# Mice, big mammals, and seeds: it matters who defecates what where.

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Abstract. By placing pseudodefecations of horse dung and cow dung mixed with guanacaste seeds (Enterolobium cyclocarpum), guapinol seeds (Hymenaea courbaril), black beans (Phaseolus vulgaris), wild lima beans (Phaseolus lunatus), and chaperno seeds (Lonchocarpus costaricensis) (all Leguminosae) in various ages and kinds of forest (and pasture) in seasonally dry Santa Rosa National Park (northwestern lowland Costa Rica), I determined that an initial seed shadow may be thinned and trimmed differentially by post-dispersal seed predation; the differences depend at least on what kind of animal defecates the seeds, what kind of seeds they are, and where the defecations occur. Spiny pocket mice Liomys salvini (Heteromyidae) were the seed predators that removed the seeds from the dung. This was a dry season experiment and therefore uncomplicated by seed burial by large dung beetles (Scarabaeidae). The Liomys mice found large seeds more readily than they found small ones, preferred to mine in horse dung rather than in cow dung, removed the seeds more thoroughly from dung with many seeds than from dung with few seeds, learned to reject toxic seeds that they found in the dung, and were more thorough in seed removal in forest than in pastures. In the first few days after pseudodefecations were placed out in the forest, there were stronger differences between horse and cow dung, and among habitats, than after the mice had 20-40 days to find all the pseudodefecations and remove as many seeds as they would. In the end, the mice not only removed the majority of the seeds from the dung, but they also removed all of the seeds from the pseudodefecations with high seed density. They also removed all of the seeds from more than half of the 5 liter pseudodefecations that contained a low concentration of seeds (20 guanacaste seeds, five guapinol seeds and 20 black beans). The latter type of trimming of the seed shadow, as opposed to simply thinning it, cannot be compensated for by density-dependent seedling survival.

### Introduction

The dispersal coterie of a tree generates an initial seed shadow. This initial seed shadow is commonly thinned and trimmed by post-dispersal seed mortality into a final seed shadow that is much reduced in density and coverage. This final seed shadow generates an initial seedling shadow in space and time. Here, I experimentally examine how postdispersal seed predation by a small forest-inhabiting tropical rodent, Liomys salvini (Heteromyidae) (Fig. 1) thins and trims portions of allospecific seed shadows that have been experimentally generated as if by defecation by two species of large herbivorous mammals. This kind of interaction between seed predator rodents and animal-generated seed shadows is undisputably as old as are small rodents and large mammals, and is as much a part of the ecology and evolution of plant recruitment as are spatially heterogeneous defeca-

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tion by dispersers and species-specific fruit and seed traits.

The experimental methodology is controlled pseudodefecations of seed-containing horse and cow dung in habitats that are rich in *Liomys* mice in the lowland dry forests and old pastures of Santa Rosa National Park in Guanacaste Province in northwestern Costa Rica. Medium-sized to large seeds (Fig. 2) were used in the experiments because they were easier to manipulate and relocate than are very small seeds. After the *Liomys* had one night or several weeks to search the dung for seeds, the dung was recollected and the seeds counted to determine the effectiveness of the mice in this kind of seed shadow thinning and trimming.

Santa Rosa's dry forests contain at least 35 species of trees whose fruits and other biology strongly suggest that for millions of years they have had their seeds in part to almost exclusively dispersed by large herbivorous mammals, nearly all of which have been extinct in the neotropics for about 10,000 or more years (Janzen and Martin, 1982). At present, horses and cattle are introduced surrogates for portions of this extinct fauna, and they conspicuously generate seed shadows (Janzen, 1981a, 1983a). In these same forests, Liomys is very common and for all practical purposes it is the only small rodent that is an intense post-dispersal seed predator on the seeds used in the experiments described here. This nocturnal heteromyid, like others such as the kangaroo rat (Dipodomys spp.) (Janzen, 1986), is an explicit forager for seeds in fallen fruits (Janzen, 1982a), in the litter, and in the dung of animals (Janzen, 1982b). The seeds it does not eat at the time are stored in deep underground tunnels and therefore killed as well. Its biology has been discussed in demographic and physiological terms (Fleming, 1983) and now its foraging behavior in Santa Rosa's forests is the subject of detailed examination. Here I examine the response of this mouse to dung species, dung seediness, seed species, seed size, seed toxicity, and habitat of defecation.

#### **Materialsand methods**

### The habitats

Santa Rosa National Park (0-350m elevation, 25km S of the town of La Cruz) contains about 10,000 ha of coastal hills and plains that have been subjected to a complicated temporal and spatial mosaic of farming, selective logging, pasturing and hunting as a wooded ranch/rangeland for at least 400 years by Europeans, and by farming and hunting by indigenous peoples for at least several thousand years before. The area receives 900-2400 mm of rainfall annually and experiences a December-May rain-free, sunny and windy dry season. Secondary successional forest, which makes up at least 90 percent of the forests of Santa Rosa, is highly deciduous during the dry season. However, at least 50% of the tree crowns and much of the understory in the primary forest on moderate slopes and bottomlands are essentially evergreen.

The experimental pseudodefecations were placed in lines through the following habitats (all the experimental sites are within 1 km of the asphalt road beginning in the Park Administration Area and continuing to the Cuesta Húmeda, about 3 km to the north).

## SF. Semi-evergreen Forest

Locally termed Bosque Humedo, this tiny patch of nearly pristine forest (*e.g.*, Janzen, 1983b) has a canopy at 20-30m height and more than half of its crowns are the nearly evergreen guapinol tree (Leguminosae: *Hymenaea courbaril*). The understory is strongly evergreen and deeply shaded even on a very sunny dry season day. It is the kind of forest that large mammals would move into for shade, understory browse, passage to other areas, and consumption of large crops of large fruits at greater than annual intervals.

### D-SF. Deciduous to Semi-evergreen Forest

This forest is immediately adjacent to the Semievergreen Forest (SF) and was generated by incomplete selective logging of evergreen species. This logging and sporadic burning has left or allowed a large number of tree species that are decidA common kind of first woody succession in the Park uplands is a virtual monoculture of the shortlived and fast growing tree Lonchocarpus minimiflorus (Leguminosae). These trees are thoroughly deciduous in the dry season. For an animal that cannot eat L. minimiflorus foliage or its abundant wind-dispersed seeds, the interior of this forest is a virtual desert. The habitat used in the present study is a 25-year-old stand on a low hill to the north of the Park dining hall.

# P-FM. Pasture and Forest Mosaic

This is a patchy jaragua (Gramineae: Hyparrhenia rufa) monoculture pasture dotted with small islands of woody secondary succession. Any point within it lies within 100m of such an island or a large forest block like DF-1 of DF-2. This site has been burned at least every 2-4 years during the past 20 years and contains much food for grass-eating vertebrates. It is also within foraging range and commuteriexploratory traffic of forest vertebrates. Horses are common at this site and it contains a large resident population of Sigmodon hispidus (Cricetidae), a seedling- and grass-eating small rodent (the hispid cotton rat). P-FM is also foraged in by *Liomvs*, though they are at a substantially lower density than in the nearby forest (e.g., Table 1).

