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## THE DISPERSION OF EGGS BY A BRUCHID BEETLE AMONG *SCHEELEA* PALM SEEDS AND THE EFFECT OF DISTANCE TO THE PARENT PALM<sup>1</sup>

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**Abstract.** Larvae of an unidentified bruchid beetle develop within and kill seeds of the palm *Scheelea zonensis*. Only one larva can develop per seed. Hence, a selective advantage should accrue to female bruchids that oviposit on previously unattacked (pristine) fruit. On Barro Colorado Island, Panama, I performed experiments to test the following hypotheses. (1)  $H_0$ : female bruchids do not distinguish between previously attacked and pristine fruit, and (2)  $H_0$ : female bruchids oviposit at random among *Scheelea* fruit. Both null hypotheses were rejected. Female bruchids oviposit more frequently on pristine fruit, and female bruchids disperse their eggs uniformly among *Scheelea* fruit.

Such sophisticated seed predators might search large areas for pristine seeds. As a result, seed-predation rates may fall slowly with distance from the parent palm. To test this hypothesis, I exposed *Scheelea* fruit at distances of 1, 8, 16, and 100 m from the nearest fruiting palm. Within 16 m, bruchid attack rates were uniformly high. However, at 100 m there was a significant decline. Other studies have found declines in seed predation rates, but only over similarly large distances. This has important implications for the mechanism by which density-dependent seed predation might contribute to the coexistence of tropical trees.

**Key words:** bruchid beetles; dispersion of eggs; oviposition tactics; Panama; *Scheelea zonensis*; seed predation; tropical forest diversity.

### INTRODUCTION

Many insects place their eggs on seeds, which their larvae then consume. Clearly, if enough eggs are placed on a single seed, competition between larvae will ensue. To minimize this competition, adults could distribute their eggs uniformly among the available seeds. This phenomenon has been observed in laboratory populations of bean weevils (Utida 1943, Oshima et al. 1973, Mitchell 1975), but the possibility and its effect on the interaction between plants and seed predators have not been considered for tropical systems.

On Barro Colorado Island (BCI), Panama, seeds of the palm *Scheelea zonensis* are preyed upon by an unidentified bruchid (Bradford and Smith 1977). This system is ideal for study of the dispersion of bruchid eggs among seeds. *Scheelea* fruits have a durable exocarp, which adult bruchids cannot penetrate. This insures that oviposition does not occur before the fruit is on the ground and the exocarp is removed. Also, casual observation suggests that supplies of *Scheelea* fruits are limited. In places the durable endocarps litter the forest floor. Most of these endocarps bear several of the small entrance holes left by the first instar of the bruchid. Moreover, in a haphazard collection of 532 endocarps, mammals or bruchids had consumed 99.4% of the seeds.

For the plant, seed predation of this magnitude can be devastating. Many seeds are never dispersed be-

yond the immediate vicinity of their parent. Janzen (1970) hypothesized that seed predators would recruit to these local concentrations and all seeds close to the parent plant would be doomed. Clearly, this could contribute to the coexistence of plant species by preventing single-species stands (Ridley 1930, Gillett 1962, Connell 1970, Janzen 1970). However, the significance of this mechanism (Hubbell 1980) and even the assumption that seed survivorship is directly related to distance to the parent plant (Connell 1978) have been challenged recently. I will evaluate these positions against the evidence from the *Scheelea*-bruchid interaction.

### METHODS

I undertook four experiments on BCI. Three test the null hypothesis that bruchid eggs are distributed randomly among *Scheelea* fruit. Of these three, the first establishes that a single bruchid can develop in a single seed. A small proportion of *Scheelea* fruits have more than one seed (Janzen 1971, Bradford and Smith 1977). Multiseeded fruits were excluded from all experiments. The second experiment tests the null hypothesis that bruchids place their eggs randomly among *Scheelea* fruit. The third experiment tests the null hypothesis that bruchids do not incorporate the presence of other conspecific eggs into their own oviposition strategy. In addition, the second and fourth experiments test the hypothesis that isolation affects the intensity of attack by bruchids. Finally, I examined the relation between seedling density and distance to parent.

Total rainfall on BCI is 267 cm/yr. There is a 4-mo dry season (December to April) during which rainfall

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TABLE 1. Survivorship of bruchid larvae in nuts of *Scheelea zonenis*.

Number of eggs on nut	Number of nuts	
	Without larvae	With a single larva
1	40	10
2	44	9
3	12	13
5	24	25

is usually <13 cm/mo. The potential vegetation has been classified as tropical moist forest (Holdridge and Budowski 1956), but some trees are deciduous in the dry season. Forest structure is heterogeneous due to frequent treefall gaps. Lianas, epiphytes, and understory palms including *Scheelea* are common.

