

## Predation by Rodents and Bruchid Beetles on Seeds of *Scheelea* Palms on Barro Colorado Island, Panama<sup>1</sup>

Pierre-Michel Forget,<sup>2</sup> Edgar Munoz, and Egbert Giles Leigh, Jr.

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama

### ABSTRACT

Predation by rodents on seeds of *Scheelea zonensis* was studied on Barro Colorado Island, Panama, during the latter half of this palm's fruiting season. The number of *Scheelea* bearing fruit declined steadily during this period. The proportion of both intact and bruchid-infested seeds among those accumulated under fruiting *Scheelea* declined, while the proportion of gnawed seeds increased. By early October, 87 percent of the *Scheelea* seeds sampled had been gnawed by rodents, and few intact or bruchid-infested seeds remained below parent palms. From August through October, agoutis, *Dasyprocta punctata*, visited *Scheelea* less and less frequently, while visits by squirrels, *Sciurus granatensis*, did not decline. To learn the fate of late-falling *Scheelea* seeds, we placed small piles of thread-marked seeds, each similar to a small *Scheelea* fruit crop, in the forest during three successive months, a total of 400 seed each month. Of these 1200 thread-marked seeds, 57.2 percent were retrieved within 20 m of their piles 7 days after placement. Of the retrieved seeds, 22.2 percent were gnawed within 1 m of their pile, 70.6 percent were carried between 1 and 20 m before gnawing, and 7.2 percent were cached (not gnawed, but buried in the ground or covered with litter). More seeds were gnawed, and fewer cached, in September and October than in August. On Barro Colorado Island, intense seed predation by rodents on *Scheelea* correlates with a previously documented forestwide low in availability of fruits of all kinds, and with a decline in egg laying by bruchids.

*Key words:* agouti; Barro Colorado Island; bruchid; palm; Panama; *Scheelea zonensis*; seed predation; squirrel.

IN CENTRAL AMERICA, BEETLES AND MAMMALS attack seeds of *Scheelea* palms at different rates at different times of year and in different habitats. On Barro Colorado Island (BCI), Panama, rodents destroy most of the seeds of *Scheelea zonensis* (Heaney & Thorington 1978; Glanz *et al.* 1982, Smythe *et al.* 1982). In some Costa Rican sites which appear to have fewer seed-eating mammals, bruchid weevils are the primary predators on seeds of *Scheelea rostrata* (Janzen 1971, Wilson & Janzen 1972, Bradford & Smith 1977), one authority is lumping *Scheelea rostrata* with Panama's *Scheelea zonensis* and other species under the name of *Attalea butyracea* (Robin Foster, pers. comm.). The contrast between Costa Rica and BCI suggests that BCI's rodents might limit populations of *Scheelea*-specific bruchids by eating so many *Scheelea* seeds (*cf.* Herrera 1989).

On BCI *Scheelea* drops fruit from May, when fruit of all kinds is abundant in the forest, through October, by which time the forest is very short of fruit, and mammals eat nearly every *Scheelea* fruit soon after it falls (Glanz *et al.* 1982, Smythe *et al.* 1982, De Steven *et al.* 1987). Wright (1990) ob-

served that *Scheelea* fruits falling late in the season on BCI, when one would expect mammals to be removing most falling fruit, were not attacked by bruchids even when protected against vertebrates. This result is consistent with Janzen's (1971) observation in Costa Rica that few of the late-fallen *Scheelea* fruits (Janzen's newly fallen endocarps, collected in September, Table 1) were infested by bruchids, even after a month of lying below the parent, while many of these fruits appeared viable. Wright (1990) proposed that progressive bruchid satiation during *Scheelea* fruiting caused the steep decline in bruchid oviposition. Both Janzen's and Wright's studies however suggest that bruchid life history might have been selected to avoid the season of most intense mammal activity.

