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HORSE RESPONSE TO *ENTEROLOBIUM CYCLOCARPUM* (LEGUMINOSAE) FRUIT CROP SIZE IN A COSTA RICAN DECIDUOUS FOREST PASTURE

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ABSTRACT

When four 400-fruit crops and one 5000-fruit crop of *Enterolobium cyclocarpum* (Leguminosae) were presented to 17 range horses in the early rainy season in a 10 ha pasture in the deciduous forest lowlands of Pacific coastal Costa Rica (Santa Rosa National Park), they consumed all of the 6600 fruits in about in about eight days. For the first six days of foraging, the horses ate an average of 46 to 71 fruits per day per horse. The horses appeared to prefer to forage in the large fruit crop. The small crops disappeared at quite different rates, apparently owing to small differences in their locations. In their daily movements, the horses made repeated trips between the fruit crops below sparse trees and the more open grazing areas. Fruit consumption rates by the horses and the timing of fruit drop by *E. cyclocarpum* trees should influence the seed defecation rates of the horses; these rates influence the probability that the seeds in the dung will be found by seed predators.

Fruits crops of different sizes are likely to be eaten at different rates or attract somewhat different dispersal agents. The phenonemon can be studied at natural fruit crops of different sizes (e.g., Howe and Vander Kerckhove 1979), or by artificially manipulating fruit crop sizes. Here I describe the results of presenting four small crops and one large crop of guanacaste fruits (*Enterolobium cyclocarpum*) to horses in a large Costa Rican pasture. Although this experiment appears artificial, it simulates potential Pleistocene interactions between horses and fruit (Janzen and Martin 1982) in that both native horses and the tree occupied Costa Rica up to 10,000 years ago, and they probably interacted much as in the interaction described below and in other studies (Janzen 1981a, b, 1982a).

Materials and methods

The fruits. *Enterolobium cyclocarpum* (Guanacaste tree) is a widespread, conspicuous and rare mimosaceous legume tree in tropical Mexico and Central America. It grows throughout the lowlands of Guanacaste Province on the Pacific side of northwestern Costa Rica. Adult guanacaste trees grow in many parts of Santa Rosa National Park (25 km south of La Cruz, between the Pan-American highway and the Pacific ocean, northwestern Guanacaste Province), where the study was conducted. The mature fruits (Figure 1) fall off the tree from late March to early May. This timing puts them on the ground and therefore within the reach of horses during the last two months of the six month dry season. Until the rains come, the fruits lie on the fully insolated hot ground and the fruit tissues contain 10–20 percent water (Janzen 1982b). Mature newly-fallen fruits are 5–20 g fresh weight (including seeds) and are indehiscent, glabrous, polished, undulating, and somewhat bumpy. They are deep chocolate brown in color. A horse picks up the entire fruit with its lips, eats it entire, but chews it throughly. The seeds are large (Figure 1b), and while the fruit is being chewed, 40–75 percent of them are spit out (Janzen 1981a).

Large plastic bags were filled with new-fallen mature dry fruits found below large guanacaste trees in central Guanacaste Province (in 1980, guanacaste fruit crops were in short supply within the park). The fruits were transported to Santa Rosa National Park and stored in open plastic bags in dry rooms until used. From these samples, four sets of 400 fruits each were chosen. The only criterion for eligibility was that the fruit be approximately intact; chipped or cracked fruits were acceptable, but those that had been broken into or fragmented were discarded. Each set of 400 fruits weighed 5.8–6.1 kg. In addition, 5000 fruits were chosen by weight from large bags that had almost no broken fruits in them. The fruits were not moistened at any time during storage and the first two days of the experiment occurred before the first rain of the rainy season. The experiment was completed before enough rain fell to noticiably moisten litter, soil or fruits. Details of moistening are important in the context of this experiment because wetted fruits are much softer and more attractive to the horses than are dry fruits, and change their flavor as well as odor.