# P. Pasture

This is a larger expanse of P-FM consisting of many ha of jaragua monoculture. It is several hundred meters from its center to woody vegetation, except for a very few widely scattered shrubs or tree sucker shoots. It is rich in Sigmodon hispidus but occupied by very few Liomys (e.g., Table 1).

# Dung

All dung used in this study was from horses or cebu cattle. Almost all dung came from the irrigated pastures of Hacienda Ahogados (approximately 15 km south of Santa Rosa), where both species of animals had been eating the same species of grass. Horse dung used in learning experiments and onenight contrasts of guanacaste seeds with wild lima beans came from free-ranging horses within Santa

uous in the dry season and much herbaceous vegetation in the understory. It is comparatively rich in fruit and foliage food for vertebrates in most years and seasons, and is the type of forest that would have been heavily visited by large herbivorous mammals seeking browse plants. Both guapinol and guanacaste (Leguminosae: Enterolobium cyclocarpum) trees occur in this forest. Many hectares of this forest type occur along the north side of the Camino Cafetal.

# DF-1. Deciduous Forest-1

This forest, locally known as Bosque San Emilio, is 20-80 year old secondary succession on a detailed mosaic of old banana plantation, roadsides, fencelines, cattle drive zones, pastures and isolated large trees (some of which are evergreen pristine forest remnants). While nearly completely deciduous during the dry season, this forest also contains a variety of scattered individuals of evergreens of various sizes and histories. This forest will return to a semi-evergreen forest (SF) after hundreds to thousands of years of succession and is characteristic of logged, semi-pastured, and burned semievergreen forest in Santa Rosa. It is very rich in fast-growing species of woody browse and herbaceous plants, ranges from 5 to 25 m canopy height. and would have been a major forage vegetation for large browsing/grazing animals. A high proportion of its woody plants are dispersed by animals.

# DF-2. Deciduous Forest-2

This extremely deciduous secondary successional forest, containing virtually no evergreen canopy or understory members, occurs in patches in the more commonplace deciduous forest (DF-1) and is uniformily 20-25 m in height. It is made up almost entirely of wind-dispersed or explosion-dispersed tree species (e.g., Gliricidia sepium, Calycophyllum candidisimum, Rehdera trinervis, Cedrela odorata, Cochlospermum vitifolium, Ateleia herbert-smithii, Luehea speciosa). In the dry season, this habitat appears to contain almost no food for a large browsing mammal except leafless twigs on understory shrubs and saplings. The particular piece of DF-2 used in this study lies on the south side of the highway to the southeast of the Bosque Humedo.

Rosa National Park; it contained some wild seeds (*Crescentia alata, Guazuma ulmifolia,* various herbaceous legumes) as well as seeds that I added.

All dung was collected between mid-morning and early afternoon and had been defecated after nightfall of the night before. The horse dung was moist but friable; it arrived in balls 3-5 cm in diameter, and was easily broken into smaller fragments at any stage of dryness. The cow dung was a wet stiff paste that was easy to mold and dried into an extremely hard block. Cow and horse dung are easily distinguished by odor. Dung from different defecations (by the same species of animal) was pooled in large buckets and thoroughly mixed before use. All pseudodefecations were made the same day that the dung was collected. The study occurred between 4 April and 20 May 1985 (the last six weeks of the dry season), and therefore no large dung beetles (and almost no small ones) visited the dung (cf. Janzen, 1983c); the dung used here was unaltered by dung beetles before its collection or after it was used in the pseudodefecations.

Seeds were counted and then mixed and kneaded into the dung by hand. The seedy dung was then packed into the bottom of a plastic bucket as a mold. The bucket was then inverted over the site of the pseudodefecation and rapped sharply to make the dung fall in place. No adjustments to the dung or the contained seeds were made after it had fallen.

Dung was placed out in one of two patterns. For

comparisons of horse and cow dung, single pseudodefecations of equal seed composition were placed on 50 cm diameter lightly swept circles 1-2 m apart. This was repeated at 20m intervals on a roughly straight line. The number of pseudodefecations per line is indicated in Table 2 and Figs. 3-6. When only one species of dung was used (for learning trials, effects of seed species, and effects of seed size), the pseudodefecations were likewise placed at 20m intervals unless otherwise mentioned below.

After an experiment, all dung remains were collected along with the litter underneath. The seeds were then recovered by manually finely dividing the dung in a 15 liter bucket of water, pouring off the floating material, repeating 3-10 times, and visually selecting the seeds from the small amount of heavy material remaining. All ungerminated seeds used here have a specific gravity greater than that of both water and dung particles; however, some germinated seeds are only slightly more dense than is water, and great care must be taken not to pour off seedlings with the dung slurry. In trial washings with known seed numbers, 100% of the seeds were recovered (n = 1000 seeds in ten trials). Visual search of dry dung was found to be errorfree only when searching for large seeds in very small amounts of dung on relatively clean soil surfaces (e.g., when counting the remaining seeds in very seedy (concentrated) rather than standard pseudodefecations).

*Table 1.* Duration and mouse density parameters for standard pseudodefecation sites and the learning experiment. Duration is the number of nights that the pseudodefecations were exposed to *Liomys* mice. An indication of mouse density was determined by setting three Sherman live traps baited with germinating guanacaste seeds for one non-moonlit night at the site (Table 2) of each pair of horse and cow pseudodefecations. The trapping was done between 20-22 May 1985. well after the mice had stopped visiting the dung to mine for seeds.

Habitat	Duration	Liomys per pseudodefecation site
SF-Semi-evergreen Forest	41	1.46
D-SF-Deciduous-semi-evergreen Forest	29	1.47
DF-1–Deciduous Forest-1	42	0.93
DF-2-Deciduous Forest-2	25	1.27
LF-Lonchocarpus Forest	23	1.00
P-FM-Pasture and Forest Mosaic	23	0.53
P–Pasture	23	0.20
Learning experiment (Table 4)	19	1.93

pseudodefecations Standard contained 20 guanacaste seeds, five guapinol seeds, and 20 black beans in 5 liters of dung. This made a cylindrical cake 28 cm in diameter and 5-7 cm tall and approximates the volume of two defecations of an adult horse or cow feeding in mixed green and dry grass. This amount of dung was chosen to approximate what an adult gomphothere or medium-sized species of ground sloth might have produced in a defecation. Concentrated pseudodefecations contained 20 guapinol seeds, or 20 guapinol seeds and 100 guanacaste seeds, or 20 guapinol seeds, 100 guanacaste seeds and 200 black beans in 0.5 liters of dung. At this degree of seediness, many seeds are on the surface of the dung and the dung resembles that of an animal that has been swallowing large amounts of a seed-rich fruit. In contemporary habitats, such seed-rich defecations are primarily generated by cattle and horses in badly overgrazed pastures containing large trees that drop large fruit crops (e.g., Enterolobium cyclocarpum, Pithecellobium saman, Guazuma ulmifolia), by tapirs (e.g., Janzen, 1982f), and by carnivores (e.g., coyotes, coati-mundis) feeding on fruit.