In this study we document the fate of fallen *Scheelea* fruit and the behavior of diurnal rodents during the later part of the fruiting season of the palm, *i.e.*, just before the end of August, when, as a rule, food for frugivores is abundant, through October when rodents are short of food. We took periodic records of the number of *Scheelea* trees bearing fruit, the proportion of fallen fruit gnawed by rodents, the proportion infested by bruchids, the frequency of diurnal rodents visiting *Scheelea* palms, and their behavior, whether foraging or eating. In addition, we examined the fate of seeds at several experimental feeding sites during the same period.

<sup>1</sup> Received 7 July 1993; revision accepted 4 January 1994.

<sup>2</sup> Present address: Laboratoire d'Ecologie Générale, Muséum national d'Histoire naturelle, 4, Avenue du Petit Château, 91800 Brunoy, France.



## STUDY SITE

The study was carried out on Barro Colorado Island, Panama (9°09'N, 79°51'W). The climate on BCI is seasonal with a well-marked dry season, of variable length and intensity, usually extending from December or January to April or May (Windsor 1990). Rainfall averages 2616 mm/yr (Rand & Rand 1982). BCI's tropical forest includes young stands about 100 yr old and primary forest several centuries old (Foster & Brokaw 1982, Piperno 1990). The number of fruiting species peaks twice, first in April and May (wind and animal dispersed species) and again in September and October (animal dispersed species) (Foster 1982a). Despite the second fruit diversity peak, overall fruit biomass becomes scarce on BCI by mid-August and continues through March (Smythe 1970, 1978). BCI supports dense populations of the two principal vertebrate consumers of *Scheelea* seeds, *i.e.*, the terrestrial agouti, *Dasyprocta punctata*, and arboreal red-tailed squirrel, *Sciurus granatensis* (Glanz *et al.* 1982, Smythe *et al.* 1982). The nocturnal spiny rat, *Proechimys semispinosus*, is a potential predator on *Scheelea* seeds, but the biomass of *Proechimys* on BCI is much lower than that of agoutis and squirrels (see Glanz 1990), so *Proechimys* probably eat far fewer *Scheelea* seeds than these others. The few trustworthy data on the diet of pacas, *Agouti paca*, suggest that it prefers soft fruit parts and cannot gnaw the very hard seeds of *Scheelea*. Unlike most rodents, pacas do not store food in hoards. Plant species nomenclature follows Croat (1978).

## METHODS

**SEED PREDATION BELOW PALMS.**—We selected the first 40 fruiting palms we encountered from a larger palm population along a 3 km loop of trails. Wright (1990) obviously used this same area. By mid-July 1990, 28 (70%) of these 40 palms were bearing fruit (Fig. 1A), and 22 of these were dropping ripe fruit. Therefore, we may assume that in 1990 *Scheelea* fruiting peaked about the middle of July, which pattern is consistent with that described by De Steven *et al.* (1987) and Wright (1990). All palms were visited once every two weeks (once weekly in mid-September) for 18 weeks beginning 30 July. In order to estimate the fraction of palms still in fruit during the study period, the presence/absence of ripe fruits in the crown were noted for each palm. Although crude, this method does not disturb the natural flow of falling fruits, and thus does not affect seed removal by mammals or bruchid infes-

tation. The cumulative percentages of predispersal predation by rodents were estimated for fallen seeds of the year that littered the ground below parents. At each periodic sample, a 0.25 m<sup>2</sup> quadrat made with polyethylene tubing was thrown once, randomly, on the ground under palms, where seeds are most dense, and the seeds within it picked up and examined for damage. We recognized three classes of damage that are mutually exclusive from the viewpoint of rodents' impact: seeds gnawed by rodents (including seeds with entrance holes, see below); ungnawed, intact (*i.e.*, bruchid-free); and ungnawed, bruchid-infested seeds, as judged from the presence of entrance holes (Janzen's [1971] Fig. 1C) to have been penetrated by bruchid larvae (judging by "entrance holes" can lead to overestimate by eight percent the infestation rate: Wilson & Janzen [1972]). In order to avoid disturbing clumps of seeds below their parents, seeds were not removed, nor were they dissected to assess bruchid infestation more precisely. Once manipulated, seeds were replaced on the ground at the same location where they were collected.

