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ATTRACTION OF *LIOMYS* MICE TO HORSE DUNG AND THE EXTINCTION OF THIS RESPONSE

BY D. H. JANZEN

Department of Biology, University of Pennsylvania, Philadelphia, Pa. 19104–4288

Abstract. When horse dung containing the large seeds of *Enterolobium cyclocarpum* (the guanacaste tree) was experimentally placed in a tropical deciduous forest in Costa Rica (Santa Rosa National Park), *Liomys salvini* (Heteromyidae) spiny pocket mice went to it and dug out the seeds. When the *Liomys* in a particular area were repeatedly offered dung containing *E. cyclocarpum* seeds, they developed an attraction response to the dung that was so strong that seed-free fresh horse dung made better bait in traps than did an oatmeal-peanut butter mix. A single exposure to seed-rich dung was not adequate to generate this response, but two exposures generated a mild response. Once moderately seed-rich dung was no longer forthcoming, the mice in an area lost their strong attraction to horse dung in 3 to 4 months; this loss was due at least in part to the mice learning that the dung no longer contained seeds, since the same individual mice that earlier had been attracted to horse dung were still present as demonstrated by capturing them with other baits.

When a horse defaecates in the forest in the forest-grassland habitats of Santa Rosa National Park in the northwestern lowlands of Pacific coastal Costa Rica, the following night the dung is often thoroughly excavated by *Liomys salvini*, spiny pocket mice (Heteromyidae) (Janzen, 1982b). The mice appear to be in search of seeds. Since large herbivores have undoubtedly been producing seed-rich dung in this habitat since well before the Pleistocene period (Janzen & Martin, 1982), the interaction between *Liomys* and the horse (and other large mammals) is probably very old. Below I report observations on development and extinction of the mice's attraction to seed-free and seed-rich horse dung. Details of the mouse–dung–seed interaction depend on the kind of seed used. I used the large seeds of the guanacaste tree (*Enterolobium cyclocarpum*), because its seeds were probably dispersed by Pleistocene large herbivores (Janzen & Martin, 1982), are presently dispersed by horses, tapirs and cattle (Janzen 1981a, 1981b, 1981c, 1982a), and are large enough to be reliably counted and recovered from dung. The seeds of guanacaste trees are among the numerous species of seeds in Costa Rican lowland deciduous forest that are avidly harvested, cached in burrows, and eaten by *L. salvini* who can live for months on a pure diet of guanacaste seeds (Hallwachs & Janzen, unpublished data).

In the early stages of exploring the seed–mouse–dung interaction, I found that when single dormant or germinating guanacaste seeds are planted in the litter at 2 to 10 m intervals in the Santa Rosa forest where the experiments were conducted, the nightly seed loss was 50 to 100% to *L. salvini;* the mouse density in this forest is 30 to 40 per ha (Janzen, unpublished data). Suffering from a severe case of Puritan faecal phobia, I guessed that a small pile of fresh horse dung placed on the guanacaste seed would olfactorily or psychologically hide the seed from the mice. On the contrary, this treatment increased the seed loss rate. Subsequent crude experiments in one small patch of forest showed that *L. salvini* could be captured at dung piles while carrying the guanacaste seeds that they had removed from them, as many as six mice could be caught at one dung pile in one night, the mice could remove as many as 1000 seeds from one dung pile in one night, seeds did not disappear from dung from which the mice were excluded, and removal rates from cattle dung were lower than from horse dung. These experiments were terminated with a trapping night in which 84% of 19 Sherman live traps baited with seed-free fresh horse dung caught *L. salvini* (remaining traps caught dung beetles) while only 13% of eight dirt-baited control traps caught mice. The following night, in a portion of forest 200 m away and therefore out of range of the mice that had experienced seed-rich dung, I got the same result with the control traps but mice in only 11% of the seed-free dung-baited traps. I then left the site for 3 months, after having accidentally created a small patch of forest occupied by *L. salvini* who associated horse dung with highly desirable guanacaste seeds, irrespective of the basis for their original attraction to the dung. Below, I describe a census of the extinction of the association and an attempt at induction of the response with other *L. salvini* with lesser rewards over the following 10.5 months in nearby patches of the same forest. The traits of this extinction are relevant to the seed–mouse–dispersal-agent interaction because large herbivore defaecation patterns are highly heterogeneous in space and because mice have small home ranges, have high population turnover, and forget. The effectiveness of seed dispersal via the guts of large mammals will depend in great part on the thoroughness with which the mice search dung for seeds.