*Experiment 1: the number of larvae per seed*

On 10 May 1981, I collected a large number of fruit with intact exocarps from the forest floor. Since their exocarps were intact, these fruit had not been exposed to bruchid attack. I removed all exocarps with a mallet. I then soaked the fruit in water for 48 h to remove as much of the mesocarp as possible. After this treatment, the fruit are visually indistinguishable from fruit whose mesocarp has been removed by mammals. Fibrous material covers the endocarp, and some pulpy fruit remains lodged in this material. Henceforth, nut will be used to denote fruit with the exocarp and most of the mesocarp removed.

These nuts were placed in the forest and exposed to bruchid attack for 48 h. To prevent mammals from disrupting the experiment, I placed the nuts in exclusion cages (2.54 × 3.81 cm mesh). I counted bruchid eggs by palpating each nut. Palpation was necessary because the eggs are frequently buried in remnants of mesocarp. The eggs are hard and large enough to be felt easily. After 48 h of exposure, large numbers of nuts had 1, 2, 3, or 5 eggs. On 15 May, I placed these nuts in cages with mesh (3 × 3 mm) sufficiently small to prevent further bruchid attack, and I placed the cages in the forest. On 13 August 1981, I dissected each nut with a hammer and examined the endosperm for larvae.

*Experiment 2: the dispersion of bruchid eggs on pristine nuts and the effect of isolation on the intensity of bruchid attack*

On 20 May 1981, I collected 420 fruit with intact exocarps from the forest floor and prepared them using the same methods described under experiment 1. I placed 20 nuts in each of 21 exclusion cages and placed the cages 1, 8, and 16 m from each of seven fruiting *Scheelea* palms. At the same time, I removed all fallen fruit with broken exocarps from the vicinity of each of the seven palms. This insured that local oviposition

sites were limited to the 20 nuts in each cage. With the exception of the experimental palm, each exclusion cage was at least 30 m from any other *Scheelea* with fruit. After 48 h of exposure, I recovered the traps and palpated each nut to count eggs.

To test the null hypothesis that bruchids place their eggs randomly, I compared the observed distribution of eggs per nut with that expected by chance. Since there were 20 nuts in a cage, the probability that an egg was placed on a particular nut,  $p$ , is .05. The probability that an egg was placed on any other nut,  $q$ , is .95. If  $n$  eggs were placed randomly on the 20 nuts in a trap, the expected variance of the distribution of eggs per nut is  $npq$  from the binomial distribution. For each of the 21 traps, I compared the variance expected by chance with the observed variance.

To examine the effect of isolation on the intensity of bruchid attack, the seven fruiting palms represent replicates and the three predetermined distances fixed treatments. Therefore, I used a mixed two-way analysis of variance to determine the effect of isolation on the number of eggs per nut (Sokal and Rohlf 1969).

*Experiment 3: the dispersion of bruchid eggs on previously exposed nuts*

I selected 20 nuts from experiment 2 that had 0, 1, or 2 eggs and 17 nuts that had 3 eggs. I separated these nuts by egg number, placed the nuts in four exclusion cages, and placed the cages in the forest 50 m from the nearest conspecific with fruit. I arranged the cages so they touched at a central point and formed 90° angles to one another. After 48 h, I retrieved the cages and palpated each nut to count eggs.

To test the null hypothesis that new eggs appeared randomly, I treated the nuts which originally had 0, 1, 2, and 3 eggs as groups in a one-way analysis of variance. I then partitioned the variation among groups into independent components to test three additional a priori hypotheses (Sokal and Rohlf 1969:226–235). These are: (1) nuts that escaped attack and nuts that were attacked during their first experimental exposure received equal numbers of eggs during their second exposure, (2) nuts that received a single egg and nuts that received multiple eggs during their first exposure received equal numbers of eggs during their second exposure, and (3) nuts that received two eggs and nuts that received three eggs during their first exposure received equal numbers of eggs during their second exposure.

*Experiment 4: the effect of isolation on the intensity of bruchid attack*

On 25 June 1981, I placed single *Scheelea* nuts in exclusion cages and placed the cages 1 m (5 cages, 5 palms), 16 m (5 cages, 5 different palms), and 100 m (10 cages) from the nearest conspecific with fruit. To insure that no conspecifics with fruit were closer than 100 m to the most isolated cages, I conducted this

TABLE 2. The distribution of bruchid eggs on nuts of *Scheelea zonensis* after one exposure to attack. Entries are number of nuts.

