. Janzen, *personal observation*). This occurs if the seed is placed in any kind of moist substrate, such as water, moist soil, cow rumen fluid, horse intestinal fluid, or horse saliva. When dormant, the seeds are extremely hard and require a force of 700–2000 N to crush (Janzen and Higgins 1979). If not scarified, the seeds will remain living but dormant for at least 5 yr submerged in water (D. Janzen, *personal observation*).

The seeds spit or dropped from the mouth by the horses on a daily diet of *Enterolobium* fruit were pooled and soaked in water. In a sample of 1000 of

these seeds, 7% germinated immediately and the remainder remained dormant for a month or more soaking in water. In a sample of 500 seeds shelled by hand from the same fruit crop, and therefore never touched by hard surfaces, 3% germinated immediately. This suggests a minimum of 4% scarification (cutting of the seed coat) by the horses' molars and that a minimum of 7% of the seeds swallowed by the horses germinated immediately in the moist horse gut irrespective of any scarification that may have occurred in the gut. In another sample of seeds hand-shelled from the same seed crop, all 500 seeds whose seed coats were broken by cutting with pruning shears germinated when placed in water.

The spit seeds that did not germinate upon being placed in water for a month or more were dried in August 1979. The seeds for force-feeding in November 1979 were drawn haphazardly from this seed pool. Also, 300 seeds from this seed pool were placed in water as germination controls for the duration of the force-feeding experiment; all of these seeds remained hard and dormant during the 70 d of the experiment.

A random sample of 10 of the seeds force-fed to the horses had an average mass of 0.793 g ($SD = 0.12$) and an average volume of 0.603 mL ($SD = 0.09$). Their specific gravity was 1.321. A random sample of 10 of the brass buttons force-fed to the horses had an average specific gravity of 1.777 ($SD = 0.24$) and an average volume of 0.631 mL ($SD = 0.26$). The seeds were 18–20 mm long, 9–10 mm wide, and 7–8 mm thick (Fig. 1). The buttons were 16-mm diameter discs, slightly convex on each side, 6–7 mm thick, and molded with the official crest of the United States of America on one side (brass buttons from military uniforms).

Dung

All dung produced by all horses during the experiment was collected. The dung was collected at dawn, once during the day, and at dusk from the horses on a daily *Enterolobium* diet. In some of the places where the horses were tethered, *Liomys salvini* mice collected *Enterolobium* seeds at night from horse dung experimentally placed at the site. However, it was found that the mice had to learn this behavior from seed-rich dung and since the horses were moved on a daily basis, it did not appear that seeds were being lost from the dung the first night. Large dung beetles (Scarabaeinae) thoroughly mined dung left out all night but *Enterolobium* seeds are too large for them to remove from the dung.

To eliminate all possibility of seed loss from dung at night from the three force-fed horses, a canvas dung-collecting bag was constructed from a duffel bag and hung on the rear of each horse at night (Fig. 2). The bag was emptied into plastic pails before midnight and at dawn. The bag was removed during the day to minimize horse distress. Diurnal dung collection for these three horses was as for the other three horses.

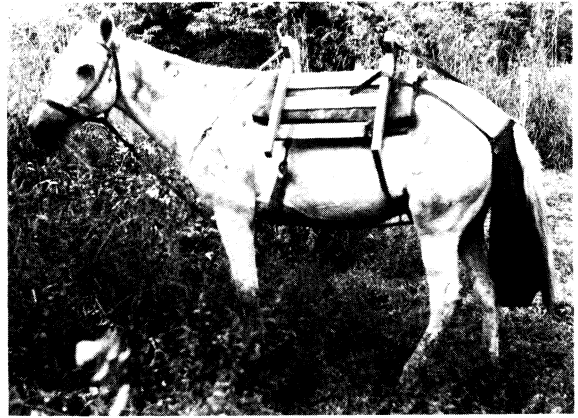


FIG. 2. A tethered gelding range horse with dung collecting bag in place. When the tail is raised to defecate, the mouth of the bag opens and is kept in place by the belly strap visible in profile. The pack saddle supports the mass of the bag as it fills with dung (Santa Rosa National Park, Guanacaste Province, Costa Rica).

