Two Costa Rican Bat-Generated Seed Shadows of Andira Inermis (Leguminosae)

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TWO COSTA RICAN BAT-GENERATED SEED SHADOWS OF *ANDIRA INERMIS* (LEGUMINOSAE)[1]

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Abstract. Bat-generated seed shadows of two mature *Andira inermis* (W. Wright) DC. trees in the deciduous forest lowlands of Guanacaste Province, Costa Rica, are highly heterogeneous; very unequal numbers of seeds are deposited beneath the trees used as feeding roosts. It is calculated that a 45-g *Artibeus jamaicensis* bat may potentially obtain as many as 1,766 joules [= 422 calories] per *Andira* fruit per round trip of 270 m between the parent tree and the feeding roost. Seed predation by *Cleogonus* weevils was found to be highest below the parent tree, intermediate under bat feeding roosts, and lowest among fruits dropped accidentally by bats between the parent tree and the feeding roosts.

Key words: Bat; Neotropical fruit; Costa Rica; seed dispersal; seed predation; seed weevils.

INTRODUCTION

To understand the interaction between tropical seed predators and tree species richness, we need to know what kinds of seed shadows are generated by dispersal agents and how the different kinds of seed shadows result in escape from seed predators (Janzen 1970, 1971). Vertebrates frequently disperse seeds, and it is reasonable to expect them to generate patchy and uneven seed shadows since their movements are greatly influenced by habitat heterogeneity. Many animals prey on seeds after they have been dispersed by vertebrates. It is reasonable to expect the thoroughness of such predation on seeds to be influenced by the heterogeneity of the seed shadow. Here, we describe two heterogeneous *Andira inermis* seed shadows that were generated by bats, and briefly describe how seed predation by *Cleogonus* weevils is influenced by this heterogeneity.

THE TREES

Andira inermis, henceforth referred to as *Andira*, is a medium-sized evergreen fabaceous tree that ranges from the Pacific coastal lowlands of tropical Mexico (Pennington and Sarukhan 1968) through Central America, the West Indies, and South America (Huber 1910, Greenhall 1956, Standley 1922). In Guanacaste Province, Costa Rica, it occurs throughout the coastal lowlands and foothills. It is most common along watercourses but also occurs as an occasional tree on mesic hillsides and flatlands. Deforestation has severely thinned the *Andira* population and most surviving adults are isolated in pastures, fencerows, or the 50 m wide strip of vegetation that is required by law along watercourses. It is the only member of its genus in Guanacaste.

The bee-pollinated flowers of *Andira* appear in February–April (Frankie et al. 1974; Frankie 1975; G. W. Frankie, *personal communication*) and the fruits from these flowers ripen from mid-May through the end of June. One of us (DHJ) has been observing the reproductive phenology of 106 *Andira* trees in Guanacaste since 1970. In general, all reproductive adults flower and many fruit on even-numbered years (this phenomenon will be described in detail in a later paper). In 1975, however, five trees were located that bore fruit that year. We chose two of these trees for intensive examination. The other three were found too late to examine the seed shadows. Since the *Andira* population in general was not in fruit in 1975, we assume that the fruits found in the near vicinity of any one of these fruiting individuals came from that individual.

Pasture Tree.—This *Andira* is in a heavily grazed complex of several hundred hectares of pasture. This pastureland is dotted with isolated mature trees of many species and borders on plowed fields and a permanent small river and accompanying riparian vegetation (Fig. 1). The site is in Finca Taboga, ≈ 10 km south of Cañas. The Pasture Tree had a diameter at breast height of ≈ 50 cm and was ≈ 25 m tall with a dense crown ≈ 15 m in diameter. The entire tree bore fruit.

There is one complication with the seed shadow of the Pasture Tree. At the point marked "b" in Fig. 1, there is an *Andira* that was found to have at least 2,000 fruits below it. These were discovered

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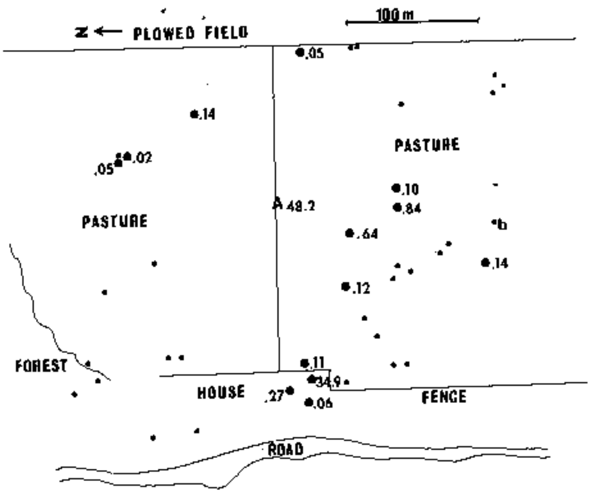

FIG. 1. Distribution of *Andira inermis* fruits and seeds below and around the Pasture Tree (A), feeding roosts (●) and unused trees (•). Numbers refer to the percent of the total seed crop that was found below each tree. A creek runs through the forest just below left side of the figure. "b" is an *Andira* tree that had at least 2,000 fruits below it of unknowable origin (see text).

well after the study was completed and by then had been thoroughly trampled into the soil by cattle. Their origin is unknown, but they could have come from a small crop in that *Andira* or been transported from the Pasture Tree. In either case, they do not confound the interpretations or data given below.

