OIKOS 38: 150–156. Copenhagen 1982

Differential seed survival and passage rates in cows and horses, surrogate Pleistocene dispersal agents

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Janzen, D. H. 1982. Differential seed survival and passage rates in cows and horses, surrogate Pleistocene dispersal agents. – Oikos 38: 150–156.

Two female Costa Rican range cattle were fed 961 and 1407 large hard dormant seeds of the guanacaste tree *Enterolobium cyclocarpum.* Of the 823 and 1111 hard dormant seeds defecated, 66 and 86% had emerged by the end of the fifth day and 87 and 96% had emerged by the end of the tenth day. By day 10, three range horses had defecated only 45, 50 and 71% of the hard guanacaste seeds they would defecate. Compared with that of the cows, the daily distribution of seeds defecated by the horses had a proportionately lower peak, was proportionately much more skewed to the right and contained many days on which no seeds were defecated. The cows killed a maximum of 14–21% of the seeds that they swallowed while the horses killed 44–83%. A lower proportion of the seeds defecated by the cows were soft (dead or alive) than was the case with the horses, one cow did not defecate heavier seeds at a different rate than it defecated lighter seeds, and one cow produced highly variable numbers of seeds per dung pile each day. Given the working hypothesis that the large caecum of the horse selectively takes large seeds out of the flow of digesta and later puts them back into it in pulses as it cleans the caecum, I hypothesize that the differences between the cow and horse in the manner of defecating guanacaste seeds is due to the much smaller caecum of the cow not acting in this manner. Additionally, a horse chews and sorts its food more carefully at first intake than does a cow with respect to large hard objects; this may be in part due to the danger to a horse of a caecum obstructed by such objects.

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Двум коровам местного Коста-Риканского скота скормили 961 и 1407 крупных твердых семян дерева гуанакасты (*Entecolobium cyelocorpum*). Из 823 и 1111 семян, выброшенных с фекалиями, 66 и 86% найдено к концу пятого дня и 87 и 96% - к концу десятого дня. К десятому дню три местные лошади выбросили лишь 45, 50 и 71% от общего количества твердых семян гуанакасты, удаленных с фекалиями. В сравнении с коровами, кривая ежедневного количества семян, выбрасываемых с фекалиями, у лошадей имеет пропорционально более низкий пик и больше уклоняется вправо, а также насчитывает меньшее количество дней, когда выбрасываются семена. У коров погибает максимум 14-21% заглатываемых семян, а у лошадей - 44-83%. Меньшая часть семян, выбрасываемых коровами, размягчена (мертвые и живые семена), чем это наблюдалось у лошадей;коровы не выбрасывают более тяжелые семена с иной скоростью, нежели более легкие; у них ежедневно выбрасывается разное количество семян в отдельных лепешках. Приняв рабочую гипотезу, что в слепой кишке у лошадей селективно задерживаются крупнные семена из потока переваренной пищи, а затем снова импульсивно выбрасываются в этот поток при прочистке слепой кишки, я предполагаю, что различия у коров и лошадей в дефекации семян гуанакасты определяются тем, что гораздо меньшая по размерам млепая кишка коров не функционирует таким образом. Кроме того, лошадь пережевывает и сортирует пищу более тщательно при заглатывании, чем корова, имея в виду, что это - очень крупнные и твердые пищевые объекты. Это частично может объясняться опасностью для лошадей засорения слепой кишки крупными твердыми пищевыми объектами.

