REMOVAL OF SEEDS FROM HORSE DUNG BY TROPICAL RODENTS: INFLUENCE OF HABITAT AND AMOUNT OF DUNG[1]

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Abstract. Horses are major contemporary dispersers of guanacaste tree seeds (*Enterolobium cyclocarpum*) in Costa Rica, and probably were in prehistoric times as well. By placing 2-L and 8-L piles of fresh horse dung containing 5, 125, or 500 guanacaste seeds each in grassland and adjacent deciduous forest (Santa Rosa National Park, Costa Rica) I determined that (1) the seeds have a much greater chance of being harvested by seed predator rodents (*Liomys salvini*) from the dung in forest than that in adjacent grassland, (2) an 8-L seed-rich dung pile hides a larger absolute number of seeds from rodents than does a 2-L seed-rich dung pile, (3) a seed has a much greater chance of being harvested from a seed-rich dung pile than from a seed-poor dung pile, and (4) the grassland rodent *Sigmodon hispidus* harvests some of the germinating guanacaste seeds from the dung but leaves hard dormant seeds behind. These findings suggest that a guanacaste seed dispersal agent that defecates small numbers of seeds in many small piles of dung in grassland will be a better dispersal agent for guanacaste tree seeds than one that defecates many seeds in a few large dung piles in the nearby forest.

Key words: Costa Rica; defecation; dung; Enterolobium cyclocarpum; *grassland; Guanacaste tree;* Liomys salvini; *pasture; Santa Rosa National Park; seed dispersal; seed predation;* Sigmodon hispidus; *tropical deciduous forest.*

The progression from adult tree to seed to another adult tree involves many complex interactions with animals. I am mapping this progression in a long-term study of the population biology of the guanacaste tree (Leguminosae: *Enterolobium cyclocarpum*) in a lowland deciduous tropical forest in Costa Rica. To date, studies have described fruit consumption, seed spitting, and seed passage through the gut by the horse as a major dispersal agent (Janzen 1981*a, b,* 1982*a,* Janzen and Martin 1982), seed survival during passage through a Baird's tapir (Janzen 1981*c,* 1982*b*) and cattle (Janzen 1982*c*), seed hardness (Janzen and Higgins 1979), seed removal from fallen fruits by spiny pocket mice (Janzen 1982*d*), seed adequacy as a pure diet for spiny pocket mice and hispid cotton rats (Hallwachs and Janzen 1982*a, b*), spiny pocket mouse attraction to dung as a seed source (Janzen 1982*e*), and fruit crop parameters (Janzen 1982*f*). Here I describe an experimental study of seed removal by native rodents from fresh horse dung as a function of the amount of dung, seed density in the dung, and the habitat in which the dung fell. The vertebrate-dispersed seed that has survived the voyage through its dispersal agent is usually subject to postdispersal seed predation. The period immediately after defecation is a particularly risky portion of the postdispersal pregermination period, since the seed is tainted at this time by a highly odoriferous marker. Here I address the specific questions of whether a guanacaste tree has a different chance of being removed from fresh horse dung if that dung is:

(1) in grassland rather than in the deciduous forest 50–100 m away,
(2) in a 2-L rather than an 8-L pile, or
(3) seed poor (2.5 seeds/L of dung) rather than seed rich (62.5 seeds/L of dung).

These variables and their numerical values are realistic approximations of the natural circumstance. Free-ranging horses feed readily on guanacaste fruits and defecate the large hard seeds throughout the mix of forest and grassland occupied by guanacaste trees. They defecate dung piles containing both large and small numbers of seeds, and they produce dung piles of different sizes. In addition, Pleistocene large mammals undoubtedly did the same to guanacaste fruits and seeds (Janzen and Martin 1982), and owing to their variation in size, produced a range of sizes of dung piles equivalent to that used here.

MATERIALS AND METHODS

Study area

The experiments were conducted in the deciduous forests and adjacent grasslands (abandoned pastures; Fig. 1A) near the main administration area of Santa Rosa National Park in the northwestern Pacific coastal lowlands of Guanacaste Province, Costa Rica. The general area (Bonoff and Janzen 1980) is quite similar to the deciduous forests described by Frankie et al. (1974) near Bagaces, 55 km to the southeast.

Horses and seeds in their dung

Free-ranging introduced horses (*Equus caballus*) eat the fruits of the large native guanacaste tree (*Enterolobium cyclocarpum*) and defecate the dormant seeds

(Janzen 1981a, b). I accept as a working hypothesis the assertion that these horses behave similarly to the extinct horses that were here 10 000 yr ago (Janzen and Martin 1982), and therefore this experiment was designed to simulate what might have happened then. When range horses are feeding on guanacaste tree fruits, the number of guanacaste seeds (flattened, smooth, oval, brown, and rock hard, with masses of 300–1100 mg and a specific gravity of $\approx$1.33 [Janzen 1981a, 1982f, Janzen and Higgins 1979]) per natural dung pile (per defecation) depends on the horse, the amount of fruit eaten previously, and the amount of time since guanacaste fruits were eaten. A dung pile may contain as few as 0–1 and as many as 150 seeds. The usual fate of guanacaste seeds defecated in dung of free-ranging horses in Santa Rosa National Park is to (1) germinate immediately (a rare and lethal event), (2) remain dormant and be mixed into the litter by the action of rain, dung beetles, and dung decomposition, or (3) be harvested by rodent seed predators.

Rodent seed predators

By the process of elimination and because of familiarity with the kinds of holes left by different species of animals digging in dung, I am certain that the seeds were removed from the dung by Liomys salvini (Heteromyidae: spiny pocket mouse) and Sigmodon hispidus (Cricetidae: hispid cotton rat), two small terrestrial rodents that feed on guanacaste seeds. L. salvini is the most-common rodent on the Santa Rosa forest floor, and S. hispidus is the most common rodent in the adjacent grassland (Bonoff and Janzen 1980; see Appendix 2). L. salvini (adult mass, 30–70 g) is largely a seed predator and is a nocturnal forager, and in the daytime lives in underground burrows (Fleming 1974). It caches seeds in its tunnels and carries them there in its cheek pouches; it can carry up to three guanacaste seeds in each pouch. In the laboratory, L. salvini can live on a pure diet of hard or germinated guanacaste seeds for 1–2 mo and maintain its body mass or gain mass (Hallwachs and Janzen 1982a). It avidly harvests guanacaste seeds from dung, fallen fruits, or forest litter (Janzen 1982d, e). Under caged conditions, an individual may remove as many as 1000 guanacaste seeds from a plate in one night and cache all of them in underground chambers, and therefore it is biologically reasonable for one mouse to harvest 500 seeds from a single pile of dung.

Sigmodon hispidus (adult mass, 50–180 g) eats herbaceous-plant vegetative structures and certain species of seeds, forages throughout the 24-h cycle, and does not hoard seeds. In the laboratory it starves to death on a diet of hard dormant guanacaste seeds and does not eat them; on a pure diet of germinating guanacaste seeds it also dies, but more slowly, since it consumes up to 10–25 seeds/d. (If other food is available, it will eat 1–3 germinating seeds/d [Hallwachs and Janzen 1982b].) In nature, S. hispidus sparingly consumes germinating guanacaste seeds but ignores hard dormant guanacaste seeds.

In either forest or grassland if L. salvini had foraged at a seed-rich dung pile, all guanacaste seeds were absent from the dung surface. Such a pile is qualitatively different from one that only S. hispidus has foraged on, and this is taken into account in some of the analyses.