On the day of collection, the dung was put into solution by running water into a bucket half full of dung. After lumps were thoroughly broken up by hand, the thin water-dung mixture was poured off and the *Enterolobium* seeds collected from the bottom of the bucket. As mentioned above, when dormant these seeds are substantially heavier than water, as are the brass buttons. Likewise, germinating *Enterolobium* seeds and seed coats sink in water and thin dung sludge, though less rapidly than do dormant seeds.

The dormant seeds were dried, accumulated, and then soaked for 1 wk in water. Seeds that were soft, but still firm and containing an apparently living seedling, were placed in soil to grow. If they grew, they were counted as "soft live" in Tables 1–2. If they did not grow, they were recorded as "soft dead," and are regarded as having been killed by intestinal fluids. Seeds that were soft and mushy were always impregnated with intestinal fluids and dead (category "soft dead" in Tables 1–2). Numerous guanacaste seed coat fragments were also found in the dung, but were not recorded.

Duration of experiments

The feeding portion of the daily experiment was terminated once a relatively continuous output of seeds was achieved, and the entire experiment was terminated when I had to leave the park. The force-feeding experiment was terminated when the park water pump broke and simultaneously a virus epidemic among the park horses depleted the herd so the experimental horses had to be put back to work. In both cases it is possible that some dormant seeds remained in the horses; only one brass button was recovered during the experiment and therefore virtually all of the buttons remained in the horses.

TABLE 1. Diary of appearance of *Enterolobium cyclocarpum* seeds in the dung of three range horses fed a single pulse of seeds on 13 November 1979 (day 0).

| | Rojo (fed 150) | | | Blanco (fed 180) | | | El Tuerto (fed 143) | | |
|------------------|----------------|-----------|-----------|------------------|-----------|-----------|---------------------|-----------|-----------|
| | Hard live | Soft live | Soft dead | Hard live | Soft live | Soft dead | Hard live | Soft live | Soft dead |
| Day 0 | | | | | | | | | |
| 1 | | | | | | | | | |
| 2 | 4 | 3 | | 5 | | | | 5 | 1 |
| 3 | 6 | | 3 | 12 | | | 1 | | |
| 4 | 1 | 1 | 2 | 1 | | | 1 | | 1 |
| 5 | | | | 4 | | 2 | 8 | 1 | |
| 6 | | | | | | | 1 | | |
| 7 | | | | | | | | | |
| 8 | 23 | | | | | 1 | 10 | | |
| 9 | 3 | | 1 | | | | 3 | | |
| 10 | 2 | | | | | | 1 | | |
| 11 | 11 | | | | | | 1 | | |
| 12 | 3 | | | | | | 1 | | |
| 13 | 2 | | | | | | 1 | 1 | |
| 14 | | | | | | | 8 | | |
| 15 | | | | | | | | | |
| 16 | | | | 1 | | | | | |
| 17 | | | | | | | 4 | | 1 |
| 18 | | | | 1 | | 1 | 5 | | |
| 19 | | | | | | | | | |
| 20 | | | | | | 1 | 2 | | |
| 21 | 2 | | | | | | 2 | | |
| 22 | 7 | | 1 | | | | | | |
| 23-24 | | | | | | | | | |
| 25 | 8 | | | | | | | | |
| 26 | 6 | | | | | 1 | 5 | | |
| 27-29 | | | | | | | | | |
| 30 | 1 | | | | | | 2 | | |
| 31 | | | | | | 1 | | | |
| 32 | | | | 1 | | | | | |
| 33 | 1 | | | | | | | | |
| 34-47 | | | | | | | | | |
| 48 | | | | | | | | 1 | |
| 49-59 | | | | | | | | | |
| 60 | | | | 6 | | | | | |
| 61-70 | | | | | | | | | |
| Σ | 80 | 4 | 7 | 31 | | 7 | 56 | 7 | 4 |
| Percent survival | 53 | 3 | | 17 | | | 39 | 5 | |