River Tree.—This *Andira* is on the margin of the thin strip of riparian forest left standing along the Rio Corobici (≈ 3 km upstream from the Pan-American Highway on Finca La Pacifica, 7 km north of Cañas). To the south and east of the River Tree are lightly grazed pastures dotted with trees, and riparian forest lies to the west and north (Fig. 2). This is the general area of the study by Heithaus et al. (1975) of resource use by bats. The River Tree had a dbh of ≈ 40 cm and was ≈ 15 m tall with a dense crown ≈ 10 m in diameter. Only the northwest half of the crown bore fruit.

The numbers of fruits on the trees were estimated by carefully counting the number of fruits present on the ends of large branches, counting the number of such large branch ends present in the canopy, and multiplying the two numbers. The numbers of fruits below feeding roosts were determined by searching the bare ground carefully on hands and knees, picking up all fruits, and later counting them individually. The number of fruits below the River Tree was estimated by carefully counting the numbers of fruits in 10 randomly placed m² quadrats on the ground in the tree crown vertical projection, and then measuring the area of the vertical projection. Numbers of fruits below the Pasture Tree were esti-

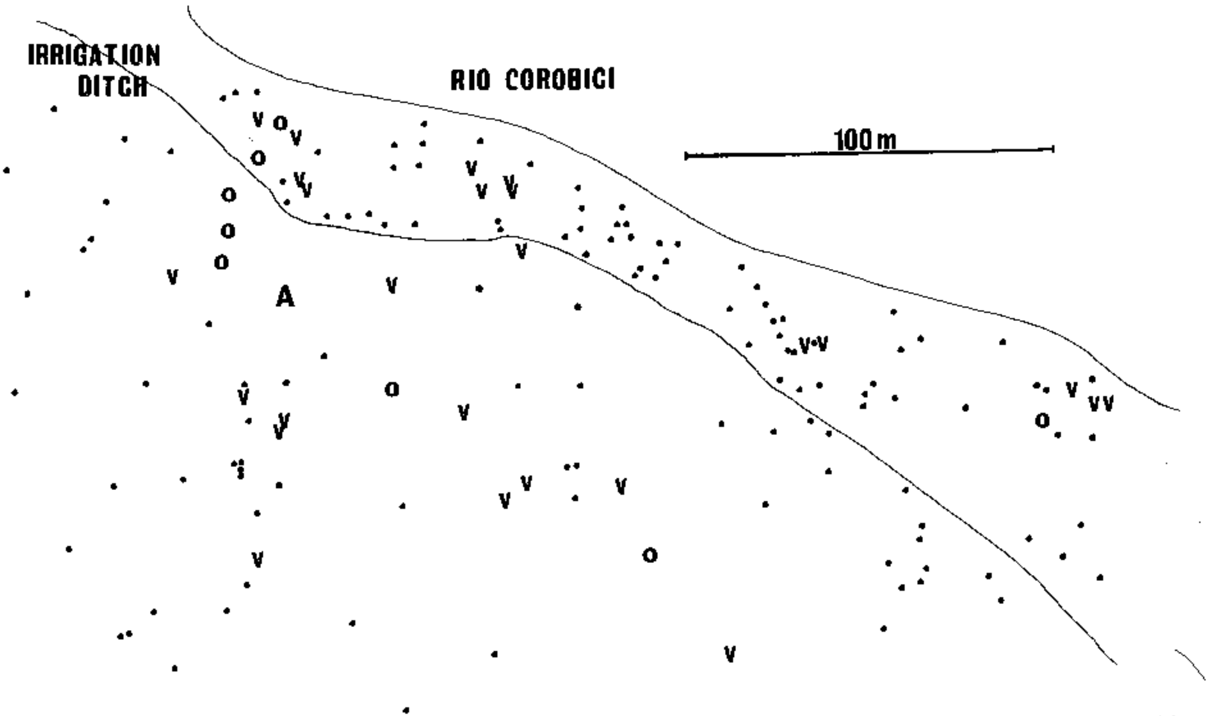

FIG. 2. Distribution of *Andira inermis* fruits and seeds below and around the River Tree (A), feeding roosts with 22 to 291 seeds beneath them (○), feeding roosts with 1 to 12 seeds beneath them (V), and unused trees (•).

mated by carefully collecting all fruits from two thirds of the area of the vertical projection of the tree crown, and extrapolating to the entire area. Fruits along the flight line from the Pasture Tree to the primary feeding roost were estimated by carefully searching the closely cropped grass in the pasture. In all cases, the large fruits are easily located as they are conspicuous against bare ground or closely cropped grass.