On 11 October, *i.e.*, toward the end of the fruiting season, a random sample of 200 rodent-gnawed seeds was collected in order to estimate levels of predation by bruchids (presence of entrance holes) among fallen seeds before their consumption by rodents. These seeds were taken from a larger sample of up to 10 seeds per palm among a population of 34 fruiting palms, *i.e.*, 40 palms less 6 whose fruit was not yet ripe by the date of collection. Decisive evidence of larvae penetration was obtained by passing a needle through visible holes into the endocarp: if the needle penetrated fully, we inferred that bruchid larvae had infested the seed before a rodent gnawed it. Since rodents remove a part of endocarp while gnawing seeds to reach endosperm (see Janzen's [1971] Fig. 1E), this method underestimates the number of holes per seed. Also, we collected 95 entire seeds, not gnawed by rodents, (all we could find on 11 October under the 34 sampled fruiting palms), and cracked them with a hammer to analyze their contents for the prevalence of bruchid infestation.

**ACTIVITY OF DIURNAL RODENTS.**—In order to correlate type of seed predation with frequency and behavior of vertebrate seedeaters at areas close to *Scheelea* palms, *i.e.*, within about 10–20 m of palms (human visibility varies with understory density), censuses of agoutis and squirrels were performed at four-week intervals, between 30 July and 2 October along the loop of trails. Nocturnal spiny rats were

not censused because they normally carry seeds to their burrows or cavities in order to consume them (Emmons 1982, Forget 1991). Each census consisted of regular one-way walks ( $N = 9$  consecutive walks per month) of 2–2½ hours starting 0600–0700. Although rodents gnawing *Scheelea* make a sound peculiar to that fruit, this sound may be confused with that from gnawing *Astrocaryum standleyanum* palm nuts, even though the latter noise is usually more strident. To avoid such errors, we simply classified rodents near *Scheelea* as foraging (*i.e.*, searching for food) or eating, without specifying what they were consuming. In contrast to the dry season, when dry leaves that crackle underfoot cover the ground, walking in the rainy season is relatively noiseless. Therefore, we are confident that the observer's (always E. Munoz) presence did not disturb the foraging and eating behavior of these animals.

The significance of temporal variation (early August, late August–early September, late September–early October) in the frequency of rodent sightings was assessed with one-way ANOVA after taking square roots of the rodent counts to normalize the data (Sokal & Rohlf 1981). A two-way contingency table of frequency of foraging (vs eating) rodents as a function of month was analyzed using G-test of independence (Sokal & Rohlf 1981).

**SEED FATE.**—During *Scheelea* fruiting, there is an incessant fruit input and output below palms, due to fruit fall and removal by mammals (coati, *Nasua nasua*, capuchin, *Cebus capucinus*, and rodents, pers. obs.). When analysing seed fate below palms, we were thus unable to accurately describe current predation rate. Therefore, to measure the current fate of removed seeds during the later part of *Scheelea*'s fruiting season, we described the fates of *Scheelea* seeds placed in small piles in the forest. We gathered freshly fallen *Scheelea* fruits in July, when they were abundant, some still with orange pericarp, cleaned off pulp and bruchid eggs, checked them for larval infestation with the aid of a needle, discarding all infested seeds, drilled holes 1.5 mm in diameter through the woody endocarp in order to pass and attach a white thread, 0.3 mm in diameter and 60 cm long, to each seed. On 3–4 August, again on 1–5 September, and finally on 1–2 October, we set out piles simulating small *Scheelea* fruit crops. In each month we set out 8 clumps of 50 seeds each (all from fresh seeds collected in July), in four pairs of clumps. The two piles in a pair were 2 m apart, while different pairs were over 100 m apart. Two pairs were placed in old forest, Forget's (1993)

*Dipteryx*-poor area, and two in young forest, Forget's (1993) *Dipteryx*-rich area. These experimental piles were 40–50 m away from the nearest *Scheelea* palms. These piles were surveyed daily between 1100 and 1400 hr until all seeds disappeared, and we searched within a radius of 20 m of each pair of clumps for thread-marked seeds.