In many habitats other than Santa Rosa, it would often be necessary to screen other animals away from pseudodefecations so as to be certain that only *Liomys* mice were removing the seeds. However, I am sufficiently familiar with the way that *Liomys* forages in dung beetle-free dung that I can detect foraging in the dung by a large mammal (such as a peccary). This happened to only three standard and four concentrated pseudodefecations during the experiments, and these seven pseudodefecations were discarded. Agoutis and smaller rodents other than Liomys may on occasion have taken a seed (although all feeding trials and field observations indicated that they did not), but in these particular experiments, Sigmodon hispidus in the pasture habitats (P-FM and P) was the only animal that may have removed a significant number of seeds. Preliminary experiments such as those described here have been conducted under exclusion cages in previous years and the results were identical to those reported here. In all the learning trials (e.g., Fig. 8) and other kinds of overnight tests, dung or plates with seeds were placed out at dusk and retrieved at dawn.

## Season of the experiments

Since the experiments were conducted in the last quarter of the dry season, the days were dry, windy and sunny. Nights were clear and often windy. The full moon occurred on 5 April and 4 May. The litter was extremely dry, and the soil was dry and hard. By the end of the third day in the forest habitats, horse dung was as dry as if oven-dried. Cow dung retained a moist core as long as 10 days, and dried progressively from the outside inwards. As mentioned earlier, at this time of year there is no dung beetle activity in the dung. These beetles would alter the story by exposing large seeds and preventing the formation of dry blocks of seed-containing dung.

<i>Tuble 2.</i> Fercent pseudoderecations mined by <i>Liomys</i> after two mgin	Table 2.	Percent	pseudodefecations	mined	by	Liomys	after ty	vo night
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Habitat	Horse dung	Cow dung	Pairs of pseudodefecations		
SF	92%	23%	13		
D-SF	93%	33%	15		
DF-I	53%	13%	15		
DF-II	13%	19%	16		
LF	100%	92%	12		
P-FM	73%	20%	15		
Р	13%	13%	15		
Total	60%	29%	101		
Average per habitat					
(n = 7)	62%	30%			
S.D.	37%	28%			

In Santa Rosa, numerous trees present their fruits to terrestrial large herbivorous mammals during the dry season (e.g.. Crescentia alata, Hymenaea courbaril, Pithecellobium saman, Enterolobium cyclocarpum, Acrocomia vinifera, Guazuma ulmifolia). Taking the entire year into account, horse and cow dung is the richest in the seeds of these trees during March-May (assuming that the animals have access to such fruit crops). The pseudodefecations used here were seasonally timed to match what would have occurred in the natural world in a Costa Rican dry tropical forest. However, in nature, large herbivores may also swallow seeds in the last half of the dry season yet not defecate them until the rainy season (e.g., viable dormant guanacaste seeds may remain in a horse for two or more months, Janzen, 1981a).

## Species of seeds

At least 40 species of viable seeds occur in the dung of free ranging horses and cows in dry forest-pasture mixes like those in Santa Rosa. Here I focus on one of these that is a favorite food of Liomys guanacaste (Enterolobium cyclocarpum) - and add in four other legumes (Fig. 2) - guapinol (Hymenaea courbaril), black beans (Phaseolus vulgaris), wild lima beans (Phaseolus lunatus) and chaperno (Lonchocarpus costaricensis). These four were chosen because of their size and toxicity. Until the end of the Pleistocene, guapinol seeds would also have occurred, along with guanacaste seeds, in the dung of mammals larger than horses and cows, mammals with the strength to break the hard pod walls and the willingness to swallow very large seeds (cf. W. Hallwachs, this volume). Plastic beads were added as seed mimics in the learning experiments.

#### 1. Guanacaste

Guanacaste seeds are avidly collected by *Liomys* mice from litter, fallen fruits, and dung; germinated guanacaste seeds are the most effective bait for *Liomys* that I know of. All indications are that a *Liomys* mouse cannot resist harvesting a dormant or germinated guanacaste seed, and a single animal will carry off as many as 500 of them from a pile in

one night. Each of the mouse cheek pouches can carry up to 3-4 guanacaste seeds. In the laboratory, Liomys mice can sustain their body weights indefinitely on a pure diet of germinated guanacaste seeds (and in nature, they germinate the seeds before eating them); they can also survive indefinitely on a pure diet of ungerminated guanacaste seeds, but on this diet there is an initial weight loss that requires weeks or months to recover (Hallwachs and Janzen, unpubl. data). These mediumsized seeds (500-1100mg, Janzen, 1982c) were cleaned of their fruit pulp and were soaked in water for four days before being placed in the pseudodefecations. The seeds that germinated during soaking were discarded; this treatment is necessary to insure that the mice are searching for ungerminated seeds in the dung and that unlocated seeds do not germinate, die, and rot into disappearance before the dung is recollected.

#### 2. Guapinol

Guapinol seeds left lying on the forest litter and in rain-rotted guapinol fruits are readily harvested by Liomys mice. Guapinol seeds are also harvested from dung, but not quite as enthusiastically as are guanacaste seeds (e.g., Fig. 5-6). In the laboratory, at least 80% of Liomys mice placed on a pure diet of ungerminated guapinol seeds survive for 1-2 weeks with little weight loss, but after this time there is a highly individual-specific response; some individuals are able to survive as long as a year on a pure diet of this seed. The large seeds (2-6 g each) were placed in the dung after being cleaned of their tightly adhering fruit pulp (cf. W. Hallwachs, this volume). Seeds required 1-2 weeks to germinate, and even then did it very slowly; the presoaking treatment, as done with guanacaste seeds, was therefore not conducted. Additionally, in the particular experiments reported here, none of the guapinol seeds germinated fast enough to be germinating before the pseudodefecation was recollected or the mice had lost interest in foraging in it. Each guapinol seed is so large that no more than one can be placed at a time in a mouse's pouch (and at times they are carried singly in the mouth instead of in the pouch). Guapinol seeds cannot be harvested directly from the fruits by Liomys until the hard indehiscent fruits rot in the rainy season (*cf*. W. Hallwachs, this volume).

### 3. Black beans

When placed out in the forest, a small number of black bean seeds are harvested by Liomys mice (see especially the learning experiments in this study), but as a pure diet in the laboratory, black beans are rejected; the animal would rather starve to death than fill its stomach with them, and better than 80% of Liomys die as quickly when given a diet of uncooked black beans as if given no food at all (Janzen, 1981b). Uncooked black beans are rich in toxic phytohemagglutinins (lectins) (Janzen et al., 1976). These medium-small seeds (140-180 mg) begin to germinate within a day of contact with a moist substrate (though this germination is often arrested in horse dung as it dries in the intense dry season sun). Black beans were included in all standard pseudodefecations and in some concentrated pseudodefecations, but the results are mostly ignored here; it was not possible to distinguish between those seeds that disappeared by germinating and then dying as seedlings and those that were harvested by the mice.