Experimental dung piles

The dung pile formed by a single defecation of a Santa Rosa range horse is $\approx$0.5–3 L in volume ($\approx$0.5–3 kg), and the average is $\approx$2 L for well-fed adult horses. The experimental dung piles (Appendix 3) were either 2 L or 8 L in volume; the 8-L piles were intended to mimic a dung pile of a much larger herbivore, such as a gomphothere (Janzen and Martin 1982). Dung was collected from horses on a grass diet, harvested so as to be free of hard materials that might scarify the guanacaste seeds, and mixed by hand. (Each dung pile was therefore a mix of dung from several horses.) Dung and seeds were mixed in a plastic bucket, and by inverting the bucket on the ground, a dung pile was formed; it was a roughly truncated dome $\approx$18 cm deep and 25 cm in diameter (2-L piles). In seed-rich dung piles (125 guanacaste seeds in each of 18 2-L dung piles, 500 guanacaste seeds in each of 30 8-L dung piles), many seeds were visible on the surface. In none of the 24 seed-poor dung piles (5 guanacaste seeds/2-L dung pile) were seeds visible on the surface at the time the piles were placed out. Piles were placed out between 1500 and 1700 in nonrainy weather, on the day of collection of the dung. Each of the three experiments was set out on a different afternoon and at 2-d intervals (14 July–2 August 1980, a time in the rainy season when there was only an occasional afternoon shower).

Each dung pile was placed in the center of an area $\approx$1 m in diameter that was scraped free of litter (Fig. 1B). Forest dung piles ($n = 36$) were below closed canopy on flat soil that had a thin litter layer. Grassland dung piles ($n = 36$) were on flat soil between dense clumps of jaragua grass (Hyparrhenia rufa), in stands that had not been burned during the previous dry season. Piles were placed no closer than 10–50 m from the occasional large woody plant in the grassland (Fig. 1A). In the grasslands, the pile was between the bases of jaragua grass clumps. The sites of the dung piles were chosen so as to be either 15–30 m into the forest from the grassland–forest edge or 40–80 m into the grassland from the forest edge. Each forest site was paired with a grassland site, and it was 70 m or more between each pair of sites. Each dung pile was left out for 10 nights, after which it was scraped by hand into a large plastic bag and removed from the site. Each dung pile was then searched for seeds by putting it in a large pot of water, stirring it thoroughly, and pouring

the floating material into a screen box. This material was rewashed with a stream of water and searched carefully for germinating seeds (no dormant seeds floated off). The remaining seeds were picked by hand from the dirt–rock mixture remaining at the bottom of the pot. Tests of guanacaste seed recovery from dung by these methods have always been 100% successful.

In addition to the guanacaste tree seeds, I added the large spherical nuts (2-cm diameter) of the common coyol palm (*Acrocomia vinifera*) to the dung piles (Fig. 1C). To each of the 8-L piles, 100 nuts were added; 25 and 1 coyol nuts were also added to the seed-rich and the seed-poor 2-L piles, respectively. Neither *Sigmodon hispidus* nor *Liomys salvini* harvests clean coyol nuts. The coyol nuts were added to the dung out of curiosity, to serve as an indicator of collared peccary foraging, and because they probably appeared in the dung of large Pleistocene herbivores in this habitat. Horses do not swallow the nuts, but cattle do.

Rodent census

There are no censuses available for either *L. salvini* or *S. hispidus* for this habitat (see Fleming 1974 for a *L. salvini* density estimate for a similar habitat). However, what is important is how many animals occur in the vicinity of a dung pile, not how many there are per unit area. Removal live-trapping (Sherman aluminum $8 \times 8 \times 23$ cm live traps, oatmeal–peanut butter bait or germinating guanacaste seed bait) was used to ascertain minimum numbers of animals of the two species in the vicinity of the dung piles.

Oatmeal–peanut butter-baited trap censuses were conducted by centering an approximately straight line of 10 traps on a dung pile the night after the dung pile was collected (i.e., night 11 of the experiment); the traps were placed at five-pace (4.5-m) intervals, and 1 of the 10 traps was placed at the edge of the bare area cleared for the dung pile. The following night, 2 (at 2-L dung piles) or 3 (at 8-L dung piles) traps baited with germinating guanacaste seeds were placed at the margins of the bare area, and in the bare area was placed a fresh dung pile that lacked seeds (Fig. 1B). On the top of this pile I placed 10 hard dormant guanacaste seeds along with 3 germinated seeds. The purpose of this elaborate bait was to capture rodents that had been unwilling to enter the traps for oatmeal–peanut butter bait, but would enter for germinating seeds. Only 20 of the total of 36 dung piles in each habitat were censused for rodent presence because not enough traps were available to do more. Which piles were to be trapped was determined by starting with the first pair of piles in an experiment and continuing until I ran out of traps.

Further details on materials and methods (Appendix 1) must be considered if the reader is to compare these results with other studies. Error estimates in this paper are given in all cases as SD.
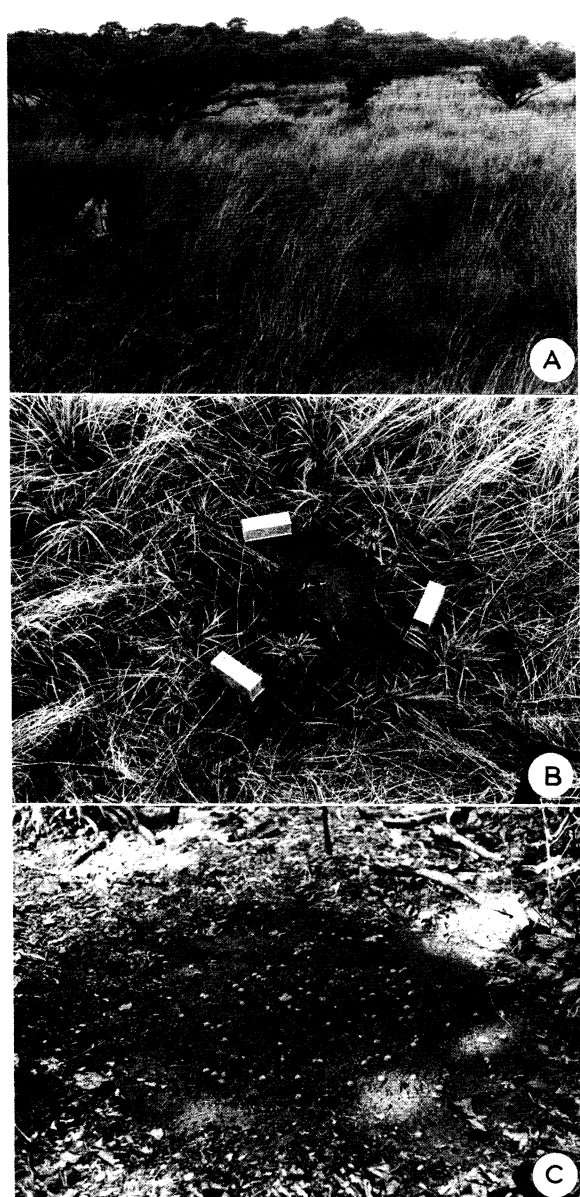

FIG. 1. (A) *Hyparrhenia rufa* grassland in which the seed-poor 2-L dung piles were placed (multibranched shrubby trees behind person are *Crescentia alata*); a dung pile is at the feet of the person. (B) An 8-L dung pile in grassland being used as bait in mouse census; there are 3 germinated and 10 dormant guanacaste seeds on the top of the pile. (C) An 8-L seed-rich dung pile in forest 10 d after placement; the 1–2 cm deep layer of dung is approximately outlined by the distribution of spherical coyol nuts.

RESULTS

General fate of dung piles

During the first two nights, the dung piles were lightly visited by ≈12 species of dung beetles, ranging in size from the 2–3 g *Dichotomius colonicus* to minute *Onthophagus* weighing only a few milligrams. By the

end of the 2nd mo of the rainy season, the time of this study, the density of these beetles was low enough that the beetles did not generally destroy the shape of the dung pile but blurred its interface with the soil. In the grasslands this blurring was minimal, but in the forest it was more thorough, and occasionally the dung pile was even somewhat flattened by their activity. However, the dung-churning activity of the dung beetles in the forest is difficult to distinguish from the intense activity of *Liomys salvini* mining for guanacaste seeds.

In the forest, usually sometime during the first two nights, the pile was found by *L. salvini* and, if the pile was seed rich, thoroughly mined for seeds. Usually all seeds visible from the outside disappear during the first night that the dung pile was torn apart by the mice. The mining by the mice flattened the dung pile to 1–4 cm in depth and spread it out over about twice the area originally occupied (Fig. 1C). Within several days after the dung pile was mined by the mice, a light rain made a slurry of the upper layer, which upon drying left a solid crust, which was not broken into during the remainder of the nights that the dung pile was exposed to the mice. I infer that most if not all the seeds removed by *L. salvini* were removed during the first couple of nights that the dung pile was mined. Seeds missed at this time are unlikely to be located by *L. salvini* until they germinate or until found by random search in the litter, later in the year.