RESULTS

The diary of appearance in dung of hard live (dormant), soft live, and soft dead *Enterolobium* seeds for the three horses force-fed a single pulse of seeds (Table 1) shows clearly that seeds do not merely pass through with the other food and appear in the dung in a single pulse. The hard live seeds required 2-33, 2-60, and 3-30 d to make the trip (\bar{x} = 13.2 d, SD = 8.3; \bar{x} = 16.0 d, SD = 22.7; \bar{x} = 13.3 d, SD = 7.3, respectively); by inspection, these three means are not significantly different from each other. The rates of passage of the soft seeds cannot be interpreted since they germinated at some unknown point in transit and changed their specific gravity at that time; it is likely that they were hard dormant seeds during most of their trip through the horse, and germinated shortly before defecation (see Discussion). I hypothesize this because had they germinated early in the trip, digestive fluids would have killed them. While the bulk of the

hard seeds appeared in the dung between day 2 and day 26 for all three horses, the 11 hard seeds (4%) that appeared between day 27 and day 70 should not be viewed as trivial in the biology of *Enterolobium* nor as mere "noise" in the horse-seed interaction. Not only did a few hard dormant seeds appear in the dung of all three horses a month or more after feeding, but also I have found occasional hard dormant *Enterolobium* seeds in fresh dung of other park horses in late July and August, at least 3 mo after they have stopped eating *Enterolobium* fruits on their own.

Of the 56%, 17%, and 44% of the seeds that survived the trip through the three horses, >90% made the voyage as hard dormant seeds (Table 1). If the horses could have been watched longer, a few more living seeds might have appeared, thereby elevating the percent survival. However, in view of the large number of *Enterolobium* seed coats encountered in the dung, and the tapering off of the number of seeds defecated

TABLE 2. Diary of defecation of *Enterolobium cyclocarpum* seeds by three horses on a steady diet of *E. cyclocarpum* fruits (begun 3 June 1979).

