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Predation of Phytelephas aequatorialis seeds ("vegetable ivory") by the bruchid beetle Caryoborus chiriquensis

Henrik Borgtoft Pedersen

Institute of Biological Sciences, Department of Systematic Botany, University of Aarhus, Nordlandsvej 68, DK-8240 Risskov, Denmark

Phytelephas aequatorialis Spruce is endemic to western Ecuador, where it is found from sea-level to 1,500 meters altitude. The palm is one of the principal producers of "vegetable ivory" or "tagua," as its hard seed-endosperm is called. The present boom in the demand for vegetable ivory has once again turned it into one of the most important non-timber forest products in Ecuador, with an annual export worth more than four million US$ (Borgtoft Pedersen 1993). For information on past and present use of vegetable ivory see Acosta-Solis 1944, 1948; Barfod 1989, 1991a, b; and Barfod et al. 1990.

Phytelephas aequatorialis is often found in dense natural or semi-natural stands. Although the palm often occurs in high densities, which may favor serious pests, there are no observations of any such pests in the lowlands below 650 m altitude. However, on the Andean slopes above 650 m the bruchid beetle *Caryoborus chiriquensis* Sharp. is a common and very efficient seed predator. The beetle may damage 60% of the seeds collected from palms in pastures and consequently it represents a serious constraint to "tagua" exploitation on the Andean slopes. This paper presents observations on the natural history of the beetle and suggests how to reduce the problem.

Study Areas and Methods

Field work was conducted in western Ecuador during a number of visits between 1990 and 1992 as part of a study of the management and economic uses of *Phytelephas aequatorialis.* Seed samples collected as part of this overall study turned out to contain many infested seeds. Considerations of how to avoid infested seed-samples led to the pilot study discussed in this paper.

Seeds were sampled in three plots. Two of these were established in pastures and one in a disturbed old-growth forest. One of the pasture plots and the forest plot were situated next to each other at 1,400 m altitude, near Palo Quemado in the Province of Cotopaxi (00°22′S; 78°55′W). The other pasture plot was situated at 1,325 m altitude, near the village of San Francisco de Las Pampas, 10 km away. Data from the two pasture plots are treated together.

Seed samples (20 seeds in each sample when possible) were collected in the plots throughout the study period whenever seeds were found. All seeds were collected within three meters from the stem of a palm. Samples were checked for beetle eggs in the umbo (the hard button at the base of the endocarp), and for number of larvae, pupae and imagines (adult beetles) in the endosperm. In some cases pores in the umbo were too obscured by mud to be examined properly for presence of eggs. Also, in the first three samples (totalling 57 seeds) the only data recorded were presence or absence of infestation of endosperm, since the samples originally were taken as part of the study on "tagua" productivity.

A cage-trial was made to investigate whether fresh seeds enclosed in endo- and mesocarp could become infested. Thirty-three seeds with endocarp, but with the mesocarp removed manually, and 20 seeds with both endocarp and mesocarp, were arranged in a bird-cage and placed in a *P. aequatorialis* palm in a pasture for three weeks (Fig. 1). The cage was used to keep rodents from eating the mesocarp. Another 20 seeds were brought back to Quito as control. All 73 seeds were harvested from the same infructescence. Infested seeds from the cage-trial were afterwards used to establish development time for the beetles.

A total of 889 seeds were examined in the present study. All seed samples were left at least two months after collection before being checked for infestation in order to allow eggs to hatch and larvae to start their development, facilitating their location.

Numeric data are generally presented as mean values (±standard deviation) and with indication of sample size (n). Range is given when relevant. When the data are included in Table 1 only mean value is given in the text. Mean and average values signify arithmetic mean.

Results and Discussion

Host-species and Distribution. Caryoborus chiriquensis is a bruchid beetle, app. 10 mm long, belonging to the subfamily Pachymerinae. The genus consists of three species (Nilsson pers. comm.), and is grouped by Lepesme (1947) among palm bruchid genera which depend exclusively on palms for at least one of their life-stages (larva or imago).

