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ASSOCIATION OF A RAINFOREST PALM AND SEED-EATING BEETLES IN PUERTO RICO¹

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Abstract. The scolytid beetle *Cocotrypes carpophagus* may attack as many as 100% of the seeds of the common Puerto Rican rainforest palm *Euterpe globosa* by the end of the fruiting season when the population densities of the beetle are at their maximum. At the beginning of fruit fall, the percentage attack is extremely small. It is hypothesized that the build-up of this seed predator on the crop each year is the selective force producing the strong inter-tree fruiting synchrony displayed by *E. globosa*. Further, this synchrony appears to prevent the beetle from depressing the palm population density to the low level characteristic of most tropical trees. It is also hypothesized that such a beetle-palm interaction could not occur on the mainland of Central America owing to the difficulty of satiating the large mainland community of vertebrates and insects that prey on palm seeds.

The sierra palm, *Euterpe globosa*² Gaertn., is an extremely common member of the Puerto Rican rainforest canopy above 500-m elevation. In mixed forest it may constitute one-fourth of the woody plant matter and be the second most common tree; it occasionally forms nearly pure stands of reproductive adults and juveniles of all ages (cf. McCormick 1970, Bannister 1970). I would like to call attention to the interaction of the sierra palm with one of its primary seed predators, the scolytid beetle *Cocotrypes carpophagus* Hornung. This interaction is of special interest to a general theory of the effect of seed predators on a plant community (Janzen 1970, 1971a), because it involves a native tropical tree growing naturally at very high density in the face of intense seed predation by a native seed predator on an island.

METHODS

On February 9, 1971, the fates of all *E. globosa* seeds were recorded in 61- by 61-cm quadrats placed at two kinds of sites with respect to reproducing adult palms. At one kind of site, the quadrat was centered on the area of highest seed density (B quadrats, Table 1); this point was within 3 m of the base of the palm and usually directly under the center of the palm crown. At the other sites, two quadrats (F quadrats, Table 1) were placed on relatively level ground free of major obstructions and 1.5–2.5 m from the B quadrat. The three quadrats at each palm thus had a configuration such that lines drawn between them and the tree formed a "Y" with the palm trunk at the base. The B quadrat, then, is between the palm trunk and the two F quadrats. The density of adult palms was such that F quadrats were often equidistant between the palm responsible for the seeds in the B quadrat and several other adult palms. The forest was on a gentle, rocky slope ap-

proximately 1.5 km south of the central recreation area of the Puerto Rican Luquillo National Forest (680-m elevation). Ten palms were sampled and all were within a 2-ha segment of the forest that contained at least 50 reproducing adult palms. Palms were chosen rather uniformly over the area; many were rejected as sample candidates because there was no place for an F quadrat (far from a parent). Other seed shadows could not be sampled because surface erosion had removed a major part of the seed crop. Inspection of other Luquillo palm forests leads me to believe that the interaction described here is representative of Puerto Rican palm forest directly undisturbed by human activities.

As in the case with other members of the pantropical genus *Cocotrypes* (Schedl 1961), adult female *C. carpophagus* (not a weevil, as reported by Bannister 1970) bore directly through the bony endocarp of an *E. globosa* fruit once it has fallen and the thin, fleshy exocarp has either rotted off (the usual case) or been chewed off by a black rat (introduced; *Rattus rattus*). Her first generation of 5–20 female offspring (less than 5% males are produced) consume the entire endosperm and embryo. I infer from Schedl's (1961) account of *C. dactyliperda*, a very similar scolytid from palm nuts, that the new females leave in search of new seeds after mating within the seed. The abandoned seed becomes waterlogged and soft, but remains recognizable for at least 1 year. A seed may survive if germination occurs shortly after the beetle's attack, but even in this case the beetle consumes a major part of the seedling's food reserves. The generation time of the beetle is about 30 days.