Accepted 27 April 1981

Introduction

Central America had a large fauna of large herbivores as recently as 10000 yr ago, and there is no doubt that they ate wild fruits and dispersed their seeds just as do the contemporary large herbivores of tropical Africa and Asia (Janzen and Martin 1981). A number of trees in Costa Rican deciduous forest produce large-seeded indehiscent fruits that appear to be the kind that would have been consumed by large Pleistocene mammals. Contemporary range horse and cattle may be viewed as ecological surrogates of the extinct large mammals; they eat these fruits and disperse the seeds in their dung. In studying the interaction between livestock and those fruits (Janzen 1981a, b), it has become clear that the numbers of seeds in a single defecation strongly influences seed survival in that it determines whether seed predator rodents will search through that dung (Janzen 1981a, b). Additionally it is clear that if different species of animals digestively kill more seeds or retain the seeds longer than do others, then they will be dispersal agents of quite different qualities. It is now clear that horses digest many seeds and a seed may spend as long as two months in a horse (Janzen 1981a, b); the present study asks whether cattle differ from horses in their seed retention time and in the number of seeds that they kill during passage, and documents the pattern of seed emergence per cow defecation. The experimental seeds are wild guanacaste tree seeds (Fig. 1) from a large native mimosaceous tree, *Enterolobium cyclocarpum.* This species was chosen because (1) the fruits are avidly eaten by range horses and cattle, (2) the comparative work with horses was done with these seeds, and (3) livestock are the primary dispersers of guanacaste seeds in contemporary Central American habitats. In view of the hypothesis that large herbivorous Pleistocene mammals were the original dispersal agents of guanacaste seeds (Janzen and Martin 1981), study of the interaction of cattle and this tree is not as artificial as it might seem. With this in mind, I fed each of two range cows a single dose of guanacaste seeds and monitored the survivorship, weight and distribution per defecation of the outcoming seeds.

Materials and methods

Animals: The cattle *(Bos taurus)* were two adult females of a race locally known as "swizo" (zebu crossed with a middle-European milk cow). Cow 1 had a new-born calf (1980) while cow 2 was barren that year (1979). They had spent their lives ranging free with a herd of about 100 zebu bulls and cows in the mixed grassland and deciduous forests of Hacienda Rosa Maria, a large cattle ranch that borders the southern boundary of Santa Rosa National Park in northwestern Guanacaste Province, Costa Rica (300 m a.s.l.). The two cows were placed in corrals about 2 wk after the beginning of the rainy season (early June) and therefore after they had begun a rainy season diet of green grass and dicot leafy browse. While corralled, throughout the experiment, both animals were fed armloads of jaragua *(Hyparrhenia rufa),* the common pasture grass growing luxuriantly in the abandoned pastures of Santa Rosa. There were dicot herbs mixed in with the diet on occasion. The grass was cut twice daily and fed in the early morning and early afternoon. The amount was deemed adequate by the owner of the cattle and as much as twice that normally gotten by a free-foraging range cow in the overgrazed pastures of Rosa Maria. However, it was not enough to satiate the cows. The fecal material appeared normal and was not conspicuously different from that produced by free-ranging individuals in the pastures a few meters from the corrals.

The three range horses that are here compared with the cows lived in Santa Rosa (see Janzen 1981a, b for a detailed description). They were adult-sized geldings, tethered in lush stands of jaragua during the rainy season, and accustomed to this diet.

Neither the cows nor the horses were used for work or released for free-ranging activity during the course of the experiments. However, they walked about in their corrals or on their tethers.

Feeding: In Rosa Maria (cows) and Santa Rosa (horses), the livestock are avid consumers of guanacaste fruits when they fall in the last third of the dry season (late March to mid-May). Cow 1 and cow 2 had undoubtedly eaten many guanacaste fruits in the wild. If these fruits are offered during the rainy season, they are also eaten eagerly even when green grass is available (though the possibility of reduced consumption rates in the rainy season has not yet been examined).

Cow 1 was induced to eat a large number of guanacaste fruits in one day in the following manner. For three days prior to the feeding of intact fruits, a small pile of de-seeded fruits were offered along with the armfuls of grass. After the cow became adjusted to confinement and accustomed to eating from a trough, she began to eat the guanacaste fruits as well. On 23 June 1980, she was given a pile of 89 fruits containing 1005 seeds. To insure that she ate all of the fruits in one day, molasses was sprinkled on the pile of fruits. All fruits were from the same guanacaste tree (growing in central Guanacaste Province, 1980 crop), fresh, and free of insect damage. That day she ate all the fruits and she spit out out 15 seeds while chewing up the fruits. While chewing her cud, she spit out another 29 seeds. On the day of feeding the fruits, she was given no grass until mid-after-noon (after about 2/3 of the fruits had been eaten). She ate the remainder of the fruits along with the grass.

