Traits for predator selection on *Pentaclethra* macroloba seeds

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ABSTRACT

Pentaclethra macroloba (Fabaceae: Mimosoidea) is a dominant species of canopy tree in Costa Rica's Caribbean lowlands, constituting up to 40% of the local tree population in some areas. It has been suggested that P. macroloba's dominance is due in part to low post-dispersal seed depredation, as few terrestrial seed predators can tolerate the high concentration of toxic alkaloids and free amino acids. Seeds are not immune from depredation, however. Several species of parrots and squirrels have been observed depredating pre-dehiscent legumes and may present selective pressure on P. macroloba recruitment. In this study, we assessed depredation patterns in P. macroloba to (1) determine if predators use legume and seed traits to select food items, (2) determine if such patterns represent an optimal foraging strategy for vertebrate predators, and (3) explore potential consequences of depredation on P. macroloba. Seed depredation was not correlated with legume valve side, legume size, seed number, or seed compartment size, though seeds at the distal end of legumes were more often extracted. Depredation patterns do not indicate that seed predators are foraging optimally and may be quickly satiated due to their low toxicity tolerance the abundance of seeds. Despite a lack of predator selection of various legume and seed characteristics, legume damage caused by depredation may interfere with the explosive dehiscence of P. macroloba and constitute a significant recruitment barrier.

I. INTRODUCTION

The leguminous tree *Pentaclethra macroloba* is a dominant species on the Caribbean lowlands of La Selva [1]. Field observations report that the dominance and success of this species is related to low seed mortality rates, due to seed toxicity [2]. Seeds contain alkaloids and amino acids that are toxic to common terrestrial seed predators, such as the Spiny Pocket Mouse (*Heteromys desmarestianus*), which is common in La Selva [1,2]. Thus, this species is abundant and its seeds and seedlings are conspicuously abundant on the forest floor [1].

However, even though the seeds are toxic, Hartshorn [2] details that there is consistent evidence of pre-dispersal seed

depredation for this species. His work reports observations of White-crowned Parrot (Pionus senilis) and gray squirrels (Sciurus variegatoides.) feeding on P. macroloba seeds from the unopened legumes [1]. As a result, at least 5% of predehiscent seed loss is due to these groups [2]. In this sense, Janzen [3] argues that seed predation has an important impact on overall seed mortality and constitutes a pressure that regulates adult plant density. Seed predator preference could influence how P. macroloba allocates resources to seed production. Seed predators have the potential to exert directional selection pressures on seed phenotype [4]. While larger seed sizes are targeted by seed predators at a much higher rate than smaller seeds [4], They also have higher rates of

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germination and seedling survival [5], and seedlings from large seeds are much more likely to recover from herbivory and other stresses [6]. We might expect that there is an optimal seed size that minimizes the negative aspects of these opposing selectional forces in *P. macroloba* that is strongly influenced by the intensity of seed depredation.

We observed vertebrate depredation upon P. macroloba seeds as evidenced by holes in legume valves. Not all legumes were depredated, nor were all seeds extracted from depredated legumes. Therefore, we suggest that there might be legume and seed traits that are being selected by predators. To examine this hypothesis we assess the following questions: (1) Is there a bias towards predating upon the left or the right valve of the seed legume? (2) What is the intensity of depredation based on legume size? (3) Is there a correlation between legume size and number or size of seeds? (4) Are predators choosing legumes with more seeds? (5) Are predators selecting legumes with larger seeds? (6) Is there a preference for seed size within the same legume? (7) Is there a preference for depredating seeds in a certain part of the legume?

We expect that: (1) there will be a bias towards depredating the right or left valve, based on the tendency of lefthandedness on parrots when grasping food [7]; (2) there will be higher depredation intensity on larger legumes, since it is possible that these contain more available seeds for predation; (3) there will be a positive correlation between legume size and number and size of seeds; (4) predators will select legumes that contain more seeds, which contain higher energetic rewards than legumes with fewer seeds; (5) predators will select legumes with larger seeds; (6) the largest seeds within each legume because larger seeds offer higher energetic rewards per unit of foraging effort;, and (7) there will be preference for depredating seeds in the legume section that tends to contain the larger seeds.

II. METHODS

Our study was conducted between April 24-25 in the Organization for Tropical Studies' Estación Biológica La Selva (83°59'W, 10°26'N), a 1615 ha reserve of Lowland Tropical Wet Forest in Costa Rica's Caribbean lowlands.

We collected 100 fallen Pentaclethra valves from sites of high legume density and assorted them into categories for data recording. We sorted the legumes by left and right valves, counted the number of undepredated and depredated valves, and logged the number of depredation sites in each valve. We randomly selected ten right-sided legumes and recorded the length, number of depredated valves, and the position of each depredated seed.