| | Vallo | | | | Sum | Colorado | | | | Sum | Negrito | | | | Sum |
|-------------|-------------|-----------|-----------|-----------|------|-------------|-----------|-----------|-----------|------|-------------|-----------|-----------|-----------|------|
| | Seeds eaten | Hard live | Soft live | Soft dead | | Seeds eaten | Hard live | Soft live | Soft dead | | Seeds eaten | Hard live | Soft live | Soft dead | |
| 0 | 70 | | | | | 31 | | | | | 14 | | | | |
| 1 | 82 | | | | | 38 | 1 | | | 1 | 28 | 1 | | | 1 |
| 2 | 37 | | 2 | | 2 | 12 | | | | | 22 | | 1 | | 1 |
| 3 | 78 | 3 | 3 | | 6 | 14 | | | | | 22 | | | | |
| 4 | 57 | 1 | 1 | 1 | 3 | 8 | 2 | | | 2 | 36 | 16 | | | 16 |
| 5 | 50 | 5 | 2 | | 7 | 10 | | 1 | | 1 | 44 | | | | |
| 6 | 90 | 2 | | | 2 | 10 | 1 | 1 | | 2 | 52 | | | | |
| 7 | 97 | 16 | 3 | | 19 | 11 | 14 | 2 | | 16 | 29 | | | | |
| 8 | 109 | 8 | 1 | | 9 | 8 | 15 | 1 | | 16 | 34 | | | | |
| 9 | 50 | 10 | 2 | | 12 | 6 | | | | | 31 | | | 1 | 1 |
| 10 | 58 | | | | | 16 | | | | | 37 | 1 | | | 1 |
| 11 | 27 | 3 | | | 3 | 27 | | 1 | | 1 | 46 | 1 | | 1 | 2 |
| 12 | 29 | | 1 | 1 | 2 | 12 | | | | | 77 | | | | |
| 13 | 25 | | 2 | 2 | 4 | 12 | | | | | 95 | | 1 | | 1 |
| 14 | 35 | | | | | 10 | | | | | 80 | | | 1 | 1 |
| 15 | 161 | 1 | | | 1 | 44 | | | | | 27 | | | 2 | 2 |
| 16 | 138 | 2 | | 1 | 3 | 54 | 6 | 2 | | 8 | 73 | | | | |
| 17 | 139 | | 3 | 2 | 5 | 45 | 12 | | 2 | 14 | 51 | | | | |
| 18 | 140 | | | 2 | 2 | 57 | 1 | | | 1 | 76 | | 2 | 1 | 3 |
| 19 | 59 | | 1 | 10 | 11 | 52 | 1 | 1 | 1 | 3 | 47 | | 1 | | 1 |
| 20 | 91 | | | | | 41 | 12 | | | 12 | 34 | 4 | | | 4 |
| 21 | 77 | 6 | 4 | 4 | 14 | 29 | 15 | 3 | 1 | 19 | 53 | | | | |
| 22 | 94 | 38 | 4 | 3 | 45 | 29 | 3 | 2 | 2 | 7 | 29 | 7 | | 1 | 8 |
| 23 | 113 | 4 | 1 | | 5 | 22 | | | 1 | 1 | 29 | 3 | | | 3 |
| 24 | 116 | 16 | 3 | 1 | 20 | 16 | 5 | 1 | | 6 | 58 | | | | |
| 25 | 80 | 10 | 4 | 2 | 16 | 15 | 67 | 1 | 1 | 69 | 36 | 10 | | 1 | 11 |
| 26 | 78 | 12 | 1 | | 13 | 25 | 15 | | | 15 | 29 | 12 | | 1 | 13 |
| 27 | 105 | 56 | 1 | 1 | 58 | 9 | 1 | | | 1 | 79 | 3 | | | 3 |
| 28 | 68 | 11 | 3 | 2 | 16 | 5 | | | | | 35 | 3 | | 3 | 6 |
| 29 | 29 | 12 | 2 | 1 | 15 | 8 | 18 | | | 19 | | | 2 | 2 | 4 |
| 30 | 45 | 101 | 5 | 6 | 112 | 13 | 3 | | 2 | 5 | | | 1 | 2 | 3 |
| 31 | 83 | 23 | 1 | 1 | 25 | 29 | 23 | | 1 | 24 | | 6 | 1 | 1 | 8 |
| 32 | 110 | 23 | 5 | 2 | 30 | 41 | 7 | 1 | 1 | 9 | 7 | | | | 7 |
| 33 | 151 | 30 | 3 | 6 | 39 | 51 | 6 | | 1 | 7 | 1 | | | | 1 |
| 34 | 161 | 34 | 5 | 6 | 45 | 65 | 5 | 1 | | 6 | | | | 2 | 2 |
| 35 | 145 | 54 | 3 | 2 | 59 | 82 | 8 | 1 | 1 | 10 | | 2 | | 1 | 3 |
| 36 | 73 | 28 | 2 | 11 | 41 | 29 | 16 | 1 | 5 | 22 | 7 | | | | 7 |
| 37 | | 8 | 1 | 9 | 18 | | 23 | | 2 | 25 | | | 1 | 1 | 2 |
| 38 | | 31 | 5 | 3 | 38 | | 16 | | | 16 | | | | | |
| 39 | | 19 | 3 | 2 | 24 | | 8 | | | 8 | | 7 | | | 7 |
| 40 | | 10 | 3 | 1 | 14 | | 7 | | | 7 | | 2 | 1 | 1 | 4 |
| 41 | | 74 | 2 | 1 | 77 | | 1 | | | 1 | | | | | |
| 42 | | 25 | 2 | 1 | 28 | | 3 | | | 3 | | | | | |
| 43 | | 9 | 2 | 1 | 12 | | 19 | | 1 | 20 | | 3 | | | 3 |
| 44 | | 28 | 3 | | 31 | | 4 | | | 4 | | 5 | | | 5 |
| 45 | | 7 | | | 7 | | 9 | 1 | 1 | 11 | | 3 | | | 3 |
| 46 | | 2 | 1 | | 3 | | | | | | | 6 | | | 6 |
| 47 | | 6 | 1 | | 7 | | 13 | | | 13 | | | 1 | | 1 |
| 48 | | 75 | | | 75 | | 23 | | | 23 | | | 1 | 1 | 2 |
| 49 | | 46 | | | 46 | | | 1 | | 1 | | | | | |
| 50 | | 7 | | | 7 | | 2 | | | 2 | | | | | |
| 51 | | 1 | 2 | | 3 | | 1 | | | 1 | | | | | |
| 52 | | | 1 | 1 | 2 | | 7 | | | 7 | | | | | |
| 53 | | | | | | | | | | | | | | | |
| 54 | | 6 | 1 | 1 | 8 | | | | | | | | | | |
| 55 | | | | | | | | | | | | | | | |
| 56 | | | | | | | | | | | | | | | |
| Σ | 3150 | 863 | 95 | 87 | 1045 | 986 | 393 | 93 | 23 | 439 | 1303 | 110 | 13 | 23 | 146 |
| \bar{x} | 85.1 | | | | | 26.7 | | | | | 44.9 | | | | |
| SD | 39.8 | | | | | 19.3 | | | | | 21.0 | | | | |
| % appearing | | 27.4 | 3.0 | 2.8 | 33.2 | | 39.9 | 2.3 | 2.3 | 44.5 | | 8.4 | 1.0 | 1.8 | 11.2 |