Cow 2 was induced to eat a large number of fruits containing 1561 seeds over 1.5 d in the same manner, except that no molasses was sprinkled on the fruits (20–21 June, 1979). This cow spit out or regurgitated 154 seeds (9.9%) while eating the fruit. I wanted both

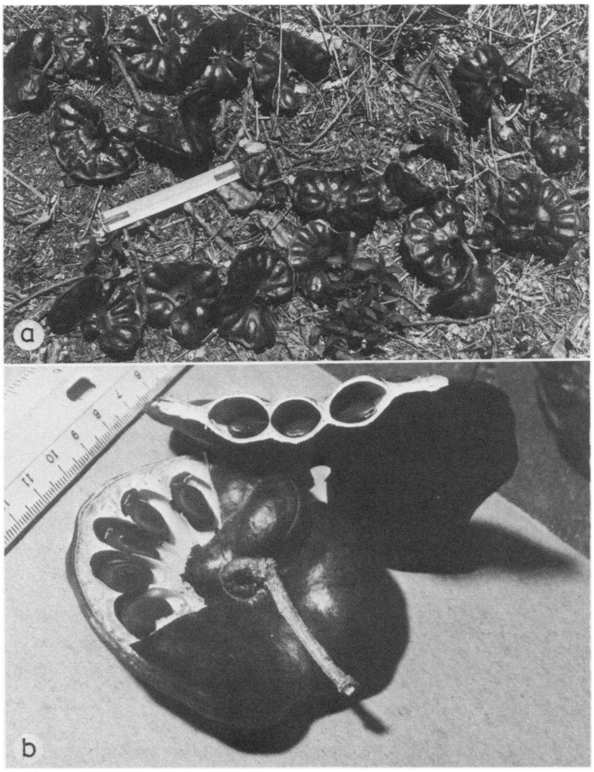

Fig. 1. a. A portion of a newly fallen crop of *Enterolobium cyclocarpum* fruits (ruler is 15 cm long). b. Indehiscent fruit of *E. cyclocarpum* with a portion of the fruit wall cut away to expose the seeds in their cavities. Santa Rosa National Park, Guanacaste Province, Costa Rica.

cows to eat a large number of seeds in one day to simulate the event of a small herd of range cows coming upon a newly fallen crop of several thousand guanacaste fruits.

The range horses customarily spit out about half or more of the seeds in the guanacaste fruits they eat (Janzen 1981a), and there is severe mortality among the guanacaste seeds that they swallow (Janzen 1981b). I wanted to get enough seeds into them in the single meal that there would be enough seeds coming out to form a distribution with a reasonable number of data points. I therefore force fed them 143 to 180 clean seeds (Janzen 1981b). This is not such a drastic departure from nature as it may seem, since in contrast to cows, horses chew the fruits so thoroughly that the seeds are no longer imbedded in fruit pulp at the time that they are swallowed. Furthermore, a free-ranging horse may swallow 200–350 guanacaste seeds per day if it has access to a large guanacaste fruit crop (Janzen 1982c).

The dung from all animals was monitored for 3 d before the experimental feeding, and no seeds were encountered. Each cow had no access to fallen guanacaste fruits in the wild for at least a month before being corralled. The three horses had not had access to wild guanacaste fruits for at least a year before the experiment.

For cow 1, each dung pat (pile) was collected separately. The seeds were washed out by putting the pat into solution in a large pail and pouring off the liquid. The large seeds have a specific gravity of about 1.3 and can easily be found in the bottom of the pail after pouring off most of the liquified dung. Cow 2's dung was pooled in 24 h aggregates. The seeds were likewise found by washing. The seeds were located in horse dung in the same manner and the seeds were pooled by 24 h aggregates (Janzen 1981b). When counting, day 1 refers to the period from dawn of the first day after feeding the seeds until dawn of the second day.

The dormant hard seeds from cow 1 were kept separate by day and weighed. These data were not collected for the other animals.

