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SEED REMOVAL FROM FALLEN GUANACASTE FRUITS *(ENTEROLOBIUM CYCLOCARPUM)* BY SPINY POCKET MICE *(LIOMYS SALVINI)*

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ABSTRACT

Even when large potential dispersal agents are missing from the habitats containing guanacaste trees *(Enterolobium cyclocarpum)*, there is no accumulation of the seeds below the parent tree over the years. By placing fruits containing known numbers of seeds below a parent guanacaste tree in Santa Rosa National Park, Costa Rica, and monitoring their disappearance, it was determined that 93.34 percent of the seeds were removed by a small forest-floor rodent, *Liomys salvini.* Another 9.6 percent of the seeds were lost by germination and unknown causes of death. This leaves only 2 percent of the seed crop to accumulate below the parent, and this number of seeds can easily be lost during the following months through germination and *L. salvini* seed predation. There is no mystery as to why the hard dormant seeds of guanacaste trees do not accumulate below seed-bearing parents in forest occupied by *L. salvini.*

In the deciduous forests of Santa Rosa National Park, northwestern Guanacaste Province, Costa Rica, guanacaste trees *(Enterolobium cyclocarpum,* Mimosaceae*)* are scarce but conspicuous and enormous members of the canopy. In some years they produce large crops of indehiscent large fruits that fall to the ground as soon as they are ripe and would have been eaten by Pleistocene large herbivores (Janzen and Martin 1982); at present they are eagerly consumed by range horses and cattle (Jansen 1981a, 1981b, 1981c, 1981d). The 300–1100 mg hard dormant ovoid seeds are dispersed by transmission through the intestinal tracts of these large animals. Tapirs *(Tapirus bairdii)* will also eat some guanacaste fruits and disperse some seeds, though as is the case with horses, they also may digest a substantial fraction of the seeds (Janzen 1981b, 1981g). Collared peccaries *(Tayassu tajacu)* also eat the fruits, but grind up the seeds in the process.

In the same habitat, spiny pocket mice *(Liomys salvini)* avidly seek guanacaste seeds as prey (along with many other species of seeds). They harvest them from fallen fruits, horse and cattle dung (Janzen 1981e, 1981f), forest floor litter and anywhere else they find them. If the fruits are given to *L. salvini* in the laboratory, they cut the seeds out of the fruit and can live on a pure diet of them for more than a month (Hallwachs and Janzen 1982). They may also disperse some guanacaste seeds by losing them, by being taken by a predator when carrying them to their underground burrows, or by dying after they have cached them in their burrows.

The fruit shadow of a guanacaste tree is therefore the site of a race between the large herbivores and the spiny pocket mice. Since a large guanacaste tree may drop as many as 5-10 thousand fruits, will the mice harvest so many seeds in the absence of the large herbivores? As a first step in answering this question, I selected a guanacaste tree in Santa Rosa that bore a crop of about 4000 fruits in March 1979 (*E.c.* number 63) and monitored seed removal by *L. salvini.* This tree was chosen not only because of its large crop, its location in a forest patch known to have a normal density of *L. salvini* (about 1 per 4 live traps at 5 m intervals, baited with oatmeal-peanut butter mix), and its ease of access, but because horses and cattle did not have access to the area at the time and there was no sign of peccary foraging in its somewhat insular patch of forest.

On 2 June 1979, the ground below the tree crown was littered with guanacaste fruits that had fallen in April and May; there were 5 to 10 fruits per m^2. The rainy season had been well underway for about 1 week and the litter and fallen pods were soggy and smelled moldy. Here and there were pods from which the spiny pocket mice had already cut some seeds (Fig. 1). At 4 haphazardly chosen points in the fruit shadow I collected the 1-4 cm thick layer of litter over a m^2 area, scraping thoroughly down to mineral soil. The fruits were removed from the litter and the litter was carefully sieved. There were 4 guanacaste seeds in the litter; presumably these were the remnants of previous seed crops (seeds that the *L. salvini* had missed). I therefore assume the background level of guanacaste seeds to be $1/m^2$ in this litter at the time of the experiment.

The seeds in a guanacaste fruit can be counted by squeezing the fruit at each large bump in the fruit surface. On each of the 4 cleaned areas and on 4 more from which all the fruits had been removed, I then placed enough fruits for an average of 108 seeds/m^2 (s.d. = 4.6); this required 8 to 13 fruits/m^2. Assuming my estimation of seeds in the litter to be correct, each of these 8 m^2 plots then contained an average of 109 seeds.

On 17 July, 46 nights later, I collected all of the litter within the 8 m^2 plots down to mineral soil, and sieved it for guanacaste seeds. At this time, there were no intact pods remaining on the litter surface but there were numerous rotting pod wall and core fragments mixed in with the rotting litter. The number of seeds in each plot ranged from 0 to 9, with a mean of 3.25 (s.d. = 2.8). Subtracting 1 seed as the background seed level, I conclude that 97.94 percent of the seeds had disappeared from the plots during the 46 day period.