In the grassland when a seed-rich pile did not have most of its seeds removed (i.e., it was not found by *L. salvini*), the pile remained dome shaped, and some of the guanacaste seeds were removed from the surface as they germinated or as the cotyledons from the germinating seeds pushed up through the dung. It appeared that the *Sigmodon hispidus* were taking guanacaste seeds off the dung surface as they became available through germination, or at a low rate throughout the 10 nights that the dung piles were exposed. At only 3 of the 36 dung piles in grassland, a *S. hispidus*-sized animal dug (sparingly) into the dung pile in pursuit of germinating guanacaste seeds.

Forest vs. grassland

In all three experiments, more seeds remained in the dung in the grassland than in the corresponding dung piles in adjacent forest (Appendix 3). In the 8-L piles in the forest, only 4.6% of the original 7500 seeds remained (1 germinating seed, 3 seedlings, 341 hard dormant seeds), while in the 8-L piles in the grassland, 75.3% of the original 7500 seeds remained (599 germinating seeds, 19 seedlings, 5027 hard dormant seeds). The bulk of the missing seeds in the 8-L grassland piles were removed from the three piles that had been foraged in by *L. salvini*. In the forest seed-rich 2-L piles, 12.8% of the original 1125 seeds remained (144 hard dormant seeds), while in the grassland seed-rich 2-L piles, 94.8% of the original 1125 seeds remained (26

germinating seeds, 17 seedlings, 1024 hard dormant seeds). Furthermore, 87% of the seeds to survive in the forest 2-L seed-rich piles were in the one dung pile that *Liomys* did not forage in. Likewise, 53% of the surviving seeds in the 8-L forest dung piles were in pile number 13, a pile only weakly foraged in by *L. salvini,* as evidenced by some guanacaste seeds remaining on its surface. In the forest seed-poor 2-L piles, 68.3% of the original 60 seeds remained (1 germinating seed, 40 hard dormant seeds), while in the grassland seed-poor 2-L piles, 98.3% of the original 60 seeds remained (1 germinating seed, 1 seedlings, 57 hard dormant seeds). In all three contrasts, the number of seeds remaining per dung pile in the forest is significantly lower than that in the corresponding set of grassland dung piles (Mann-Whitney U tests, $P < .01$).

Instead of viewing the comparison as between forest and grassland, one may choose to contrast piles foraged in by *L. salvini* and piles not freely foraged in by this small rodent. In this case, forest pile 13 of the 8-L piles would be deleted from the set of forest piles because it was missed, and grassland piles 8, 22, and 30 would be deleted from the set of corresponding grassland piles because they were foraged in. If one again calculates the differences between the forest and grassland with these modified samples, the differences become even greater. (Compare the second set of means for forest and for grassland in Appendix 3A and in 3B.)

No difference in removal was found for the coyol palm nuts in any of the comparisons of forest and grassland or between other pairs of dung types (Appendix 3). Neither of the rodents that eat guanacaste dormant or germinating seeds can feed on coyol nuts, and therefore are not likely to carry them off. The occasional coyol nut that was missing from the dung piles was probably removed by a naive rodent that carried it a metre or so and dropped it after trying to open it (*L. salvini* was found to do this in preliminary trials).

Large vs. small dung piles

Within the grassland, the 8-L dung piles retained a significantly lower percent of their hard dormant guanacaste seeds than did the seed-rich 2-L dung piles ($\bar{x}_{15} = 66.9 \pm 29.6\%$; $\bar{x}_9 = 91.1 \pm 2.9\%$; Mann-Whitney U test, $P < .01$). This is true even if the three 8-L dung piles heavily foraged in by *L. salvini* are removed from the grassland experiment. However, if the germinated seeds are added into the census, there is no difference between the percentage remaining in the two sizes of dung piles, irrespective of whether the dung piles heavily foraged in by *L. salvini* are considered.

Within the forest, the 8-L dung piles retained the same percent of their guanacaste seeds as did the 2-L seed-rich dung piles ($\bar{x}_{15} = 4.7 \pm 8.8\%$; $\bar{x}_9 = 12.8 \pm$

32.7%; Mann-Whitney U test, $P > .05$). Seed-rich 2-L dung pile number 1 was not found by $L.$ $salvini$ and therefore is not equivalent to the other forest dung piles. When this data point is deleted, and pile 13 of the 8-L dung piles is deleted for the same reason, the percent seeds retained by the two sizes of dung piles in the forest is still not different.

If the forest 8-L piles ($n = 14$) and 2-L seed-rich piles ($n = 8$) that were heavily foraged in by $L.$ $salvini$ are compared for the absolute numbers of remaining seeds, significantly more seeds remained in the 8-L piles than in the 2-L seed-rich piles ($\bar{x}_{14} = 11.6 \pm 9.6$; $\bar{x}_8 = 2.8 \pm 1.7$; Mann-Whitney U test, $P < .01$). In the grassland 8-L dung piles, many more seeds remained than in the 2-L seed-rich dung piles, if the piles foraged through by $L.$ $salvini$ are excluded from the comparison (piles 8, 22, and 30). However, the 8-L piles initially contained four times as many seeds as did the 2-L seed-rich piles, and therefore the comparison is meaningless. The number of seeds removed per 8-L dung pile ($\bar{x} = 45.7 \pm 34.0$) is significantly greater than the number removed per 2-L seed-rich pile ($\bar{x} = 6.0 \pm 3.9$; Mann-Whitney U test, $P < .01$). In summary, if the dung is seed rich, the percent seeds it loses to small rodents is the same whether it is an 8-L or 2-L dung pile. However, in the forest an 8-L dung pile retains a larger number of seeds than does an equally seed-rich 2-L dung pile, and in the grassland an 8-L pile has more seeds removed from it than does an equally seed-rich 2-L dung pile.

Seed-rich vs. seed-poor dung piles

In the forest, the percent guanacaste seeds remaining in the seed-rich 2-L dung piles was significantly less than that remaining in the seed-poor 2-L dung piles ($\bar{x}_9 = 12.8 \pm 32.7\%$; $\bar{x}_{12} = 66.7 \pm 39.4\%$; Mann-Whitney U test, $P < .01$). Seed-rich 2-L forest pile 1 was not foraged in by $L.$ $salvini,$ and therefore may be deleted from the experiment in a comparison of the foraging effectiveness of this mouse at two different values of seed richness. However, such a deletion is not biologically reasonable because there is no way to know which of the seed-poor 2-L forest piles were not visited by $L.$ $salvini.$

Likewise, in the grassland a significantly lower percent of the seeds remained in the seed-rich 2-L piles than in the seed-poor 2-L piles ($\bar{x}_9 = 91.1 \pm 2.9\%$; $\bar{x}_{12} = 95.0 \pm 9.0\%$; Mann-Whitney U test, $P < .01$). The same difference is true for the numbers of seeds removed, but this is a nonsense comparison since there were so many more seeds available for removal from the seed-rich 2-L piles than from the seed-poor 2-L piles.

Rodent abundance

Using oatmeal–peanut butter bait in Sherman live traps (11th night of the experiment), 77% of the animals caught in the forest sites were $L.$ $salvini$ ($n = 35$), while in the grassland 94% of the animals caught were $S.$ $hispidus$ ($n = 32$; Appendix 2). These proportions are in rough agreement with the results of several thousand trapnights associated with other studies in these two habitat types (Bonoff and Janzen 1980, D. H. Janzen, $personal$ $observation$). The number of rodents per trapnight ranged from 0.13 to 0.27 over the six sites.

Using germinating guanacaste seeds as bait in Sherman live traps next to fresh dung piles on the 12th night of the experiment, the number of rodents per trapnight ranged from 0.03 to 0.07 over the six sites (Appendix 2). If these data are pooled with the records of rodents caught in the oatmeal–peanut butter-baited trap placed next to the scar left by collecting the first dung pile, an average of 0.8 $L.$ $salvini$ was caught at the exact site of each of the forest dung piles, and an average of 1.15 $S.$ $hispidus$ was caught at the exact site of each of the grassland dung piles. Only one $S.$ $hispidus$ was caught at a forest dung pile, and only one $L.$ $salvini$ was caught at a grassland dung pile.