Seeds: A sample of 20 of the guanacaste seeds defecated on day 5 by cow 1 had a specific gravity of 1.319 which does not differ from the value of 1.321 recorded in the trials for the horses (Janzen 1981b). However, there are other guanacaste trees that produce seeds with a specific gravity as low as 1.24 and as high as 1.38. All seeds recorded here as "hard dormant" are viable, if I may infer from germination tests on thousands of other normal-appearing hard dormant guanacaste tree seeds (unpubl.). The seeds and fruits fed to both the cows and horses were normal in color, shape and surface texture (smooth flattened ovals). A "soft live" seed (Tab. 2) is a seed that has begun to germinate in the digestive fluid of the cow and then was defecated before it was killed. A seed was regarded as "soft live" if when placed in shallow water it continued to take up moisture and the cotyledons emerged from the seed coat. A "soft dead" seed is one that germinated in the cow and then was defecated after the digestive fluids had killed it. In addition to the seeds recorded in Tab. 1 for cow 1, there were a very few seed coat fragments (these were not censused for cow 2). In contrast, horse dung contains many fragments of guanacaste seed coats from the seeds killed by the digestive processes in the horse (Janzen 1981b).

Results

Seed survival: While at least 17–56% of the seeds that were fed to the horses survived the trip through the animal, at least 79 and 86% survived the trip through the cows (Tab. 1). However, by soaking in water a control set of 1000 of the seeds fed to the cows, it was determined that a small fraction would have germinated irrespective of the digestive abilities of the animals' guts. Subtracting this amount, I calculated that 925 and 1379 hard dormant seeds were swallowed by the two cows; 89 and 81% of these seeds were defecated by the cows in a hard dormant state (Tab. 1). The seeds used to feed the horse had been so thoroughly pre-soaked

Tab. 1. Fate of *Enterolobium cyclocarpum* seeds fed as single dose to two cows and three horses[2].

	Cow 1	Cow 2	Horse 1	Horse 2	Horse 3
Total seeds fed	961	1407	150	180	143
% seeds surviving passage	86	79	56	17	44
Total hard dormant seeds fed[1]	925	1379	150	180	143
% hard dormant seeds surviving passage[1]	89	81	53	17	39
% defecated hard dormant[1] seeds that were defecated by day 5	66	86	14	71	18
% defecated hard dormant[1] seeds that were defecated by day 10	87	96	50	71	45

1. These seeds were all viable.
2. In part based on data extracted from Janzen 1981b.

Tab. 2. Diary of seed defecation by two adult range cows fed a single dose of *Enterolobium cyclocarpum* seeds.

	Cow 1							Cow 2
Day	Number hard seeds per defecation	Total hard seeds	$\bar{X}$ hard seed weight (mg)	s.d. hard seed weight (mg)	Number soft live seeds	Number soft dead seeds	% defecated of hard seeds defecated (823)	% defecated of hard seeds defecated (1111)
0	0,0,0,0,0,0,0						961 seeds swallowed	1407 seeds swallowed
1	2,2,1,0,0,0,0	5	663	120	2		0.6	10.8
2	7,5,2,2,0	16	651	107			1.9	33.8
3	38,27,21,12,12	110	662	109	2	14	13.4	24.5
4	81,24,21,8,5,5,5,1	150	669	113	2	4	18.2	13.6
5	53,52,33,32,24,22,19,14,11	260	648	111		3	31.6	3.0
6	7,6,6,5,5,4,3,3,2,1	42	635	125		1	5.1	5.0
7	10,3,3,2,1,1,0	20	645	133		3	2.4	3.4
8	21,8,5,4,4,3,2,1	48	662	112			5.8	0.6
9	10,9,6,4,3,1,1,0,0	34	648	115		1	4.1	0.8
10	9,5,4,3,3,2,1,1,1,1	30	627	131			3.7	0.5
11	8,4,3,3,2,2,0,0	22	626	106			2.7	0.6
12	4,2,1,1,1,1,0,0	10	726	92		2	1.2	0.6
13	2,2,2,1,1,0,0	8	664	70			1.0	1.2
14	2,2,1,1,1,0,0,0,0	7	646	118			0.9	0.2
15	0,0,0,0,0,0,0		N/A	N/A				
16	5,5,4,4,3,2,0	23	638	141			2.8	0.4
17	2,2,0,0,0,0,0,0	4	661	101			0.5	0.1
18	4,3,1,1,1,0,0,0	10	604	116			1.2	0.9
19	2,2,1,1,1,0,0	7	660	97			0.9	
20	0,0,0,0,0,0,0		N/A	N/A				
21	2,2,1,0,0,0,0	5	736	97			0.6	
22	2,1,1,0,0,0,0	4	673	140			0.5	
23	1,1,1,1,0,0,0,0	4	718	65			0.5	
24	1,1,0,0,0,0	2	801	33			0.2	
25	1,0,0,0,0,0,0	1	524	N/A			0.1	
26	1,0,0,0,0,0	1	629	N/A			0.1	
27	0,0,0,0,0,0		N/A	N/A				
28	0,0,0,0,0,0,0		N/A	N/A				