THE FRUIT

The association of bats with *Andira* by humans is an old one. "Andira" means "bat" in a Brazilian Indian language and a Brazilian name for *Andira* is "morceguiera" (Huber 1910). Costa Ricans living near the Pasture Tree informed us that bats came every night and carried *Andira* fruits to their feeding roosts in nearby trees and that bats were responsible for the seeds and fruits scattered about far from the Pasture Tree. *Andira* fruits are described as being typical "bat fruits" and are known to be eaten by bats (Docters van Leeuwen 1935, Pijl 1957, 1972; Greenhall 1956; Heithaus et al. 1975; Huber 1910). Bat chew marks, easily distinguished from those of rodents and parrots, were conspicuous on the uneaten flesh of the dropped fruits.

Ripe *Andira* fruits are green and indehiscent single-seeded oblong spheres 3 to 5 cm in length. They are borne on long stems that project outside of the *Andira* canopy surface. The glabrous fruit epidermis is paper-thin but tough and lacks noticeable flavor or odor. The spherical seed is ≈ 1.5 cm in diameter and surrounded by a tough and fibrous husk 2 to 5 mm thick. It is much too large for a Neotropical fruit bat to swallow entire. Between the husk and the green epidermis is a 2 to 5 mm thick layer of crisp and juicy white pulp. The pulp tastes like that of a poorly ripened pear and a large bag of ripe fruits has an aroma of slightly spoiled peaches. This odor could be detected at least 100 m downwind from the Pasture Tree.

Freshly fallen and intact ripe fruits from the Pasture Tree had a mean weight of 11.25 g ($n = 144$) and those from the River Tree weighed 2 to 8 g more. The average fresh weight of nine seeds from the Pasture Tree was 2.99 g or 26.6% of the fresh fruit weight. The husk constituted 14% of the fresh fruit weight. The average fresh pulp weight (including epidermis) was 6.68 g for fruits from the Pasture Tree ($n = 50$) or 59.4% of the fruit weight.

The nutrient content of the pulp (including epidermis) of an average *Andira* fruit from the Pasture Tree is given in Table 1. These values were obtained by removing the pulp from 50 freshly fallen intact ripe fruits, weighing the pulp and then drying it to constant weight. The nutrient content was determined by M. J. Trlica's laboratory at Colorado State University (and subcontractors to that laboratory). Since the Pasture Tree produced an estimated 44,428 fruits (Table 2), it made available to the bats 225 liters of water and 199.83 megajoules [= 47,760 kcal] of potential energy (see later paragraphs for methods of calculating energy content).

TABLE 1. Estimated nutrient content of the 6.68 g of fleshy pulp on an 11.25 g fresh ripe *Andira inermis* fruit ($n = 50$, fruits intact and freshly fallen from beneath the Pasture Tree)

Item	Amount (g)
Water	5.07
Total available carbohydrate (TAC)	0.2104
Lipid	0.0201
Other organic matter	1.3003
Nitrogen	0.0308
Potassium	0.0193
Calcium	0.0186
Phosphorus	0.0034
Magnesium	0.0032
Sodium	0.0003
Iron	93 ppm
Other ash	0.0037

Although bats were clearly the major consumers of the *Andira* fruit, a flock of *Aratinga* parrots was observed feeding on the fruits in the River Tree and distinctive semicircular parrot bill marks are occasionally seen on *Andira* fruits below *Andira* trees. Once on the ground, the fruits have their pulp occasionally removed by small rodents, leaf-cutting ants and miscellaneous small insects. Cattle and pigs show no interest in feeding on the abundant fruits even when pasture forage is very sparse.

THE BATS

It is impossible to know which species of bats carried the fruits to the various feeding roosts mapped in Figs. 1 and 2, but numerous bats were seen moving in and out of the canopies of the Pasture Tree and *Cocoloba*-1. One bat, the size and shape of an *Artibeus*, was seen hanging with an *Andira* fruit in its mouth in *Cocoloba*-1. *Artibeus lituratus* and *Artibeus jamaicensis* were netted under the River Tree (identified by D. Wilson). The partly eaten fruits below the *Andira* trees and the feeding roosts had typical bat tooth marks on them. *Artibeus* spp. have been reported feeding on *Andira* fruits in older literature (Huber 1910, Greenhall 1956, Pijl 1957).