It is clear that germinating guanacaste seeds are an adequate bait for both $L.$ $salvini$ and $S.$ $hispidus$ (Appendix 2). This is not surprising as I have captured large numbers of $L.$ $salvini$ using either hard and dormant, or germinating guanacaste seeds as bait in other studies in this habitat. The interest of $S.$ $hispidus$ in germinating guanacaste seeds was somewhat of a surprise because they cannot survive on a pure diet of them in the laboratory (Hallwachs and Janzen 1982b) and because they do not eat all those available on the surface of the dung pile, to say nothing of those deep in the dung (which they do not dig for).

On four different occasions, two $L.$ $salvini$ were taken at the same forest dung pile (one with oatmeal–peanut butter bait and another with germinating guanacaste seed bait the following night). This event was particularly dramatic at the site of the 2-L seed-poor dung piles, since there were two such cases at this site and at both dung piles, the five guanacaste seeds buried in the dung were not removed.

I view this trapping program as adequate to demonstrate that $L.$ $salvini$ is much more abundant in the forest than in the grassland, and that $S.$ $hispidus$ is much more abundant in the grassland than in the forest. It also shows that there are enough animals present in each habitat to account for the missing seeds over a 10-night period. If only those $L.$ $salvini$ trapped (33 animals in total) had removed seeds from the forest piles, each animal would have had to remove only 247 guanacaste seeds to account for the 8155 missing. However, there are undoubtedly many more $L.$ $salvini$ present at the sites than were captured, if for no other reason than the fact that only 20 of the 36 forest dung piles were censused. Likewise, in the grassland 1815 seeds were removed, and 39 $S.$ $hispidus$ were captured at the 20 grassland dung piles (out of 36) that were censused for rodents. Each $S.$ $hispidus$ would have to

eat only 47 seeds over 10 nights to account for this number of seeds. Furthermore, it is clear that at a few grassland dung piles the *S. hispidus* had substantial assistance from *L. salvini* in removing seeds (e.g., grassland 8-L dung piles 8, 22, and 30).

Subjective impressions

As mentioned in the materials and methods, it was easy to predict the number of seeds remaining by a glance at the intact dung pile on the day of collection. Those with severe seed removal were flattened down to ≈2–4 cm in depth and the surface of the pile finely divided. No guanacaste seeds were visible, but coyol nuts were scattered about on the surface. Occasionally there was an empty guanacaste seed coat on the surface of the dung. The seed-rich 8-L and 2-L piles that still contained most of their guanacaste seeds had a very different appearance. Numerous guanacaste seeds were visible on the surface of the dung and most of these were hard and dormant. There was an occasional seedling poking up through the dung. The dung pile not only retained its original domed shape, but the surface was dotted with relatively large lumps of horse dung (the individual units characteristic of horse dung).

Coyol nuts were sometimes rolled 2–5 cm from the edge of the dung mat and a guanacaste seed was found occasionally at this distance at a seed-rich grassland pile with few seeds removed. At one grassland pile, a *S. hispidus* had constructed a small nest in the grass at the edge of the cleared area and pulled two coyol nuts into it as well as three hard guanacaste seeds (along with the remains of at least 10 half-eaten germinated guanacaste seeds).

If a grassland dung pile still contained a large number of guanacaste seeds, the surface of the pile usually had 10–50 chipped seed coats and cotyledon fragments scattered about on it, and up to twice as many fragments on the bare soil immediately adjacent to the dung pile. Observation of animals in the laboratory leads me to believe that these uneaten cotyledon parts are refuse left by *S. hispidus* rather than by *L. salvini*, as the latter species tends to eat all of a germinated seed's embryo or carry it off to a burrow.

DISCUSSION

The results of the three sets of experiments show clearly that a guanacaste seed defecated by a horse (1) is much less likely to remain in the dung for the first 10 d after defecation in the forest than in the adjacent grassland, (2) has the same probability of surviving in a large pile of horse dung as in a small pile of horse dung, if the density of seeds in the dung is high and equal in both, and (3) is more likely to survive if accompanied by only a few rather than many guanacaste seeds in a particular pile of horse dung. The primary cause of these patterns appears to be the relatively high interest in guanacaste seeds by *Liomys salvini* as compared with *Sigmodon hispidus* and the restriction

of *L. salvini* largely to forested habitats. While this study was directed at only a subset of the challenges to guanacaste seeds, it is important to stress at this point that a seed that escapes rodents in the grassland is still confronted with two major abiotic mortality factors once it becomes a seedling: severe dry season desiccation and fire.

While *L. salvini* were very thorough in locating and mining the seed-rich forest dung piles, they did miss one pile entirely (a 2-L pile) and only weakly searched another (an 8-L pile). If these piles had been left out for many more weeks, I suspect that they would eventually have been found and mined by *L. salvini*, as this was found to be the case in preliminary trials of longer duration before the experiments reported here. Another study just completed in the same forest (Janzen 1982*e*) shows clearly that the odor of the dung piles aids the mice in locating them. Or, to put it another way, the mice respond to a large and smelly novel object in their habitat by going to it and exploring it. As the dung pile decomposes and its odors begin to blend with those of the general litter background, it becomes progressively less of an unusual object, and correspondingly, its discovery will have to be through random search. This means that an unlocated dung pile will probably have to wait longer to be searched, the longer it goes undiscovered.

In the grassland, the situation appears to be quite different. In a grassland study preliminary to the one described in detail here, I found most dung piles to retain their seeds for as long as 45 d, even when there was a low density of *L. salvini* in the grassland along with the high density of *S. hispidus*. It appears that if the *L. salvini* density is low, the dormant hard guanacaste seeds in a horse dung pile may escape intense seed predation entirely.

That the percent seeds removed from the 8-L and 2-L forest seed-rich dung piles was not different did not come as a surprise, as I found in preliminary experiments that it is virtually impossible to satiate the *L. salvini* with anything approximating realistic amounts of dung–seed mix. In one trial, 5000 seeds were mined out of 15-L conical piles of dung in two nights from each of five dung piles in habitats where four to six *L. salvini* were live-trapped at single dung piles over three nights of trapping with oatmeal–peanut butter bait. By observing caged animals tearing apart dung balls and by examining dung piles only partly mined by *L. salvini*, it appears that the animals literally burrow through the dung from the top to bottom and sides to center, pouching seeds as they find them. Once the seed density is in the range of a few per 0.5 L of mined dung, it appears that *L. salvini* either lose interest or simply cannot find the seeds among the bulk of dung. If there is more dung in the pile, then a greater absolute number of seeds is left behind at this point. Since the ratio of seeds to dung was the same in the two sizes of seed-rich piles, it is not surprising to find

that the percent seeds left behind was approximately the same as well.

In the grassland, the seeds were primarily harvested off the surface of the piles by *S. hispidus*, and not thoroughly even from this exposed position. I cannot explain why relatively more seeds were removed from the surface of the grassland 8-L dung piles than the 2-L seed-rich dung piles, as is required for the two piles to lose the same percent of their seeds (since the 8-L dung piles have a smaller surface to volume ratio than do the 2-L dung piles).

The very striking difference in seed removal from forest seed-rich and seed-poor dung piles appears to be the result of the way that *L. salvini* hunts for seeds. In an as yet unpublished study, I have found that after being attracted to a novel object in the habitat, the mouse explores it superficially, and if no seeds are found, it neither mines into it nor later explores it more thoroughly. However, if even one seed is found, the entire dung pile is thoroughly mined for seeds. In the present experiment, not only are the seeds buried within the dung pile, but the density is so low that a cursory mining inspection by the mouse is unlikely to uncover a seed. Where some but not all seeds were removed from a forest 2-L seed-poor dung pile, the pile was very likely searched by a *L. salvini* that found one seed but could not find all of them because seeds were too diluted among a large bulk of dung.