#### 4. Wild lima beans

Wild lima beans are rich in cyanide (Clegg *et al.*, 1979) but the mice harvest them readily from litter and dung (*e.g.*, Fig. 7). In the laboratory, about 90% of wild-caught mice can subsist without weight loss for at least two weeks on a pure diet of ungerminated wild lima beans. These medium-small seeds (40-60 mg) were collected from ripe dry pods (on a single large herbaceous vine) in the Park. Only the gray (slow germinating) color morphs were used in experiments and wild lima beans were used only in over-night exposures of pseudo-defecations to mice.

## 5. Chaperno

This tree, *Lonchocarpus costaricensis*, bears the same common name as does the other five species of *Lonchocarpus* in the Park (Janzen and Liesner, 1980), but only *L. costaricensis* seeds were used in the experiments reported here. *L. costaricensis* seeds contain at least two uncommon amino acids

that cause a mild weight loss in *Liomys*, and eight flavonoids that thoroughly repel Liomys when place in laboratory chow (Janzen et al., 1986). Liomys would rather starve to death in the laboratory than eat L. costaricensis seeds (this applies to the seeds of the other five species of Lonchocarpus in the Park as well), quickly learn to reject the seeds when they encounter them in dung or on the forest litter, and do not open the conspicuous winddispersed fruits that are abundant on the litter under the parent trees. These medium-sized seeds (250-350 mg, Janzen, 1982d) were collected from mature wind-dispersed fruits (from large trees) in the Park. Their presence in dung was meant to represent the case where a mammal has consumed seeds that are truly toxic or directly repellent to Liomys.

## 6. Beads

At the end of the learning experiment (Fig. 8, Table 4), white plastic 5 mm diameter spherical beads (Fig. 2; with a hole for stringing on thread) were mixed with the seeds on the food plates. These artificial seeds were dense enough (95-100mg each) to sink in water but less dense than is an ungerminated legume seed.

# Mice

Liomys salvini forages for seeds and insect pupae (and at times other insects) on the forest floor at night. Five other species of small rodents have been trapped occasionally in tens of thousands of trapnights in these habitats: Sigmodon hispidus, Nyctomys sumichrasti, Reithrodontomys gracilis, Oryzomys fulvescens, Oryzomys talamancae and Ototylomys phyllotis. However, the details of their biology in the forest and laboratory make it obvious that with the exception of S. hispidus in the pasture, they were not involved in seed harvest from the pseudodefecations in these experiments.

*Liomys* usually does not eat hard seeds where they are found, but instead carry them in their cheek pouches to a deep underground tunnel system where they are eaten or cached. Even if a seed cache is forgotten or the owner eaten and its tunnel not taken over by another mouse, the seeds so



Fig. 1. Adult female Liomys salvini (Heteromyidae) on balls of intact horse dung.

harvested are treated here as having been preyed upon; the tunnels are 30-90 cm below the surface of the ground and seedlings in them have no chance to reach the surface. There are also some hints of very temporary surface caches among the litter — if some of these are not recollected, the mouse may on rare occasions be a disperser as well as a seed predator; here, however, I treat *Liomys* as purely a seed predator. Additionally, *Liomys* are heavily preyed on by carnivores, and such predation results in a certain amount of a rather bizarre form of seed dispersal because the prey will have seeds in their pouches.

The *Liomys* mouse traits of greatest importance to the present study are the following.

1. It explores new objects, such as dung, novel fruits, newly turned soil, new traps, etc. (Janzen, 1982e).

2. If seeds are encountered on the dung pile surface, or if it has previous seed-collecting experience from dung, it (and its associates) thoroughly mines through the dung looking for seeds (Janzen, 1982e).

3. When mining through dung, different species of dung are mined more avidly than are others (present study).

4. If a defecation or other point seed source contains more seeds than can be carried in a single trip to the tunnel, the mouse continues to move back and forth with new seeds loads until it exhausts the seeds, is interrupted by (potential) predators, or dawn comes.

5. It can survive on a pure diet of some species of seeds (e.g., guanacaste, guapinol, wild lima beans), other species are of somewhat less value (e.g., black beans), and others are absolutely unacceptable (e.g., chaperno) (Janzen, unpublished laboratory results).

6. Novel seeds are usually harvested when first encountered, but after being sampled (bitten, apparently usually in the tunnel), they are later rejected when encountered.

7. It may forage as far as 30-70 m from the tunnel entrance (e.g., Fig. 10).

8. It lives in the same area of perhaps 0.20 to 0.50 ha for much of its lifespan of two or less years (Janzen, unpublished demographic study).

9. In the forested habitats where the experiments were carried out, its resident density is 20-100 animals/ha, though not all these animals may be foraging on the ground surface on a given night (Fig. 9).



*Fig.* 2. Seeds placed in pseudodefecations: largest, guapinol (*Hymenaea courbaril*); dark ovoids with pale ovoid marking, guanacaste (*Enterolobium cyclocarpum*); C-shaped pale, chaperno (*Lonchocarpus costaricensis*); black beans (*Phaseolus vulgaris*); smallest, wild lima beans (*Phaseolus lunatus*); white spheres, plastic beads (scale in mm).

10. It weights 14-65g as forager that consumes 1-5g of dry seeds per night in the laboratory (Janzen, unpubl. data).

In short, the forest floor is at times a seething monoculture of *Liomys* that are selectively capturing the seeds in litter, fruits and dung. They continue to harvest previously missed seeds until they germinate (which does not occur in the dry season).

#### **Experiments and results**

# 1. Are seeds differentially removed from horse and cow dung?

On the days immediately following lines of paired pseudodefecations, one of three different results is readily visible. For example, after two nights, in four of the seven habitats with standard pairs of pseudodefecations, the horse dung was significantly more frequently mined by *Liomys* searching for seeds than was cow dung (by inspection, habitats SF, D-SF, DF-1, P-FM) (Table 2). In one habitat (LF), both horse and cow dung were extremely heavily and identically mined. In two habitats (DF-2, P), only trivial mining had occurred in either kind of dung. In sum, when there is moderate mining of pseudodefecations, the horse dung is mined significantly more frequently (by inspection) than is cow dung during the first few days after pseudodefecation.

However, dung lies in place for weeks to months in the dry season, since there are no dung beetles to degrade it. Furthermore, it is the number of seeds that remain after the dung is thoroughly incorporated in the litter that is the most important in determining the final seed shadow thinning and trimming by *Liomys*. After 23 to 42 nights (Table 1), it was clear that the mice had no more interest in mining in the pseudodefecations (there was no further change in the dung topography and fallen leaves accumulated on the surface). These pseudodefecations were collected and their seeds extracted (Table 3). In six of the seven habitats (SF, D-SF, DF-1, DF-2, L-F, P-FM) significantly more guanacaste seeds had been removed from the horse dung than from the cow dung (significance by inspection). Furthermore, in the same six habitats, significantly more (by inspection) of the horse dung pseudodefecations than of the cow dung pseudodefecations had been totally cleaned of guanacaste seeds. If all piles are considered together, 91% of the 2020 guanacaste seeds in 101 horse pseudodefecations were removed, in contrast to 67% from 101 cow pseudodefecations; likewise, 56% of the horse dung pseudodefecations lost all of their guanacaste seeds, while only 2% of the cow dung pseudodefecations lost all of theirs. If the data are pooled by habitat rather than by all pseudodefecations, essentially the same results are obtained (Table 3).