Artibeus bats are well known to carry fruits of many species out of the parent tree canopy and consume them at a nearby feeding roost. To date, however, records of the discarded seeds are largely from caves or, if from feeding roosts, no attempt was made to describe a tree's seed shadow (Huber 1910; Greenhall 1956, 1965; Osburn 1865; Vázques-Yanes et al. 1975; Hall and Dalquest 1963; Vaughan 1970; Pijl 1957, 1972).

TABLE 2. Dispersal fate of 44,428 *Andira inermis* seeds from the Pasture Tree on 19 May 1975, and of 11,952 seeds from the River Tree on 21 June 1975

	Pasture Tree		River Tree	
Location	Distance from parent (m)	% of seed crop	Distance from parent (m)	% of seed crop
Hanging on parent (estimated)	0	13.5	0	51.0
Intact fruit below parent	0	42.3	0	16.8
Bat-chewed fruit below parent	0	5.9	0	23.3
Dropped between Pasture Tree and *Cocoloba*-1	70 ($\bar{x}$)	0.95		
Dropped elsewhere between Pasture Tree and roosts	≈50	0.07		
Below feeding roosts:				
Cocoloba-1	140	34.9		
Cocoloba-2	119	0.05		
Andira (not in fruit)	142	0.27		
Acrocomia	120	0.05		
Guazuma-1	60	0.64		
Guazuma-2	82	0.12		
Guazuma-3	89	0.84		
Guazuma-4	90	0.14		
Guazuma-5	90	0.10		
Guazuma-6	120	0.02		
Guazuma-7	132	0.11		
Guazuma-8	147	0.06		
Guazuma-9	165	0.14		
Guazuma-1			21	1.79
Trichilia			24	1.05
Simarouba			33	0.64
Anacardium-1			39	2.43
Guazuma-2			38	0.90
Anacardium-2			49	0.54
Luehea			207	0.20
Cassia			120	0.45
25 other trees with fruits below				1.64

THE SEED SHADOWS

The distribution of seeds and fruits around the Pasture Tree is illustrated in Fig. 1 and Table 2. We are fairly confident that most seeds and fruits were found because they are large and at this time of year the ground beneath the trees was largely bare of vegetation. There are many possible causes for the extreme heterogeneity of this seed shadow (we may add by way of definition that a "heterogeneous seed shadow" is one in which the seeds are patchily and unevenly distributed over the surface of the seed shadow).

1) Trees are not uniformly spaced in the pastureland. Furthermore, it is probable that if there were many trees nearer to the Pasture Tree, the bats would have used closer trees as major feeding roosts (as they did at the River Tree, Fig. 2).

2) The bats clearly ignored certain species of adult trees. *Pithecellobium saman*, *Tabebuia rosea*, *Luehea candida* and *Chlorophora tinctoria* were all within the area containing trees used by the bats but were not used as feeding roosts. They were leafless during much of the time the *Andira* was in fruit and this may partially explain why they were not used. However, two *Crescentia alata* were also ignored and yet were in heavy leaf. The frequently used *Guazuma ulmifolia* have many more small branches than any of the species mentioned above and are only semideciduous in this site. Aside from the essentially evergreen *Andira*, the *Cocoloba* is the most heavily leafed species of tree near the Pasture Tree and has a very opaque crown.

3) The bats clearly ignored certain areas. *Cocoloba*-2 was the same size and distance from the Pasture Tree as *Cocoloba*-1. However, *Cocoloba*-1 received 34.9% of the seed shadow while *Cocoloba*-2 received only .05% of the seed shadow. *Cocoloba*-1 was over a well and muddy swale, and directly downwind from the Pasture Tree while *Cocoloba*-2 was over a dry pasture and directly upwind from the Pasture Tree. It is likely that these physical differences between the microsites of the two *Cocoloba* trees are at least partially responsible for the bats' preferences.

4) In flying from the Pasture Tree to *Cocoloba*-1, the bats did not fly there directly but rather down the fencerow and then over to *Cocoloba*-1. This flight pattern was inferred from the fact that 422 fruits were found evenly distributed in a corridor 8 m wide and centered on the fence while only 17

fruits were found in two parallel corridors 8 m wide on each side of the corridor containing the fence. Such apparent use of landmarks in flight between the parent tree and feeding roosts can generate quite linear heterogeneity in seed shadows. Riverbeds and other sharp contours could serve the same purpose in more natural circumstances.

In summary it appears that the bats favored a feeding roost that was downwind from the parent tree, over a moist area, and based in a densely leafed crown. The close proximity of people and livestock did not seem to bother the bats. A favored feeding site was only 2 m above the Hacienda washhouse, which was in turn only a few feet from the base of *Cocoloba*-1.