Statistical analyses were conducted in JMP (v. 5.1.2, SAS Institute, Inc. 2004). We tested for a bias for depredation on the right versus left sides of the legumes with a paired t-test. We then analyzed through a regression the intensity of predation based on legume size. We tested for the relationship between legume size and both number of seeds and the size of the largest seed contained in the legume with two regression analyses. We then compared the number of seeds and size of the largest seed in depredated legumes versus the number and size in predated legumes with a Wilcoxon two-sample test. We tested to see if the predators were choosing the larger seeds within a legume by comparing the size of a depredated seed to the size of an undepredated seed both from the same legume by running a matched-pairs t-test. Positional skew of depredation r was calculated as

$$r = \frac{p_o - p_e}{p_e}$$

where:

$$p_0 = \frac{p_1 + p_2 + p_3 \cdots p_x}{n}$$

$$p_{\rm e} = \frac{n}{2} + 1$$

 p_1 - p_x = the position of x depredated seed compartments; and

n =total number of seed compartments in the legume

Depredation was random when r = 0, a positive r value indicated depredation was concentrated on the distal end, while a

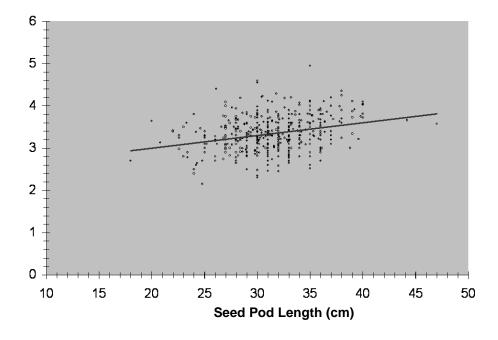


Figure 1. Correlation of largest seed size (along vertical axis) and seed legume length (y = 2.4111 + 0.0303x, $r^2 = 0.084$, P < 0.0001).

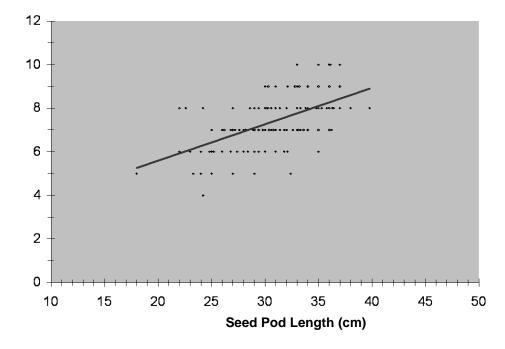


Figure 2. Correlation of seed number (along vertical axis) and seed legume length (y = 3.5286 + 0.1228x, $r^3 = 0.192$, P < 0.0001).

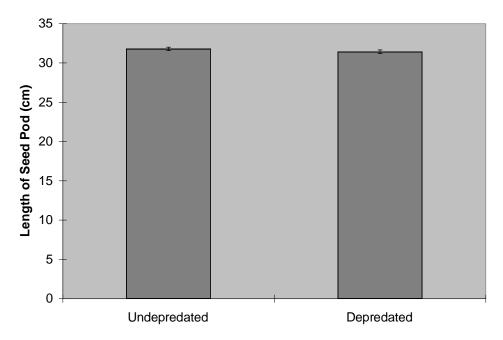


Figure 3. Comparison of mean legume length in undepredated and depredated seed legumes (\pm SE, Wilcoxon 1-way sign ranks test, df = 1, x^2 = 0.550, P = 0.458).

negative r indicated proximal depredation. Deviation of r from 0 was assessed with a Wilcoxon 1-sample signed-rank test

III. RESULTS

Twenty-two percent of all seed valves (N = 3972) showed evidence of depredation, from which approximately 5% of all seeds were extracted. Depredation was similar between left and right valves (paired t-test, P = 0.915), and thus only right legume valves were used for remaining analyses.

Valve length was a predictor of both seed number (Fig 1; $r^2 = 0.084$) and size (Fig 2; $r^2 = 0.192$). Depredated and undepredated valves did not differ in valve size (Fig 3, P > 0.05) or seed size (Fig 4, P > 0.05), though seed number was significantly different between depredated and undepredated valves (Fig 5, P > 0.0161).

Among depredated valves, neither seed length (Fig 6) nor the size of the largest seed (Fig 7) were correlated to depredation intensity. Within depredated valves, the sizes of the largest depredated and undepredated seeds were similar (Fig 8, P > 0.05).

