

## SHORT COMMUNICATION

# Bruchid beetle infestation and the value of *Attalea butyracea* endocarps for neotropical rodents

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Frugivorous and granivorous vertebrates often discriminate against seeds and fruits infested by insects (Sallabanks & Courtney 1992). Insects may actively render seed or fruit unpalatable or unusable to vertebrates as a strategy to maximize the amount of food available to themselves (Janzen 1977). Nevertheless, vertebrates sometimes do not differentiate between sound and infested seeds or fruits (Dixon *et al.* 1997, Weckerly *et al.* 1989), or even prefer insect-infested seeds and fruits to sound ones (Sallabanks & Courtney 1992, Semel & Andersen 1988, Steele *et al.* 1996, Valburg 1992). Possible reasons for vertebrates to prefer infested seeds include: (1) seeds with larvae having a higher nutritional value than sound ones, because larvae synthesize fat and/or proteins (Sallabanks & Courtney 1992, Valburg 1992) or other nutrients such as vitamins (Havera & Smith 1979, Semel & Andersen 1988, Steele *et al.* 1996); (2) seeds with larvae tasting better than sound seeds (Borowicz 1988); and (3) seeds with larvae may be more easily opened and consumed than sound seeds (Borowicz 1988).

Infestation-based discrimination among seeds is of great potential relevance for the population dynamics of the plants and the insects, as well as the vertebrates, involved. For example, a preference for infested seeds may result in top-down control of insect population levels by vertebrates, which could in turn enhance plant reproductive success (Herrera 1989), whereas vertebrates rejecting infested seeds may result in insect population outbreaks (Herrera 1989). Insect outbreaks could in turn negatively affect vertebrate population levels, and ultimately influence plant reproductive success

by altered rates of seed predation and dispersal by vertebrates. A preference for sound seeds may induce vertebrate behaviours preventing insect access to seeds, such as the rapid sequestering and burial of seeds by scatter-hoarding rodents (Vander Wall 1990).

Here, we study how bruchid infestation affects the attractiveness of large stony palm endocarps (*Arecaceae*) to rodents. Palm fruits and seeds are among the most important food sources for a wide diversity of vertebrates and invertebrates in tropical and subtropical forests around the world (Zona & Henderson 1989), and represent a keystone food resource for rodents during the periods of fruit shortage in the forest (Forget *et al.* 1994, Wright 1990). Palm seeds may be heavily depredated by bruchid beetles (Coleoptera: Bruchidae) and rodents, which are among the few animal species capable of penetrating the endocarp (Bradford & Smith 1977, Janzen 1971). At the same time, many large-seeded palm species rely on scatter-hoarding of endocarps by rodents for seed dispersal (Forget & Milleron 1991, Forget *et al.* 1994, Smythe 1989, Zona & Henderson 1989).

How bruchid beetle infestation of endocarps affects handling and consumption by rodents is of obvious importance for the population dynamics of palms, rodents and bruchids, but is still poorly understood. Sallabanks & Courtney (1992) suggest that bruchids compete with rodents. For example, Forget *et al.* (1994) argues that the agouti *Dasyprocta punctata* and the squirrel *Sciurus granatensis* prefer *A. butyracea* endocarps that are less likely to contain a developed bruchid larva. Silvius (2002), in contrast, reports that *D. leporina* and *S. igniventris* prefer infested *A. maripa* palm endocarps to uninfested ones. She hypothesized that larvae are attractive food to mammals because of their high nutritional value and because larvae can be extracted with much less effort than seeds.

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We compared the nutritional value of bruchid-infested and sound endocarps of the palm *Attalea butyracea* in Central Panama. We determined the energetic value and accessibility of bruchid larvae and seeds, and evaluated whether rodents discriminated between larvae and seeds, and between infested and sound endocarps.