The distribution of seeds around the River Tree was less grossly distorted than that of the Pasture Tree (Fig. 2 and Table 2) but it was nevertheless far from homogeneous. The parent tree had 23.3% of the seeds dropped below it at the time of the census (21 June 1975). On this date, an estimated 51% of the fruits were still hanging on the parent tree. Eight feeding roosts away from the parent received a total of only 8% of the seeds; a large *Anacardium excelsum* (evergreen with large leaves superficially like those of a *Cocoloba*) received about a third of these seeds. Within the range of the farthest seeds found by us from the River Tree, 25 other adult trees received a total of 1.64% of the seeds and at least 102 trees $>$ 6 m tall had no seeds at all below them. There was no obvious correlation of intensity of use with tree size or proximity to the river or irrigation ditch. However, all but two of the heavily used trees are within 50 m of the parent tree (Fig. 2). Trees with large branches and sparse branchlets, and those with small finely compound leaves, were not used as feeding roosts. The following tree species were used one or more times as a feeding roost as evidenced by an accumulation of seeds below it: *Guazuma ulmifolia*, *Licania arborea*, *Dalbergia retusa*, *Andira inermis*, *Hymenaea courbaril*, *Anacardium excelsum*, *Spondias mombin*, *Spondias purpurea*, *Trichilia* spp., *Bursera simaruba*, *Simarouba glauca*, *Cordia alliodora*, *Casearia guianensis*, *Cassia grandis*, *Gliricidia sepium*, *Ficus* sp., and *Luehea candida*.

ECONOMICS OF BAT FLIGHT

Does a bat obtain enough energy from eating a fruit to pay for the flight from the parent tree to the feeding roost? The answer to this question is not trivial, as they could be visiting the tree primarily for water, protein or minerals. It depends on the distance to the feeding roost, the energy obtained from the fruit pulp, and the cost of bat flight.

From Table 2 we calculate that the total distance flown in dispersing *Andira* fruits around the Pasture Tree was 4,606 km (including fruits dropped in flight). This involved transport of 17,048 fruits, or an average of 270 m flown per fruit. To determine the total cost of feeding would require also knowing the distance from the sleeping roost to the Pasture Tree, an impossible figure to obtain without radio tracking.

Examination of the *Andira* fruits below the Pasture Tree and the feeding roosts suggests that, on the average, the bats eat about half the pulp from a fruit before dropping it. Assuming that a bat extracts all the lipid and total available carbohydrate (TAC) from the pulp it eats, and assuming that a gram of lipid provides 9,500 calories [$\approx$ 39.75 kJ] and a gram of TAC provides 4,200 calories [$\approx$ 17.57 kJ] (M. J. Trlica, *personal communication*, Schmidt-Nielsen 1960), a bat potentially obtains 538 calories [= 2.25 kJ] from half the pulp on an *Andira* fruit (see Table 1 for nutrient content of fruit). There are no data available on the digestive efficiency of a frugivorous bat. However, since the value of 2.25 kilojoules is based on cell contents rather than structural potential energy in the fruit, we accept 100% efficiency as a reasonable approximation. If the reader has a favored smaller value, then the numerical values in the following paragraphs should be scaled down accordingly.

To determine the cost of flight requires some extrapolation. It is difficult to know what weight to use for the average bat carrying *Andira* fruits. In Guanacaste Province, freshly netted *Artibeus jamaicensis* weigh $\approx$ 45 g and *Artibeus lituratus* $\approx$ 60 g (D. Wilson, T. Flemming, *personal communication*). This agrees with the 50 to 70 g values, respectively, usually given for these bats in the literature (Morrison and McNab 1967, McNab 1969). We will base our calculations on 45 and 60 g for these two species of bats. There are no data available on *Artibeus* O_2 consumption in flight. However, Thomas and Suthers (1970, 1972) and Thomas (1975) have calculated that 87- to 101-g *Phyllostomus hastatus* use 23 ml $O_2 \cdot g^{-1} \cdot h^{-1}$. *Phyllostomus hastatus* is in the same family as *Artibeus* and like *Artibeus*, largely frugivorous. Using 23 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ as a representative metabolic rate while in flight for *Artibeus* allows the estimate that a 45 g *A. jamaicensis* would consume 24.2 ml of O_2 during a round trip of 270 m at 10 km/h if carrying an 11.25 g fruit for half that trip. Assuming that using 1 ml of O_2 costs 20.08 J or 4.8 calories, the bat expends 485.3 J [= 116 calories] on such a trip. A 60-g *A. lituratus* would expend 640 J [= 153 calories] on the same trip. We assume selection of fruits is instantaneous. If the bats spend much time fluttering about in the tree selecting a fruit then the cost would be increased. Such an addition cannot be calculated with the figures at hand.