Tree number	Number of eggs							Variance		
	0	1	2	3	4	5	6	7	Observed	Binomial
Distance 1 m										
1	4	11	2	2		1			1.48	1.24
2	2	8	4	4		1	1		2.37	1.85
3		4	8	2	4	2			1.73	2.47
4		2	4	6	7	1			1.21	2.90
5		3	14	3					0.32	1.90
6		2	9	5	3	1			1.09	2.47
7	20								...	...
Distance 8 m										
1	2	3	5	7	3				1.48	2.19
2		6	5	5	4				1.29	2.23
3	6	13	1						0.30	0.71
4			1	4	8	4	2	1	1.46	4.04
5	1	13	6						0.30	1.19
6	4	12	3	1					0.58	1.00
7	3	11	5			1			1.17	1.24
Distance 16 m										
1*				3	5	5	3	3	3.54	4.94
2	1	3	7	5	4				1.31	2.28
3	4	7	6	3					0.99	1.33
4	1	11	5	2	1				0.89	1.47
5		3	7	6	4				1.00	2.42
6	6	6	4	4					1.27	1.24
7	1	2	9	4	3	1			1.42	2.33

\* The final seed had 11 eggs.

experiment in the 50 ha of forest on BCI that has been mapped by Dr. Stephen Hubbell. I prepared the nuts exactly as in experiment 1. Every 24 h, I recovered each nut and placed a new nut in each cage. Mammals removed three nuts from the most isolated cages. To test the null hypothesis that isolation does not affect the intensity of bruchid attack, I examined the frequency of nuts with and without eggs.

#### *Isolation vs. seedling density*

I measured the distance from the adult palm to all conspecific seedlings in wedge-shaped transects which extended for 18 m from the base of 24 adult palms. Each wedge described an arc of at least 30°. I chose the adult palms haphazardly, and I chose the direction for each transect with the help of a compass and a random number table. If a second conspecific adult came closer than 18 m to a transect, the transect was cut short. Seedlings from several cohorts are included in the counts.

## RESULTS

### *Experiment 1*

Larvae developed in 47 of the 127 nuts that initially supported more than one egg (Table 1). In each of these 47 nuts, a single larva was present, and the larva had consumed about one-third of the endosperm. Thus, the supposition that a single larva develops within each endosperm is supported.

Four to seven days after an egg is deposited on a nut, the larva begins to drill into the endocarp. Multiple entrance holes were present on at least 40 of the 47 nuts that supported a single larva and on most of the 80 nuts that did not support a larva. The cause of the deaths of these larvae is not known, and I did not find the remains of any dead larvae. The same phenomenon occurs under natural conditions. The endocarps of *Scheelea* seeds are durable and persist on the forest floor. Most of these endocarps have several small bruchid entrance holes, but there is never more than one large exit hole per seed.

### *Experiment 2*

Female bruchids found 20 of the 21 sets of nuts during the 48 h of exposure. The distributions of eggs among nuts are presented in Table 2. For 17 of the 20 sets of nuts, the observed variance is less than the variance expected by chance. The null hypothesis that eggs are randomly distributed among nuts is rejected ( $P < .002$ , Binomial Test). Rather, female bruchids distribute their eggs uniformly among nuts.

The number of bruchid eggs per nut varies significantly among the seven replicate palms ( $F = 22.1$ ,  $P < .005$ ). Also the interaction term (palm  $\times$  isolation) is significant ( $F = 24.8$ ,  $P < .005$ ). This means that isolation affects the intensity of bruchid attack, but the direction of the effect varies among palms. For example, for palms 1 and 7, the number of eggs per

TABLE 3. The distribution of new bruchid eggs on previously exposed nuts of *Scheelea zonensis*. Entries are number of nuts.

Number of new eggs	Number of eggs initially present			
	0	1	2	3
0	0	0	2	2
1	0	7	4	3
2	6	5	6	1
3	6	6	7	3
4	4	0	1	7
5	4	1	0	1
6	0	1	0	0
Total number of nuts	20	20	20	17
Total number of eggs	66	46	41	47

nut actually increased with isolation, and for palms 3 and 6, the number of eggs per nut decreased with isolation (Table 2). Clearly there is no consistent effect of isolation on bruchid attack rates ( $F = 0.39, P > .50$ ).