per day, I suspect that nearly all of the seeds were out of the horses by the termination of the experiment.

Each diary of appearance of *Enterolobium* seeds in the dung of the three horses on a daily diet of *Enterolobium* fruits (Table 2) appears to represent a reasonable approximation to the sequential daily summation, by a horse, of many patterns like the one in Table 1. Vallo was the best seed-swallower ($\bar{x} = 85.1$ seed/d, $SD = 39.8$) and by about day 21 appeared to have arrived at a fairly steady rate of seed defecation. From day 21 to day 44 he defecated an average of 33 hard seeds/d ($SD = 24$). His maximum for 1 d was 101 seeds (day 30) as compared with a maximum of 67 and 16 for the other two horses (day 25 and day 4, respectively). The other two horses defecated substantially fewer seeds per day than did Vallo, but each also swallowed only about one-third as many seeds as did Vallo. Negrito defecated about one-third as many hard seeds as did Colorado, but actually swallowed more seeds than did Colorado.

As with the horses that were fed a single pulse of seeds, the horses that swallowed seeds daily defecated >90% of the seeds that survived the trip (30%, 42%, 9.4%) as hard dormant seeds. For Vallo and Colorado, the horse dung was censused for seeds for only 20 d after the last seeds were fed (Table 2), and 25% of the hard seeds to emerge from the three horses given a pulse of seeds appeared after day 20 (Table 1). It is therefore likely that the actual seed survival recorded for Val and Colorado would have been at least 33% greater had a longer census been possible.

There is a striking pattern in the daily total seeds defecated by Vallo (Table 2). Starting with day 22, there appears to be a peak in seed defecation every 2–5 d (day 22, 24, 27, 30, 35, 38, 41, 44, 48). Colorado shows the same peaks but at longer intervals. Negrito did not defecate enough seeds to distinguish any peaks, if there are any. While no quantitative data are available on the matter, these peaks in seed defecation per day by Vallo and Colorado were even more striking to observe in the field because they were generated by one or two defecations; the remainder of the dung produced by the horse on a peak day contained in total the usual number of one to 10 seeds.

Only one of the 57 brass buttons appeared in the horses' dung during the 70 d of the experiment. El Tuerto defecated it along with one seed on the 20th d after feeding.

DISCUSSION

When a horse eats *Enterolobium* fruits for only 1 or 2 d, as probably occurs when a large herd happens upon a small fruit crop below one tree, for several weeks it will generate dung that contains a few seeds per day (at best one to five seeds per dung pile). If it feeds daily on *Enterolobium* fruits, the horse will defecate a higher number of seeds per day, and continue to do so for several weeks after the last fruits have

been eaten. Some dung piles may contain several tens of seeds and many will contain as many as five seeds. Since *Enterolobium* fruits fall from the parent during the second half of the dry season (late March–early May), the horse may eat seeds in the dry season and defecate them in the rainy season which begins in early May. The fate of seeds defecated in different seasons is currently under study.