The results are in the same direction for guapinol seeds (Table 3), though more pseudodefecations were totally cleaned of these (larger) seeds than of guanacaste seeds (and see below with reference to seed size).

*Table 3.* Thoroughness of removal of guanacaste and guapinol seed by *Liomys* from pairs of horse dung (HD) and cow dung (CD) pseudodefecations in seven habitats (*cf.* Table 1 for duration). Thoroughness was determined after the mice had lost interest in mining in the dung piles, and therefore unequal duration of pseudodefecations (Table 1) is irrelevant to data analysis.

Habitat	guanaca	guanacaste seeds				guapinol seeds			
	% seeds removed	% seeds removed		% piles all seeds gone		% seeds removed		% piles all seeds gone	
	HD	CD	HD	CD	HD	CD	HD	CD	
SF	98	71	77	0	100	75	100	39	
D-SF	94	50	67	7	100	64	100	27	
DF-I	92	53	57	0	95	57	81	13	
DF-II	90	70	40	0	93	75	73	40	
LF	99	87	87	8	98	100	92	100	
P-FM	83	62	40	0	76	64	67	40	
Р	84	83	13	0	81	77	60	33	
All piles	91	67	56	2	92	72	81	40	
(n = 2020  seeds,	101 pseudodefe	ecations)			(n = 505	seeds, 101 p	seudodefecati	ons)	
All habitats $(n = 7)$	91	68	54	2	92	73	82	42	

Table 4. Removal of four species of seeds simultaneously mixed into 1 liter of horse dung or on a plate in the forest (n=20 seeds per seed species). See Fig. 8 for the time course of the experiment.

Seeds	Percent seeds removed from dung (n = 8 nights)*		Percent seeds removed from plates (n = 9 nights)		
	average	S.D.	average	S.D.	
guanacaste	94.4	3.02	99.7	1.00	
wild lima bean	50	4	84	11	
black beans	31	13	38	13	
chaperno	7.0	5.4	6.3	5.0	

\*The first two nights of 10-night experiment were deleted from calculations because the majority of the *Liomys* were learning their seed preferences during those two nights.



*Fig. 3.* Time course of percent guapinol seeds remaining in concentrated pseudodefecations (A) and percent pseudodefecations still intact (B) in Semi-evergreen Forest (SF) (1985).

# 2. Are seeds of different sizes differentially removed from horse and cow dung?

The mice eventually remove the same percent of guanacaste and guapinol seeds from each dung type when the results are summed within or between habitats, or for the pseudodefecations as a whole (Table 3). However, the mice removed all guanacaste seeds from only 56% of the horse pseudodefecations, while they got all the guapinol seeds out of 81% of the same pseudodefecations; in like manner, they got all the guanacaste seeds out of only 2% of the cow pseudodefecations, but they harvested all of the guapinol seeds out of 40% of the same pseudodefecations (Table 3). Observing the piles during the seed harvest, it was clear that



*Fig. 4.* Time course of percent guapinol seeds remaining in concentrated pseudodefecations (A) and percent pseudodefecations still intact (B) in Deciduous Forest-2 (DF-2) (1985).

the mice first harvested all the guanacaste seeds that they could find, and then the guapinol seeds were harvested on subsequent nights (this is reflected in the faster rate of removal of guanacaste seeds than guapinol seeds from concentrated pseudodefecations as well, *cf.* Fig. 5a, 6a). The total removal of guapinol seeds from most of the pseudodefecations was due not to there being fewer guapinol seeds (5) initially than guanacaste seeds (20) but to the mice not being able to find all the (smaller) guanacaste seeds before turning to the slightly less preferred guapinol seeds.

To examine the recovery of yet smaller seeds (at the species level), I placed out 20 pseudodefecations of 2 liters of horse dung eacht at 50m-plus intervals in forested areas (along the gradient from SF to DF-2) where no experiments had been done with the mice. Each relatively concentrated pseudodefecation contained 100 guanacaste seeds



*Fig. 5.* Time course of percent guapinol and guanacaste seeds remaining in concentrated pseudodefecations (A) and percent pseudodefecations still intact (B) in Deciduous Forest-1 (DF-1) (1985).

and 100 much smaller wild lima bean seeds. Each pseudodefecation was collected the morning following the night during which the mice discovered it. The mice were substantially more effective in harvesting the guanacaste seeds in a pile of dung than they were in harvesting the much smaller wild lima bean seeds (Fig. 7a). To control for seed preferences in this experiment, small plates, each containing 100 guanacaste seeds and 100 wild lima beans, were placed out in the same forest type in the same pattern, but located so as not to be found by the same individual mice that had collected seeds from the horse dung. The mice liked the wild lima bean seeds well enough to take all of them, and approximately equal numbers of each species of seed remained on the plate if the mice were interrupted while working (Fig. 7b). However, the possibility remains that the mice were willing to search harder in dung for guanacaste seeds than for wild lima beans, or that wild lima beans are more olfactorily cryptic than are guanacaste seeds.

# 3. Are there inter-habitat differences in the number of seeds captured from a dung pile?

The pseudodefecations in the forest habitats (all the habitats except P and P-FM) generally had a high percent removal of the seeds from their dung, but LF was exceptionally high (Table 3). This intense seed harvest in LF is evident in the high percent of mining of pseudodefecations on the first two nights as well (Table 2). On the other hand, only 13% of the horse dung piles in the pasture habitat (P, Table 3) had all of their seeds removed. Furthermore, this line of pseudodefecations was only trivially mined during the first two nights that it was in the field (Table 2). The same applies to the extremely deciduous DF-2 forest site.

Once the mice had done all the harvesting from the dung piles that they were going to do (Table 3), there was no biologically significant difference in the percent seed capture from the pseudodefecations in the different forest habitats sampled in this experiment.

# 4. Does seediness of dung influence percent seed removal?

When very seedy pseudodefecations (concentrated pseudodefecations) were placed out in the same habitats but within the foraging ranges of different Liomys than those that had harvested the seeds from the standard pseudodefecations, all guanacaste and guapinol seeds were removed from all pseudodefecations in less than 14 days (Fig. 3-6). This is clearly significantly more rapid and thorough seed removal than was the case in the standard pseudodefecations (Table 3). Additionally, in 56% of the 106 very seedy (concentrated) pseudodefecations, all the seeds were removed the first night that a pseudodefecation was encountered by a mouse. Among the 20 very seedy horse pseudodefecations that contained both guanacaste and guapinol seeds, 86% of the pseudodefecations lost all of their guanacaste seeds and 22% lost all of their guapinol seeds during the first night that the pseudodefecation was mined. The same figures for 20 cow pseudodefecations are 41% and 7%. It was usual for the mice to remove all of the guanacaste seeds and part of the guapinol seeds from a particular pseudodefecation and then to gradually remove the remaining guapinol seeds during several subsequent nights.