Data for the percentage of seeds consumed or scatterhoarded were analyzed with one-way ANOVA for the effect of months after arcsine square root transformation.

## RESULTS

**SEED PREDATION BELOW PALMS.**—By August, when food is becoming scarce on BCI (see Smythe 1970), the proportion of intact *Scheelea* seeds among those laying on the ground below parent palms decreases (Fig. 1B). By this time, most seeds remaining below these palms were either gnawed or "infested" by bruchids (Fig. 1B). Later yet, when progressively fewer *Scheelea* palms were bearing fruit (Fig. 1A), the cumulative proportions of seeds underneath the trees infested by bruchids declined; whereas, the cumulative proportion of seeds gnawed by rodents increased. On 7 October, 87 percent of the seeds sampled ( $N = 228$  seeds) were chewed by rodents.

Of the 200 rodent-gnawed seeds collected on 11 October, 77.5 percent had large ( $> 10$ –15 mm) openings and large ( $> 2$  mm) tooth marks, at either the center or the extremity, and 22.5 percent had small ( $< 10$  mm), narrow openings and small ( $< 1$  mm) tooth marks, mostly at one extremity. Direct observations of rodents eating seeds confirmed that agoutis make the larger tooth marks, and the larger openings, and squirrels the smaller ones. Twenty-four percent of seeds eaten by agoutis were also infested by bruchids: the infested seeds averaged  $1.8 \pm 1.6$  (mean  $\pm$  SD) bruchid entrance holes each (range 1–4 holes;  $N = 37$  seeds). Sixty-four percent of seeds eaten by squirrels were infested: these averaged  $2.5 \pm 1.3$  bruchid entrance holes each (range 1–5 holes;  $N = 29$  seeds) ( $t = 1.99$ ;  $P < 0.05$ ). These data suggest that the seeds chewed by agoutis contain fewer bruchids than those chewed by squirrels. Finally, of 95 either intact or bruchid-"infested" seeds collected on 11 October, 64 contained one large fully developed bruchid larva each, 21 were empty (possibly aborted), and only 10 had a live embryo.

**ACTIVITY OF DIURNAL RODENTS.**—Agoutis and squirrels accounted for 75.5 percent and 24.5 percent of all observations ( $N = 216$ ), respectively, a result

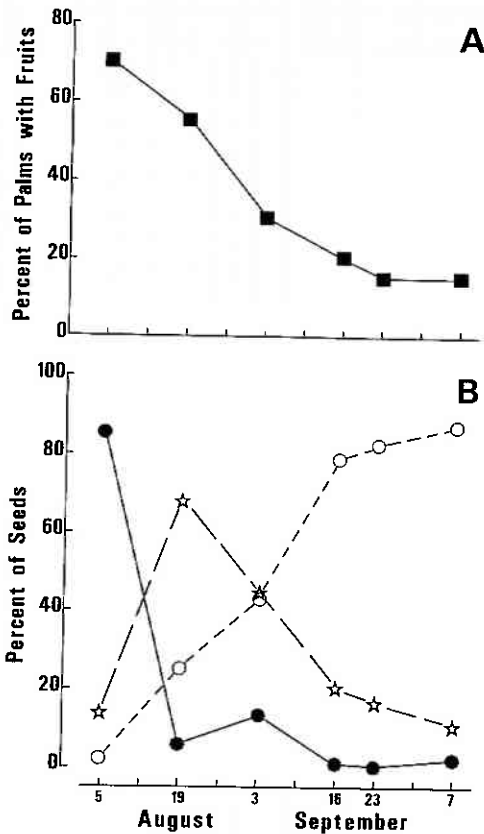


FIGURE 1. (A) Percentage of *Scheelea zonenis* palms ( $N = 40$ ) bearing fruit. (B) Cumulative percentages of seeds intact (full circles), apparently infested by bruchid beetles (stars), or gnawed by rodents (open circles) below palms from 5 August throughout 7 October 1990 at Barro Colorado Island. At each census, the number of seeds randomly sampled was 333, 170, 225, 302, 285, and 228.