As a control for seeds lost to germination and subsequent death as seedlings (there were no seedlings in the plots or elsewhere beneath the parent tree), I simultaneously placed 34 of the same tree's fruits containing 394 seeds on a soil-litter mix in a large wooden tray. The tray was screened to keep out horses and placed in a *L. salvini*—free habitat nearby, but it nevertheless received about the same weather as did the fruits exposed to *L. salvini.* After the same 46 day period, the rotted fruits were dissected and found to contain 356 hard dormant seeds (i.e., 90.4% of the seeds were in the same dormant state as at the beginning of the experiment), 4 seedlings (only one of which had pushed out of the fruit), 8 living soft seeds just beginning to germinate, 11 that had germinated but then died, and 15 unaccounted for. I assume that the 15 unaccounted for germinated and died early in the experiment, and had rotted beyond recognition by the end.

I therefore assume that as many as 9.6 percent of the seeds missing from below the parent tree could be due to causes other than *L. salvini.* However, the actual figure is probably lower because many of the seeds that died in the control would have been taken by *L. salvini* before they could have germinated.

The experiment suggests that the *L. salvini* may be removing a minimum of 88.53 percent of the seeds below a large guanacaste tree that is not visited by large mammals. If this is a general event, and examination of fruits crops below many guanacaste trees over a 4 year period in Santa Rosa convinces me that it is, it is likely the primary explanation for why a large reservoir of dormant seeds does not accumulate in the soil below a guanacaste tree growing in forest free of large mammals.

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Resumen

Aun cuando hacen falta grandes agentes dispersores de semillas en los habitats poblados por árboles de guanacaste *(Enterolobium cyclocarpum),* no se produce acumulación de semillas bajo el árbol productor, durante los años de reproducción. Usando el método de colocar frutos que contienen números conocidos de semillas bajo un árbol reproductivo en el Parque Nacional Santa Rosa, Costa Rica, y anotando cuando estos desaparecieron, se ha determinado que el 93,34 por ciento de las semillas fueron "cosechadas" por un pequeño roedor del bosque, *Liomys salvini.* Un 9,6 por ciento de las semillas germinaron o murieron por causas desconocidas. Solamente un 2 por ciento de las semillas quedan al pie de su productor, y este número puede ser fácilmente eliminado, durante los meses siguientes, por germinación

o por depredación por *L. salvini.* Así se explica el porqué, las semillas duras, latentes del guanacaste no se acumulan bajo sus árboles en un bosque habitado porque contiene *L. salvini.*

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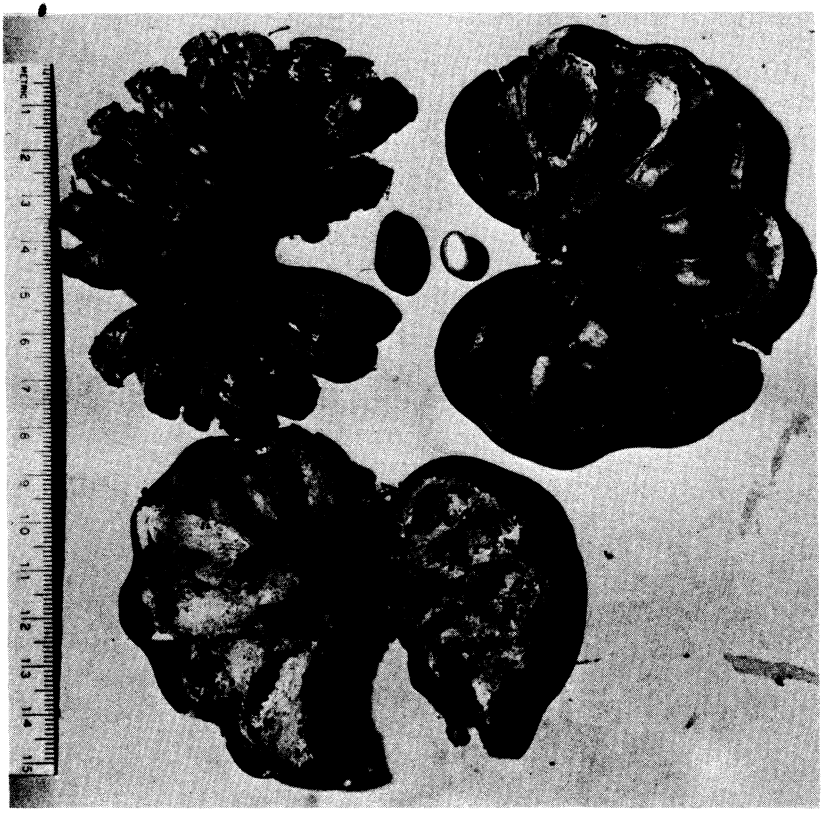

Fig. 1. Fruits of *Enterolobium cyclocarpum* in various states of decomposition. Upper right: intact fruit from which 3 seeds had been taken by *Liomys salvini;* I replaced the seeds for the photograph. Upper left: intact fruit with the outer fruit wall removed by leaf-cutter ants, leaving the inner seed cavities intact. Lower: fruit from which all the seeds have been removed by *Liomys salvini.* Santa Rosa National Park, Guanacaste Province, Costa Rica (May 1979).