Since all the dung piles were placed among mice initially naive to horse dung with guanacaste seeds, the results with the seed-poor dung piles represent the result when large herbivores are so rare that an individual mouse encounters seed-rich large-mammal dung only a few times in its lifetime. However, even seed-poor dung piles cannot be expected to contain surviving guanacaste seeds for more than a few days if they are put down in an area where mice have been trained by other experiments to know that horse dung signifies guanacaste seeds (Janzen 1982*e*).

I suspect that a germinating guanacaste seed generates substantially more of an odor cue than does a hard dormant guanacaste seed. I tried to minimize this confounding effect by intially removing seeds that would be likely to germinate during the experiment; however, the controls showed that at least 2.7% of the seeds germinated during the experiment and therefore were not subject to the same search rules as were the hard dormant seeds. The absence of germinating seeds from piles foraged in by *L. salvini* could be due to extremely accurate location of germinating guanacaste seeds by this mouse or by seed removal to a level whereby through chance none of the small number of remaining hard seeds was a germinator. No numerical information can be derived from the germinating seeds found in the grassland dung after the 10th d because the *S. hispidus* selectively removes germinating seeds. However, the number of germinating seeds in the seed-rich grassland piles is substantially greater than would

be expected by applying a 2.7 germination percent to a sample of 500 or 125 seeds (Appendix 3A and B). I suspect that some process in the intensely insolated grassland piles led to increased guanacaste seed scarification.

The partitioning of the two species of small terrestrial rodents between the two major habitats is compatible with their feeding biologies, since the seeds that *L. salvini* eats are largely missing from the grassland, and the grassy and herbaceous vegetation eaten in bulk by *S. hispidus* are largely missing from the forest. However, as is clear from the occasional grassland pile with most of its seeds missing and from the trapping records in Appendix 2, each of the mice does occasionally forage in the habitats occupied primarily by the other species. The detailed locations of these seemingly misplaced individuals are highly predictable. In the forest, all *S. hispidus* were caught in or near small treefalls or when the end of a trapline came within a few metres of the forest edge. To get to those treefalls well within the forest, the *S. hispidus* must occasionally cross unbroken forest as well. However, in a forest rich in *L. salvini*, the occasional germinating guanacaste seed or seedling taken by *S. hispidus* is probably a trivial amount of mortality when compared with that caused by the *L. salvini* that seek guanacaste seeds wherever they occur (in fruits, in dung, loose in the litter) and eat them in all stages. *L. salvini* forages freely in treefalls, and a dung pile placed in one is probably no less likely to be mined for seeds than is one in adjacent forest.

In the grassland, *L. salvini* are most frequently trapped near isolated shrubs or rock outcrops, but their capture sites are not restricted to them. These animals are not necessarily short-term transients even when found several hundred metres from the forest, as evidenced by the fact that if there is a mouse that is taking seeds from dung near a tree or bush in the grassland, it can be counted on to continue to do so for at least 2 mo. The relative frequency of these *L. salvini* in the grassland is accurately represented by the observation that 3 of the 24 seed-rich grassland piles of dung put out were heavily mined by them.

The fate of the seeds removed from dung by *L. salvini* and *S. hispidus* in various habitats in Santa Rosa is currently under study (as well as that of the seeds that remain). However, it is easy to state at this point that easily 99% of the guanacaste seeds harvested by *L. salvini* are later eaten from their underground caches. It appears that *S. hispidus* either kills the germinating seed (by eating all or part of the seed) or ignores it. The closest approximation to caching seeds was the nest with three hard seeds in it a few centimetres from the dung pile. In captivity, *S. hispidus* shows no interest in hoarding hard or germinating guanacaste seeds, though it may carry an individual germinating seed into a nest to eat it. Since piles of seed-rich dung were left with many visible dormant seeds on their

surface in the presence of a high density of *S. hispidus* that were eating germinating seeds at the dung pile and could be baited into the trap with germinated seeds, I conclude that *S. hispidus* is a trivial force in moving hard dormant seeds away from the concentration in the dung pile. *S. hispidus* does not mine into dung for guanacaste seeds as evidenced by the lack of mining into piles exposed to it, and by the nearly perfect retention of seeds and seedlings by seed-poor dung piles (1 germinating seed lost out of the 60 initially placed in the dung).

Another study in progress shows that earlier in the rainy season, dung beetle density at horse dung piles may be great enough to result in guanacaste seeds being inadvertently buried by falling down the burrows made by the larger dung beetles below the dung. The dung beetles do not incorporate seeds as large as guanacaste seeds into the dung they are burying. At the time of the present experiments (last half of July), dung beetle density and foraging activity were so low that they did not make more than zero to five holes beneath each dung pile, and this is not adequate to account for removal of more than one to two guanacaste seeds (D. H. Janzen, *personal observation*). However, guanacaste seeds that fall down dung beetle burrows are probably safe from small rodents until they germinate.

L. salvini and *S. hispidus* may seek out horse dung in search of dung beetles as well as seeds, since they consume these beetles unenthusiastically in the laboratory. However, unless a nocturnal rodent burrows through the horse dung, it is unlikely to capture the common nocturnal species of large dung beetles because they do not roll balls of dung away from the pile but rather bury it in tunnels below the dung pile. *S. hispidus* clearly does not tear dung piles apart, and *L. salvini* does not do so if it does not encounter seeds on the surface, which implies that the search of the pile is not highly motivated by search for dung beetles.

From the viewpoint of the maternal parent guanacaste tree, different large herbivores will be of different value as dispersal agents. Ignoring what happens in transit through the animal (where there may be substantial seed mortality and rejection [Janzen 1981a, b]), the defecation pattern of the animal or the animals will determine how many seeds land in predator-rich habitats and how many land in predator-free habitats. For example, from this standpoint alone, the tapir (*Tapirus bairdii*) may be an excellent dispersal agent of guanacaste seeds since it preferentially defecates in water (Janzen 1981c), and *L. salvini* does not forage in water. On the other hand, a horse that moves into the forest to eat guanacaste fruits and then moves well out into the grassland to defecate the seeds may cause many seeds to escape from *L. salvini* but expose those same seedlings to severe desiccation and fire. Perhaps when we know more of the defecatory seed shadows generated by large mammals this discussion can be

elaborated, but more hypotheses are not useful at this time.

While I have only weakly explored this subject, I am certain that the dung of some species of mammals may be repellent to *L. salvini* and perhaps other vertebrate seed predators as well. When I put out fresh range cow dung with guanacaste seeds in it in the Santa Rosa forest along with horse dung, the *L. salvini* removed the seeds from the horse dung in the first one to two nights and required as many as 7 d to remove the seeds from the much more liquid cow dung. Peccary feces in the same forest remains undisturbed, even when rich in species of small seeds that the mice eat readily in the laboratory. Deposits of bat feces and chewed pellets rich in intact *Ficus* seeds on the forest floor are ignored by *L. salvini* that are busily harvesting other species of seeds only a few centimetres away.

While I have not yet surveyed large-mammal dung for this trait, I suspect that there may be interspecific differences in the location of defecated seeds relative to the surface of the dung piles made by different species. Especially in very liquid dung, such as that from some range cattle on a rainy season diet of water-rich foliage, the seeds may sink to the bottom where they will be located by only the most determined *L. salvini*.

A horse feeding on a steady diet of guanacaste fruit, to say nothing of what happens when it eats fruit intermittently, does not defecate a uniform density of guanacaste seeds per day or per dung pile (Janzen 1981a, 1982c). Piles with a high concentration of seeds may be quite lethal, in that they lead to thorough dung search by *L. salvini*. In such a case, it appears that in a large dung pile, a slightly greater proportion of seeds may survive than in a small pile. For example, using the mean values generated by the present experiment, an animal that averages 500 guanacaste seeds/8-L dung pile will generate 11.6 surviving seeds per dung pile if all piles are found by *L. salvini*, while if those 500 seeds are spread out among four 2-L dung piles, each one-fourth as large, there will be an average of 9.5 surviving seeds per 500 seeds. Two seeds may seem like a small difference when dealing with so many seeds, but by this time in a recruitment attempt the tree no longer has tens of thousands of surviving seeds. Furthermore, when considering selection for traits that put fruits into one animal as opposed to another, or fruit traits that influence the way seeds exit from the animal, it is relative differences that matter, rather than absolute amounts.