When very concentrated pseudodefecations contained only guapinol seeds, the overall rate of seed removal was essentially the same from horse as from cow dung (Fig. 3-4), though a very large sample size would probably show a slightly higher removal rate from horse dung as can be seen in the first six nights in Fig. 3a. Once concentrated pseudodefecations have baked in the hot sun for 3-6 days, there appears to be no moisture difference between the two dung types and the way the mice harvested seeds suggested that the dry dung type made no difference to them.

When very seedy dung contained both guanacaste and guapinol seeds, the guanacaste seeds were removed more rapidly than were the guapinol seeds, and this occurred with both horse dung and cow dung (Fig. 5-6). The time course of seed removal (Fig. 5-6) makes it clear that if there is to be a differential effect of cow and horse dung on the final capture of seeds by *Liomys*, some other process has to interfere within a very few days of defecation (*e.g.*, removal of seeds by a secondary dispersal agent — another rodent, dung beetles (*cf.* Estrada and Coates-Estrada, this volume), or rain surface erosion).

# 5. Do the mice show different responses to different species of seeds?

Since many of Santa Rosa's tree species have seeds that are rejected or semi-rejected by Liomys, there should be occasions when large herbivore dung contains toxic as well as edible seeds. When four species of seeds — guanacaste, black beans, wild lima beans, chaperno — were placed together in 0.5 liter horse pseudodefecations (such a pseudodefecation is so seed-rich that there is no doubt that the *Liomys* encountered all kinds of seeds), the removal percentages by the (initially mostly naive) *Liomys* went through a 2-4 night learning phase,



*Fig. 6.* Time course of percent guapinol and guanacaste seeds remaining in concentrated pseudodefecations (A) and percent pseudodefecations still intact (B) in Deciduous-Semi-evergreen Forest (D-SF) (1985).

and then remained relatively constant (first half of Fig. 8). Guanacaste seeds were universally collected from the start, and chaperno seeds were almost universally rejected after the learning phase. Black beans and wild lima beans showed different but intermediate levels of harvest. When the same seeds were then offered to the same free-ranging mice on small plates, there was no substantial overall change in removal percent except that wild lima beans were then more thoroughly removed when they did not have to be located in the dung (second half of Fig. 8, and Table 4); the latter result is similar to that illustrated in Fig. 7. The sources of variation in the daily percentages of seed removal in this experiment will be discussed later.

In the standard pseudodefecations, it was obvious that about half of the black beans were rejected (although this cannot be determined from



*Fig.* 7. Percent seeds removed from 1 liter pseudodefecations (A) and from small plates (B) in the forest (100 seeds per site (DF-1) per plant species). Open bars = guanacaste seeds and hatched bars = wild lima bean seeds. *Liomys* mice removed the seeds and had only one night to collect from each site once they had located the site (dark of the moon, April 1985).

the final collections of the pseudodefecations because the germinated black beans died of rotting and confinement). After the first few nights of Liomys foraging through a horse dung pseudodefecation, it was usual for there to be one to ten of the original 20 black beans scattered on the dung surface. Horse dung was so dry that the beans were generally still present 1-2 weeks later, but they did very gradually disappear. Likewise, they were clearly left in the surface of the cow dung (immediately adjacent to pits and tunnels from which guanacaste and guapinol seeds had been removed). However, since cow dung was more moist than the horse dung, the black beans often germinated; these leafy seedlings were then eaten off of the tops of the cow dung by some other animal(s) than the Liomys.

In the concentrated pseudodefecations, the usual pattern was that 10-50% of the original 200 black beans was removed at the same time as the

guanacaste and guapinol seeds, and then the pseudodefecation, liberally sprinkled with black beans, accumulated litter and was no longer of interest to the mice. In four cases, peccaries found these piles and ate all the black beans.

## Discussion

#### Details of the experiments

The differential removal of seeds from horse and cow dung is not a simple consequence of a single variable such as odor, moisture or hardness when dry. First, cow dung is more moist and more sticky than is horse dung. As cow dung piles dried up, the mice become more willing to mine in them. On the other hand, extremely wet horse dung gets no less intense treatment than does relatively dry and friable horse dung. Second, cow dung has a strong odor that could mask the odor of the seeds and/or be somewhat repellent to the mice. Horse dung has a strong but different odor. When the seeds were in very seedy dung piles, seeds were often removed from the surface of fresh cow dung without the mouse digging further into the dung. Since such seeds are contaminated with cow dung, the odor of the dung itself may not be repellent in moderate doses. Third, as it dries, cow dung becomes so hard that the mice that attempted to extract seeds had to work extremely hard. They cut tunnels into the dung block (leaving a small pile of chips on the ground outside), and guapinol seeds were often observed rigidly imbedded in the walls of a tunnel with only part of their supporting substrate gnawed or scratched away. Such a hard block of cow dung may also prevent escape of the odors of hard (or germinating) seeds, or guide odors in such a manner that the seed is hard to locate. By way of contrast, the horse pseudodefecation was usually reduced to a pile of small fragments during the first 1-2 nights of being mined by Liomys, and the mouse could get its nose to within a centimeter or less of any remaining seed. The mice were often very delicate in the way that they removed seeds from horse dung; the seeds disappeared yet the pseudodefecation appeared only slightly flattened;



*Fig. 8.* Time course of percent seeds removed by *Liomys* mice during one night exposures at fixed stations in the forest (*cf.* Table 4 for additional information). The vertical line indicates the date of change from putting seeds in dung to putting seeds on small plates at the same sites.

they do not dive in and throw dung in all directions as does a collared peccary looking for seeds.

There are at least two ways that naturally occurring seeds might be permanently hidden in horse dung that falls in the dry season, yet be found by the mice in my pseudodefecations. First, a seed that has spent days to months in the gut of a horse may be maximally clean of seed odors as compared with those that I put in the pseudodefecations after a minimum of processing. Second, some of the naturally-occurring seeds will be imbedded in the very center of the balls of horse dung. These might be missed by the Liomys if they have virtually no odor and if there are no dung beetles to tear apart the dung and expose the seed. On the other hand, laboratory Liomys that have had experience with extracting seeds from horse dung are very thorough in tearing apart each horse dung ball irrespective of whether it contains a seed.

The thoroughness of seed removal from any dung pile is related to how many mice search in a pseudodefecation as well as the manner in which each one searches. The number of mice that encountered a pseudodefecation was clearly related to a number of environmental variables.

### 1. The phase of the moon

Three years of mouse live-trapping and release in



*Fig.* 9. Number of *Liomys* mice captured on a fully moonlit night in very dry forest (A, 24 animals) and two weeks later in the dark of the moon after the rains have started(B, 66 animals). The site (DF-1; Bosque San Emilio Mouse Plot) is a 10 m grid and covers  $230m \times 230m$  (529 Sherman live traps); the bait was germinated guanacaste seeds. Females are represented by closed figures, males by open figures.

the Santa Rosa forest have made it clear that once the moon is half or more full, there is a reduction in the number of *Liomys* active above ground and/or the number of hours that they forage per night (compare also Fig. 9a and 9b). The more deciduous the overstory trees, the more intense the effect. Pseudodefecations made during the more moonlit half of the moon cycle had longer to dry out before the mice first mined in them. The final effect was probably negligible, but any process that depended on the rate of seed removal during the first few days after a pseudodefecation would have been influenced. During the rainy season, this effect would be less because moonlit nights are often cloudy and because the dung beetles ignore the moon and would render the dung into finely divided fragments and seeds in the first night. Then, when the *Liomys* did come to forage in it, the results would be the same irrespective of when in the moon cycle defecation occurred.