Five palm genera have been listed as hosts for species of the genus *Caryoborus: Astrocaryum, Dictyocaryum, Jessenia, Mauritia* and *Phytelephas* (Nilsson, pers. comm., Couturier and Kahn 1992, Lepesme 1947). The species *Caryoborus chiriquensis*, however, has only been recorded from *P. macrocarpa* (Lepesme 1947) and *P. aequatorialis* (pers. obs.), but since it has been collected from a species of *Phytelephas* in western Panama (Johnson, pers. comm.), *P. seemannii* may be included in the host-list, because it is the only species of *Phytelephas* known from Panama (Barfod 1991b). The total distribution of the beetle appears to include Venezuela, Panama, Colombia, and Ecuador (Lepesme 1947, Johnson and Nilsson, pers. comm.).

In Ecuador I have found seeds infected by *C. chiriquensis* in the provinces of Pichincha, Cotopaxi, Cañar, and Loja, and, according to Nilsson, the bruchid has been collected in the province of Carchi, i.e., it is distributed throughout the western Andean slope from north to south in Ecuador. The altitudinal range was registered along a 40 km transect in the Provinces of Pichincha and Cotopaxi (on the road from Santo Domingo de Los Colorados to Las Pampas de San Francisco). It showed the bruchid to be present from 650 m to 1440 m altitude (observed at 650, 850, 1,025, 1,210, 1,290, 1,310, 1,330, and 1,440 m. altitude). This distribution matches the distribution

1. *Phytelephas aequatorialis* palm with a bird cage. *Phytelephas aequatorialis* seeds with and without mesocarp, all with endocarp, were placed in the cage and later examined for infestation by the bruchid beetle *Caryoborus chiriquensis.*

of *P. aequatorialis* (see Barfod 1991b) above 650 m.

Phytelephas aequatorialis is common throughout the western lowlands up to an altitude of 1,500 m. Because of its many uses the palm often escapes the axe when forest is converted to pasture or agricultural land, and in this way it becomes part of various land use systems (Fig. 2a).

The seeds on which the larvae feed are almost entirely made up of the extremely hard endosperm. Seeds are 5–7 cm long, average weight (dry weight) in the study area is 36.3 ± 12.3 g (n = 610), and average density is 1.35 g/cm^3 ± 0.08 (n = 36). One infructescence contains 25.1 ± 5.3 (n = 39) fruits, each with an average of 4.9 ± 1.5 seeds (n = 447) (Fig. 2b). Each of the seeds is surrounded by its own, one millimeter thick, endocarp. In the endocarp an oval button-like structure, about 1–1.5 cm long, can be seen

Table 1. Infestation of Phytelephas aequatorialis *seeds by the bruchid beetle* Caryoborus chiriquensis.

	Infested endosperm	Individuals per seed[1]	Cocoons per seed[2]
Seeds cleaned by rodents			
Pasture	61% (n = 262)	22.1 ± 15.6 (1–71, n = 85)	25.6 ± 16.6 (1–71, n = 56)
Forest	12% (n = 197)	16.6 ± 18.4 (1–78, n = 21)	19.7 ± 13.6 (10–54, n = 9)
All	40% (n = 459)	21.0 ± 16.2 (1–78, n = 106)	24.8 ± 16.2 (1–71, n = 65)
Seeds cleaned manually			
Pasture	0% (n = 227)	—	—
Forest	1% (n = 130)	—	—
All	0% (n = 357)	—	—
Cage trail			
Seeds without mesocarp:	100% (n = 33)	29.4 ± 14.9 (1–55, n = 33)	29.6 ± 14.2 (2–55, n = 27)
Seeds with mesocarp:	0% (n = 20)	—	—
Control:	0% (n = 20)	—	—

[1] Average number ± standard deviation of individuals (larvae, pupae, imagines) per seed. Range and sampling size is given in parenthesis.

[2] Average number ± standard deviation of cocoons per seed. The data include both cocoons with pupae and with fully metamorphosed imagines. Range and sampling size is given in parenthesis.

(Fig. 3a). The umbo, as the structure is called, is formed by the funicle and the adjacent endocarp and mesocarp tissue (Barfod, pers. comm.), i.e., the umbo penetrates the endocarp. The umbo itself is penetrated by numerous pores.