Depredation location was significantly different from random expectation (Wilcoxon 1-sample signed-rank test = 14689, df = 290, P = 0.000), concentrated on the distal half of legumes (r = 0.49)

IV. DISCUSSION

Contrary to expectations, patterns of seed depredation do not indicate predator selection based upon legume side, size, seed number, or seed compartment size. This contradicts the findings of various studies, including Celis Diez et al. [8], which found that predators (birds and rodents) preferred larger seeds. The lack of legume valve preference is interesting in light of Friedman's 1939 study [7] in which he found that among seven species of Amazona parrots the individuals were 66.97 per cent left-handed. As we did not distinguish between depredation by parrots and squirrels, potential evidence of handedness is obscured by our methodology.

Our sampling methodology did not allow us to examine the issue of seed size preference in fine resolution, but because of their clear positional preference for seeds in the distal end of the legume, we suspect that

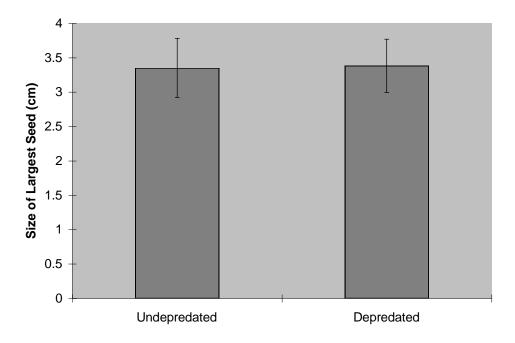


Figure 4. Comparison of largest seed size in undepredated and depredated legumes (\pm SE, t-test, t = 0.909, P = 0.364).

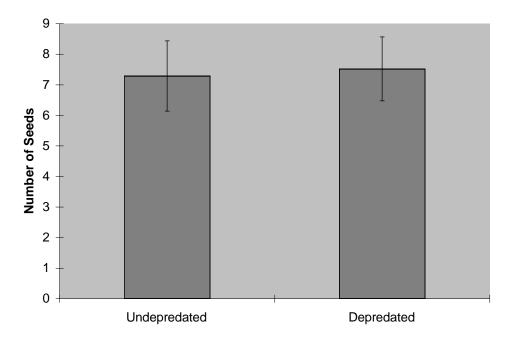


Figure 5. Comparison of number of seeds between undepredated and depredated seed legumes (\pm SE, Wilcoxon 1-way sign ranks test, df = 1, x^2 = 4.791, P > 0.0161).

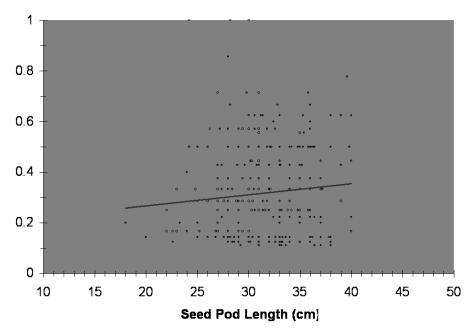


Figure 6. Correlation of legume length and depredation intensity (n.s.).

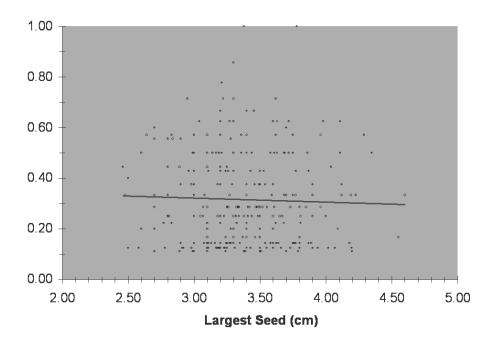


Figure 7. Correlation of largest seed size and depredation intensity (n.s.).

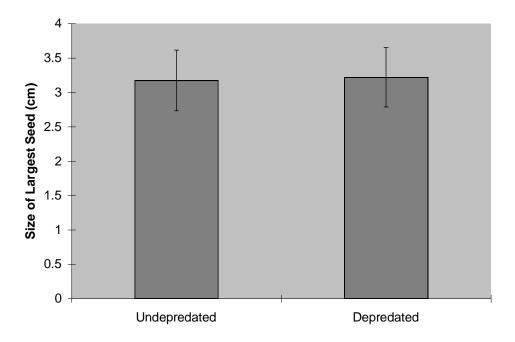


Figure 8. Mean size of largest undepredated and depredated seeds within depredated legumes (\pm SE, paired t-test, t = -1.491, P = 0.137).

seed predators were choosing from among the largest seeds in each legume. Although observation suggests larger seeds are contained in the distal end of the legume, relationship between compartment position and seed size remains unexamined. If such a relationship exists, a preference for seed location, and a generally larger seed size, could influence how P. macroloba allocates resources to seed production. Seed predators have the potential to exert directional selection pressures on seed phenotype [4]. Larger seed size increases germination rates and seedling survival, and helps seedlings recover from herbivory and other stresses [6]. However, Gómez's 2003 study [4] demonstrated that larger seeds are targeted by mammalian seed predators (rodents and boars) at a much higher rate than smaller seeds. We might expect that there is an optimal seed size that minimizes the negative aspects of these opposing selectional forces in P. macroloba. The equilibrium seed size resulting from these two selectional forces should be strongly influenced by the intensity of seed depredation.