The value of an animal that defecates a few seeds in a large volume of dung is evident from this study. The parent tree may evolutionarily influence this seed dilution by the kind of animal into which the seeds are directed, by the pattern of presentation of fruits to the animal, by fruit traits that determine the rate at which the animal eats the fruits, and by seed traits that influ-

ence seed passage rate. Guanacaste trees are undoubtedly involved in all four kinds of selection. First, horses are big animals, and therefore a large seed may be hidden in the dung. Second, the fruits fall from an individual tree over 3–6 wk (a few each day); this presentation pattern seems ideal to distribute the seeds maximally among the large mammals in the area and among their dung. Third, when hand feeding guanacaste fruits to horses (Janzen 1981b) and watching them feeding free on artifically placed fruit crops, it became clear that after a horse has eaten 10–20 fruits it stops eating them. This number of fruits has a volume far less than the stomach volume of a horse. Later in the day, the horse again will feed on guanacaste fruits if available. It appears that the fruit contains some chemical properties such that it is desirable to eat only a small amount at a time. Finally, guanacaste seeds do not pass quickly through a horse along with the other digesta (Janzen 1981a); this results in their exit being spread out over many days of defecation. The slowness of passage through the horse is maximized by having very dense seeds, and this trait is certainly under evolutionary control of the parent tree.

A small literature is emerging which shows that the microhabitat in which a dispersed seed lands can strongly influence the probability of that seed being taken by a rodent seed predator. Proximity to an ant nest may be critical to whether a seed is dispersed or eaten by an ant or rodent (O'Dowd and Hay 1980, Perry and Fleming 1980, Davidson and Morton 1981). Proximity to a rodent shelter from vertebrate predators may alter both the chance of a seed being preyed on by a rodent and that rodent's realized interspecies seed preferences (Reigel 1941, O'Dowd and Hay 1980, Hay and Fuller 1981). Seeds in bird feces seem to be of lower interest to *Peromyscus* mice than those in fruit or clean in the litter (Stiles 1980). *Peromyscus* mice will, however, harvest *Opuntia* cactus seeds from jackrabbit pellets at certain times of year (Reigel 1941). Dung that dries rapidly (hardens) and is in microhabitats where it is quickly covered by shifting sand may protect its seeds from seed predation by baboons (Hamilton et al. 1977). While I am not in a position to enumerate all the reasons why *L. salvini* does not extend its foraging range into the grassland, it is clear that its habitat-specific foraging behavior has a strong influence on guanacaste seed survival in the present study.

In conclusion, the exact location of a guanacaste tree seed shadow matters in more than just its location with respect to physical environmental heterogeneities. Postdispersal seed predation by rodents in a guanacaste tree's habitat is a complex event related to more than just the presence of rodents and seeds. The relationship of seeds to the dung in which they are found is more than that of a simple container and contents. The reproductive sequence involving the tree,

horse, and rodents is clearly one that would be severely disrupted by the removal of the horse from the system, as must have happened ≈10 000 yr ago.

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APPENDIX 1

Addendum to materials and methods

Study area.—Santa Rosa National Park was a functional cattle ranch for at least 150 yr, but was taken out of operation in the mid-1960s and virtually all cattle removed by mid-1978. The sites for the three experiments were chosen such that within them, nearly treeless jaragua (*Hyparrhenia rufa*) grassland of several hectares abuts directly against 10–20 m tall forest patches of equal or greater extent. The forest is away from riparian sites, on gently rolling topography crossed by small plateau edges, and contains at least the following characteristic trees and shrubs: *Allophyllus occidentalis, Brysonima crassifolia, Gliricida sepium, Enterolobium cyclocarpum, Annona purpurea, Annona holosericea, Annona reticulata, Acacia collinsii, Acacia farnesiana, Acacia tenuifolia, Simarouba glauca, Lonchocarpus minimiflorus, Lonchocarpus costaricensis, Spondias mombin, Diphysa robinioides, Pithecellobium saman, Cordia panamensis, Cordia alliodora, Cedrela odorata, Calycophyllum candidissimum, Guazuma ulmifolia, Cochlospermum vitifolium, Bursera tomentosa, Bursera simaruba, Ateleia herbert-smithii, Apeiba tibourbou, Luehea speciosa, Luehea candida, Alibertia edulis, Rourea glabra, Erythroxylon havanensis, Genipa americana, Hemiangium excelsum, Randia echinocarpa, Swietenia macrophylla, Trichilia americana, Pisonia macranthocarpa, Tabebuia ochracea, Tabebuia rosea,* and *Jacquinia pungens.* Almost all of these plants are deciduous during the dry season (late December through early May). The forest is secondary successional of 20–80 yr age, and has been subjected to selective logging, occasional light fires, and intense browsing by cattle and horses. This forest–grassland mosaic, with forest edges constantly advancing and retreating with fluctuations in fire and grazing patterns, is similar to that which I have observed in eastern Africa and I suspect is similar to the habitat in which the Pleistocene megafauna and contemporary Santa Rosa trees interacted (Janzen and Martin 1982).

The forest experimental dung piles were located such that each was below closed canopy yet below understory that was open enough to walk through easily and see several tens of metres without major obstructions. Treefalls were avoided because the rodent fauna in them tends to be a mixture of the forest and grassland rodent fauna; an examination of the effects of forest rodent fauna on the dung in contrast with this mixed fauna will require yet another set of experiments.

The jaragua grasslands contain widely scattered shrubs and sucker shoots of woody species in the adjacent deciduous forests (Fig. 1A). These woody plants were avoided in dung pile placement for the same reason that the treefalls in the forest were avoided. The jaragua was introduced into the Park in the 1940s from eastern Africa; there is no evidence that there was native grassland in the Park immediately prior to cattle ranching, and wherever fire is excluded, the Park's jaragua grasslands revert to young forest in 5–20 yr. At present, the grasslands are burned every 1–3 yr. In the grassland experiments, the sites were chosen such that they were not burned in the 1980 dry season but were burned in the 1979 dry season. They were therefore covered with a dense stand of dead jaragua stems left from the 1979 rainy season and these dead stems were thickly interspersed with new 50–100 cm tall green grass foliage from the 1980 rainy season. It is in this kind of habitat and successional stage that *Sigmodon hispidus,* the common grassland rodent, reaches its maximum density in the Park.

The soil surface in the forest ranged from flat to undulating over broken rocky outcrops, and was covered with a thin litter layer largely made up of rotting leaves and stems that had fallen during the previous dry season. In the grassland, the soil surface was covered with a dense layer of rotting old grass leaves and stems between the bases of the clumps of jaragua plants.

The experiments were conducted at a time in the rainy season when an afternoon shower occurred every 2–3 d. The nonrainy weather ranged from clear skies to broken clouds. There was no nocturnal rain during the experiments. The habitats and the weather are representative of thousands of square kilometres of northern and central Guanacaste Province, with the proviso that outside of the Park the habitat has adequate livestock and fire to keep the pasture grass height down to 10–50 cm, and the forest understory is largely free of saplings and seedlings edible to livestock.

Horses and seeds in their dung.—When range horses have free access to the mosaic of grassland and forest in the Park, they forage on grasses in the open and frequent the forest for shady resting places and in search of fallen tree fruits (Janzen 1982a) and leafy browse. Large guanacaste trees (*Enterolobium cyclocarpum*) grow scattered through the forest and the grassland, and their newly fallen fruits are avidly eaten by range horses (and previously by cattle) during the last 2 mo of the dry season (late March to early May). Some of the seeds survive the passage through the horse, and nearly all survivors are defecated in the hard and dormant state. The seeds may take as long as 2 mo to pass through the horse (Janzen 1981b), and the dung is defecated throughout the forest and grassland. Seeds that germinate in the dung always die by being taken by rodents or by being too poorly rooted to survive the upcoming dry season; survivors are the dormant seeds that become incorporated into the litter.