that none of the controls germinated in water. However, some seeds exited in a soft (dead or alive) state and if these are removed from the calculation, then the horses defecated 17–53% of the hard dormant seeds swallowed as hard dormant seeds.

Of the 925 hard dormant seeds swallowed by cow 1, only 34 were defecated in the soft state (4%) and cow 2 defecated no soft seeds (Tab. 2). In contrast, 12–18% of the seeds defecated by the horses were soft (Tab. 1, Janzen 1981b). These differences among the cows and horses were expected since while on only a few occasions seed coats were found in the cow dung, seed coats were commonplace in the horse dung. From all of the animals except one horse, the majority of the soft seeds were dead at the time of defecation.

The weights of the seeds passing through cow 1 were recorded each day (Tab. 2). A sample of 300 seeds taken at random from the same fruit crop as produced the fruits cow 1 ate, had a mean weight of 653 mg per dormant hard seed (s.d. = 118). Since this mean is not different from the weights of any daily set of more than five seeds defecated by cow 1 or from the grand mean of all seeds defecated by cow 1 ($\bar{X}$ = 652 mg, s.d. = 119), there is no hint that seeds of a particular weight were more likely to survive the passage than were seeds of any other weight.

Duration of trip: As the cow experiments were (unavoidably) terminated after day 28 and 18 (Tab. 2), I cannot state the maximum time a cow may carry a guanacaste seed in its intestinal tract. However, it was at least 26 and 18 d in the case of these two cows. The three horses carried seeds at least 33, 60 and 48 d. I suspect that both kinds of animals may carry a few dormant hard guanacaste seeds for as much as months more, but quite different experiments will be required to demonstrate that. Certainly the percent seeds potentially carried a long time by a cow is much smaller than the percent potentially carried a long time by a horse. With respect to the transit time of the majority of the seeds defecated (i.e., in the case of cows, the great majority of the seeds swallowed), the cows and horses differed substantially. By day 5, the cows had defecated 66 and 86% of the seeds to be defecated and by day 10, 87 and 96% of the seeds had been defecated (Tab. 1). The horses on the other hand had only defecated 14, 18 and 71% by day 5 and 45, 50 and 71% by day 10. On day 5, the cows and horses are not significantly different ($t_{3\,d.f.}$ = 1.99, n.s.) but by day 10 they are ($t_{3\,d.f.}$ = 3.88, $p < 0.05$, all tests on arcsin transformed data). The hard seed defecation pattern of the cows was characterized by a rapid and continuous buildup to day 4–5 or day 2, followed by a rapid decline to a long tail (Tabs 2, 3). The horses did have a few days of seed-rich dung (Tab. 3) but the pattern is much more irregular and on many days there were no hard seeds defecated even when a horse still had numerous seeds inside. Since the

Tab. 3. Comparison of seed defecation patterns by two cows and three horses fed a single dose of *Enterolobium cyclocarpum* seeds.

Day (Number hard seeds defecated)	% of defecated hard dormant seeds that were defecated on day n Cow 1 (823)	Cow 2 (1111)	Horse 1 (80)	Horse 2 (31)	Horse 3 (56)
1	1	11			
2	2	34	5	16	
3	13	25	8	39	2
4	18	14	1	3	2
5	32	3		13	14
6	5	5			2
7	2	3			
8	6	1	29		18
9	4	1	4		5
10	4	1	3		2
11	3	1	14		2
12	1	1	4		2
13	1	1	3		2
14	1				14
15					
16	3			3	
17	1				7
18	1	1		1	9
19	1	discontinued			
20					4
21	1		3		4
22	1		9		
23	1				
24					
25			10		
26			8		9
27					
28					
29	discontinued				
30			1		4
31					
32				3	
33			1		
34–59					
60				19	
61–70					
71			discontinued	discontinued	discontinued

distribution of defecated seeds is highly skewed toward long duration time in the animal in both cows and horses, a mean of the time in the animal has not been calculated. Cow 1 and cow 2 defecated the largest number of seeds on days 5 and 2; the horses produced the largest number on days 8, 3 and 10 (Tab. 3). The respective medians are on days 5 and 3, and days 10, 3 and 13.

