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SIMULATION OF *ANDIRA* FRUIT PULP REMOVAL BY BATS REDUCES SEED PREDATION BY *CLEOGONUS* WEEVILS

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ABSTRACT

By cutting 1/3, 2/3 and all of the fruit pulp off of ripe *Andira inermis* fruits, the intensity of seed predation by *Cleogonus* weevils was lowered from 97.5 percent in the controls to 92.5, 92.5 and 83.5 percent, respectively. Removing the fruit pulp simulates what the bats do to *Andira* fruits during seed dispersal. I conclude that dispersal of *Andira* seeds by bats may increase seed survival by more than just removing them from the vicinity of the parent tree.

Andira inermis is a scarce evergreen fabaceous legume tree in the deciduous and riparian forests of Santa Rosa National Park in northwestern Guanacaste Province, Costa Rica. It is native to the lowlands of Mexico, Central America, some Caribbean islands, and northern South America. In Santa Rosa, as elsewhere (Janzen *et al.* 1976), the seeds in its 2–3 cm diameter single-seeded ovoid fruits are dispersed by phyllostomatid bats (*Artibeus* spp.) that pluck the fruits from the tree and carry them one at a time to a feeding roost which may be as many as 150 m away, but is more likely to be within 50 m if the habitat is forested. The ripe fruits are leaf-green in color and have a juicy pulp surrounding a large fibrous nut. After chewing off a variable amount of the pulp (usually 1/4 to 3/4 of it), the bat drops the intact nut with its attached pulp remnants and contained large seed, and returns to the *Andira* tree for another fruit. In contemporary habitats, bats appear to be the only natural dispersal agents of the seeds from the tree crown. However, once the bats have dropped the seeds there may be secondary dispersal of the seeds by rodents and in Pleistocene times the seeds may have been dispersed from the crowns by large mammals that ate the fruits (Janzen and Martin 1982).

The removal of fruit pulp from the *Andira* nut by bats may increase seed survivorship for the following reason. At the same time that the bats are harvesting the *Andira* fruits, in the tree crown and on the ground below there are adults of three species of large black weevils (Curculionidae: *Cleogonus armatus, C. rubetra, C. fratellus*). These adults are mating, feeding, and ovipositing on the green-colored mature and nearly mature fruits (Fig. 1). Oviposition begins shortly before the fruits are sufficiently ripe for the bats to start removing them, and continues as long as the fruits are available on the tree, on the ground beneath the tree, and dispersed away from the tree. The *Cleogonus* larvae mine through the fruit pulp for a few days before tunneling through the fibrous nut wall (endocarp) and into the full-sized relatively soft seed. As many as five larvae may complete their development while consuming the seed contents, but a seed is killed if only one or more larvae develop in it. If a bat removes a fruit from the tree before a weevil oviposits in it, or if a bat chews off fruit pulp containing eggs or larvae before one or more larvae get into the nut, the bat increases the probability that the seed will survive.

Normally, better than 90 percent of the *Andira* seeds on the ground beneath the parent tree are killed by *Cleogonus* larvae (Janzen *et al.* 1976 and unpublished censuses). If all the fruits on a branch are picked at the time that the bats are harvesting fruits, or if a large sample of ripe fruits is shaken from the tree, the seed mortality due to *Cleogonus* usually ranges between 70 and 100 percent. If a sample of nuts and partly eaten fruits is collected from beneath a bat feeding roost and the larvae allowed to develop, the seed mortality usually ranges between 30 and 90 percent. There are five mutually non-exclusive hypotheses as to why the seed mortality beneath a bat feeding roost is lower than that beneath the parent tree. Since it is the seeds beneath the bat feeding roosts that will probably produce the next generation of *Andira,* these hypotheses are relevant to understanding the impact of bats on *Andira.*

1. By selecting the most exposed fruits in the *Andira* crown, the bats may remove fruits with an exceptionally low intensity of oviposition; adult *Cleogonus* weevils are most inclined to feed and oviposit on fruits in the center of clusters and nestled among leaves.

2. The patch of seeds below the bat feeding roost may be far enough from the main concentration of adult weevils at the parent *Andira* that a significantly lower number of weevils find each fruit than is the case below the parent *Andira.*

3. The nuts that have been thoroughly cleaned of pulp by the bats may not offer suitable oviposition sites for *Cleogonus,* and therefore the seeds that already had weevil larvae in them at the time they were picked are the only ones that are killed.

4. The bats may pick some fruits before the weevils have oviposited in them (and therefore the interaction contains a race between the bat and the weevils, as far as the seed is concerned).

5. The consumption of fruit pulp by the bats may remove a significant number of eggs and larvae that had not yet mined into the nut or seed.

Here, I report the results of an experiment designed to test the last two of these hypotheses.

The source of the experimental fruit (*Andira inermis* 200) is growing approximately 50 m west of the beginning of the trail to Playa Nancite, where this trail leaves the road at the north end of Playa Naranjo; Playa Naranjo is in the lowlands of Santa Rosa National Park. This tree bore a crop of about 10,000 fruits in May 1979 and ripe fruits were collected from the crown on 23 May by moderate shaking of the branches into a long-handled butterfly net. The crown is 3 to 6 m above the ground and the fruits taken were representative of those in the central portions of the crown margins. With this type of fruit collection at this time in the life of the fruit crop, about a quarter of the fruits on a branch were ripe enough to fall off. I do not know at exactly what stage of ripeness the bats select *Andira* fruits and therefore I cannot know what fraction of these would have been regarded as too green by a bat; however, the handfull that I tasted had about the same flavor as those that had been dropped below feeding roosts after having been partly eaten by roosting bats.