Rodent seed predators.—While it cannot be known with certainty which of the vertebrate seed predators in the habitat has removed which guanacaste seed from a pile of horse dung, by the process of elimination the choice can be narrowed to *Liomys salvini* (Heteromyidae) and *Sigmodon hispidus* (Cricetidae), two small terrestrial rodents that feed on guanacaste seeds. The only large terrestrial seed predator in the habitat is the collared peccary (*Dicotyles tayassu*). This animal roots up and tears apart a dung pile or other substrate containing desired seeds; none of the experimental dung piles was torn apart during the experiments described here.

There are three arboreal rodents in the habitat and these rarely forage on the ground. Numerous observations of *Coendu mexicanum* and *Sciurus variegatoides* (prehensile-tailed porcupine and variegated squirrel) in Santa Rosa and in a zoo suggest that they do not prey on guanacaste seeds either on the parent tree or on the ground after the fruits have fallen. *Ototylomys phyllotis* (Cricetidae), the climbing rat, showed no interest in hard ungerminated seeds in the labo-

ratory, though *O. phyllotis* will on occasion eat fragments from newly germinated guanacaste seeds or seedlings (W. Hallwachs, *personal communication*). As they appear to forage on the ground only when in search of a particularly desirable food item, and as they were never trapped on the ground in the rodent censuses at the dung piles (though they were surely foraging in the foliage overhead), I assume they were not responsible for the removal of guanacaste seeds from the horse dung.

Two large terrestrial rodents, the paca (*Aguti paca*) and agouti (*Dasyprocta punctata*), forage throughout the grassland and forest of the Park, and could have removed guanacaste seeds from the dung. However, I doubt this to be the case because captive pacas and agoutis show no interest in eating hard dormant guanacaste seeds. (Though wild agoutis will eat and bury dormant guanacaste seeds, and even shell them out of the fruit, wild agoutis offered fresh horse dung in the forest showed no interest in digging into the dung [W. Hallwachs, *personal communication*].) Finally, when an agouti digs a seed out of substrate, it leaves a characteristic type of hole that, while common in the forest floor in the vicinity of the experiments, was never seen in the dung piles in these experiments. The two rodents will eat very newly germinated guanacaste seeds but leave very diagnostic wide incisor marks on the discarded seed coats. No trace of this type of damage was seen at the dung piles. Again, I assume that these two large rodents were not responsible for the removal of guanacaste seeds from the horse dung.

By close observation of the removal of seeds from dung piles in the forest other than those described here, it was made quite clear that virtually all the guanacaste seeds disappear from the dung in the forest before they have time to germinate. If taken while germinating, it is almost always within 24 h of when the seed begins to swell. In view of the strong disinterest of *Sigmodon hispidus* (rare in the forest) and *Ototylomys phyllotis* in dormant guanacaste seeds, and in view of the fact that either of these animals eats the germinating seeds only sparingly and only when seeds are advanced in germination state, I assume here that all the guanacaste seeds removed from the dung piles in the forest were removed by *Liomys salvini*.

In the grasslands, there is no doubt that *Sigmodon hispidus* was responsible for the removal of guanacaste seeds from dung piles. This is evidenced by catching them when using germinating guanacaste seeds as bait (Appendix 2), by finding chewed up germinating guanacaste seeds in habitats where only *S. hispidus* can be trapped, and by finding seed coats of germinated seeds with incisor marks that match those of *S. hispidus*. On rare occasions, *S. hispidus* will carry a hard dormant guanacaste seed a few centimetres from the dung pile, presumably while testing its edibility. A dung pile that has been foraged on by *S. hispidus* but not *L. salvini* is conspicuous in that its surface is covered with dormant and germinating guanacaste seeds in situ, and a few fragments of chipped up germinating seeds are scattered about. One that has been foraged on or in by *L. salvini* never has guanacaste seeds on its surface. On occasion, these differences are taken into account in the analyses of the experimental results.

The eventual fate of the guanacaste seeds removed from the dung is not the subject of this study. However, both species of rodent eat germinating seeds as soon as they remove them from the dung. I likewise assume that all hard dormant seeds carried off have been either eaten or cached by *L. salvini*. What fraction of these cached seeds escape through germination in abandoned burrows or through being misplaced by the rodent is now under study, but for the purposes of the experiments described here, a realistic working hypothesis is that after the seeds' removal from the dung, better than 99% of them are killed by the rodent that carried them off.

The *Liomys salvini* and *Sigmodon hispidus* individuals exposed to the experimental dung piles had not been exposed to horse or cattle dung that contained guanacaste seeds for at least a year, unless they had migrated to the area from distances of a kilometre or more. Other trapping experiments with these two species of rodents at Santa Rosa cause me to believe that movements of such a distance are rare but can occur. The results from the 2-L seed-poor dung piles lead me to believe that the rodents around these piles were initially naive about dung and seeds at the time of the experiment, since the seeds were rarely found. If seed-poor dung is placed in areas containing mice that have recently harvested seeds from horse dung, the mice thoroughly tear the dung apart in search of seeds (Janzen 1982e).

Experimental dung piles.—It is essential in a study such as this that the seeds placed in the dung have a very low and equal chance of germinating throughout the duration of the experiment, since a germinated seed has a very different chance of being found and removed by a small rodent than does a hard dormant seed. With this in mind, all the seeds used came from one tree's crop (tree 35 in Santa Rosa National Park) and were soaked in water for 10 d prior to use (all germinating seeds, ≈4%, discarded), and germination controls were established. During the course of the experiment, five subsamples of 500 each of these seeds were kept in moist dung of the depth, origin, and aeration of the dung piles, but the subsamples were not exposed to seed predators; 2.7% of these seeds germinated. To minimize and equalize the chances of scarifying seeds, all horse dung was collected by hand in such a manner as to avoid soil contamination (abrasive materials), held in thoroughly clean plastic buckets and bags, and placed out with the help of a plastic bucket as a mold for the dung pile. Seeds were mixed into dung by hand.

The dung for the 2-L pile experiments came from the herd of ≈17 range horses kept in the jaragua pastures near the Park administration area. The much larger amount of dung needed for the 8-L dung piles came from the large horse herd at Hacienda Ahogados, a large horse ranch to the south of the Park. Care was taken to collect dung from horses that had been maintained on a grass diet, avoiding dung from animals that had been fed grain. Grain-fed horses produce dung containing sorghum and other seeds, and these seeds induce *Liomys salvini* to search through the dung quite independently of the guanacaste seeds within. Since the dung was pooled and mixed, each experimental dung pile was a mix of dung ranging from 1 to 6 h in age and from four to eight horses. Because of this treatment, each dung pile contained dung whose origin was in common with that of at least three to five other dung piles.

If a dung pile fractured at the time it was dumped from the plastic bucket mold, the pieces were packed gently back into place. The ground below each dung pile was scraped clean of litter (Fig. 1B) because I knew that the large dung beetles (Scarabaeidae) and rodents would spread the dung pile out over this area, and I wanted to be certain that the soil surface could be later thoroughly searched for seeds.

The dung piles were left out for 10 nights because numerous pilot experiments have shown that after such a period, there is no further interest by large dung beetles and the rodents have lost interest in searching through the dung pile for hard dormant seeds. (Germinating seeds are removed for indefinite periods from the grassland dung piles, though this is of small significance because as mentioned earlier, seedlings do not survive if they appear in the dung pile rather than in the litter later on.) At this particular time in the rainy season, the rain was not heavy enough to have washed the dung pile remains into the surrounding litter by surface water runoff after 10 d. Had there been heavy rain during the experiment, I would have had to collect the litter for at least

50 cm around the dung piles and wash through it as well in order to insure recovery of all remaining seeds.

After collecting the dung from the site, the soil surface was very closely scraped with finger tips until only a hard surface remained. Likewise, the bare ground around the dung pile was searched. Dormant seeds were encountered in the soil surface, and these were added to the dung. The soil seed bank at Santa Rosa contains both guanacaste seeds and coyol palm nuts at very low density. However, by scraping the litter surface clean before putting down dung piles, and by only removing the 10-d-old dung only down to the firm soil surface, I eliminated the possibility that some of the seeds recorded after 10 nights were in fact contaminants. In addition, horse dung in Guanacaste Province commonly contains some guanacaste seeds even as late as 3 mo after the beginning of the rainy season (3 mo after the end of the tree's fruiting season [Janzen 1981a]). I used this horse dung for a wide variety of experiments at this time of year and estimate the dormant guanacaste seed density to be $\approx$ 1 seed/10 L. Since this amounts to <1% of the seeds added to the seed-rich dung piles and 2.5% of the seeds added to the seed-poor dung piles, and since the analyses performed do not dwell on topics requiring 1–2.5% accuracy, I ignored these contaminant seeds.