Experiment 3

Bruchids responded differently to nuts which initially supported different numbers of eggs (Table 3). There is significant heterogeneity among the mean number of new eggs placed on the different groups of nuts ( $F = 3.54, P < .05$ ). Only one of the three remaining a priori hypotheses can be rejected. Female bruchids preferentially placed their own eggs on nuts which had previously escaped attack ( $F = 7.85, P < .01$ ). However, given that a nut had been attacked, the number of eggs present did not affect the oviposition tactics of later arrivals. Nuts with one vs. two or three eggs ( $F = 0.05, P > .50$ ) and nuts with two vs. three eggs ( $F = 2.76, P > .10$ ) did not receive different numbers of eggs during their second exposure to bruchid attack.

Experiment 4

During 24 h of exposure, bruchid eggs appeared on 60.0% ( $N = 35$ ), 57.1% ( $N = 35$ ), and 10.4% ( $N = 67$ ) of the *Scheelea* nuts placed 1, 16, and >100 m from the nearest conspecific with fruit, respectively. The frequency of attacked nuts differs significantly among the three distances ( $G_H = 18.04, P < .001$ ). As in experiment 2, attack rates are equal for nuts isolated from fruiting conspecifics by 1 and 16 m ( $G_H = 0.03, P > .9$ ). Virtually all of the heterogeneity arises from lower attack rates on the nuts isolated by 100 m or more from fruiting conspecifics.

Isolation vs. seedling density

The average number of seedlings per transect was 16.9. Sample size is too small to examine seedling shadows for individual palms. Therefore I lumped seedling counts from all 24 transects to obtain estimates of seedling density. The composite data show

an obvious inverse relation between seedling density and distance to the nearest conspecific adult (Fig. 1).

DISCUSSION

Only one bruchid larva can develop in a single endosperm of *Scheelea zonensis*. Therefore female bruchids that preferentially oviposit on pristine nuts will enjoy a selective advantage, and, in fact, pristine nuts are the preferred oviposition site (Table 3). However, the presence of a single egg does not insure that larvae from subsequent eggs will face an established competitor. The survivorship of eggs and larvae is low. For example, 3 mo after oviposition, larvae survived in only 20% of the nuts which initially supported a single egg (Table 1). Given 80% mortality of eggs and larvae, the probability is  $.8^n$  that no larvae become established in a nut with  $n$  eggs. Thus, the larvae of a female that oviposits on nuts that currently support the minimum number of eggs will be less likely to encounter an established competitor. As a result, females should disperse their eggs uniformly among nuts. This occurs among nuts exposed to bruchid attack for one 48-h period (Table 2).

The outcome of a second exposure to bruchid attack (experiment 3) only confirms this observation in part. As expected, nuts that had escaped attack during their first exposure were the preferred oviposition site. However, no preference was exhibited for nuts that had previously received one, two, or three eggs (Table 3). Apparently, in experiment 2, female bruchids were able to distinguish nuts with different numbers of eggs, while in experiment 3, they only distinguished nuts that had (one or more eggs) or had not (zero eggs) been attacked before. There are two possible explanations for this difference. First, the nuts were handled after their initial exposure in experiment 3. This may have erased some cue which the bruchids use to determine the previous level of attack. Another coleopteran seed predator uses a chemical cue in this regard (Oshima et al. 1973), so this possibility cannot be ruled out. However, in experiment 3, female bruchids did oviposit more frequently on nuts that had

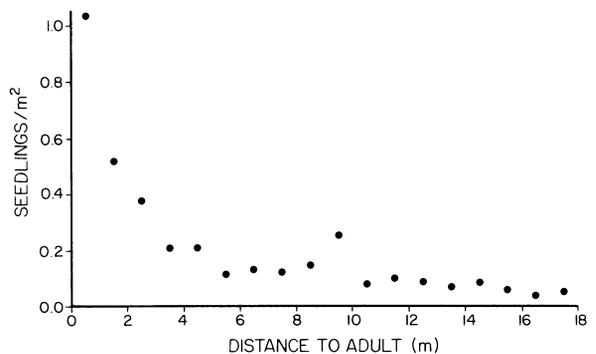


FIG. 1. The relation between seedling density and distance to the nearest conspecific adult for *Scheelea zonensis*.

not been attacked before (Table 3). So the erasure of some cue is not entirely consistent with the results of experiment 3. A consistent explanation for the results of experiments 2 and 3 emerges if a female bruchid (1) can determine whether or not eggs are already present on a nut and (2) can count the number of eggs she has deposited on a particular nut but (3) cannot count the number of eggs previously deposited by another female. However, any inferences about the sensory abilities of the beetles are speculative.