During a 15 minute period the five artificial fruit crops were put in place in the southern end of the 10 ha horse pasture near the administration area of the park. At this time, the 17 horses in the pasture were 100–200 m away at a right angle to the wind current across the pasture and out of sight behind hills. The configuration of the crops was such that 40–60 m separated the periphery of each crop from that of the next in line, and all five crops were in an approximately straight line. At one end of the line was a small crop, followed by the large crop, followed by the three remaining small crops. The fruits in each small crop were spread haphazardly on a fine scale and uniformly on a large scale over an area approximately 20 m in diameter. Such an area and configuration of fruit distribution is a reasonable approximation to the fruit shadow beneath a medium-sized *E. cyclocarpum* tree, although on occasion strong winds may scatter the fruits sufficiently as to increase the area of the fruit shadow to perhaps as much as twice that used here. The large crop was spread in the same manner over an oval area about 30 m in diameter. This crop approximates the fruit shadow of a large adult guanacaste tree. In the case of the four small crops, the fruit shadow had a density of approximately 1.27 fruits per m^2. In the crop of 5000, the density was 7.07 fruits per m^2. However, in putting out the large fruit crop, the fruits were somewhat more heterogeneously scattered and there were occasions when a square meter would contain as many as 20 fruits. Such heterogeneity of pattern often occurs beneath large guanacaste trees that have dropped a fruit crop of approximately this size.

The seeds in a guanacaste fruit can be censused by counting the number of domes on the surface of the fruit over each seed, and by this method I determined that each of the small fruit crops contained 4432, 4441, and 5046 seeds. The large fruit crop contained approximately 58,260 seeds (based on the mean of 11.65 seeds per fruit derived from the above four samples of 400 fruits each). The fruits used in this experiment were derived the crop of one large tree and therefore were quite homogenous in color, odor, shape and size.

The fruit crops were censused every day between 0800 and 0900 hours, by counting the remaining fruits while walking through sections of the fruit shadow. When the crops ahd more than 200—300 fruits, my counts are accurate to about 5 percent. At lower numbers, there is about a 1 percent error in counting.

The horses: During the course of the experiment (6 May through 18 May, 1980) there were 17 horses in the pasture. However, on occasion, between one and three of these horses were removed for a morning or afternoon of work as a park patrol animal. The horses were all geldings and of adult size. All of these horses had previous experience feeding on naturally fallen guanacaste fruits, and at least six of these horses were the subjects in feeding experiments where guanacaste fruits were offered by hand (Janzen 1981a, b, 1982a). In general, these horses were avid consumers of guanacaste fruits. However, usually after eating 5—20 fruits, each of these horses lost interest and moved on to forage on other food items before returning to consume another 5—20 guanacaste fruits several hours later.

This particular horse pasture is a continuous stand of heavily grazed jaragua (*Hyparrhenia rufa*) with scattered woody sucker shoots mixed in with patches of herbs that are largely inedible to horses (e.g., *Crotalaria maypurensis*). There are a moderate number of small trees at the south end of the pasture and the fruit crops were largely under the shadows of these trees. In their normal foraging movements throughout the pasture before I put out the fruit crops, it was commonplace for most of these horses to pass through the south end of the pasture at least once a day, if not more often. The small fruit crop farthest from the large one was directly under one edge of the canopy of a large guanacaste tree that did not produce any fruit in 1980. No natural guanacaste fruit crops fell into this pasture in 1980. By early May, the horses had trampled and grazed this pasture down to practically bare ground and there was very little grass present. They were being given hay as supplementary feed but in fact showed little interest in it, preferring to forage for bits of regrowth. The horses were not starving to death, but certainly should not be viewed as being overfed. Food availability to these horses approximates that of free-ranging horses not able to leave a deciduous forest region during the end of the dry season.

When the fruit crops were put out, the wind (breeze) was blowing at right angles to a line between the crops and the horses. However, despite the fact that the persons putting out the crops were out of sight from the horses, the horses quickly perceived that something had changed and moved to the crops and began to feed within 30 minutes. I suspect that the crops were therefore first located by odors carried to other parts of the pasture by turbulence.

Other animals: There were no cows in the pasture so I know that no animal other than the horses removed entire fruits; white-tail deer (*Odocoileus virginianus*) occasionally cross this pasture but they do not eat entire guanacaste fruits. However, there are spiny pocket mice (*Lionys salvini*) in this pasture. They behave towards these fruit crops as they do toward any other guanacaste fruit crop (Janzen 1981e). *L. salvini* cuts the large seeds out of the fruit and carries these seeds off for later consumption (seed predation). *L. salvini* also collects the seeds that are spit out by the horses. The horses were seen to spit many seeds and on occasion there were hundreds of clean seeds on the ground in the fruit shadows. At the end of the experiment there were no visible loose seeds in the pasture, indicating thorough seed removal by *L. salvini.* However, it appeared that the mice were occupied picking up loose seeds and spent little time cutting seeds out of fruits. During the entire experiment I only saw two fruits with their seeds removed by *L. salvini.* The mice were therefore not a factor contributing to the rate of disappearance of fruits in this experiment.