Adult *E. globosa* are strongly synchronized with each other in fruit production. There is almost no seed fall from early May to early January (Bannister 1971, and observed in the study). By February 9, 1971, approximately half of the trees with fruit at the study site had dropped most of their seeds (e.g.,

¹ Received May 5, 1971; accepted November 2, 1971.

² Also known as *Prestoea montana* (Howard 1968).

TABLE 1. Condition of 4,017 *Euterpe globosa* seeds from quadrats close (B) and far (F) from parent palms on February 9, 1971. Attack is by the scolytid beetle *Cocotrypes carpophagus*

Tree	1970 Percentage of seeds attacked	Number of seeds	1971 Percentage of seeds attacked	Number of seeds	Number of seedlings 1-3 years old
1 B	95.1%	122		0	4
F ₁	100%	9		0	1
F ₂	100%	46		0	1
2 B	99.8%	537		0	55
F ₁	83.4%	6		0	0
F ₂	100%	6	0%	1	0
3 B	98.0%	343		0	10
F ₁	100%	3		0	0
F ₂	100%	11		0	0
4 B	100%	99	0.4%	541	0
F ₁	100%	7	0%	11	1
F ₂	100%	4	0%	7	0
5 B	97.6%	169		0	5
F ₁	100%	23	0%	1	0
F ₂	100%	16	0%	1	1
6 B	100%	64	0%	185	2
F ₁	100%	1	0%	7	2
F ₂	100%	15	0%	21	6
7 B	100%	172		0	15
F ₁	100%	3	0%	4	2
F ₂	100%	34		0	12
8 B	100%	38	0%	264	5
F ₁	100%	49	0%	15	3
F ₂	100%	15	15.0%	20	12
9 B	100%	160	0.6%	778	11
F ₁	100%	13	0%	10	0
F ₂	100%	5	14.3%	7	2
10 B	100%	61	11.0%	36	44
F ₁	100%	2	0%	1	1
F ₂	100%	69	20.0%	5	0

trees 4, 6, 8, and 9 in Table 1). The population flowers during the rainy season (June-September); the previous dry season (February; Odum, Drewry, and Kline 1970) is probably the cue used for the initiation of flower primordia. The samples in Table 1 were taken during the early part of the period of fruit fall and during the dry season.

RESULTS

Of the 1,765 seeds from the 1970 seed crop in the B quadrats, 99.0% had been attacked (eaten out) by the scolytids by the date of the sample collection. Of the 17 unattacked seeds, 12 had badly discolored and soggy endosperm, and appeared dead. Of the 1,804 seeds from the 1971 seed crop in the B quadrats, 0.9% had been attacked by scolytids, though more than 99% of the 1971 seeds had been on the ground long enough (2-4 weeks) for the fleshy pericarp to have been chewed or rotted off. Under tree number 9 they had been on the ground long enough

for germination to have started. In both B and F quadrats, the seeds attacked in 1971 had either one adult beetle in them (very newly attacked), or 6-15 newly emerged adults, plus nearly mature larvae and pupae.

Of the 337 seeds from the 1970 seed crop in the F quadrats, 99.7% had been attacked by scolytids. The endosperm of the single unattacked seed was badly discolored. Of the 111 seeds from the 1971 seed crop in the F quadrats, 4.5% had been attacked by scolytids. While a slightly higher percentage of the 1971 seeds in the F quadrats had been attacked than in the B quadrats, this difference is not statistically significant at the 5% level. Even if larger samples show this difference to be significant, it will probably be obliterated or reversed as the seed crop ages, owing to a faster rate of scolytid population increase in the B quadrats where seeds are closer together than in the F quadrats.

The B quadrats have produced 151 seedlings over the past 3 years while the F quadrats have produced 44. If we assume that the total number of seeds in each quadrat is representative of previous years' seed shadows, then this 3:1 seedling ratio was produced by a ratio of seed shadow intensities of about 8:1 (3569:448).