About 1000 of the fruits collected from the crown were placed in a large cloth bag, and from this bag 800 were drawn blindly for the experiment. To determine the weevil infestation of fruits at the time that they were taken from the crown, 200 of these fruits were left intact. To simulate the effects of a bat eating 1/3, 2/3 and all of the fruit pulp from a fruit, this amount of pulp was scraped off of each of 200 fruits. Each of these four 200-fruit samples was then divided into subsamples of 20 fruits each. All fruit choice and allocation to categories was done by naive helpers and therefore without reference to signs of feeding scars by the weevils. Each subsample was stored in an open plastic bowl at ambient temperature. The fruits were sprinkled heavily with water about once a week to simulate being rained on. After a month to allow weevil larval development (there is no egg dormancy in *Cleogonus* weevil eggs), each fruit was cut in half and its contents scored for the presence of weevil larvae. All but three fruits were either intact with a solid white living seed or thoroughly eaten out by *Cleogonus* larvae; the three exceptions were moldy and rotting but were counted as having been killed by weevil larvae because larval attack may have this effect when the larva dies shortly after entry (there was one of these seeds in each of the three treatments).

As is evident in Table 1, when the fruit was left intact, the seed mortality was 97.5 percent. This figure is consistent with past levels of seed predation recorded for fruit samples collected from this particular *Andira* tree. A mortality of 97.5 percent is significantly greater than the mortality in any of the other three treatments (e.g., intact vs. 1/3 of fruit pulp removed, Kruskal-Wallis test, p less than 0.05). The result of 1/3 pulp removal was identical to that for 2/3 pulp removal; 92.5 percent of the seeds were killed by *Cleogonus* in both cases. When all of the fruit pulp was removed from the nut, the seed predation intensity was even further lowered; the value of 83.5 percent is significantly lower than that obtained with any of the other three treatments (e.g., 2/3 removed vs. all fruit pulp removed, Kruskal-Wallis test, p less than 0.05).

It therefore appears that simply the act of cleaning fruit pulp off the nut by the bat will increase seed survivorship irrespective of the other bat-seed interactions. Since uninfested nuts that have been thoroughly cleaned of fruit pulp do not become infested by *Cleogonus* even if they are left directly below the parent tree (and therefore within centimeters of adult weevils), it appears that a bat may save an *Andira* seed from seed predation by *Cleogonus* even if it does not carry off the fruit. On the other hand, if the bats collect the fruits late in the life of the fruit crop, most if not all of the seeds will already have larvae in them and are doomed no matter where the bats drop them.

The results of these experiments support the notion that the outcome of the *Andira-Cleogonus*-bat interaction is dependent on much more than simply how far and where the bat carries the *Andira* fruit to eat off its pulp. The interaction is influenced by how long the ripe fruits have been on the tree before the bat picks them, by the location of the fruit in the crown when picked, by how thoroughly the bat cleans off the fruit pulp before dropping the nut, and by where the bat drops the nut.

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Resumen

Al eliminar artificialmente 1/3, 2/3 y toda la pulpa del fruto maduro de *Andira inermis,* la intensidad de depredación de semillas por gorgojos *Cleogonus* disminuye de 97.5 por ciento en los testigos hasta 92.5, 92.5 y 83.5 por ciento en los tratamientos, respectivamente. Eliminar la pulpa del fruto es equivalente a lo que hacen los murciélagos al alimentarse con los frutos, conducente a la dispersión de las semillas. Concluyo que la dispersión de semillas de *Andira* por los murciélagos, posiblemente aumenta la supervivencia seminal por otras razones además de su simple remoción de la vecindad del árbol que las produce.

Literature Cited

Janzen, D. H. and P. S. Martin 1982. Neotropical anachronisms: the fruits the gomphotheres are. Science (215:19–27).

Janzen, D. H.; G. A. Miller; J. Hackforth-J.; C. M. Pond; K. Hooper, and D. P. Janos 1976. Two Costa Rican bat generated seed shadows of *Andira inermis* (Leguminosae). Ecology 56:1068–1075.

Table 1. Effect of cleaning fruit pulp off ripe *Andira inermis* fruits on seed mortality by *Cleogonus* weevil larvae.

Replicate (20 seeds per)	Percent seed mortality by *Cleogonus* spp.			
	Intact fruit	1/3 of fruit pulp removed	2/3 of fruit plup removed	All of fruit pulp removed
1	100	90	90	85
2	95	90	95	95
3	100	100	90	80
4	90	95	95	70
5	100	85	85	85
6	100	95	100	85
7	100	100	100	85
8	95	85	85	75
9	100	90	95	85
10	95	95	90	90
$\bar{X}$	97.5	92.5	92.5	83.5
s.d.	3.53	5.4	5.4	7.1
n	10	10	10	10

Figure 1. A mated pair (on right) of *Cleogonus* weevils on a lightly-attacked ripe fruit of *Andira inermis.* The small holes in the fruit are feeding punctures made by the female (underneath the male) and will also be the oviposition sites. Fruits in this stage of attack are often harvested by bats.