## 2. The dry season

The mice forage less actively (fewer mice and/or fewer hours spent foraging) when the ground surface is covered with dry leaves (which are noisy to forage among) and when the overhead trees are deciduous. For example, in Fig. 9a are displayed the capture locations for the 24 Liomys mice captured in a 529-trap  $10 \times 10m$  grid  $(230 \times 230m)$ square) on a full-moonlit night at the end of the dry season and just a few days before the rains begin; in Fig. 9b are the parallel data for a night two weeks later (during the dark of the moon) after the rainy season has started. This dry season reduction in foraging activity is probably due to increased visual and sonar perception by owls and other nocturnal predators in deciduous forest during the dry season.

During the dry season the dung dries much faster than in the rainy season (irrespective of dung beetle presence). A block of cow dung will be a better protection for seeds in the dry season than in the wet season. It also means a changing dynamic between seed odors, dung odors, litter odors and *Liomys* olfactory perception when the season changes from dry to wet (or vice versa). On the other hand, cow dung moistness may lure some seeds into lethal germination in the dry season (as happened with well over half of the black beans in these experiments).

### 3. The absolute density of Liomys

How many mice actually visit a single pseudodefecation and from how far do they come? I have

captured up to six mice in 10 traps at a single horse pseudodefecation in one night, but it is commonplace to capture one to three Liomys at a single point in the forest in one night, irrespective of whether there is a dung pile there. When a set of three Sherman livetraps baited with germinating guanacaste seeds was placed at each of the standard pseudodefecations in the forest in the current study, an average of 1-2 Liomys were captured per site on a single night in the dark of the moon (Table 1). During the period of about 20-40 days that the standard pseudodefecations were placed out (Table 1), I suspect that each of the pseudodefecations was visited by one to five Liomys, with an average of about three per pseudodefecation. A number of mice greater than one per pseudodefecation means that learning incentives are diluted but the chances are increased that one of the visitors is a fanatically eager searcher in dung for seeds.

If one uses a large trapping grid to determine how far the mice range, the result is a very large number of small and non-overlapping apparent home ranges (e.g., Fig. 10). However, this is in fact a map of the burrow entrances of each mouse. If a patch of 80 traps is set in a 10m diameter circle within the grid, and no other traps are set in the grid that night, mice are captured within that circle that have traveled as far as 50m from their previously-mapped area of major burrow entrances; such a trapping was done at station F-18 and at station S-6 in Fig. 10, and the dotted lines connect the mice caught with sites of their home burrows. The same experiment was then conducted at F-6 and S-18, but prior to trapping, each of these two sites was seeded with horse dung rich in guanacaste seeds on three nights at three day intervals. The number of Liomys caught in the dung-baited circles (ll and ll) was not significantly greater than in the control circles (7 and 8) (Fig. 10); they always forage such distances. In such a Santa Rosa forest, a defecation is always well within the foraging ranges of a number of Liomys mice and is also within 10-20m of a main burrow system. Even if there are hundreds of guanacaste seeds in the defecation, for example, a single mouse has time to harvest all seeds if the dung is found in the early evening.



*Fig. 10.* Density and approximate locations of burrow entrances for 106 *Liomys* mice in the Bosque San Emilio Mouse Plot (21-27 July 1984) as determined by three nights of trapping with a trap at each intersection of a 5 m grid (1058 traps per night). Solid or dotted figures indicate that the mouse was captured three times, squiggly lines indicate two capture times, and open squares one capture. A set of 80 traps (within a 10m radius circle) was then rotated four times among stations F-6, F-18, S-6 and S-18 on 16 mutually exclusive and alternating nights in August 1984; mice trapped at these stations are indicated by dotted lines. Stations F-6 and S-18 had been prebaited with three 5 liter pseudodefecations of guanacaste seed-enriched horse dung on 1, 4 and 7 August and the first trap night was 9 August, 1984.

# 4. The ability of the mice to remember the site and return to it

On rare occasions a pseudodefecation was only partly cleaned of guanacaste seeds, even though the remaining seeds were evident on the dung surface. It is possible that a foraging mouse did not find its way back to the pseudodefecation. However, it is more likely that only one mouse was foraging at the dung and it was interrupted by a predator or dawn caught up with the mouse; such piles are almost invariably cleaned of their seeds during the following night.

It is very difficult to predict the percent removal of a seed or seeds from dung according to their toxicity or other kind of unacceptability to the mice. There are many different components to this aspect of the interaction.

1. If the seed encountered is novel to the mouse, it is very frequently removed on the first encounter irrespective of its edibility. Apparently a novel seed is taken into the tunnel system and sampled; if found undesirable, on the subsequent or nearly subsequent encounter that species of seed is either left in place or taken a few centimeters away, sampled, and discarded. When white plastic beads (Fig. 2) were placed on the food plates along with seeds during the last three nights of the experiment plotted in Fig. 8, the mice removed 49, 89 and 97% of the beads on subsequent nights; that the percent removed did not jump from 49 to 100% on the second night was undoubtedly due to a mixture of slow learners and mice that did not experience the beads until the second or third night because other mice had removed them before they could get to them.

2. A seed may remain novel to the population of mice as a whole for a number of nights at the site of a single pseudodefecation, since as mentioned above, a mouse cannot collect the novel seeds from a pseudodefecation until the mouse before it has been sufficiently trained to leave some for the latecomer mouse to learn with. If ambient conditions are such that mice are foraging at greater than nightly intervals, the duration of novelty effects may be prolonged. Likewise, each time a new mouse changes its foraging area to include the pseudodefecation, a new mouse has to be trained. It was commonplace in the learning experiment plotted in Fig. 8 to have a pseudodefecation or plate retain all of its (highly unacceptable) chaperno seeds for 2-4 nights and then lose all of them in one night but then to retain them on the following night. I interpret such a total loss of chaperno seeds to mean that a naive mouse had found the dung pile.

3. The mice appear to forget or at least have doubts. Even after they had been exposed, for

example, to chaperno seeds for over a week, the mice that generated Fig. 8 often picked up 1-3 seeds and carried them off 20-100cm before discarding them on the litter surface. This creates a kind of microdispersal that may be highly significant to a plant species whose seeds all germinate with the first rains (such as is the case with chaperno). This kind of microdispersal was the cause of most of the small fluctuations in chaperno seed removals from the dung and plate arenas throughout the learning experiments (Fig. 8).