Duration of trip for seeds of different weights in cow 1: No batch of hard seeds defecated on one day had a mean weight different from that of the seeds defecated on any other day (Tab. 2). Since guanacaste seeds within a fruit crop are very similar in shape and volume, and since this volume is directly proportional to weight (unpubl.), I doubt that the specific gravity of the seeds in any daily defecated batch differs from that of any other daily batch. The data in Tab. 2 suggest that soft seeds pass through faster than hard ones (soft seeds have a lower specific gravity) but in fact no conclusions can be drawn because a soft seed becomes soft at an unknown point along the journey. Inspecting the raw data, I find no indication in the daily records that there is a distribution over time of very heavy or very light seeds that is different from that of medium-weight seeds.

Hard seeds per defecation from cow 1: Even though cow 1 passed seeds through rapidly and digested few of them, she did not generate a uniform or high number of seeds in each defecation. The number of hard seeds in a single defecation ranged from 0 to 81 during the period of defecation (day 1–26, Tab. 2). There were defecations containing less than 10 seeds on every day but the 3rd and 5th, and after the 5th day, defecations with 0–5 seeds were the usual case. On each day, the seeds were not evenly distributed among the 5–10 defecations. For example, even on the day of the 81-seed defecation a defecation with only 1 seed also occurred. Cow 1 defecated an average of 7.51 times per 24 h (the frequency of 5, 6, 7, 8, 9, and 10 times per day was 5, 24, 63, 80, 36, 10 respectively). Considering only the 26 day period during which she defecated seeds, there was an average of 4.26 seeds per defecation (n = 193, s.d. = 9.73). However, this average is highly misleading because of the large number of zeros and values very far above the mean. Only 20 (10.4%) of the defecations contained 4 or 5 seeds.

Force-fed fruit-free seeds vs. seeds in fruits: The cow was fed the seeds in the fruits and therefore chewed both seeds and fruits before swallowing them. This appears to have resulted in little or no scarification of the seeds. While this may be due to the more rounded edges of cow molars, I also have the impression that cows do not grind the fruit and seed mass as intensely as do horses. Cows appear to make no effort to separate the seeds from the fruit when chewing while horses chew until many of the seeds are separated from the fruit mass. When I placed my ear against the side of the head of a cow that was chewing guanacaste fruits, I but rarely heard the molars bounce off the hard seeds. However, when a horse was chewing guanacaste fruits, the sound of molars hitting a hard seed was heard frequently. The data for horses in Tab. 1 (derived from Janzen 1981b) was based on horses force-fed guanacaste seeds and therefore the seeds were not contacted by the molars. Even in this case, there was substantially less seed survival in the horses than in the cows. However, in the Janzen 1981b study, four horses were also fed entire guanacaste fruits as part of a study of the effects of continuous input of guanacaste seeds. It was clear from the early part of the seed defecation record of these four horses that when they were fed guanacaste seeds in fruits, they had the same kind of seed defecation pattern as did horses force-fed fruit-free seeds.

Discussion

Cows are quite different from horses at all levels of interaction with guanacaste seeds. When a cow eats a guanacaste fruit, it holds the long axis of its head roughly horizontal and allows almost no seeds to fall out as the fruit is chewed. A horse chews up a guanacaste fruit while holding the long axis of the head nearly vertical and allows many seeds to fall out, and actively pushes seeds out of its mouth with its tongue as it chews. Even when a cow chews its cud, it only spits out a few seeds, suggesting that guanacaste seeds are small enough and/or dense enough to pass on through the orifice into the second chamber of the stomach rather than come back up with the large particle regurgitate for a second chewing. Once the seeds have been completely swallowed, the cow digests only a few of them and defecates the bulk of those that will be defecated in the first 5–10 d after feeding. The horse digests many of the swallowed seeds and has a much more attenuated daily record of distribution of seeds among the dung.