Oviposition: As long as the seeds remain in the dense globular infructescence, they are well protected against the bruchid beetle. However, once the mature infructescence disintegrates and the fruits fall to the ground (Fig. 2b), the protective yellow fruit-mesocarp is quickly consumed by rodents such as squirrel (*Sciurus aestuans*) and guatusa (*Dasyprocta* sp.,—a rodent the size of a large rabbit, often hunted for its tasty meat), leaving the seeds protected only by the endocarp. The hard endocarp may offer protection against many potential predators, but *Caryoborus chiriquensis* lay its eggs in the pores of the umbo, and once the eggs hatch, the larvae penetrate to the endosperm through the pores.

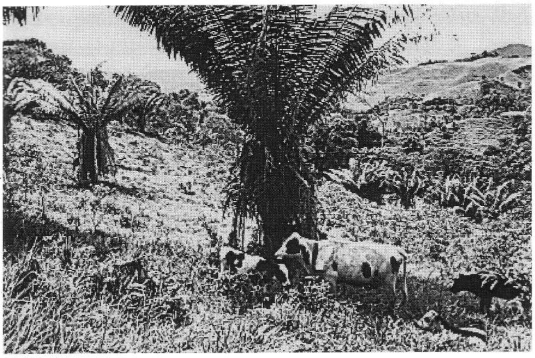
Eggs, or parts of eggs, in the umbo are a useful indication of the endosperm being infested: 74% of the seeds examined with eggs in the umbo (n = 129) were found to have an infested endosperm. Among those collected without mesocarp and with no detectable eggs in the umbo, only 19% turned out to have infested endosperm (n = 118). In the cage-trial it was found that all 28 seeds with eggs in the umbo had infested endosperm, while 5 seeds with infested endosperm had no recognizable parts of eggs left in the umbo. Generally the eggs are easily observed (Fig. 3a), and their presence may be used by farmers or dealers to predict infestation. Later, as the endosperm is consumed and turned to powder by the larvae, the seeds lose weight. In dry seeds the change is significant and may be also used to detect infestation.

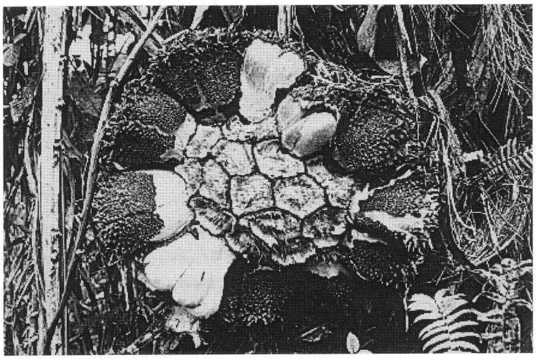
Infestation: Examination of 357 seeds from fresh fruits, from which the mesocarp was removed manually, revealed only one seed with infested endosperm, while 40% of the seeds collected on the ground without mesocarp had infested endosperm. The cage-trial showed 100% of seeds placed without mesocarp to be infested, while 0% of the seeds with mesocarp were infested (Table 1). These data suggest that intact mesocarp is an efficient protection against the beetle.

Infestation rates from forest and pastures are given in Table 1. In the forest only 12% of the seeds collected without mesocarp were infested, while the corresponding percentage for pasture was 61%.

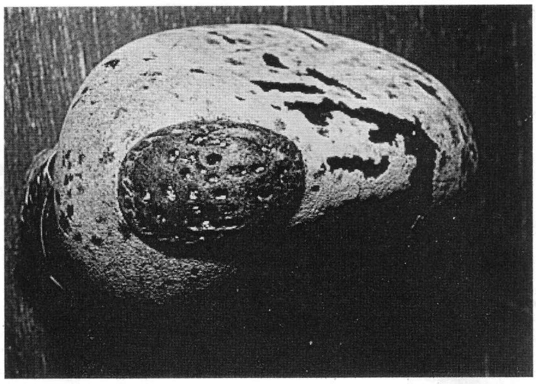
Though sample sizes are rather small, this suggests that the forest offers some kind of protection of the seeds, e.g., it may be more difficult for the beetle to localize individual palms and/or seeds in the forest, or the beetle may have more predators in the forest than in the pasture.