DISCUSSION

The data suggest that there is the following interaction between the palm and the beetle. As new seeds begin to accumulate in large numbers on the forest floor in January, the few scolytids surviving (i) on seed crops from palms out of phase with the general population or (ii) from the previous year's crop suddenly have a large amount of food available and have close to an exponential rate of population growth for three to four generations. By August, the combination of seed germination and the scolytids will have removed almost all of the viable seed crop. The scolytid population then probably declines rapidly and survives only in the form of those rare individuals that locate a seed crop that is out of phase with the remainder of the population, or those that survive as free-living adults. The beetle has no known alternate host in the palm forest, though it feeds on the seeds of at least twenty species of palm seeds over its pantropical range according to Schedl (1961). The beetle cannot aestivate with low mortality in the waterlogged seeds and probably cannot easily aestivate outside of them. The beetle population probably provides the selective pressure that has resulted in synchronized fruiting within the population. Were the palms not synchronized in their fruiting, they would probably be much less abundant than they are at present.

The compound hypothesis stated above is worth some more-detailed explanation even at this prim-

itive state of our knowledge of *E. globosa* and *C. carpophagus*. Two strong processes select against attenuation of the palms' fruiting period beyond the end of the fruiting season. First, the later in the fruiting season (that a palm drops its seeds) the higher should be the scolytid density in the forest and the shorter should be the half-lives of newly dropped seeds. With a generation time of 1 month for the beetle, we may expect that a palm that drops its seeds between July and September will have the lowest chance of producing a new adult. Second, since *E. globosa* is obligatorily outcrossed (Bannister 1970), trees flowering out of season may be selected against through lack of pollination. Later fruiting would thus require changes in developmental time as well as flowering time.

Some enigmatic process is also selecting against attenuation of the beginning of the fruiting season. This process is not seed predation by vertebrates, since those birds that eat *E. globosa* fruits (e.g., ruddy quail dove, *Geotrygon montana*; red-necked pigeon, *Columba squamosa*; Puerto Rican parrot, *Amazona vittata*—Recher 1970, Bannister 1970) only eat the pericarp and drop or regurgitate the seeds unharmed (C. Kepler and A. Kepler, personal communication). Introduced black rats (*Rattus rattus*) appear to eat only the pericarp of *E. globosa* fruits. Currently (as well as in the recent past) there appears to be no vertebrate population on Puerto Rico that preys on large seeds.

The slightly higher percentage of seed attack on the 1971 crop in the F quadrats, as contrasted with the B quadrats, should not be viewed as a negation of the general hypothesis that clumped seeds should suffer higher overall predation than widely spaced ones (Janzen 1970, 1971b, 1971c). At the low beetle densities early in the fruiting season, the adult palm will temporarily successfully satiate them. However, as the beetle population builds up, the beetles should find all the seeds in the B quadrats faster than in the F quadrats. This should result in a final higher rate of seedling production per seed in the F quadrats than in the B quadrats. The accuracy of this interpretation is supported by the data on the number of seedlings per plot; while the intensities of the seed shadows in the B and F quadrats are at a ratio of 8:1, the ratio of seedlings is 3:1. The difference between these two ratios is even more dramatic if we note that any particular B quadrat is likely not to have been directly under one of the inflorescences some of the years (each tree produces one to five inflorescences) and therefore many of the seedlings recorded in a B quadrat may have been produced during years when the B quadrat had a seed density characteristic of an F quadrat. The reverse is not true, owing to the distance of F quadrats from parent palms.

In tropical climates such an interaction system as described above should be able to exist only on relatively small islands. If the palm seeds fell to a large bird and rodent community such as characterizes mainland tropical rainforests, the selective pressure for synchronization of the palm population would be largely removed. The same reduction of selective pressure would occur if there were numerous other palm species available whose seeds could serve as alternate hosts for the scolytid when *E. globosa* seeds were unavailable. On the other hand, the selection for synchronization within a palm's seed crop would be strongly increased. (An *E. globosa* palm may take several months to shed its seeds.) Further, there would be strong selection for a more fruitlike endocarp so that animals would be more likely to remove the seeds from below the parent palm. Currently in Puerto Rico, such selection is probably very mild since it would be hard to carry the seed to a point not close to at least one parent palm but yet within a forest occupied by *E. globosa*. The primary selection for dispersal is probably for longer distances to newly opened habitats such as new landslides.