4. The seeds may be of variable desirability to the mice. For example, an intermediate and small number of black beans were often removed from the dung and plate experiment in Fig. 8. Many of the beans removed were eaten at the dung or plate, numerous others were handled but rejected at the dung, and yet others were carried a few centimeters away and then discarded. There were also inter-mouse differences in removal of wild lima beans; even when they were on the feeding plates in the learning experiments, some wild lima beans were left behind by mice that had had many nights of opportunity to harvest and eat them.

Are there inter-habitat differences in the number of seeds captured from a dung pile? While the forest habitats (all but P and P-FM) had generally high removal of the seeds from their dung, the Lonchocarpus forest had a very high initial removal rate and a high final percent removal. This suggests a large number of Liomys, very hungry mice, or both. At least 95% of the canopy of this forest is Lonchocarpus minimiflorus, which bears seeds rejected by Liomys. It is therefore unlikely that it can sustain or produce a high density of Liomys. The forest is also somewhat of an island in a relatively inhospitable and sterile habitat, the jaragua-filled pasture habitats (P and P-FM) (jaragua seeds are not available to Liomys). As 1985 appears to be a year of exceptionally high *Liomys* density, I suspect that the Lonchocarpus forest was a haven for mice dispersing through the grassland, but a haven populated by starving mice.

Only 13% of the horse pseudodefecations in the pasture habitat (P, Table 3) had all their seeds removed. Likewise, the initial rate of mining in both horse and cow dung was very low. I am certain

that these low harvest rates are primarily due to the low numbers of *Liomys* in the habitat (*e.g.*, Table 1). Furthermore, even though *Sigmodon hispidus* likes to burrow in horse and cow dung, it often ignores ungerminated guanacaste and guapinol seeds. If it picks them up, it then leaves them lying in the litter within a meter of the dung. When it encounters a germinating seed, it sometimes eats it (also see the pasture experiments in Janzen, 1982b).

While I do not report it in detail here, another habitat was sampled with concentrated pseudodefecations (100 guanacaste seeds, 20 guapinol seeds. 200 black beans) during this study. Pairs of horse and cow pseudodefecations were placed at 20m intervals in the open rocky creek bed of the Quebrada Cafetal, and paired with pseudodefecations placed 1-2m into the forest from the quebrada (creek) margin. During the first four days, all forest pseudodefecations had all of their guanacaste and guapinol seeds removed but only 32% of the 32 creekbed pseudodefecations had all or part of their guanacaste and guapinol seeds removed. However, after three weeks (18 April-10 May), all guanacaste and guapinol seeds had been removed from the creekbed pseudodefecations except for 11 guapinol seeds left in one pseudodefecation (all guanacaste and guapinol seeds were gone from the forest pseudodefecations by this date). While such a number does not appear to be biologically significant, it is noteworthy that the upcoming rains may wash those 11 seeds into potentially very high quality sites for germination.

### Implications for the plants

The different seed shadows produced by different species of large mammals in a tree's disperser coterie have the potential of being differentially thinned and trimmed by post-dispersal seed predation. Not only did the *Liomys* mice, for example, harvest different percentages of the guanacaste and guapinol seeds from horse than from cow dung, but they were also differentially effective in removing all guanacaste and guapinol seeds from a specific pseudodefecation. While one might argue that thinning of an initial seed shadow does not necessarily have much negative effect on the final distribution of adult trees (owing to inversely densitydependent factors), it is clear that trimming a seed shadow potentially eliminates any chance of an adult tree appearing at some sites, irrespective of how well the seedlings might have grown in those sites. Furthermore, the probability of appearance of an adult tree at a given site is very dependent on the number and temporal distribution of seedling attempts made at that site; thinning a seed shadow has a high potential for negatively influencing the appearance of new adult trees when seed numbers are low at a given site. The lower is seed density, the greater the chance that seed shadow thinning will turn into seed shadow trimming.

The experiments also make it clear that one of the multitude of selective pressures on seed size (volume probably being more relevant than actual weight in this case) will be the ability of postdispersal seed predators to locate seeds when those seeds are contained in large volumes of animal dung. Simultaneously such seed predators are selecting for particular seed odors, seed shape and other traits influencing the probability that a seed will be located.

At first glance it would appear that seeds that are toxic to a potential post-dispersal seed predator such as Liomys would be unaffected by seed harvest by this seed predator. However, some toxic seeds will die in the deep burrows after they have taught a mouse that a seed species is inedible. Almost all mice will have to learn, even if the mouse can remember from one year to the next, because better than 70% of the mice contacting a seed species that is new to the season are too young to have ever encountered it previously as a newlyfallen seed. Even once the mouse knows that a particular seed is undesirable, there will still be some microdispersal of undesirable seeds away from the dung. If the seed species is only very rarely encountered in dung, or if the Liomys density is very high, a given mouse may also encounter a toxic seed so rarely that it never does learn to reject it at the defecation site.

It is tempting to take the details of experiments like these and try to predict from them the impact on, for example, the guanacaste or guapinol population were the Liomvs to be exterminated from the habitat or were there to be yet other large mammals introduced into the habitat. However, with the present state of overall knowledge of what matters to such tree species, such statements should be restricted to a very general level. For example, if there were no Liomys and Santa Rosa supported a natural density of self-sustaining cattle and horses (much as it did for several hundred years before it became a national park), it is certain that guanacaste seedlings and saplings would be much more abundant than they are at present. At present, virtually all guanacaste seeds are consumed by peccaries when grinding up the fruits or Liomys that extract the seeds from the fruits (there are essentially only point seed shadows). However, guapinol seed shadows would not be directly affected because neither horses nor cows consume guapinol fruits (or their contained seeds) in nature. Guapinol could well, however, be indirectly affected through the production and maintenance of breaks in the general vegetation and along watercourses, and through the increased dispersal of seeds of other large trees such as guanacaste and cenicero (Pithecellobium saman). Likewise, were large ground sloths to be reintroduced to Santa Rosa, they might well consume large amounts of guapinol fruits and defecate the seeds in fibrous horse- or elephant-like dung in many sites of high quality from the viewpoint of the tree. Such friable dung might well be thoroughly cleaned of guapinol seeds by the Liomys population with the final result being only a slight increase in the density or coverage of the guapinol seed shadow as compared with that presently generated by agoutis (cf. W. Hallwachs, this volume), whose fruits the ground sloths would be eating. On the other hand, if the new megafaunal addition had dung much like cow dung, it might well do a high quality dry season performance of placing guapinol seeds in the habitat and encasing them in rain- and termite-soluble yet relatively Liomys -proof containers. If the large herbivore did not also defecate some very desirable seeds (e.g., guanacaste seeds) along with the guapinol seeds, the mice might be even less likely to find the guapinol seeds.

It is clear that the impact of dispersers and seed

predators on the population biology of a particular plant is not something that can be predicted given the highly fragmented and sketchy knowledge we have at present on both the animals and the trees. On the other hand, the interactions have all the properties of being structured, characterizable, and predictable given enough knowledge of both the habitats and what the organisms do in them. Give us a couple of hundred more years of careful close observation. We are at the stage parallel to medicine when it didn't know what red blood cells were or did, and still puzzled over the seat of the soul.

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