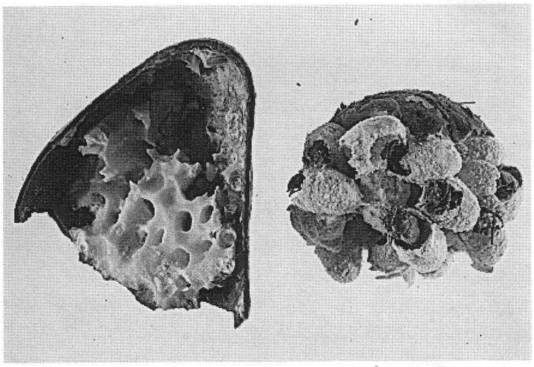
Each infested seed may contain from 1 to 78 individuals (larvae, pupae, imagines), averaging 21.0. The corresponding data from the cage-trial showed a range from 1 to 55 and an average of 29.4 individuals. Number of cocoons (excluding data from seeds with one or more larvae) are 24.8 for seeds collected on the ground and 29.6 for seeds from the cage-trial (see Table 1 for details).





2. A. (Upper photo) *Phytelephas aequatorialis* is often spared when forest is converted to pastures. B. (Lower photo) Mature disintegrating infructescence of *P. aequatorialis*. The infructescences contain about 25 fruits, each with an average of 5 seeds. The yellow (white on the photo) mesocarp is a favored food for both wild and domestic animals.





3. A. (Upper photo) A seed of *Phytelephas aequatorialis* still enclosed in the endocarp. *Caryoborus chiriquensis* lays its white eggs in the pores of the umbo. B. (Lower photo) Left, the remaining endosperm of an infested seed is seen attached to part of the endocarp. To the right a number of cocoons with imagines are seen.

Since the numbers of cocoons are as high as or higher than the overall average of individuals (which includes larvae), they suggest a high survival rate for larvae. The maximum number of living imagines found in one seed is 44, but it is likely that seeds with higher numbers of larvae would have resulted in up to 78 imagines, had the endocarp not been broken in order to examine the seeds. The average number of individuals per seed in the pasture is higher than the average number in the forest (21.8 as compared to 16.6), but the difference is not statistically significant (Students t-test: $t = 1.3$, $p = 0.2$).

In most cases (154 out of 182) the larvae consumed only part of the endosperm (Fig. 3b), suggesting that food rarely is a limiting factor. Not surprisingly seeds which have their endosperm consumed completely generally contain a high number of individuals (47.4 ± 11.2, range 26–78, $n = 28$).

Seed mortality due to infestation has not been studied, but it is most likely very close to 100%, even when just a single or a few larvae are present. The embryo is embedded in the endosperm near the umbo, and since this is where the larvae enters, that area is the first to be consumed.

Development Time. Development time for the beetles under natural conditions is unknown. Table 2 shows data from beetles reared in the laboratory (room temperature) from 33 infested cage-trial seeds.

Cocoon formation had started after 100 days, after 130 days most of the pupae in their cocoons could move and a few imagines were observed. At 145 days only imagines, still in their cocoons, were found. Checks at 160 and 175 days showed most cocoons to contain live imagines, while checks at 190 and 225 days showed mainly dead imagines. Mortality during the pupal stage (from when cocoons had been formed until metamorphosis had

Table 2. Development time for Caryoborus chiriquensis *at room temperature.*[1]

Days[2]	Development stage	Number of seeds examined
80	Larvae	5
100	Cocoons being made, larvae in cocoons still mobile	5
115	Cocoons, mainly with immobile pupae	5
130	Cocoons mainly with mobile and almost completely metamorphosed pupae	5
145	Cocoons with imagines, 96% alive (49 out of 52)	4
160	Cocoons with imagines, 96% alive (74 out of 77)	2
175	Cocoons with imagines, 100% alive (30 out of 30)	1
190	Cocoons with imagines, 25% alive (24 out of 96)	3
225	Cocoons with imagines, 4% alive (5 out of 116)	3

[1] Seeds used when determining development time had their mesocarp removed manually and were placed for three weeks in the field for infestation.