consistent ( $G = 0.24$ ,  $df = 1$ ,  $P > 0.05$ ) with the observed frequency of seed damage (large and small openings) attributed to them. Months differ significantly in the number of agoutis ( $F = 10.5$ ,  $df = 2, 24$ ,  $P < 0.001$ ) but not in the number of squirrels ( $F = 0.49$ ,  $df = 2, 24$ ,  $P = 0.62$ ) observed near *Scheelea* (Fig. 2A). Squirrels were regularly observed near *Scheelea*, while agoutis visited such areas less and less frequently in successive months from August onward (Fig. 2A). Agoutis showed no significant change in their behavior ( $G = 2.8$ ,  $df = 2$ ,  $P > 0.05$ ), which consisted mostly of foraging (Fig. 2B). In contrast, squirrels foraged progressively less ( $G = 18.25$ ,  $df = 2$ ,  $P < 0.001$ ) (Fig. 2B), and were progressively more often seen eating seeds, especially those of *Scheelea*.

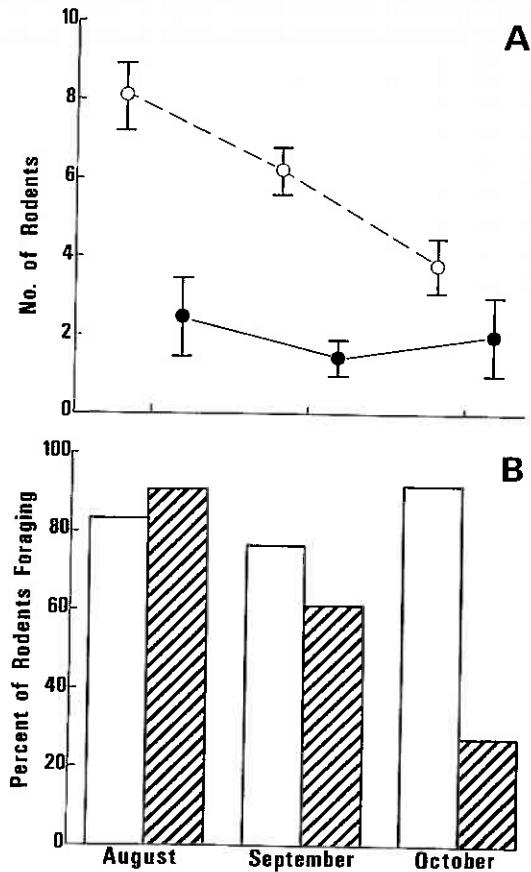


FIGURE 2. (A) Number (mean  $\pm$  SD) of *Dasyprocta punctata* (empty circle) and *Sciurus granatensis* (full circles) observed during censuses ( $N = 9$  walks per month) within 10–20 m of *Scheelea* palms along a 3-km loop of trails on Barro Colorado Island, Panama. (B) Frequency of foraging (vs eating) *D. punctata* (empty bars) and *S. granatensis* (hatched bars) during censuses. The total number of rodents observed is 73, 56, and 34 individuals for *D. punctata*, and 22, 13, and 18 individuals for *S. granatensis* in August (30 July–9 August), September (25 August–5 September) and October (23 September–5 October), respectively. Note that squirrels were observed foraging less and less, thus eating more and more.

**SEED FATE.**—All seeds placed in clumps were removed from the piles within 7 days. Of the 1200 marked seeds placed in the forest during our three experiments, 686 (57.2%) were retrieved (Table 1). Of the seeds retrieved 7 days after the experiments started, 22.2 percent were gnawed and dropped  $< 1$  m from the center of the pile, 70.6 percent were removed 1 to 20 m away and gnawed, and 7.2 percent were not gnawed but cached less than 20 m away. Cached seeds are identified as

TABLE 1. Seed fate in *Scheelea zonensis* palms throughout the late fruiting season expressed as the mean ( $\pm$  SD) of the percent of seeds ( $N = 400$  seeds per month) removed by animals and retrieved gnawed within 1 m from feeding sites, gnawed between 1 and 20 m, cached within 20 m, or not retrieved at four sites 7 days after the experiments started on 3 and 4 August, 1 and 5 September and 1 and 2 October 1990 at Barro Colorado Island. All seeds were removed. Range is for four experimental sites with 100 seeds each.