Methods

Study Sites

Santa Rosa National Park is about 25 km south of La Cruz in Guanacaste Province in northwestern Costa Rica, between the Pan-American highway and the Pacific ocean (9 to 350 m elevation). The three study sites are the borders of three trails that wind through a continuous patch of lightly disturbed forest of 40 to 80 years in age and many hundreds of hectares in extent. Most of the 200 tree species are deciduous, but a few evergreen species combined with creekside evergreen vegetation give a semi-deciduous aspect to the site during the 6-month rain-free dry season. The forest is bordered by patches of jaragua grassland (*Hyparrhenia rufa*) that were the home of large horse and cattle populations until the middle of 1978. These animals consumed all of the new-fallen guanacaste tree fruits and defaecated their seeds throughout the mix of forest and grassland. *Liomys salvini* is the only common small nocturnal terrestrial rodent seed-predator throughout this forest (Fleming 1974; Bonoff & Janzen 1980) and it also ranges occasionally into the grassland. A variety of unpublished experiments and censuses have made it clear that *L. salvini* is the only vertebrate in this forest that collects ungerminated guanacaste seeds from horse dung. The population of *L. salvini* is continuous throughout this forest, but owing to relatively sedentary behaviour and small home ranges (one ha or less), the mice along each of the three trails are to be viewed as three distinct replicate groups. There is no reason to suspect that there are differences in behaviour among these three groups of mice.

Hubbell's Woods Trail I (HWI). This footpath, along which I accidentally created a set of mice trained to search in horse dung for seeds, leaves the asphalt access road to the Park approximately 75 m north of its only four-way intersection.

Nature Trail (NT). This broad footpath passes through the forest 200 to 250 m to the southeast of HWI, and the portion of the trail used in this study is the terminal loop, beginning at the main fork and passing by the bat caves. The trail begins near the historic Casona. The vegetation along NT is 10 to 30 years younger than that along HWI but the *L. salvini* density is the same.

Bosque Húmedo (BH). This narrow and little-used footpath winds through the forest understory to the north of the asphalt access road as it passes through a patch of exceptionally evergreen forest 3 km toward the Pan-American highway from the main administration area. The vegetation along BH is more moist and shady than that along HWI or NT, but the *L. salvini* density is about the same as on the other trails.

None of the three study sites has been exposed to cattle or horse dung since these large herbivores were largely removed from the Park in 1978; occasionally a park guard's horse passes down the asphalt access road, but the dung that falls there is quickly dried by the sun and is not generally available to the mice that live along the trails where I worked. Furthermore, these horses did not have access to guanacaste fruits during the period of this study because of a general failure of the guanacaste fruit crop in 1980 within the Park.

Mammal Trapping

Oatmeal–peanut-butter baits. About 2 Tbs. of chunk-style Skippy peanut butter were kneaded into a litre of rolled oats oatmeal and about a tsp. of this bait placed in the back of a 7 × 8 × 22 cm Sherman aluminium live trap. Traps in which OPB had been used were disassembled and washed thoroughly between each night of trapping. OPB traps were never used as dung-baited or dirt-baited traps (and vice versa), never stored with other types of traps, and never handled by someone who had been recently working with dung. Likewise, the dung- or dirt-baited traps had never been baited with OPB. However, the 28 traps used on 1–2 August 1979 were old and well-used traps that had been subject to many kinds of bait; they were thoroughly washed before use. If an OPB trapline had to be checked the same morning as a dung-baited trapline, the latter was always checked second or by a different person, and neither touched the materials being handled by the other. Likewise, two persons collected the dung and control traps and kept all materials separate. Dung and control traps were always placed out in the same relative order (two dung traps followed by a control, except for one set of stations central to the line where three dung traps were followed by a control trap), but the exact locations of the traps varied by 0–2 m between trapping events.

In both OPB traps and dung (and control) trapping, the traps were placed at approximately 7–10 m intervals next to the trail. *Liomys salvini* foraging ranges are such that it is commonplace to catch the same mouse repeatedly among all of a set of three traps placed this far apart. Based on other trapping in Santa Rosa forests (1979–1980), if a single station were to be trapped repeatedly over a period of 2 weeks or more, 2 to 4 different *L. salvini* are likely to be captured there. Examination of the individual trapping records in the study reported here suggests that at least two different mice regularly foraged in the vicinity of each of the 40 trapping stations.