TABLE 3. Fate of *Andira inermis* seeds in different parts of the seed shadow

	% attacked by *Cleogonus* weevils	% intact and alive	% moldy (dead)	Total seeds examined
Pasture Tree (collected 19 May 1975)				
Under parent tree:				
Fruit intact	54	25	20	790
Fruit chewed by bats	64	23	14	1,571
Combined	61	24	16	2,361
Under *Cocoloba* (34.9% of seed crop)	31	65	5	1,491
Under other feeding roosts (2.54% of seed crop)	33	53	14	927
Scattered in open pasture (0.95% of seed crop)	10	26	65	149
River Tree (collected 21 June 1975)				
Under parent tree:				
Fruit intact	90	9	2	134
Fruit chewed by bats	94	5	1	297
Combined	93	6	1	431
Under feeding roost:				
Anacardium-1	96	4	2	291
Guazuma-1	93	6	1	212
Trichilia	95	5	0	123
Guazuma-2	94	5	1	105
Simarouba	89	8	4	79
Anacardium-2	81	16	3	68
Cassia	70	28	2	53
Luehea	36	64	0	22

Since 2.25 kJ are theoretically available in the half of the fruit pulp eaten by the bat, a 45-g *A. jamaicensis* could obtain a profit of ≈ 1.77 kJ [= 422 calories] per round trip (to say nothing of the other nutrients and water that could be obtained from the fruit). If the 45-g *A. jamaicensis* had simply hung from a branch during the 1.25-min round trip, it would have consumed only 35.98 kJ [= 8.6 calories] in the same time (assuming a resting but awake metabolism of 1.5 ml $O_2 \cdot g^{-1} \cdot h^{-1}$, as reported by McNab [1969] for *A. lituratus*). At this time of year near the Pasture Tree, night time ambient temperatures are 23 to 26°C, which is within the range at which these bats hold their resting metabolic rate constant (McNab 1969). An intuitive feel for the size of the profit possible from eating one-half an *Andira* fruit, assuming 100% use of the fats and available carbohydrates present in the food, may be gained by the observation that a 45-g *A. jamaicensis* could make a 1,266 m round trip and a 60-g *A. lituratus* could make a 951 m round trip at zero profit.

At this point, an immediate note of caution is due. As has been stressed by numerous authors (see reviews in Pijl 1957 and Greenhall 1956), frugivorous bats usually chew the fruit fragments, apparently press out the liquids and swallow them, and then spit out much of the solid remains. We cannot know what fraction of the nutrients in the *Andira* pulp are actually received by the bat, and what part ejected. The profit figures given in the previous paragraph are thus all maximum possible values, values that are probably not attained by a bat. Likewise, some of the items listed in Table 1 may be contained in the solid parts of the pulp, and thus unavailable to the bat. Much of the nitrogen, for example, may be tied up in the thin but hard epidermis. On the other hand, the fruit pulp has a very fragile and juicy texture (like that of a ripe peach or pear) and thus for obvious reasons apparently can be maximally extracted by the bat's mouth.

SEED PREDATION

The seeds of *Andira* in Guanacaste are subject to very heavy predation by the larvae of three sibling species of *Cleogonus* weevils (Janzen 1975, D. R. Whitehead, *personal communication*). The adult beetles oviposit on the ripe fruit while it is still on the tree and on fallen fruits in all stages of loss of fruit pulp. The larvae mines in the fruit pulp for a short time and then eats directly into the seed. The mature larva bores out of the seed and pupates underground. Adult emergence occurs many months later. An attacked seed does not survive. Some of the "moldy" dead seeds recorded in Table 3 are undoubtedly the result of beetle death after initiation of attack of the seed. Of the seeds left below the parent *Andira*, virtually none are free of attack by *Cleogonus* by the end of the fruiting season. The high percentage of mortalities recorded under the parent tree (Table 3) are well before the weevils have finished their season's activities. To record the degree of seed predation at any given time, the fruits are collected and allowed to incubate for a month away from adult beetles. Larvae do not move from fruit to fruit. After a month, the number of seeds lacking damage from beetle larvae is the number unattacked.

The data in Table 3 show clearly that, at the time of collection, seeds from below the bats' roosts in the pasture habitat are subject to about half the intensity of weevil predation as those below the Pasture Tree. The percent mortality of seeds below *Cocoloba*-1 was almost identical to that under the other feeding roosts. As the samples from the small feeding roosts were not kept separate, we cannot ask if differences in the sizes of small piles of seeds below feeding roosts affect the predation intensity.