Increased seed predation by both vertebrates and insects, such as in the mainland community, should not only change the direction of selection pressures, but should lower the frequency with which an adult palm reproduces new adults; this should lead to densities of large palms more similar to those commonly encountered in well-drained mainland rainforests. It is of interest in this context that those lowland mainland habitats where large palms are very common are either highly seasonal (with the season having the same depressant effect on the array of seed predators as does the absence of alternate hosts in Puerto Rican forests), or are very swampy with the seeds falling into water where they are protected from many predators. We may suspect seed toxicity or some direct behavioral mechanism of escape for the small palms (e.g., *Geonoma*, *Asterogyne*) which become very common in the understory of Neotropical mainland rainforests. On the other hand, these palms may be such outstanding competitors in the heavily shaded understory that they maintain a high density in spite of very high predation.

Viewed the other way round, we may note that the establishment and maintenance of a terrestrial rodent population in the Puerto Rican rainforest may be rendered very difficult by the nearly total lack of production of intact seeds during the greater part of the year by a major part of the plant community. The problem is aggravated if there is an occasional very wet dry season with the result that the palms do not initiate flower primordia. The scolytid population might survive on the seeds produced by those few trees growing in exceptionally dry sites, but such

survival should be less likely for a rodent population.

The Puerto Rican palm forest differs in a major way from mainland forest sites. In view of the large number of seedlings produced, a comparatively large number of young palms must die through direct competition rather than by being eaten as seeds (and thereby sustaining a large animal population) as would be the case on the mainland. This suggests that a proportionately larger emphasis in the evolutionary history of *E. globosa* may have been on the competitive abilities of the seedlings rather than on escape from predators. It also suggests that the equilibrium number of Puerto Rican rainforest tree and understory shrub species might be increased through the introduction of a more effective *E. globosa* seed predator. In view of the ease with which humans have moved insects and rodents about the tropics, we may be shortly provided with an experiment similar to that conducted with chestnut blight and Dutch elm disease.

We may also predict that, over evolutionary time, *C. carpophagus* may have been periodically eliminated from Puerto Rico through weather events leading to occasional failure of all the palm crops on the island in a given year. This should have led to episodes of greatly intensified competition between *E. globosa* and other understory shrubs and saplings, as well as broadening of fruiting synchronization at the population level. Both *E. globosa* and *C. carpophagus* have been recorded from other Caribbean islands (Schedl 1961, Bannister 1970) and there may be some chance to examine their interaction at a less intense stage in their coevolution. This is complicated, however, by the ease with which *Cocotrypes* species have been transported about the Neotropics by man in recent years (Schedl 1961). It is also possible that if *C. carpophagus* is made temporarily extinct from an island such as Puerto Rico, its very similar congener, *C. dactyliperda*, will be the first to reinvade. A tantalizing bit of information in this connection is that only *C. dactyliperda* has been recorded from Cuba, while only *C. carpophagus* has been recorded from Puerto Rico (Schedl 1961). However, Schedl points out that *C. dactyliperda* is probably of Old World origin, and Cuba may therefore be a simple case of competitive displacement by a recently introduced insect.

Perhaps the most intriguing complication of all is the hypothesis advanced by S. Wood (personal communication) that *C. carpophagus* may have been in-

troduced to Puerto Rico from the Old World tropics around 1900. While I personally doubt this, if it proves to be the case, we then have an example of an animal arriving on an island where a very large food resource is unexploited and then becoming integrated with the community as if it had been there for a very long time. This is quite similar to the introduced African cotton-strainer bug *Dysdercus fasciatus* developing large populations in the forest on Costa Rican *Sterculia apetala* seeds that were probably all eaten by deer, peccaries, and agoutis prior to contemporary heavy hunting (Janzen 1972).

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