*Attalea butyracea* (Mutis ex L.f.) Wess. Boer (synonym: *Scheelea zonensis* L.H. Bailey) is an arborescent palm that ranges from southern Mexico to Colombia (Henderson 2002). *Attalea butyracea* (henceforth *Attalea*) is abundant in Central Panama, especially in secondary forest. Mature trees bear 1–3 infructescences per year, with 100–1400 fruits each (Henderson 2002, Janzen 1971, Wright 1990). The fruits are drupes containing a hard, indehiscent endocarp surrounding one seed, occasionally but seldom 2–4 seeds (Bradford & Smith 1977, Henderson 2002, Janzen 1971). Fruiting occurs during the rainy season, from May to December, with a peak in June–August (Forget *et al.* 1994, Wright 1990).

The most important vertebrate seed predators and dispersers of *Attalea* in Central Panama are squirrels (notably *S. granatensis* Humboldt 1811) and the Central American agouti (*D. punctata*) (Glanz *et al.* 1982, Janzen 1971). The rodents scatter-hoard and bury numerous endocarps as food reserves for later consumption outside the fruiting season. They function as dispersers because many cached seeds are never recovered and thus allowed to germinate and establish into seedlings (Glanz *et al.* 1982, Smythe 1989).

Seeds are also predated by the bruchid beetles *Speciomerus giganteus* (Chevrolat) Nilsson & Johnson and, to a lesser degree, *Pachymerus cardo* Fåhræus (Silvius 2005, Wright 1990). *Speciomerus giganteus* lays its eggs on fallen endocarps after the tough exocarp and juicy mesocarp have been removed by frugivorous animals or decay. The first instar larva drills its way through the endocarp and then feeds on the endosperm and embryo (Silvius 2005, Wright 1983, 1990). The thick endocarp provides excellent protection against predation of the bruchids, which stay inside the endocarp as larvae, pupae and adults for 3–9 mo (Silvius 2002). Where and how *P. cardo* infests seeds is not known. Typically, a single larva consumes one entire seed plus the inner layer of the endocarp wall.

Endocarps for chemical analyses and preference experiments were collected in Soberania National Park, near Gamboa, at the start of Pipeline Road. To obtain sound endocarps, we collected fresh, intact fruits in July–August 2004, removed exocarp and mesocarp as described in Wright (1983), and then stored the seeds in the forest in a wire enclosure (35 × 35 × 35 cm) covered with fine mesh to protect them against infestation by bruchids, until the endocarps were used. Infested endocarps were collected from unmanipulated fruit piles below adult palms that were exposed to beetles during the same period. Infested endocarps based on the entrance

holes that the *Speciomerus* first instar leaves when boring towards the seed (Janzen 1971, Wright 1983, 1990) were selected. Because survivorship of larvae is low (Wright 1983), we chose endocarps that had two or more entrance holes, ensuring that each actually contained a larva. Our selection of sound and infested endocarps was corroborated at the end of the preference experiment (see below) by opening endocarps and verifying their status.

To determine how the energy content differs between bruchid-infested and sound endocarps, we used endocarps containing either an intact *Attalea* seed or a full-grown *Speciomerus* larva without any seed remains. We used a Parr bomb calorimeter (Bradford & Smith 1977, Semel & Andersen 1988) to compare the energy density between ten larvae and nine 1-g seed fragments.

To determine whether the effort required to access the endocarp content differs between infested and sound endocarps, we measured the size of holes gnawed to extract the endocarp content. We used callipers ( $\pm 0.01$  mm), and calculated opening size as length × width. Measurements were made on endocarps that rodents opened and left at the tent pegs in the field experiment (see below).

To determine whether rodents eat larvae and bruchids, and whether they discriminate between larvae and seeds, we let captive rodents in the Summit Botanical Garden (10 km from Gamboa) choose between living full-grown *Speciomerus* larvae and fresh *Attalea* seeds, offered to them without surrounding endocarp so that the rodents had direct, unblocked access to the endocarp contents. We gave each of three individually housed variegated squirrels (*S. variegatoides*) a Petri dish with ten larvae and ten seeds, and recorded the order in which the squirrels consumed these items. The three animals were normally fed fruits and seeds, and had previously been given seeds and larvae to make them familiar with both items. We also gave larvae and seeds to captive agoutis, but not in an experimental setup, because these animals were not individually housed. Agoutis and squirrels were also given adult bruchids to see whether they would eat them.