The horses are clearly killing (digesting) a substantial fraction of the seeds that they swallow. Some of this mortality is unavoidable in that $\approx 3\%$ of the seeds will begin to germinate the moment they are in a moist environment, and 2 d is the minimum for the trip through a horse. I suspect that only a few hours' immersion in the digestive fluids of a horse will kill a germinating seed. This is likewise under study. At least another 4% of the seed death can be blamed on the horse through its scarification of the seeds during chewing. However, even when the seeds were forced to the horse, and therefore never touched by the teeth, there was substantial digestive seed predation (e.g., Blanco, Table 1). It is most likely that the inorganic acids in the horse's stomach, or the organic acids and digestive enzymes in the remainder of the intestinal tract scarified the seeds and led to their germination and consequent death by digestion. Digestive seed predation was also the result obtained when a captive Baird's tapir (*Tapirus bairdii*) was fed *Enterolobium* seeds (Janzen 1981b).

The primary sites of seed digestion in the horse are probably those portions of the digestive system where the seeds are retained as the horse's finely chewed fodder passes rapidly on by them (the passage rate of fodder through a horse is normally 2–4 d; Argenzio et al. 1974). While corners, folds, and eddies in the intestinal loops are candidates for sites of seed retention, the caecum is a more likely site. In contrast to bird caeca (e.g., Björnhag and Sperber 1977), mammal caeca somehow selectively remove large hard objects from the digesta flow and retain them for unknown periods of time (e.g., Hoelzel 1930, Björnhag 1972). I suspect that the pulsed pattern of seed defecation evident in Vallo's dung (Table 2) represents the periodic partial voiding of the caecal contents into the large intestine, as is known to occur in rabbits (Björnhag 1972) and birds (Björnhag and Sperber 1977). It was very conspicuous for Rojo, Blanco, and El Tuerto that appearance of seeds after about day 18 often occurred in dung that was foul-smelling and noticeably more finely degraded than usual. I hypothesize that the brass buttons, only one of which appeared even after 70 d, were permanently retained in the caecum owing to their very high specific gravity. Whatever cleansing process gradually cleaned the heavy *Enterolobium* seeds from the caeca was not capable of removing the heavier brass buttons.

As a first step to understanding the site of seed degradation, three nylon mesh bags containing a total of

25 hand-shelled *Enterolobium* seeds from the same 1979 seed crop (tree 35) were placed in the small intestines of a thrice-fistulated adult pony on an alfalfa-hay diet at the University of Pennsylvania's New Bolton Veterinary Center and left for 9 d. Of the 25 seeds, only one germinated, strongly suggesting that the intestinal chemicals are not adequate to scarify the seed coat. Digestive fluids of large mammals in general are not adequate to scarify these seeds. I kept 20 *Enterolobium* seeds from a different tree continually circulating through my own digestive tract for 30 d; only one germinated (Janzen 1981b). It was killed by my digestive processes but the other 19 remained dormant and undamaged.

Whether the soft live seeds appearing in the dung should be counted as live or dead depends on the site and season of dung defecation, the subsequent action of dung beetles and mice on such seeds, and whether a dung pile is a microhabitat in which an *Enterolobium* seedling can survive. These parameters are subjects of ongoing study. However, the usual case is seedling death by rodent herbivory or desiccation. It is the hard and dormant seeds in the dung which should be viewed as "successful." Provided that they escape seed predation by rodents, their normal fate is to become incorporated in the soil seed bank and then germinate in the rainy season of some subsequent year, after soil physical and chemical processes have eventually scarified the seed coat. There is no evidence that passage through the horse "enhances" germination of the surviving seeds, since the hard dormant seeds that have passed through a horse sit in water for many months without germinating, just as do 97% of the seeds that are hand-shelled out of the same fruit crop and placed directly in water.

While the Baird's tapir gave very similar results to those obtained with the horse (Janzen 1981b), a preliminary trial with a cow (*Bos taurus*) gave very different results. Over a 2-d period, an adult "Swizo" range cow was fed 1407 *Enterolobium* seeds in fruit fragments. A sample of 300 hand-shelled seeds from the same fruit crop displayed 2% germination in water. This means that the cow swallowed 1379 hard and dormant seeds that would not have germinated simply by being moistened. By day 6 and 9, 73% and 83% of this single seed pulse had been defecated as hard live seeds. No soft live or dead seeds were found in the dung. No horse had a seed passage rate anywhere near as fast, nor a seed survival rate anywhere as high. A range cow is clearly very different from a horse as a potential *Enterolobium* seed disperser. In another preliminary trial, I hung a nylon screen bag containing 20 *Enterolobium* seeds in the rumen of an adult Jersey cow on a normal fodder diet at the New Bolton Center mentioned above, and after 9 d there was no seed germination or digestion.