Dung bait. Horse dung between 0 and 4 h of age was collected between 1200 and 1500 hours for use as bait that evening. Several different dung piles originating from several different horses were pooled in a large plastic pail or bag and kept sealed until used. A small handful of fresh dung was laid in the middle of a 20-cm square of flimsy nylon netting, and the corners were gathered together to form a dung-filled net bag. I then twisted the corners together and wedged them between the rear trap door and the trap ceiling so as to suspend the dung ball about 3 cm over the posterior lip of the trap treadle. This arrangement prevented the dung ball from setting off the trap and maximized the difficulty that dung beetles had in setting off the trap while trying to get to the dung.

Large *Dichotomius* dung beetles are an ever-present nuisance when using dung bait during the first two-thirds of the rainy season (May–October). There is no way to know if they significantly reduced trapping success of mice attracted to dung; they set off between 1 and 4 of the dung-baited traps in each of the rainy season surveys cited in Table I. To subtract such traps from the number used would falsely increase the number of mice per trap that apparently were attracted to dung, and therefore traps sprung by dung beetles were included in the category 'empty traps'. In the present study the results are sufficiently dramatic that the elimination of traps with dung beetles would not change the qualitative conclusions.

Control traps. These were baited with balls of moist earth treated just as were the dung balls,

Table I. Trapping Outcome and Treatment Regime for Three Forest Sites for *Liomys salvini* Live Trapped with Dung, Dirt or Oatmeal–Peanut-butter Baits

	Percentage of traps catching *Liomys salvini* per night per site													
	1–2 Aug.		5–9 Nov.		29–31 Nov.		3–5 Jan.		7–9 March		1–3 May		15–17 June	
Site	Dung	Dirt	Dung	Dirt	Dung	Dirt	Dung	Dirt	Dung	Dirt	Dung	Dirt	Dung	Dirt
HWI	84	11	19	0	33	8	37	0	44	8	0	0	4	8
BH			0	0	7	8	0	0	37	0	4	0	0	8
NT	11	11	0	0	0	0	0	0	7	0	4	8	0	0

	10–11 Nov.	4–6 Jan.	8–10 March	2–4 May	17–19 June
	Oatmeal–Peanut-butter	Oatmeal–Peanut-butter	Oatmeal–Peanut-butter	Oatmeal–Peanut-butter	Oatmeal–Peanut-butter
HWI	35	40	40	28	30
BH	30	23	35	28	33
NT	35	25	23	28	28

Treatments

Seed-enriched dung placed out 6 times (25 June–31 July) on HWI	Seed-enriched dung 3 times on HWI and BH; seed-free dung 3 times on NT (19–28 Nov.)	Dung-free seed lines to census mice (1–3 Dec.)	Seed-enriched dung 1 time on all 3 lines, and dung-free seed lines (5–7 Jan. 1980)

On 1–2 August there were 19 dung-baited traps and 9 dirt-baited traps per site; on all other dates there were 27 dung traps and 13 dirt traps per site. On all oatmeal–peanut-butter traplines, 40 traps were used.

and were of the same size. Only dirt-contaminated and new netting was used in control traps. Throughout the course of the experiment, control traps were never baited with anything except dirt and were kept isolated in their own containers. They, like the dung traps, were new at the beginning of the experiment. Two persons worked together when setting a dung and control trap line.

Mouse response and treatment. The mice caught with OPB bait ate some oatmeal and extracted the peanut chunks for storage in their pouches. The captured animals were therefore rewarded, but they were also traumatized as indicated by the fact that roughly half of the mice captured on a given OPB trapping bout were not captured again at that site with that bait for 1–4 months, but were then often recaptured at that trap site with that bait. However, if a different bait is used, such animals are likely to be recaptured the night after capture with OPB bait. While the animals caught with horse dung bait or dirt balls tore the bait ball to shreds, there were no seeds present so they were not rewarded. Trapping trauma was undoubtedly increased by marking, which required firmly holding the mouse while snipping 2–3 mm deep thin V-shaped notches out of the margin of one or both ear pinnae. All animals trapped were individually marked except those on 1–2 August 1979. Traps were set between 1600 and 1800 hours and the mice removed between 1800 and 2000 hours. When released, the mice usually remained motionless for a few seconds and then ran-jumped-bounced 1–10 m rather directly to an apparent burrow entrance and disappeared below ground. There were also intrinsically trap-shy mice, as evidenced by occasions when 1 to 3 guanacaste seeds placed adjacent to traps baited with a variety of baits were removed, but the traps and their contents left undisturbed. *Liomys salvini* occasionally enters unbaited traps while exploring the novel object.