To determine whether rodents discriminate between bruchid-infested and sound endocarps, we carried out a field experiment in and around Gamboa, Central Panama (9°6'N, 79°40'W), a forested village in which variegated squirrel *S. variegatoides* Ogilby 1839 and the Central American agouti *D. punctata* Gray 1842 are common. The forest is classified as tropical humid forest. Annual rainfall ranges between 1900–3000 mm. We placed 60 pairs of one sound and one infested endocarp throughout Gamboa at intervals of at least 50 m to ensure independence. The experiment started on 14 January 2005, during the season of low fruit abundance in which rodents are known to use *Attalea* endocarps. We monitored the timing and order of endocarp handling and removal over 116 d, at 1, 3, 5, 7 and 10 d after placement, and 13 more times with

intervals of 5–15 d. Handling was recorded as gnawed, pulled, eaten or removed.

To be able to determine the order of handling even if both endocarps were handled within a single time interval, we used a new method for presenting the endocarps. First, we thread-marked all endocarps by drilling a 1-mm hole through the distal end, and tying ~20 cm of cotton thread to it. Rodents can easily cut this thread when removing a seed. Then, for each pair of endocarps, we hammered a yellow plastic tent peg into the ground, passed 1 m of cotton thread (0.3 mm diameter) through a hole in the peg, and tied the thread ends together to form a loop. The thread marks of infested and sound endocarps were tied to opposite sides of this loop, and the endocarps were placed on the ground, at equal distance from the peg. The thread on the infested endocarp's side was marked with permanent ink. A rodent now handling an endocarp would pull that endocarp away from the peg, and pull the other endocarp closer to the peg. Thus, if both endocarps within a pair were handled in the same time interval, the relative position of the threads would tell the order of handling; the thread furthest from the tent peg belonged to the endocarp handled last. Observations on thread positions where the endocarps were handled in different time intervals showed that this method was reliable.

Forget (1993) found that thread-marking does not affect handling and removal of endocarps by rodents. To verify that piercing of *Attalea* endocarps also did not affect seed quality and larval development, we placed 40 thread-marked endocarps, 20 infested and 20 sound, inside a rodent enclosure in the forest. After 100 d, we opened them with a hammer and determined seed and larvae condition. All 20 sound endocarps were intact, and all 20 infested endocarps had a bruchid larva in them, hence there was no evidence for any effect of piercing. This test also confirmed our ability to discriminate reliably between sound and infested endocarps based on larval entry holes.

Sound endocarps contained more biomass than infested endocarps. The fresh mass of seeds ( $1.48 \pm 0.28$  g;  $n = 76$ ) was more than twice the fresh mass of full-grown larvae ( $0.60 \pm 0.22$  g;  $n = 106$ ); the dry mass of seeds ( $1.13 \pm 0.21$  g;  $n = 76$ ) was more than three times the dry mass of larvae ( $0.34 \pm 0.14$  g;  $n = 106$ ). The energy density of dry mass did not differ significantly between seeds and larvae (mean  $\pm$  SD:  $27.3 \pm 2.0$  kJ g<sup>-1</sup> versus  $24.8 \pm 4.4$  kJ g<sup>-1</sup>,  $n = 10$ ;  $t$ -test:  $t_{17} = 1.55$ ,  $P > 0.05$ ). Thus, because seeds have more dry mass, sound endocarps contained 3.7 times more energy (30.8 kJ) than endocarps with a fully grown larva (8.4 kJ). Under similar digestibility and accessibility, rodents would obtain more energy from a seed than from a larva. Among 22 endocarps opened by agouties, obtained from the field experiment (see below), sound endocarps had significantly larger openings than infested ones ( $t_{20} = 7.32$ ,  $P < 0.0005$ ). Openings made for extracting a seed

( $116 \pm 31.8$  mm<sup>2</sup>;  $n = 10$ ) were three times as large as openings made for extracting a larva ( $38.1 \pm 17.5$  mm<sup>2</sup>;  $n = 12$ ). We obtained insufficient squirrel-handled endocarps to make the same comparison for squirrels.