Horses eat *Enterolobium* pods because of the nutrients in the fruit wall and even spit out 39–75% of

the seeds (Janzen 1981a). They show no interest in eating shelled seeds, either intact or pulverized. Yet nutrient analysis of the fruit walls and the seeds (D. Janzen, *personal observation*) suggests that they may actually get more nutrients out of digesting the seeds than the fruit tissue. *Enterolobium* seeds, like other legume seeds, are rich in nutrients as measured by standard analyses. However, they are also rich in protease inhibitors (C. Ryan, *personal communication*) and contain 2% albizzine and 1% pipercolic acid (E. A. Bell, *personal communication*). The hard and the newly germinated seeds are an excellent pure diet for the mouse (*Liomys salvini* (Heteromyidae) and lethal as a pure diet for the rat *Sigmodon hispidus* (Cricetidae); the latter can, however, live for 10 d with no sign of ill health on a pure diet of the germinated seeds if they have been boiled (W. Hallwachs and D. H. Janzen, *personal communication*). In short, it is not clear if the horse gains or loses by digesting *Enterolobium* seeds. It is therefore not clear if the horse should be viewed as an accidental or deliberate digestive seed predator.

What sort of dispersal agents are horses, from the viewpoint of *Enterolobium*? Contemporary horses must on occasion move the seeds very long distances. A large *Enterolobium* tree near an old Costa Rican ranch house could have come from a seed brought from as much as 20–60 d ride away. However, this is not the sort of dispersal on which selection operates (just as it does not operate on long-distance seed dispersal to islands). Furthermore, there is no reason to associate the longest distance moved by a seed with the "best" dispersal. A herd of wild horses foraging at the end of the dry season through a combination of forest and grassland that contains *Enterolobium* trees, as is currently found in Santa Rosa National Park and lightly developed ranchlands of lowland Pacific coastal Costa Rica, will generate a diffuse and widespread seed shadow made up of the seeds of many individual *Enterolobium* trees. One defecation is likely to contain the seeds from many individual trees even if a given tree's fruit crop is visited consecutively for many days. Furthermore, since an individual horse grazes, browses, and gathers fruits in all parts of the forest/grassland habitat, a herd should generate a seed shadow that encompasses practically all microhabitat types. However, to the degree that horses defecate more frequently along trails and at often-frequented resting or watering places, the seed shadow will be likewise intensified in these microhabitats. The fates of *Enterolobium* seeds in such microhabitats is the subject of an ongoing study, and it is clear that the importance of horses to *Enterolobium* will depend on the kinds and frequencies of these fates.

A habitat containing wild horses, such as the *Enterolobium* habitat in the Pleistocene, would have very different *Enterolobium* seed shadows than a habitat without these animals, and consequently should have

very different local distribution patterns of the adult trees. Since free-ranging horses migrate locally in response to seasonal changes in browse, grass, water, and fruit availability (based on my own observations and information from 60–80 yr old cowboys at Santa Rosa), the seed shadows horses generate should have two quite different aspects. First, there should be the local seed shadow falling largely within hundreds to thousands of metres of the parent trees. This seed shadow should be intense and contribute most of the recruitment for each successive generation. It should also serve to move genetic information over distances not much different from those crossed by pollinators moving between flowering *Enterolobium* trees. Second, there should be a much more diffuse and attenuated seed shadow, generated by horses moving tens of kilometres and into quite different habitats. For example, in the early part of the century during the later part of the dry season at Santa Rosa, free-ranging horses moved up into the pastures and evergreen forests 10–20 km into the northeast (400–800 m elevation) on the lower slopes of the volcanoes of the Guanacaste Cordillera. When the rains came, they moved back to the lower elevation deciduous forests and pastures of the park. By eating *Enterolobium* seeds in March–April at Santa Rosa and then defecating them in the foothills, and then by consuming foothill *Enterolobium* seeds and defecating them in Santa Rosa in May, the horses certainly moved genetic material much further than would any pollinator. There is no reason to believe that Pleistocene horses (and other large herbivores) would not have done the same to Pleistocene *Enterolobium* trees in habitats such as currently occur in Guanacaste.