The single fruits dropped in flight along the fence had the lowest attack by weevils; only 10% of these widely scattered fruits had weevil larvae in their seeds. This low percent mortality from weevils may well represent the degree of infestation of fruits at the time they are plucked from the tree by the bats. On the other hand, the pasture fruits have an extraordinarily high percent of moldy seeds. It is possible that many of these represent seeds in which the young developing larva was killed by heat and desiccation (this occurs occasionally with the larvae of other seed eating insects in Guanacaste during the dry season). The fruits are fully exposed to the sun's rays and often suspended on closely cropped grass blades above the moist soil.

Beneath the River Tree the percent seed mortality by weevil larvae was > 90% (Table 3), which is close to the 99% plus value usually found below parent *Andira* late in the fruit season (D. H. Janzen, *personal observation*). This census was made nearly a month later than the census from the Pasture Tree. The combined seed mortality of 84% by weevils beneath the feeding roosts around the River Tree is also very high. It might well have arrived at total destruction had the seeds been left for another month. On the other hand, the rainy season had begun nearly a month previously and thus the surviving seeds would have had the opportunity to escape by germinating if this were a forested habitat.

Under the individual feeding roosts, the percent seed mortality by predation shows a striking decline as the number of seeds in a site declines (Table 3). It also declines somewhat with distance from the parent; the three furthest large seed piles have the lowest percent seed mortality (Tables 2 and 3). Unfortunately, the very small numbers of seeds below the 25 other feeding roosts in the vicinity of the River Tree were not examined for seed predation. It is among these seeds that we expect even lower seed mortality than the 36% recorded for the 22 seeds below the *Luehea candida* feeding roost.

Cleogonus weevils are large, shiny black, and quite conspicuous on the large green fruits. Beneath a heavily fruiting *Andira* there may be thousands in sight at one time during daylight hours. They readily come to feed on the exposed seeds of *Andira* fruits cut in half. As a crude assay of beetle density, two piles of 10 halves each were placed on the ground beneath the parent *Andira* and beneath the various feeding roosts in the afternoon. The number of weevils present was censused several hours after dark. The census data show that some weevils had found their way to all of the feeding roosts in the vicinity of the Pasture Tree. The numbers of adult beetles on the cut *Andira* fruit was not related to the number of seeds below a feeding roost (e.g., *Cocoloba*-1 had 52 weevils on the cut fruit while *Guazuma*-9 had 171 [16 June 1975], yet *Cocoloba*-1 had nearly 200× as many seeds as *Guazuma*-9). Many variables influence the number of weevils present at a given pile of seeds at any one instant and it will take much larger samples to distinguish among the various important variables. At the River Tree, all but 1 of the 19 roosts assayed had weevils on the cut fruits and 3 had as many or more weevils on their piles of cut fruits than did the River Tree.

DISCUSSION

It is not obvious why the bats leave the parent *Andira* to eat the fruit. There should be selection for tree traits that cause vertebrate dispersal agents to leave the parent tree after they have eaten seeds. We therefore expect that there has been strong selection for tree and branch morphology and perhaps odor such that the bats find it difficult or unpleasant to roost in the *Andira*. However, exactly what traits this selection has produced are unclear. It is also unclear if all bats are equally susceptible to these traits if such exist; the large number of chewed fruits below the parent *Andira* may indicate that a substantial number of individuals are immune to such postulated traits. It is noteworthy that the greater the profit the bat makes from each fruit, the less severe will have to be such traits. Since the bat is potentially recovering at least 3 to 4× as much energy from the fruit as it expends in removing it to a feeding roost, the *Andira* may not have to be very objectionable for the bats to leave. Once the bat has left the *Andira*, it does not go merely to the closest other tree to feed. That certain trees are ignored suggests that the eagerness (willingness?) to leave the *Andira* to feed may also be conditioned by the availability of highly desirable feeding roost trees in the vicinity. Whatever the case, it is not expected that the bats left the Pasture Tree merely to escape predators; the concentration and conspicuousness of bats in *Cocoloba*-1 was as great as it would have been had all the bats stayed in the Pasture Tree to feed. Furthermore, in this heavily agriculturalized habitat, virtually all potential predators have been extirpated.

In addition to the calories that the bats may obtain from the *Andira* fruits, Table 1 shows that they may be obtaining a wide variety of other nutrients. It is impossible to know if they are attracted to *Andira* fruits primarily for the water, the calories, or the other nutrients. At the end of the time of the ripening of the Pasture Tree fruit crop, *Spondias purpurea* and *Anacardium excelsum* fruits, both taken by *Artibeus* bats, were just maturing. However, fresh seeds of neither were found mixed with the *Andira* fruits under the feeding roosts. Under some of the *Guazuma* trees in the pastureland around the Pasture Tree, there were old seeds of *Spondias, Anacardium* and *Eugenia*, suggesting that at other times of year these *Guazuma* served as feeding roosts for flights from other trees.