Dung Piles

The dung piles mimicked a horse defaecation and were placed at 5–8-m intervals on the litter adjacent to the three trails in the study sites. Each pile was a fresh defaecation from one of the same horses that generated the dung for the bait in the traps. A seed-enriched dung pile was made by scooping out the centre of the pile, scattering 20 guanacaste seeds over the depression, and lightly covering them with dung. Guanacaste seeds are flattened, polished, smooth brown ovals 15 to 20 mm long and 5 to 10 mm thick, and each weighs 300 to 1100 mg; a *L. salvini* can carry about six at a time in its pouches. The dung piles resembled a natural moderately seed-rich defaecation in that the seeds were easily located if the dung pile was dug into, but were not encountered unless the mouse did that. This is the sort of moderately seed-rich dung pile produced by a horse that is consuming 10 to 30 guanacaste fruits per day. When guanacaste seeds were put out without dung as a measure of mouse presence, great care was taken to avoid contamination with dung odours.

Program of Reinforcement and Trapping

As briefly mentioned in the introduction, the HWI site was exposed to seed-enriched dung piles six times between 25 June and 31 July 1979. HWI and NT were then dung- and dirt-trapped on 1–2 August 1979. On 5–9 November 1979, HWI, NT and BH were dung- and dirt-trapped, followed by trapping to determine the intensity of dung response and to determine the numbers of mice that could be trapped on the three trails in one night. On 19–28 November I attempted to reinforce strongly the attraction to dung on HWI by twice putting out fresh dung piles with seeds and refilling the emptied dung piles once. Simultaneously I gave the BH site its first dose of seed-enriched dung by doing the same thing and performed a control with NT by putting out seed-free dung. Immediately after, on 29–31 November, I again dung- and dirt-trapped all three sites. Shortly after that, I assayed *L. salvini* activity by putting out small piles of dung-free guanacaste seeds at all three sites. A month later, I again dung- and dirt-trapped all three sites, then OPB-trapped all three, and then put seed-enriched dung at all three. This meant that the HWI site had received seed-enriched dung eight times between 25 June 1979 and 5 January 1980, the BH site received seed-enriched dung twice (21–28 November 1979, 6 January 1980), and the NT site received seed-enriched dung once (7 January 1980). The sites were then dung- and dirt-trapped, immediately followed by OPB trapping, on 7–10 March, 1–4 May, and 15–19 June 1980. This schedule was then stopped because the differential attraction response to dung and dirt traps had extinguished.

Results

Initial trapping (1–2 August 1979). The 84% success with dung-baited traps on HWI is highly significantly greater than the 11% success with dirt-baited control traps (Table I), and leaves no doubt that the mice were attracted to seed-free dung in a habitat where seed-rich dung had been deposited repeatedly during the previous 2 months. The equal and low success rate of dung-baited and dirt-baited traps on NT (Table I) shows clearly that when the mice have not been entrained to seed-rich dung, they are not sufficiently attracted to seed-free dung to enter the traps any more than if the traps were baited with dirt. There was a high density of mice at NT at this time, as shown by a different census at the site using OPB-baited traps in May through mid-July 1979 (Bonoff & Janzen 1980).

After a 3-month recess (5–12 November 1979). The 19% success with dung-baited traps on HWI (Table I) suggests some extinction of the attraction to dung demonstrated on 1–2 August (no mice were taken with any control traps or with dung-baited traps on NT and BH). The mice were neither torpid nor had left the area, as demonstrated by 30 to 35% trap success with OPB-baited traps on 10–12 November (Table I), and by recapturing 4 of the 5 mice that had been caught in August using dung as bait.

Reinforcement and response initiation (19–28 November 1979). On each night of 21, 23 and 27 November, I placed 40 seed-enriched dung piles along HWI; within these nights the mice harvested 2385 of the 2400 guanacaste seeds. I did the same along BH and the mice got 2270 of the seeds. The same number of dung piles were placed along NT but, being seed-free, they were not dug through by the mice. The above treatments should have reinforced the attraction to dung on HWI, initiated it on BH and had no effect on NT mice.