Captive squirrels and agoutis readily ate *Speciomerus* larvae and adults offered to them without surrounding endocarp. Squirrels strongly discriminated between *Speciomerus* larvae and *Attalea* seeds offered without surrounding endocarp. Each of the three captive squirrels first consumed nine or ten larvae before eating any seeds. Thus, rodents eat bruchid larvae, and even prefer the larvae to seeds if not enclosed in a stony endocarp.

Endocarps in the field experiment were handled by rodents in 43 of the 60 pairs. Dental marks on 26 endocarps left at the tent pegs showed that this handling was by agoutis and squirrels. Most endocarps (85%) had agouti marks, but this does not imply that agoutis handled most endocarps: squirrels tend to take endocarps into trees before opening them, while agoutis often open endocarps where they find them. Infested endocarps were the first to be handled in 17 pairs and sound endocarps were the first in 26 pairs, hence there was no significant difference in the order of handling (Binomial test:  $P = 0.395$ ). The time until handling did not differ between sound and infested seeds either (Log-rank test on Kaplan–Meier survival estimates:  $\chi^2_1 = 0.3$ ,  $P = 0.578$ ). Thus, there was no evidence for rodents discriminating between bruchid-infested and sound *Attalea* endocarps.

Our results indicate that bruchid larvae in *Attalea* endocarps are attractive food to rodents, as suggested by Silvius (2002). Captive agoutis and squirrels readily ate larvae when presented without the surrounding endocarp, and preferred larvae to seeds. This observation is in line with earlier reports of rodent feeding on animal matter (Silvius 2002 and references therein). A sound endocarp contained almost four times as much energy as did a bruchid-infested endocarp. However, not all of the energy in seeds will be extractable (digestible) to mammals (Norconk *et al.* 1998). Moreover, the lower energy content of infested endocarps compared with sound endocarps was offset by the relatively low energy investment required to extract the contents of infested endocarps. Our accessibility measurements corroborate earlier qualitative observations by Silvius (2002) and Janzen (1971), who suggest that seeds are more difficult to extract than larvae because of their shape and texture, and because seeds stick to the endocarp wall. Silvius (2002) furthermore suggested infested endocarps are more easily opened because larval feeding causes the endocarp wall to become thinner.

Nevertheless, agoutis and squirrels in our field experiment did not discriminate between endocarps with larvae and endocarps with intact seeds, in disagreement with our prediction. Possibly, rodents are unable to determine whether endocarps are infested or not through the thick stony endocarp wall. Alternatively, rodents may

not discriminate between infested and sound endocarps because the difference in net nutritional value does not merit strong selectivity.

We conclude that beetle larvae do not render endocarps unattractive to rodents. Bruchid-infested endocarps represent suitable food to rodents, provided that the rodents use the endocarps before the beetles hatch. This condition is likely met, because most beetles emerge at the onset of the next rainy season (Wright 1990), which is after the period of low fruit abundance during which rodents rely heavily on cached seeds. This implies that rodents may in fact not experience any competition with the beetles, in disagreement with Sallabanks & Courtney (1992). Rather, the *A. butyracea* system may resemble the *A. maripa* system in which mammals purposely feed on larvae (Silvius 2002). Thus, prevention of seed infestation should not be an incentive for rapid sequestering and burial of *Attalea* seeds by rodents, unlike in other large-seeded tree species (Jansen *et al.* 2004, Vander Wall 1990).

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