After washing the seeds out of the dung, they were scored as to their activity state and counted. However, some germination occurred in the bags of dung and soil after they were collected and before they could be washed. I have enough experience with grading germinating guanacaste seeds so that I can distinguish seeds that are 1–2 d into germination from older germinating seeds, and the seeds that germinated in the bags were counted as "hard dormant"; they constituted <5% of any sample of hard dormant guanacaste seeds recorded here.

The coyol nuts (Acrocomia vinifera) added to the dung were collected from the litter below a single palm, where they had lain for $\approx$11 mo (during which time all vestiges of fruit pulp had rotted off). They were soaked in water, and only those that sank were used; at least 99% of intact coyol nuts dense enough to sink in water contain living seeds. These very hard nuts offer a good example of interspecific differences in treatment of seeds by animals that forage in dung. If peccaries find coyol nuts they crack them with their molars, and if agoutis find them they gnaw them open (neither occurred in this experiment); however, Liomys salvini cannot gnaw them open (though it will try under starvation conditions) and leaves them where encountered, even though the seed inside the nut is a very high-quality food item for the mouse if the nuts are broken for it.

Rodent census.—I was careful to choose areas for the experiments that had not been trapped previously; the number of trap-shy animals was therefore as low as possible. However, other trapping programs with L. salvini have shown that there are some animals that will enter the trap for one bait, but not for another which is quite acceptable to other conspecifics. While the use of oatmeal–peanut butter bait is standard in trapping small rodents, I have found that germinating guanacaste seeds are a superior bait. However, they are large enough to obstruct the movement of the trap treadle of a Sherman live trap, and great care must be taken to insure that the seeds are placed as far back as possible in the trap. The hard dormant seeds were added to the dung piles set out to attract L. salvini that had learned to forage in them (Janzen 1982e) because there are mice in the habitat that will collect seeds near a trap but not go in it. In these particular experiments in all cases where the hard dormant seeds were removed, a L. salvini was taken in the adjacent trap, and it had carried the seeds into it. I have no reason to suspect that there were many mice foraging at the dung piles that were not counted in the mouse census.

APPENDIX 2

Small rodent occurrence at dung pile sites as measured by removal live-trapping.

Pile type	Site	Number of dung piles trapped	Oatmeal–peanut bait on 11th night		Germinating seed bait on 12th night		Total animals at dung pile site	
			Liomys salvini	Sigmodon hispidus	Liomys salvini	Sigmodon hispidus	Liomys salvini	Sigmodon hispidus
8-L dung (500 seeds)	forest	11	8	6	3	0	5	1
	grassland	11	2	13	0	4	1	9
2-L dung (125 seeds)	forest	3	5	0	1	0	3	0
	grassland	3	0	7	0	2	0	7
2-L dung (5 seeds)	forest	6	14	2	2	0	8	0
	grassland	6	0	10	0	3	0	7
Total forest		20	27	8	6	0	16	1
Total grassland		20	2	30	0	9	1	23

APPENDIX 3

Number of seeds remaining in piles of fresh horse dung after 10 nights in grassland and adjacent forest.

Pile number	Acrocomia vinifera nuts	*Enterolobium cyclocarpum*					Pile number	Acrocomia vinifera nuts	*Enterolobium cyclocarpum*				
		Ungerminated	Germinating seeds	Intact seedlings	Seedlings cut off by rodent	Total alive			Ungerminated	Germinating seeds	Intact seedlings	Seedlings cut off by rodent	Total alive

A. 8-L piles of dung

	Forest							Grassland					
	(100 initially)	(500 seeds initially)						(100 initially)	(500 seeds initially)				
1	100	19				19	2	100	419	60	3	1	482
3	100	5				5	4	100	390	54			444
5	99	10			1	10	6	100	423	21	1	2	445
7	100	12				12	8‡	100	142	5	1	2	148
9	100	12			1	12	10	99	444	31	2		477
11	100	16			2	16	12	100	412	78	4		494
13*	100	178	1	3		182	14	100	396	53			449
15	98	9				9	16	100	419	59			478
17	98	3				3	18	100	414	51	2	2	467
19	97	18				18	20	99	397	28		2	425
21	97	9			1	9	22‡	100	18	5			23
23	97	2				2	24	100	298	71		12	369
25	99	39				39	26	99	420	23		1	443
27	99	2				2	28	99	414	60	6		480
29	98	7				7	30‡	99	21				21
Σ	1482	341 (4.5%)	1	3	5	345 (4.6%)	Σ	1495	5027 (66.9%)	599	19	22	5645 (75.3%)
$\bar{x}_{15}$	98.8	22.7				23.0	$\bar{x}_{15}$	99.7	335.1				376.3
SD_{15}	1.2	43.9				45.0	SD_{15}	0.5	148.2				166.7
$\bar{x}_{14}$	98.7†	11.6†				11.6†	$\bar{x}_{12}$	99.7§	383.7§				430.8§
SD_{14}	1.2†	9.6†				9.6†	SD_{12}	0.5§	80.5§				91.0§

B. Seed-rich 2-L piles of dung

	Forest							Grassland					
	(25 initially)	(125 seeds initially)						(25 initially)	(125 seeds initially)				
1‖	25	125				125	6	25	120	2	2	1	124
2	25	3				3	7	25	116	2		2	118
3	25	5				5	8	25	112	2			114
4	21	1				1	9	25	110	5	6		121
5	24	2				2	10	25	117	3			120
11	25	4				4	15	25	113	5	5	1	123
12	25	3				3	16	25	115			3	115
13	25	1				1	17	25	112	5	4	2	121
14	23	0				0	18	25	109	2		7	111
Σ	218	144 (12.8%)				144 (12.8%)	Σ	225	1024 (91.1%)	26	17	16	1067 (94.8%)
$\bar{x}_9$	24.2	16.0				16.0	$\bar{x}_9$	25	113.8				118.6
SD_9	1.4	40.9				40.9	SD_9	0	3.5				4.4
$\bar{x}_8$	23.8¶	2.37¶				2.37¶							
SD_6	1.6¶	1.7¶				1.7¶							

* Pile not heavily foraged in by *L. salvini*.

† Summary statistics based on deletion of pile 13.

‡ Pile heavily foraged in by *L. salvini*.

§ Summary statistics based on deletion of piles 8, 22, and 30.

‖ Pile not foraged in by *L. salvini*.

¶ Summary statistics based on deletion of pile 1.

APPENDIX 3
Continued.

		Enterolobium cyclocarpum							*Enterolobium cyclocarpum*				
Pile number	*Acrocomia vinifera* nuts	Ungerminated	Germinating seeds	Intact seedlings	Seedlings cut off by rodent	Total alive	Pile number	*Acrocomia vinifera* nuts	Ungerminated	Germinating seeds	Intact seedlings	Seedlings cut off by rodent	Total alive
						C. Seed-poor 2-L piles of dung							
			Forest							Grassland			
	(1 initially)		(5 seeds initially)					(1 initially)		(5 seeds initially)			
1	1	5				5	2	1	4		1		5
3	0	0				0	4	1	5				5
5	1	1				1	6	1	5				5
7	1	5				5	8	1	5				5
9	1	5				5	10	1	5				5
11	1	3				3	12	1	5				5
13	1	0		1		1	14	1	4			1	4
15	1	5				5	16	1	5				5
17	1	4				4	18	1	4	1			5
19	1	4				4	20	1	5				5
21	1	3				3	22	1	5				5
23	1	5				5	24	1	5				5
Σ	11	40 (66.7%)		1		41 (68.3%)	Σ	12	57 (95.0%)	1	1	1	59 (98.3%)
$\bar{x}_{12}$	0.9	3.3				3.4	$\bar{x}_{12}$	1	4.8				4.9
SD_{12}	0.3	2.0				1.8	SD_{12}	0	0.5				0.3