	August	September	October	Total
% Gnawed <1 m	16.25 $\pm$ 12.3 (range 1–30)	8.75 $\pm$ 6.4 (range 2–16)	13.00 $\pm$ 8.2 (range 2–21)	12.7 $\pm$ 9.0
% Gnawed 1–20 m	27.50 $\pm$ 4.7 (range 21–32)	53.25 $\pm$ 6.3 (range 39–68)	40.50 $\pm$ 11.2 (range 29–55)	40.4 $\pm$ 14.3
% Cached <20 m	9.00 $\pm$ 5.3 (range 4–16)	0.75 $\pm$ 0.9 (range 0–2)	2.50 $\pm$ 2.0 (range 0–5)	4.1 $\pm$ 4.8
% Lost	47.25 $\pm$ 10.4 (range 32–54)	37.25 $\pm$ 12.0 (range 20–46)	44.00 $\pm$ 17.9 (range 19–61)	42.8 $\pm$ 13.3

seeds that were either buried several cm under the ground or hidden beneath the litter. No significant difference occurred in the proportion of seeds gnawed within 1 m ( $F = 0.38$ ,  $df = 2,9$ ,  $P = 0.698$ ) but a significantly greater proportion of seeds were found destroyed (*i.e.*, gnawed) between 1 and 20 m in September and October than in August ( $F = 6.67$ ,  $df = 2,9$ ,  $P = 0.016$ ) (Table 1). More seeds were scatterhoarded (*i.e.*, cached) in August ( $F = 7.53$ ,  $df = 2,9$ ,  $P = 0.012$ ) (Table 1).

## DISCUSSION

While availability of fruit for BCI's diurnal rodents is decreasing from August through October (Smythe 1970), rodents are preying with increasing intensity on *Scheelea* seeds. By early October, 87 percent of seeds remaining beneath palms were destroyed. Rodents do not hesitate to consume bruchid-infested seeds during the latter part of the fruiting season of the palm. However, below fruiting *Scheelea*, rodents choose seeds, selecting those which are less likely to contain a developed bruchid larva, that is, seeds with fewer bruchid entrance holes (see Wright 1983). Intact seeds remaining underneath palms are more likely to be chewed by rodents in the following months.

Although *Scheelea* ranks first in squirrel diets on BCI (Glanz *et al.* 1982) and only third in agouti diets (Smythe *et al.* 1982), agoutis appear to be BCI's primary *Scheelea* consumers. BCI may have twice as many squirrels as agoutis (Glanz 1982, 1990), but an agouti weighs 8 times as much as a squirrel (Eisenberg & Thorington 1973). The contrast between how squirrels and agoutis exploit *Scheelea* appears to be related to their different modes of exploiting resources and storing them. When fruit availability is low, squirrels focus their activity around

*Scheelea* palms (*cf.* Glanz *et al.* 1982; Fig. 2B), where their preferred food, their arboreal caches, and the partly bruchid-infested seeds below parent palms, are to be found. On the other hand, the frequency of agoutis progressively decreases near *Scheelea* palms (Fig. 2A): they tend to forage further away (Smythe 1978), eating *Scheelea* seeds they have buried earlier, and also alternative foods such as germinating seedlings of *Astrocaryum standleyanum* (N. Smythe, pers. comm.) and *Gustavia superba* (Forget 1992).

Experiments showed that rodents rapidly remove all intact fresh *Scheelea* seeds in August–October, with only a small fraction (7%) of them being buried for later consumption, and, that a large proportion of these seeds is removed away from the seed pile (that is, usually below palms) to be chewed.