Results

The daily rate of disappearance of the fruits varied strongly from crop to crop (Table 1 and 2). While crop 1 was almost completely eaten by 1000 hrs on the third day after being put out, the other three small crops were still 1/2–2/3 present. The large fruit crop lost many more fruits per day than did any small crop. Its fruit loss rate was relatively constant for the first six days (11–16 percent of the original each day) and then became erractic and abruptly declined when the number of remaining fruits fell below 850. While observing the horses, I was left with the distinct impression that there were more fruits removed per day from the large fruit crop because more horses foraged there, rather than because they ate more there once they had arrived.

Much of the inter-crop variability in rates of fruit removal seemed related to the behavior of the horses. At the beginning of the experiment, small crop number 1 was directly in the line of arrival of the bulk of the horses at the time they started to moved toward the fruit crops, and crop 1 was the one that disappeared most rapidly. The large fruit crop was next in line, though down wind from from crop 1. The horses moved into it next. They discovered it when too many horses initially moved into the area of the small crop (number 1) and they started to fight amongst each other over places to feed. The fleeing horses encountered the large crop. Once the larger crop had been discovered by all horses, it became the focal area of interest for most of them. Part of its attractiveness appeared to be that a horse could feed on fruits without to close to another horse; biting and kicking was common among the horses and at least three horses were conspicuous in not tolerating other horses that were attempting to feed within 1–3 m.

Crop number 1 was exhausted during the first two days, and some horses located the two most distant small crops (number 4 and 5) on day two or three. The same individuals were repeatedly seen feeding there during the day. The remainder of the horse tended to concentrate on the large crop. However, as the large fruit crop diminished in density, again fighting was noticed amongst individuals feeding at that crop and simultaneusly, horses began to appear in greater numbers at the two most distant small crops. It is somewhat enigmatic that crop number 3 was the slowest to be eaten, since it was the same distance the large crop as was crop number 1. A major horse trail even passed through the center of crop number 3, but somehow this crop did not attract horses as did the others. The only difference that was conspicuous between its location and the other locations was that the fruit shadow of crop number 3 was slightly more shaded than were the others. However, these horses frequently forage in the shade and stand in the shade during the day, so shade was probably not a contributing factor.

A horse did not simply walk into the fruit shadow, eat the ten closest fruits, and walk on. First, some small patches of fruit within the large crop were not touched until very near the end while others were eliminated early in the life of the crop. This is because a horse often moved to a small patch of fruit and ate all of them in that patch before moving on (if not disturbed by another animal while feeding). A horse generally did not eat more than 5–20 guanacaste fruits in any one feeding bout. Once it fed at one patch and ate its fill, it then moved out of the fruit crop rather than pick up scattered fruits lying amongst the little patches. However, if a horse was disturbed by other horses, it moved while feeding and then picked up isolated fruits as well as fruits from patches. Second, the horses sometimes broke fruits by stepping on them as they walked through the crop. Fragments from these broken fruits worked their way down between the grass blades and were less frequently located by the horses than were intact fruits perched somewhat higher on the vegetation. A third source of heterogeneity in fruit removal was associated with fallen branches and especially the large fallen leaves of the palm *Acrocomia vinifera.* Fruits that fell beneath a fallen branch or spiny palm leaves were left until the very last. I was left with the distinct impression the horse was reluctant to stick the front part of its head underneath or through dense vegetation to get at a fruit. The fruits under palm leaves were the very last to be eaten and this is probably related to the 5–10 cm long, sharp spines which project in many directions from a fallen *Acromia* leaf. However, all fruits were eventually eaten by the horses. It was evident that the horses located fruits by both vision and odor.

These horses occasionally dropped fragments of fruits while chewing up fruits. Neither the small fragments nor the seeds they spit out were picked up by horses at later times, although more thorough harvest of fruit fragments might have occurred if the horses had been starving.