Large Neotropical frugivorous bats may be flying as far as 10 km from their sleeping roosts to feeding areas (Williams 1968, Williams and Williams 1967, Fleming 1975). Probably, it is the few seeds that they drop on the way home that have the maximum chance of surviving predation by *Cleogonus* weevils. Presumably the 10% predation rate on fruits dropped in the open pasture would apply to these fruits dropped very far from the Pasture Tree. We have no way of estimating this number since that would require knowledge of the total number of bats visiting the tree each night during the approximately 1 mo when fruits were available on the Pasture Tree. However, whatever their number, the high predation rates of seeds below the parent *Andira* and heavily used feeding roosts strongly suggest that recruitment of *Andira* trees may occur only through those seeds carried far from the parent or dropped singly in flight at closer distances.

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LITERATURE CITED

Docters van Leeuwen, W. M. 1935. The dispersal of plants by fruit-eating bats. Gard. Bull. Str. Settl. **9**: 58–63.

Fleming, T. H. 1975. The role of small mammals in tropical ecosystems. *In* Small mammals: Their Productivity and Population Dynamics, IBP, Vol. 5, p. 269–298. Cambridge Univ. Press, Cambridge.

Frankie, G. W. 1975. In press. Pollination of widely dispersed trees by animals in Central America, with an emphasis on bee pollination systems. *In* J. Burley and B. T. Stiles [eds.] Variation, Breeding and Conservation of Tropical Forest Trees. Academic Press, New York.

Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J. Ecol. **62**:881–919.

Greenhall, A. M. 1956. The food of some Trinidad fruit bats. J. Agric. Soc. Trinidad Tobago. **56**:3–26.

———. 1965. Sapucaia nut dispersal by greater spear-nosed bats in Trinidad. Caribbean J. Sci. **5**:167–171.

Hall, E. R., and W. W. Dalquest. 1963. The mammals of Veracruz. Univ. Kansas Publ. Mus. Nat. Hist. **14**: 165–362.

Heithaus, E. R., T. H. Fleming, and P. A. Opler. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology **56**:841–854.

Huber, J. 1910. Mattas e madeiros amazonicas. Bol. Mus. Goeldi **6**:91–225.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. **104**:501–528.

———. 1971. Seed predation by animals. Annu. Rev. Ecol. Syst. **2**:465–492.

———. 1975. Interactions of seeds and their insect predators/parasitoids in a tropical deciduous forest, p. 154–186. *In* P. W. Price [ed.] Evolutionary Strategies of Parasitic Insects and Mites. Plenum Press, New York.

McNab, B. K. 1969. The economics of temperature regulation in neotropical bats. Comp. Biochem. Physiol. **31**:227–268.

Morrison, P. R., and B. K. McNab. 1967. Temperature regulation in some Brazilian phyllostomid bats. Comp. Biochem. Physiol. **21**:207–221.

Osburn, W. 1865. Notes on the Cheiroptera of Jamaica. Proc. Zool. Soc. London **82**:61–85.

Pennington, T. D., and J. Sarukhan. 1968. Arboles tropicales de Mexico. Inst. Nac. Invest. For., Mexico, 413 p.

Pijl, L. van der. 1957. The dispersal of plants by bats (Chiropterochory). Acta Bot. Neerl. **6**:291–315.

———. 1972. Principles of Dispersal in Higher Plants. Springer-Verlag, Berlin. 161 p.

Schmidt-Nielsen, K. 1960. Animal Physiology. Prentice-Hall, Englewood Cliffs, New Jersey. 118 p.

Standley, P. C. 1922. Trees and shrubs of Mexico, Part 2. Contrib. U.S. Natl. Herb. **23**:171–515.

Thomas, S. P. 1975. Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. J. Exp. Biol. **63**:273–293.

Thomas, S. P., and R. A. Suthers. 1970. Oxygen consumption and physiological responses during flight in an echolocative bat. Fed. Proc. **29**:265.

Thomas, S. P., and R. A. Suthers. 1972. The physiology and energetics of bat flight. J. Exp. Biol. **57**: 317–335.

Vaughan, T. A. 1970. Flight patterns and aerodynamics, p. 195–216. *In* W. A. Wimsatt [ed.] Biology of bats, Vol. 1. Academic Press, New York.

Vázquez-Yanes, C., A. Orozco, G. François, and L. Trejo. 1975. Observations on seed dispersal by bats in a tropical humid region in Veracruz, Mexico. Biotropica **7**:73–76.

Whitehead, D. R. 1976. The neotropical genus *Cleogonus* (Curculionidae).

Williams, T. C. 1968. Nocturnal orientation techniques of a neotropical bat. Ph.D. thesis. Rockefeller University, New York.

Williams, T. C., and J. M.. Williams. 1967. Radio tracking of homing bats. Science **155**:1435–1436.