The intensity in removal of and predation upon fallen intact and infested seeds by rodents between late August and early October is concomitant with the decline in the level of bruchid oviposition by August as described by Wright (1990). Larvae need about a week to penetrate a *Scheelea* seed, and two to six months to grow to full size (Wright 1983, S. J. Wright, pers. comm.). Thus, the earlier a bruchid egg is laid on a *Scheelea* seed, the greater the chance of its becoming an adult bruchid rather than dying when a rodent eats its seed. Our study shows that intense seed removal and predation by rodents lower the probability that seeds remaining below parent palms will be infested by bruchid larvae, and therefore may limit the bruchid population that will reproduce in the next wet season. If rodent predation depresses bruchid numbers sufficiently, then the steep August–October decline in bruchid oviposition may reflect a combination of satiation by early falling *Scheelea* fruits (Wright 1990) of the (rodent-limited) bruchid population

and selection against laying eggs so late that rodents will inevitably destroy them. It follows that timing of the reproductive behavior of bruchids might have been selected to favor adult emergence and oviposition during the first part of the rainy season (see Wilson & Janzen 1972, Wright 1990) when rodents are satiated with food (see Sinythe 1970, 1978; Glanz *et al.* 1982; Smythe *et al.* 1982) and when *Scheelea* seeds accumulate underneath palms (pers. obs.).

Maximum seed predation occurs at the two tails of the *Scheelea*'s fruiting season: bruchids consume nearly all early-falling *Scheelea* seeds, while rodents consume nearly all late-falling fruits (Wright 1990, this study). To explain the timing of fruitfall (Janzen 1978) in *Scheelea*, later studies should test the hypothesis that seeds produced and dispersed (*i.e.*,

scatterboarded) in the middle of *Scheelea*'s fruiting season have the greatest chance of escaping both bruchids and rodents. If the timing of fruit ripening is under genetic control (see Wright 1990), then the escape of mid-season seed crops would select for individuals that, on the average, ripen fruit in July–August, when *Scheelea* fruit production actually peaks. The total amount of food available in BCI's forest, and the times when it appears, varies from year to year (Foster 1982b; Giacalone-Madden *et al.* 1990; Leigh 1990, Table 4; Worthington 1990, Table 6 and Fig. 3) with inevitable effects on the timing of maximum survival of *Scheelea* seeds and seedlings. Therefore, one may expect variation among *Scheelea* in timing of fruit production, variation which may be essential to the survival of both bruchids and rodents.

## LITERATURE CITED

- BRADFORD, D. F., AND C. C. SMITH. 1977. Seed predation and seed number in *Scheelea* palm fruits. *Ecology* 58: 667–673.
- CROAT, T. B. 1978. Flora of Barro Colorado Island. Stanford Univ. Press, Stanford, California.
- DE STEVEN, D., D. M. WINDSOR, F. E. PUTZ, AND B. DE LEON. 1987. Vegetative and reproductive phenologies of a palm assemblage in Panama. *Biotropica* 19: 342–356.
- EISENBERG, J. F., AND R. W. THORINGTON, JR. 1973. A preliminary analysis of a neotropical mammal fauna. *Biotropica* 5: 150–161.
- EMMONS, L. 1982. Ecology of *Proechimys* (Rodentia, Echimyidae) in South-Eastern Peru. *Trop. Ecol.* 23: 280–290.
- FORGET, P.-M. 1991. Scatterhoarding of *Astrocaryum paramaca* by *Proechimys* in French Guiana: comparison with *Myoprocta exilis*. *Trop. Ecol.* 32: 155–167.
- . 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica* 24: 408–414.
- . 1993. Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* 94: 255–261.
- FOSTER, R. B. 1982a. The seasonal rhythm of fruitfall in Barro Colorado Island. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: seasonal rhythms and long-term changes*, pp. 151–172. Smithsonian Institution Press, Washington, D.C.
- . 1982b. Famine on Barro Colorado Island. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: seasonal rhythms and long-term changes*, pp. 201–212. Smithsonian Institution Press, Washington, D.C.
- , AND N. V. L. BROKAW. 1982. Structure and history of the vegetation of Barro Colorado Island. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: seasonal rhythms and long-term changes*, pp. 67–81. Smithsonian Institution Press, Washington, D.C.
- GIACALONE-MADDEN, J., W. E. GLANZ, AND E. G. LEIGH, JR. 1990. Adición: fluctuaciones poblacionales a largo plazo de *Sciurus granatensis* en relación con la disponibilidad de frutos. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *Ecología de un Bosque Tropical*, pp. 331–335. Smithsonian Tropical Research Institute, Balboa.
- GLANZ, W. E. 1982. The terrestrial mammal fauna of Barro Colorado Island: censuses and long-term changes. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: seasonal rhythms and long-term changes*, pp. 455–468. Smithsonian Institution Press, Washington, D.C.
- . 1990. Neotropical mammal densities: how unusual is the community on Barro Colorado Island, Panama? In A. H. Gentry (Ed.). *Four neotropical forests*, pp. 287–313. Yale Univ., New Haven, Connecticut.
- , R. W. THORINGTON, JR., J. GIACALONE-MADDEN, AND L. R. HEANEY. 1982. Seasonal food use and demographic trends in *Sciurus granatensis*. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: seasonal rhythms and long-term changes*, pp. 239–252. Smithsonian Institution Press, Washington, D.C.
- HEANEY, L. R., AND R. W. THORINGTON, JR. 1978. Ecology of neotropical red-tailed squirrels, *Sciurus granatensis*, in the Panama Canal zone. *J. Mammal.* 59: 846–851.