The horse movements to the area the fruit crops were highly predictable. Shortly after dawn, or sometime even before, two to five horses moved from the open central grassy area of the pasture to the wooded are where the fruit crops were and began feeding on fruits. After 15 to 30 minutes of doing this, these horses left and returned to the more open parts of the pasture. Throughout the first half of the morning, different horses moved to the crop and fed a short time before moving back into the pasture. In the last half of the afternoon, the process was repeated. Many horses were seen to make at least two different visits during the day to the fruit crop and many made three or four trips. The salient feature of this activity was that they were willing to walk 100–300 meters from the grazing area to the fruit crops, eat some fruit and then return to the grassy area on a repeated and daily basis.

There is no doubt that different horses consumed different numbers of fruits per day but I was not able to document these rates. All 17 horses in the pasture did eat guanacaste fruits. They ate an average of 46 to 71 fruits per horse per day up through day six (Table 2), by which day the fruit crops had been severely decimated.

Once the fruit crops had been consumed, horses were not observed to return and search the are intensely, although just as before the experiment, at least once a day an occasional horse wandered through the site of a fruit crop or stopped and grazed there.

Discussion

The situation presented to these horses represents that of a herd of horses moving into a previously horse-free piece of grass-forest habitat in which there are five medium-sized to large forest-edge guanacaste trees that have accumulated a fruit shadow beneath each near the end of the dry season. In this experiment, the horses grazed but moved periodically to the fruit crops and ate a number of fruits before they returned to grazing again, just as do range horses in similar situations when free-ranging. The horses showed a preference to feed in the large fruit crop once it was located, and showed different intensities of feeding at different small crops on a given day. Most of these horses preferred to feed in the general vicinity of other horses but some horses would not allow other horses to feed in close proximity. This suggests that the rate and pattern of fruit consumption by horses may be determined by the pattern of distribution of fruit on the ground as well as by the absolute numbers of fruits and horses present.

Because all the fruits were eventually eaten by the horses over 12 days, the rate of removal from a crop might seem to be insignificant. However, in natural circumstances there are three processes that are importantly related to the rate of removal of fruits. First, if there is a low density of horses and the fruits are being fed on near the end of the dry season, then some crops or crop fractions run the risk of being thoroughly wetted. It is only a matter of days until thoroughly wetted fruits are sufficiently decomposed that the horses will not eat them. Second, in the forest that contains guanacaste trees along grassland-forest edges, the *L. salvini* density is often high enough to harvest the seeds from the fruits almost as fast as they fall. It becomes a race between the mice and the horses as to which animal gets the seed. In short, the best fruit removal rate may well be the fastest. However, high speed of removal can occur through a few or many horses, depending on fruit consumption rates and seed spitting intensity. Third, the more guanacaste seeds swallowed per day, the greater the chance of seed-rich dung being produced by the horse. The more seed-rich a dung pile, the greater the chance that a *L. salvini* will be stimulated to thoroughly search the dung pile for seeds (Janzen 1982d).

The system clearly involves a balance between fruit traits, horse consumption behaviour, and horse numbers. Even when there are large numbers of fruits present, the horse eats far fewer in a meal than are required to fill its stomach (and then goes back to grazing for a while). This implies that some chemical trait of the fruit causes the horse to register "enough" after eating 5—20 fruits. It appears that the tree maximizes the spread of the seeds among and within the horses not only by dropping the fruits gradually (over 3—6 weeks) but by causing the horse to mix the fruit with other fodder. The result of this inter-and intra-horse dilution of seeds should be both a geographically more diffuse seed shadow and fewer seeds in any given pile of horse dung. As mentioned above, the latter is of value to the plant because it minimizes the chance the *L. salvini* in the habitat will find the seeds in that pile of horse dung.