It is commonplace to speak of hard legume seeds as having “enhanced” or “improved” germination after passing through a dispersal agent, owing to scarification of the seed coat. Given the state of knowledge of dispersal biology, such statements are premature and misleading. There is no intrinsic reason why an increase in the percentage of seeds germinating upon defecation (as compared to the percent germination of seeds that have not passed through an animal) is an “improvement” in the context of anyone but a farmer trying to grow seedlings. Success in the breaking of dormancy of seeds is not necessarily measured by the length of the period of dormancy (inverse of the germination rate) but is based on a complex interaction with habitat and weather conditions at the time of germination.

The picture that is beginning to emerge for *Enterolobium* in Santa Rosa National Park is the following: In normal dispersal, after the fruits fall, some of the seeds are swallowed by a large mammal. Some of these survive the trip without scarification, enter the soil seed bank, and eventually germinate years hence once the seed coat has been scarified by soil action such as scratching during erosion or chemical etching.

The seeds left below the parent in uneaten fruits, and the seeds spit below the parent by potential but uncooperative dispersal agents, are taken as prey by *Liomys salvini* mice. While an *Enterolobium* seedling germinating in a dung pile is picturesque, its chances of surviving the dung beetles, mice, dryness, and root exposure characteristic of dung piles are very slim. In such a system, it is not at all certain that scarification during passage through the mammal gut is the event that natural selection has favored during the evolution of the *Enterolobium*-disperser interaction.

Why then is the *Enterolobium* seed coat not so impervious that nearly all seeds survive the trip through the animal? First, for a cow-like animal, it appears that it is largely impervious. However, this does not mean that *Enterolobium* seed traits necessarily or even likely evolved under selection by animals with cow-like gastrointestinal tracts. Second, the seed that is so impervious that the horse does not kill it by molar or chemical scarification may then be so slow to be scarified by soil processes that it has significantly fewer generations than the less impervious morph. Third, the seed we now see may be a relatively imperfect fit to any one dispersal agent or disperser coterie because over evolutionary time dispersal agents are periodically appearing and disappearing. Their selective pressure as individuals and as a group is then not constant long enough to generate evolutionarily the perfect seed coat with respect to those dispersers and the environment of the adult tree, to say nothing of whether such a seed is biologically possible. Certainly the Pleistocene loss of horses (and other potential dispersers, D. H. Janzen and P. S. Martin, *personal communication*) is one such disappearance event, and there is simply no way to know how much *Enterolobium* seed coat imperviousness has changed over the last 10 000 yr in the absence of the big dispersers. There has long been a strong bias among field biologists against studying the two most easily studied species of the large herbivores, range cattle and horses. The 1979 state of the art was “larger mammals that graze may be effective in the long-distance transport of seed, but we have only anecdotal records of internal passage times of seeds for species whose foraging ranges are known” (Levin 1979). It is indeed ironic that there is not a single paper in *Ecology*, *Journal of Animal Ecology*, or *Journal of Ecology* on the field ecology of the two large herbivorous mammals that have had the greatest impact on habitats the world over, and are our only chance even to begin to understand the impact that the New World Pleistocene megafauna must have had on New World vegetation.

ACKNOWLEDGMENTS

This study was supported by NSF grant DEB 77-04889. G. Vega, R. Glass, D. Hofmann, A. Pescador, A. Herre, J. Petersen, M. Bonoff, and W. Hallwachs aided in field work. The manuscript was constructively criticized by W. Hallwachs. Servicios de Parques Nacionales de Costa Rica in

general, and F. Chaves in particular, generously provided facilities, horses, and habitats. W. J. Donawick and G. Topkiss aided with the experiments at the New Bolton Center.

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