- HERRERA, C. M. 1989. Vertebrates, frugivores and their interaction with invertebrate fruit predators: supporting evidence from a Costa Rican dry forest. *Oikos* 54: 185-188.
- JANZEN, D. H. 1971. The fate of *Scheelea rostrata* fruits beneath the parent tree: predispersal attack by bruchids. *Principes* 15: 89-101.
- . 1978. Seeding pattern of tropical trees. In P. B. Tomlinson and M. H. Zimmermann (Eds.). *Tropical trees as living systems*, pp. 83-128. Cambridge Univ. Press, London, England.
- LEIGH, E. G., JR. 1990. Introducción: ¿por qué hay tantos tipos de árboles tropicales? In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *Ecología de un Bosque Tropical*, pp. 75-99. Smithsonian Tropical Research Institute, Balboa.
- PIPERNO, D. R. 1990. Fitolitos, arqueología y cambios prehistoricos de la vegetación en un lote de cincuenta hectareas de la isla de Barro Colorado. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *Ecología de un bosque tropical*, pp. 141-152. Smithsonian Tropical Research Institute, Balboa.
- RAND, A. S., AND W. M. RAND. 1982. Variation in rainfall on Barro Colorado Island. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: seasonal rhythms and long-term changes*, pp. 47-59. Smithsonian Institution Press, Washington, D.C.
- SMYTHE, N. 1970. Relationship between fruiting seasons and seed dispersal methods in a neotropical forest. *Am. Nat.* 104: 25-35.
- . 1978. The natural history of the Central American agouti (*Dasyprocta punctata*). *Smithson. Contrib. Zool.* 257: 1-52.
- , W. E. GLANZ, AND E. G. LEIGH, JR. 1982. Population regulation in some terrestrial frugivores. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: seasonal rhythms and long-term changes*, pp. 227-238. Smithsonian Institution Press, Washington, D.C.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd edition. W. H. Freeman and Company, New York, New York.
- WILSON, D. E., AND D. H. JANZEN. 1972. Predation on *Scheelea* palm seeds by bruchid beetles: seed density and distance from the parent palm. *Ecology* 53: 954-959.
- WINDSOR, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. *Smithson. Contrib. Earth Sci.* 29: 1-145.
- WORTHINGTON, A. H. 1990. Comportamiento de forrajeo de dos especies de saltarines on respuesta a la escasez estacional de frutos. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *Ecología de un bosque tropical*, pp. 285-304. Smithsonian Tropical Research Institute, Balboa.
- WRIGHT, S. J. 1983. The dispersion of eggs by a bruchid beetle among *Scheelea* palm seeds and the effect of distance to the parent palm. *Ecology* 64: 1016-1021.
- . 1990. Cumulative satiation of a seed predator over the fruiting season of its host. *Oikos* 58: 1016-1021.
-