Oviposition tactics will affect the interaction between plant and insect. For example, the proportion of seeds that survive attack will be minimized by insects that place their eggs uniformly among seeds. Also, insects that indiscriminately place their eggs on any available seed will not be compelled to leave the concentration of seeds in the immediate vicinity of the parent plant. As a result, predation rates may drop very quickly with increasing isolation from the parent plant. On the other hand, insects that prefer pristine seeds may range more widely once the seeds in the immediate vicinity of the parent plant have been saturated with eggs. As a result, the dispersal distances necessary to reduce seed predation rates may be large.

Connell (1978) reviewed several studies that examined the relation between seed predation rates and isolation from conspecific adults. His conclusion that isolation "generally" does not affect predation rates may be premature. There is no difference in the viability of seeds "near" and "far" from conspecific adults for *Euterpe globosa* (Janzen 1972a), *Spondias mombin* (Janzen 1975), *Sterculia apetala* (Janzen 1972b), and *Scheelea rostrata* (Wilson and Janzen 1972). However, the "far" seeds in these studies were only 5.5, 0, 17.5 (discounts seeds in open pasture), and 8 m, respectively, from a conspecific adult or a conspecific seed shadow created by fallen seeds. On the other hand, seeds of *Andira inermis* that are dispersed 49 m or more from their parent are much less susceptible to weevil predation than seeds that are dispersed shorter distances (Janzen et al. 1976). Also, the intensity of bruchid attack on seeds of *Scheelea zonensis* is uniformly high within 16 m of the adult but significantly lower at 100 m (Table 2, experiments 2 and 4). In sum, there probably is an inverse relation between seed predation rates and isolation, but the effect occurs over relatively large distances.

This raises questions about the effect of seed predators on the spatial pattern of tropical plants. Janzen (1970) hypothesized that seed predators recruit to the concentration of seeds below a fruiting plant and kill all seeds within some threshold distance from the parent plant. This is not the case for *Scheelea zonensis*. The density of seedlings is greatest within 1 m of the parent and falls exponentially with distance (Fig. 1). The oviposition tactics of the bruchid seed predator may be partly responsible. The concentration of seeds below a fruiting *Scheelea* attracts female bruchids (S.

J. Wright, *personal observation*). Nevertheless, some seeds survive immediately beneath their parent (Fig. 1). This may be due to failure of all eggs on a seed or some seeds may simply be overlooked. More important, as female bruchids aggregate at a fruiting *Scheelea*, the number of eggs per fruit must increase, and the number of pristine fruit must decrease. At some point, the female bruchid must decide whether (1) to continue adding eggs to the fruit beneath the palm or (2) to leave in search of dispersed fruit or another fruiting *Scheelea*. Within 24 h, bruchids oviposited on 10.4% of the single, isolated (>100 m from a *Scheelea* adult) nuts which I placed in the forest. Clearly, some female bruchids range widely through the forest. As a result, eventual predation rates must be substantial for even the most isolated seeds (*Scheelea* seeds are vulnerable to bruchid attack for several months before germination). In sum, occasional escape of seeds close to their parent (Hubbell [1980] emphasized this possibility) and reasonably high predation rates on isolated seeds combine to generate an inverse relation between seedling density and distance to parent (Fig. 1).

Janzen (1970) hypothesized that seed predators contribute to the coexistence of tropical plant species by preventing recruitment close to seed-producing conspecifics. Connell (1970) advanced a similar hypothesis but emphasized the role of seedling mortality. Despite the activities of seed and seedling predators, (1) conspecific nearest-neighbor distances are small, (2) adult spatial patterns are aggregated, and (3) the density of juveniles is inversely related to distance to a conspecific adult in seasonally dry forest in Costa Rica (Hubbell 1979). On Dalia Island in Gatun Lake, the spatial pattern of adults of *Scheelea zonensis* is random (S. J. Wright, *personal observation*), and on BCI, seedling density is inversely related to distance to a conspecific adult (Fig. 1). These observations do not support the Janzen and Connell hypotheses, but they are not particularly damaging either. Any factor which lessens the intensity of aggregation of conspecific plants could contribute to the coexistence of plant species. A host of factors affect the spatial pattern of plant populations, and most of these increase the tendency toward aggregation (e.g., Pielou 1960, Barbour 1973). It would be naive to expect a single factor to overwhelm all others to produce uniform spatial patterns. The crucial prediction of the Janzen and Connell hypotheses is that the spatial patterns of plant populations are less aggregated in the presence of seed and seedling predators, than in their absence. This prediction has not been tested, but it may be possible to do so on isolated islands where plants exist without their seed predators.

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