Both the seed digestion and passage rate differences among these two animals are counter-intuitive if intuition is based on the fact that horses pass forage through rapidly (2–4 d) and do not digest it thoroughly, while forage may take 2–3 times as long to move through a cow and be much more thoroughly digested in the process (Janis 1976). I hypothesize that the difference is at least partly based on the large and well-developed caecum in the horse. I have hypothesized that many of the dense guanacaste seeds are diverted into the horse caecum and remain there to be removed in small batches as the caecum periodically cleans itself. This hypothesis is being tested at this time (Janzen unpubl.). A long residence in the caecum exposes the seed coat to potential chemical scarification for much longer than would be the case if the seed went through the intestinal tract at the same rate as the small particle digesta. Whatever the ability of the seed coat to withstand chemical degradation, the longer the seed coat is subject to this process, the more likely it is to become permeable to water and initiate germination. A germinating guanacaste seed can only survive a few hours in the horse digestive tract (Janzen study in progress). Second, this pattern of seed handling by the horse gut should minimize the seed-dung ratio in the horse's feces, with the consequences that the seed shadow will be more diffuse, and seed predators that search in the dung for seeds will be less likely to find them (Janzen 1982a, b).

The working hypothesis that the caecum is the site of seed retention by horses leads to a hypothesis as to why horses bother to spit out large hard seeds and why cows do not. A cause of colic (abdominal pain) in riding horses is obstruction of the caecal orifice with hard objects eaten along with vegetative forage (Van Soest pers. comm.). If a horse were to eat a large number of guanacaste fruits in a short period and not spit out the seeds, there could be impaction of caecal material with a high concentration of seeds. It is perhaps relevant that a common cause of appendicitis in humans is impaction of the appendix with grape seeds and other small objects. A cow has a very small caecum of 1–2 l volume. Apparently only a small amount of digesta is processed by it. Since guanacaste seeds are not strongly delayed in their passage through a cow, there is no need to postulate that they are being delayed in the caecum. On the other hand, they do not all pass through in the 4–8 d used by the vegetative digesta. I suspect that just as stones, nails and other hard objects settle to the bottom of bovid rumens and may take a long time to be passed on, the guanacaste seeds are being mildly delayed by being held up in the depths of the rumen. It is likely that the seeds unaccounted for in the two cows were lodged at this site if they were not already digested.

How the various detailed differences between the cow and the horse relate to their quality as dispersal agents of guanacaste seeds will depend on other variables such as exact sites of defecation, differential foraging by mice in horse and cow dung, foraging responses of mice to patterns of mixing of seed-rich defecations with seed-poor defecations (Janzen 1982a, b), seasonal movements of cows and horses as the dry season comes and goes, the relative effect of other dietary items on seed passage and survival, and the availability of other animals as dispersal agents. While the horse was in Costa Rica during the Pleistocene (Janzen and Martin 1981), there was no large bovid cow-like animal south of Nicaragua. On the other hand, *E. cyclocarpum* ranges north into the lowlands of Mexico, and the lowland tropics of northern Central America and southern Mexico were subject at the least to Pleistocene bison, animals that might well have treated guanacaste fruits and seeds as do contemporary cows.

It is easy to imagine that the three kinds of guanacaste seed shadows that may by generated by horses, cows, or horses and cows would be quite different not only because of the way that the guts of horses and cows treat the seeds, but because of the different group sizes and ranging patterns of the two animals. Likewise, it is easy to imagine that the details of the distribution of adult guanacaste trees over the lowlands of Central America would be quite different with any of these three seed shadows. When mastodonts, mammoths, and ground sloths are considered as yet additional dispersal agents (Janzen and Martin 1981), even more kinds of seed shadows may be postulated.

Acknowledgements – G. Vega, A. Herre, M. Bonoff, J. Petersen, A. Wolff and R. Glass aided in the field work. This study was supported by NSF DEB 88-11558 and Servicio de Parques Nacionales de Costa Rica.

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