We expected that predators would select the largest, most energy rich seeds.

This is consistent with the Optimal Foraging Theory, as greater energetic gain would outweigh the cost of handling and searching time. However, our data was not consistent with this assumption, as we failed to find that predators chose larger seeds. Schluter [9] found a similar contradiction to the Optimal Foraging Theory in his study of Galapagos ground finches. He hypothesized that when food is abundant and predators are quickly satiated, animals are not pressured to forage optimally [9].

The same may be of Pentaclehtra macroloba and its seed predators. As we only found a seed depredation rate of 5% and an overall legume depredation rate of 22%, P. macroloba seeds are relatively abundant and easy for seed predators to find. Janzen [3] described how most vertebrates are generalists with high microflora diversity in their digestive systems due to their wide diet. Therefore, they are able to handle small amounts of toxicity without being harmed. Hartshorn [2] inferred that white-crowned parrots and gray squirrels possess digestive systems capable of processing the toxic chemicals contained in P. macroloba seeds. Since the two animals are still vulnerable to high levels of

toxic compounds, they may only safely consume a minimal number. This follows Schluter's 1982 study [9], as Optimal Foraging Theory may not apply to this system.

Despite a lack of predator selection of various legume and seed characteristics, depredation of P. macroloba may be constitute a significant recruitment barrier. We observed an overall pre-disperal seed depredation of approximately 5%, which is the percentage that Hartshorn [2] reported for P. macroloba seed depredation by whitecrowned parrots (Pionus senilis) and gray squirrels (Sciurus variegatoides) at La Selva. We also found that about 22% of legumes were depredated to some extent, and we suspect that this could have negative effects on reproductive success. P. macroloba disperses its seeds via elastic dehiscence [1], and holes chewed in the predators legumes bγ seed compromise the dispersal capability of these legumes. The seeds are expelled from the legume up to ten meters from the parent tree, and once on the ground there is little secondary dispersal due to seeds' high toxicity [10]. The Janzen-Connell model predicts a decrease in seed survival with decreased distance from parent tree; therefore, decreased seed dispersal ability due to legume damage from seed predators may reduce seedling recruitment and overall parent fitness.

To further elucidate patterns of depredation in *P. macroloba*, we suggest several lines of investigation. Observation suggests that a high proportion of legumes contain aborted seeds, a fact not considered in the present study but one which bears on any seed selection strategy by vertebrate seed predators. Future studies must consider only viable seeds. Furthermore, depredation by different predators must be distinguished in order effectively assess predator preference and untangle the confounding effects of multiple selection strategies of different predators.

REFERENCES

 Hartshorn, G.S. 1983. Pentaclethra macroloba (Gavilán). In D.H. Janzen (ed.) Costa Rican Natural History.

- Chicago: The University of Chicago Press
- Hartshorn, G. 1972. Ecological Life History and Population Dynamics of Pentaclethra macroloba and Stryphnodendron excelsum. Ph.D Thesis. University of Washington. 73-76.
- 3. Janzen, D.H. 1971. Seed Predation by Animals. Annual Review of Ecology and Systematics 2: 465-492.
- Gomez. J. M. 2003. Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. Evolution: 71-80
- Parciak W 2002 Environmental variation in seed number, size and dispersal of a fleshy-fruited plant. *Ecology* 83: 780-793.
- Bonfil, C. 1998. The effects of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus* rugosa and *Q. laurina* (Fagaceae). American Journal of Botany 85(1): 79-87
- 7. Friedman, M. and M. Davis. 1939. Left-handedness in Parrots. The Auk 55(3): 478-480.
- Celis-Diez J.L., Bustamante R.O, Vasquez, R.A. 2004. Assessing frequency-dependent seed size selection: a field experiment. Biological Journal of the Linnean Society 81(2): 307-312.
- 9. Schluter, D. 1982. Seed and patch selection by Galapagos ground finches: relation to foraging efficiency and food supply. Ecology 63(4): 1106-1120.
- Angulo, M. 1993. Depredacion en semillas de *Pentaclethra macroloba*. In Organization for Tropical Studies Coursebook 93-2. Duke University, Durham, North Carolina.



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