Test of reinforcement and response initiation (29–31 November 1979). A 33% success with dung-baited traps on HWI (Table I) showed that the dung attraction had increased over that recorded before reinforcement with seed-rich dung piles. Five of the mice had been captured previously using dung as bait. On BH, the 7% success (indistinguishable from the control) shows that the attraction to dung cannot be initiated by three exposures to seed-enriched dung over a 6-day period. Again, the zero trapping success on NT showed that seed-enriched dung is necessary to initiate a strong attraction to dung. I put out piles of 20 dung-free guanacaste seeds each near the sites of the traps and dung piles on 1–3 December and within 2 to 10 nights all were harvested by the mice, demonstrating that the mouse density was still high at all three sites.

After a 1-month recess (3–5 January 1980). On HWI, there was 37% success with the dung-baited traps, but no mice in any other traps (Table I). Seven of the mice had been captured earlier in dung-baited traps and it is clear that they retained their attraction to dung at least a month. The low trap success everywhere except on HWI was not due to a diminution of mouse density as demonstrated by the 23 to 40% trap success with OPB-baited traps on 4–6 January (Table I).

Final reinforcement and attempt at response initiation (5–7 January 1980). I placed 20 seed-rich dung piles along all three trails, and in addition placed 20 piles of dung-free seeds on the litter. Along all three trails, the seeds were gone from the dung within several days; the dung-free seeds required 6 to 156 days to be removed, strongly suggesting that without an odour cue, it can be a very long time before a *L. salvini* finds them by random search. This placing of seeds should have reinforced the attraction to dung by the HWI mice, might have increased attraction to dung by the BH mice (if any attraction ever existed), and should not have had any effect on the NT mice, judging by the negative results from the November exposure to seed-rich dung by BH mice.

After a 2-month recess (7–9 March 1980). HWI mice showed no sign of extinction of the response (Table I), and NT mice showed no sign of initiation of the response. However, the 37% success with dung-baited traps on BH strongly suggests that the second dung treatment (January) initiated an attraction to dung. This suggestion is reinforced by the fact that two of the mice were the same two that had been caught in dung-baited traps in November on BH. Again, immediate subsequent trapping with OPB-baited traps showed that the mouse density was as high as usual at all three sites (Table I). Half the mice caught at all three sites had been captured in a previous trapping session.

After a 4-month recess (1–4 May 1980). On all three trails, the dung-baited and dirt-baited trap successes are indistinguishable, and also not distinguishable from the successes in areas or times that have not experienced seed-rich dung. The response has extinguished. When the trails were trapped with OPB bait, the results were no different from the previous OPB-bait trapping bouts. Nine of the 33 mice had been previously captured in dung-baited traps; 10 of the mice were young of the year and could not have been exposed to seed-rich dung (*L. salvini* reproduction occurs in January–May). Only three mice were adults that had not been captured previously, and no young of the year were taken in dung-baited traps.

On 15–19 June I repeated the 1–4 May trapping regime with essentially the same results (Table I).

Discussion

At least 4 months is required to extinguish the attraction to seed-free horse dung by *L. salvini* once it has been initiated and reinforced numerous times with seed-rich dung over a 6-month period. Three exposures to seed-rich dung over a 6-day period did not induce attraction to seed-free dung, but by giving another exposure a month later, an attraction response was generated. This conclusion presupposes that before 1979 the mice living along HWI were no different from the mice along the other two trails; unfortunately there was no earlier trapping attempt with seed-free dung as bait.

Numerous exposures to seed-rich dung should be required to generate a strong attraction response by *L. salvini* because (a) with any given exposure to seed-enriched dung, part of the animals that are thereby entrained to dung will not happen to be foraging in the area the subsequent night of assay trapping, and (b) the first mouse to discover the seeds in the dung will probably get all of them and subsequent mice will therefore not be entrained or will even have their attraction dampened. Extinction of the response should occur through forgetting, negative reinforcement, and population turnover.