[2] Days are counted from the middle of the three week infestation period, i.e., days are ± 10 days.

been terminated) was 4.5% (n = 3720. All imagines remained in their cocoons during the whole study period, and no exit holes were encountered at any time. Among all infested seeds examined (182 collected and 33 from the cage-trial) only six have been found with exit holes in the endocarp. It is not known whether the imagines await some environmental trigger such as rain before they make the exit holes (see e.g., Wilson and Janzen 1972), or whether they are unable to make holes in the dry endocarp (caused by the dry conditions under which they have been stored).

It is also possible that, under natural conditions, they wait for a partial breakdown of the endocarp, or for the umbo to fall off. The latter seems to happen more quickly, since many endocarps without umbo have been found in the field. Another possibility is that the beetles depend in part on rodents or other animals to break the endocarp in search for larvae. Janzen (1971) suggests the foraging for larvae of *Caryobruchus buscki* as a possible explanation why rodents chew holes in the endocarp of *Scheelea rostrata* seeds. In the present study most live imagines quickly became very active, trying to escape, when the endocarp and cocoons were broken during checks.

Conclusion

Phytelephas palms are the only known host for *Caryoborus chiriquensis* and the beetle certainly appears to be a well adapted and highly specialized predator on the seeds of this genus: it lays its eggs in the pores of the umbo and, in this way, it gains access through the hard endocarp. Furthermore it is able to consume the extremely hard endosperm of the seeds.

The present work, though only a pilot-study, gives some suggestions on how to reduce the problem which the beetle causes to "tagua" exploitation on the Andean slopes. Since seeds become infested only after the mesocarp has been removed, farmers may collect the fruits as they fall, remove the mesocarp manually and transport the seeds with endocarp out of the area as quickly as possible. This method is somewhat laborious, but it provides an additional benefit since the mesocarp can be used as fodder for pigs and chickens (Koziol and Borgtoft Pedersen 1993). Alternatively seeds with endocarp and mesocarp may be dried on location. Once dry, the mesocarp and endocarp is easily removed with a single blow from a hammer or stone, leaving only the seed (which command a higher price). Drying however may be difficult, especially during the rainy season, and the fruits must be protected against rodents that remove the mesocarp. Therefore, a better suggestion may be to ship seeds with endocarp and mesocarp to the Province of Manabí and dry them near the "tagua" processing industries in Manta, where dry almost desert-like areas exist.

This study also suggests that infestation rates are much lower in the forest than in open pastures. Thus if "tagua" is collected without mesocarp it is best collected in the forest. Because of this, increased exploitation may give farmers economic reasons to maintain more land as forest or at least with diverse agroforestry systems rather than turning the land into pastures.

Further studies may provide other and more attractive ways of solving the problem than those suggested here, since a number of questions remain unanswered. Does the imago depend on other host plants (possibly not since infestation rates are so high in pastures with a long distance to other species of plants apart from the grasses)? Are there any seasonal variations in infection rates? Is the beetle only found close to *Phytelephas* palms (how close to the extraction areas can the seeds be stored safely)? Which natural predators do the beetles have (how can their number be increased)?

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CHAPTER NEWS AND EVENTS

News from the Texas Chapter

The Texas Chapter of the IPS participated in the Houston Home and Garden Show at George R. Brown Convention Center on February 15. Members handed out chapter newsletters and solicited memberships for both the local chapter and for the IPS.

The group met on April 8 for a tour of Moody Gardens in Galveston. The tour started with the Rainforest Pyramid and also took in the many excellent palms planted outside at Moody Gardens. In addition to the Moody tour, members and guests visited the garden of member Henry Homrighaus and the home of Alfred Loeblich and Wendy Ann Aldwyn in Galveston.

Cycad Society Sponsors Trip to Mexico

The Cycad Society sponsored a tour to Mexico for March 6-13, 1995 to visit Mexican cycads in their native habitat. This first of a kind tour was led by Bart Schutzman, of the University of Florida. Bart is one of the leading authorities on the cycads of the New World. This was a special opportunity to see *Dioon edule* in its mountain forest habitat, *Ceratozamia mexicana* in cloud forest, and *Zamia loddigesii* and *Dioon spinulosum* in lowland forest. Of course, participants were able to view many other kinds of plants and animals in the Vera Cruz area, including palms.