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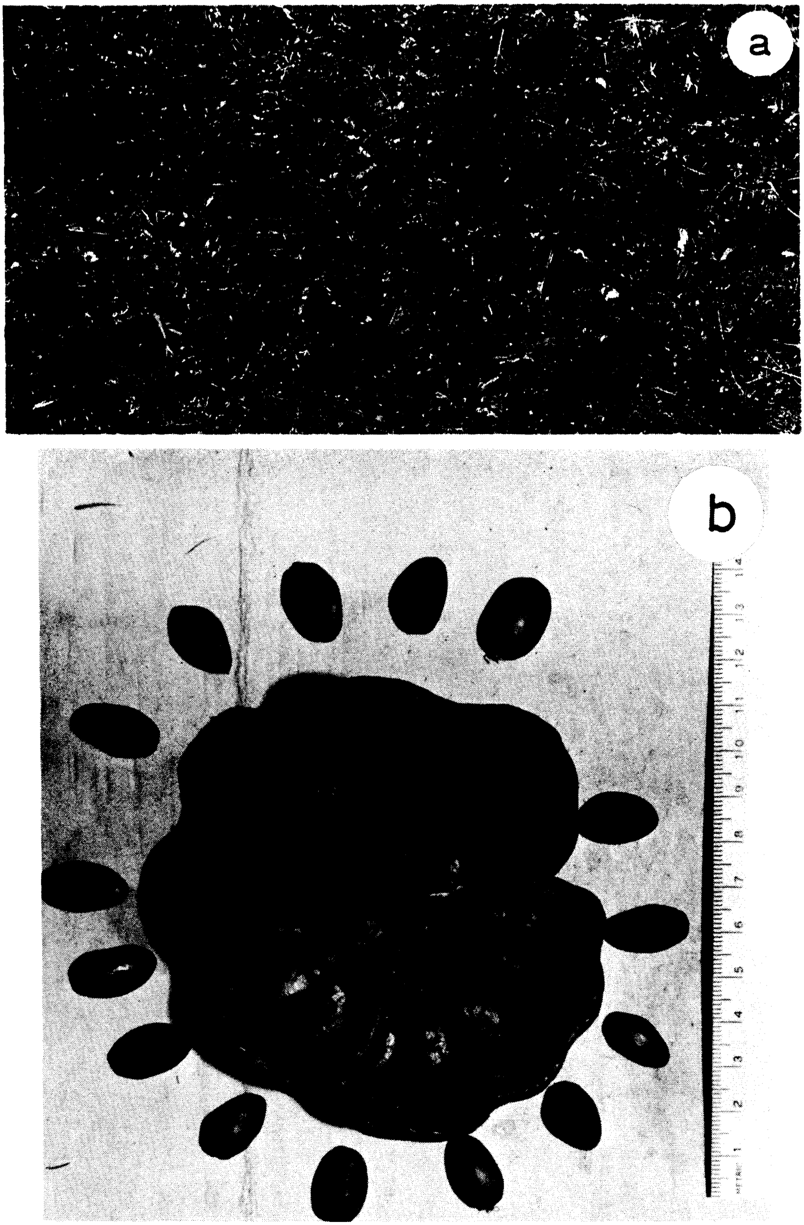
Table 1. Persistence of *Enterolobium cyclocarpum* fruits in 5 artificial fruit crops of 2 sizes fed on by 17 horses in one large pasture (start 6 May 1980).

Day	Percent of orginal pods remaining					
	Crop 1 (400 pods)	Crop 2 (5000 pods)	Crop 3 (400 pods)	Crop 4 (400 pods)	Crop 5 (400 pods)	Total (6600 pods)
1	29	86	83	75	90	82
2	12	70	84	75	72	68
3	3	55	80	61	61	54
4	2	43	80	27	27	41
5	2	31	61	18	12	30
6	1	17	51	3	2	16
7	1	12	27	1	0.3	11
8	1	2	17	1	0	3
9	0.5	0.3	1	1	0	0.3
10	0	0.1	1	0	0	0.1
11	0	0	1	0	0	0.1
12	0	0	0	0	0	0

Table 2. Number of guanacaste fruits removed each 24 hours from 5 artificial crops of two sizes fed on by 17 horses in one large pasture.

Day	Crop 1 (400 pods)	Crop 2 (5000 pods)	Crop 3 (400 pods)	Crop 4 (400 pods)	Crop 5 (400 pods)	Total eaten per day	Total eaten per day per horse
1	286	717	68	99	39	1209	71
2	67	798	0	3	73	941	55
3	37	725	17	56	46	881	52
4	4	594	0	135	133	866	51
5	0	606	78	36	36	782	46
6	3	720	40	57	38	858	51
7	1	230	94	9	8	342	20
8	0	496	38	0	1	535	32
9	1	101	63	1	all gone	166	10
10	1	8	0	4	—	13	0.8
11	all gone	5	0	all gone	—	5	0,3
12	—	all gone	2	—	—	2	0.1
13	—	—	all gone	—	—	0	0

Figure 1. a) A small portion of an accumulated fruit shadow of *Enterolobium cyclocapum* below a large adult (livestock excluded from the area). b) A normal intact fruit of *E. cyclocarpum* with seeds laid next to the fruit radial to where they occur. Santa Rosa National Park, Costa Rica.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