Why do *L. salvini* go to the dung piles in the first place? I suspect that the mice investigate any novel non-threatening object in their habitat. For example, while I was exploring the responses of the mice to seeds in another part of the forest used for this experiment (July 1979), I set out four lines of 80 dung-free piles of five guanacaste seeds at 10 m intervals. After 2 weeks, 12 to 18 of these piles remained in each line. I concluded that the mouse density was either very low in this area or the remaining piles had been placed in small lacunae in *L. salvini* foraging patterns. I then hung a small nylon netting bag of fresh horse dung on a string about 10 cm above each of the remaining piles. In the following night, 96% of the 57 seed piles were taken by the mice. First, this suggested that the result was due to the 57 seed piles having been placed in small lacunae in mouse foraging patterns rather than that there was a low density of mice. Second, it suggested that the mice were intrinsically attracted to horse dung, since I had never used it in these areas before. To test this suggestion, I later constructed two more 80-pile seed lines, and after 10 days each had 11 remnant seed piles. I hung a small bag of moist dirt in a nylon bag over each of these and got 91% removal of the seed piles. I then set a line of 40 hanging bags of dung, each bag alternating with one of 40 hanging bags of moist soil. Each was 10 cm above five clean guanacaste seeds on the litter and at 10 m intervals. After the third night, 81% of the piles below dung bags and 91% of the piles below dirt bags had disappeared; over the next three nights all but one pile below a dung bag disappeared and all but two below a dirt bag disappeared. It is the novel object, rather than dung per se, that first attracts *L. salvini*. This working hypothesis is consistent with the occasional capture of a mouse in a dirt-baited control trap and even the occasional capture of a mouse in a dung-baited trap in an area that has never been exposed to seed-enriched dung.

The most straightforward scenario, then, is that a mouse is attracted to a horse dung pile the first time one appears in its foraging area. It examines the dung pile. If it is rewarded with a seed, the mouse digs further until all or most seeds are located. If the seeds have very little odour of their own (as is probably the case with the 1 to 2-year-old dormant guanacaste seeds used in these experiments), a seed may be missed even after intensive search. In this situation, the probability that a seed will be found should decline with a decrease in (a) the seed/dung ratio, (b) the number of other seeds in the dung, (c) the size and olfactory conspicuousness of the seed, and (d) the mouse's previous experience with seed-rich dung.

Horse dung in these forests attracts a large array of dung beetles. This raises the possibility that *L. salvini* are initially attracted to the dung to harvest dung beetles rather than seeds. In captivity, *L. salvini* are at best unenthusiastic consumers of dung beetles (but eat eagerly many other species of insects). In the field, it is commonplace to have all the guanacaste seeds removed from a dung pile rich in dung beetles, yet have no insect parts left as a sign of predation on dung beetles. The dung beetles are usually well-buried in horse dung and the mouse would have to dig after them. When the seed-free horse dung was put out on the NT, it attracted a moderate number of dung beetles but there was no disturbance of the dung pile in the manner characteristic of that of *L. salvini* when digging for seeds. These seed-free but dung beetle-rich dung piles initiated no dung attraction response in the mice on the NT. Finally, the failure of dung-baited traps to catch more mice than control traps in areas not exposed previously to several bouts of seed-enriched horse dung implies that dung beetles were not the reward to the mice. Dung-baited traps usually attracted dung beetles, and if a mouse were searching for them it would have to walk on the trap treadle to examine the dung used as bait.

In the laboratory, response to fresh horse dung by newly caught *L. salvini* is variable (in the three study areas all mice were released immediately after capture so they were not tested). Some mice ignore it indefinitely while others wake from a deep sleep, go directly to it, tear it to shreds in a few seconds, and go back to sleep. The sources of this variation are being studied. However, since the dung of vertebrates often contains seeds that are highly edible to *L. salvini*, it is not surprising to find that dung is one of the novel objects in the habitat which the mice find worth investigating. Furthermore, if a mouse finds that a particular kind of dung regularly yields valuable seeds, it is not surprising to find the mouse developing a very strong search response to that odour.

Numerous additional field studies are needed to thoroughly relate the findings of this study to the disperser–tree–rodent interaction system in this tropical deciduous forest. However, a few working hypotheses can be formulated. If a horse or other large mammal wanders into a part of the forest that its species only rarely visits and leaves behind a very seed-rich pile of dung, it is likely that the *L. salvini* will get all or most of the seeds (Janzen, 1982b). On the other hand, if the dung is sufficiently seed-poor for the seeds to be not readily apparent, the seeds may escape detection and find their way into the litter. This process would greatly increase the value of dispersal agents that fed in such a manner that there was a low seed/dung ratio in their dung. In a part of the forest often frequented by large mammals that occasionally or frequently defaecate dung rich in seeds, it seems that the chances of seed survival may be very low at any seed/dung ratio. The number of guanacaste seeds escaping to the seedling stage might then be somewhat equally distributed between the very few that are missed by mice thoroughly searching a seed-rich dung pile and the very few that escape after the mouse has harvested them (through mouse death, sloppy hoarding behaviour, seed germination in the cache in the burrow, etc.). Whatever the balance of these various processes, it is clear that high quality seed dispersal does not necessarily occur simply by having a large mammal eat a lot of fruit and dump seed-rich dung in the forest.

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