

Palms Use a Bluffing Strategy to Avoid Seed Predation by Rats in Brazil

Constança de Sampaio e Paiva Camilo-Alves and Guilherme de Miranda Mourão¹

Laboratório de Vida Selvagem, Embrapa Pantanal, Caixa Postal 109, Corumbá, Mato Grosso do Sul 79320-900, Brazil

ABSTRACT

The goal of this study was to ascertain why the production of variable seediness is advantageous for *Attalea phalerata* palms. Our hypothesis was that variation reduces seed predation by the spiny rats *Thrichomys pachyurus* and *Clyomys laticeps*. Although there is a positive correlation between endocarp size and number of seeds, endocarps sometimes contain more or fewer seeds than expected; palms bluff about the number of seed per endocarp. Therefore, rats do not know how many seeds an endocarp contains. To model rats' predating behavior, we applied Charnov's Marginal Value Theorem. The model shows that rats attack endocarps only when the energy gain is higher than the energy available in the habitat. Hence, it is not advantageous to eat all the seeds inside an endocarp. This explains why 45 percent of forest endocarps and 35 percent of savanna endocarps were still viable after predation. We then applied the model to two simulated endocarp populations with less variability in the number of seeds per endocarp size and determined that viable diaspores after predation were reduced to 15 percent. With less variability, palms cannot bluff about the number of seeds inside endocarps and predators can predict accurately how many seeds they should try to eat. Uncertainty about the number of seeds diminished predation but gave selective advantage to multiseeded fruits. Therefore, the bluffing strategy would be evolutionarily stable only if it were counterbalanced by other forces. Otherwise, predators would win the bluffing game.

Abstract in Portuguese is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: *Attalea phalerata*; *Clyomys laticeps*; marginal value theorem; multiseeded fruits; Pantanal; predator–prey interaction; *Thrichomys pachyurus*.

IN PLANTS WITH INDEHISCENT FRUITS there are advantages in brood reduction: from the standpoint of offspring, it would reduce rivalry and concentrate maternal resources on fewer seeds. From the maternal standpoint, seed dispersal may be enhanced and the probability of successful seedling establishment may increase (Augspurger 1986; Uma Shaanker *et al.* 1988; Casper 1990; Casper *et al.* 1992; Arathi *et al.* 1996, 1999; Akhalkatsi *et al.* 1999; Sasaki & Felipe 1999). Moreover, because fruit set is resource-limited (Stephenson 1981, McDade & Davidar 1984, Bronstein 1988, Gorchov 1988, Ehrlen 1992), resources allocated to produce multiseeded diaspores would eventually lead to a reduction of the total number of fruits and a decline of maternal fitness. Fewer seeds per fruit allow for a compensatory increase in seed size or number of fruits (Adams 1967, Primack 1978, Marshall *et al.* 1985). On the other hand, a few studies indicate that plants may experience reduction in seed predation when they produce multiseeded fruits (Downhower & Racine 1976, Bradford & Smith 1977, Heithaus *et al.* 1982, Garrison & Augspurger 1983). Although the authors observed that brood reduction would enhance dispersal distance or increase the probability of seedling establishment, their results also indicate that within multiseeded fruits the probability of attack per seed is lower than in single-seeded fruits, increasing germination success. Thus, seed predation may play a role in maintaining the production of multiseeded fruits.

The fruit of *Attalea* spp. palms (species formerly classified under the genus *Scheelea* are now all synonymized under the genus *Attalea*; Henderson *et al.* 1995) is a drupe with three layers: a thick exocarp covering an oily, fibrous mesocarp, which in turn encloses a hard woody endocarp. Seeds are enclosed in the hard endocarp and

encapsulated individually. Fruits are the unit of dispersion and eventual seedlings from the same endocarp are strong rivals because they germinate near each other (1–4 cm), but only one of them may eventually become a successful adult plant. *Attalea* spp. seeds are intensely consumed by bruchids or rodents, usually involving predation of much more than 70 percent of the diaspores (Janzen 1971a, Wilson & Janzen 1972, Bradford & Smith 1977, Wright 1983, Forget *et al.* 1994, Quiroga-Castor & Roldan 2001, Silvius 2002, Silvius & Fragoso 2002, Pimentel & Tabarelli 2004).

Attalea butyracea (former *Scheelea zonensis* and *Scheelea rostrata*; Henderson *et al.* 1995) populations in Panama and in Costa Rica have fruits with one seed, but a small proportion of the fruits have two or three seeds. Bradford and Smith (1977) found that the survival rate of multiseeded fruits after pre-dispersal predation is much greater than that of one-seeded fruits. They observed that predators had to attack more than once a multiseeded nut to kill all the seeds inside. As a result, seed survivorship increases with seed number. The authors proposed that multiseeded fruits are a strategy to reduce predation by bruchids. However, we believe that the production of multiseeded fruits *per se* may not be sufficient to reduce predation in the long term. Within a palm population consistently producing two-seeded fruit, animals could learn to attack each endocarp twice or even be selected to do this, as it would increase their fitness. This would happen because it is energetically favorable to deplete each fruit before investing in searching another endocarp. In that case, palms producing two-seeded fruit would lose their advantage.

In this study, we use Charnov's Marginal Value Theorem (1976) to demonstrate that variation in the number of seeds, rather than the absolute number of seeds, is what reduces predation on *Attalea phalerata* (Mart. ex Spreng) diaspores by the spiny rats *Clyomys laticeps* and *Thrichomys pachyurus* in Brazil's Pantanal. The fruits of the studied species contain from one to five seeds and this variation is previously

Received 15 August 2008; revision accepted 29 April 2009.

¹Corresponding author; e-mail: gui@cpap.embrapa.br

revealed by the number of carpels per flower (C. Camilo-Alves and G. Mourão, pers. obs.), indicating that this characteristic is intrinsic to the plant and is not caused by other factors such as pollen restrictions. The goal of this study was to test if a variable number of seeds per endocarp reduce seed predation by deceiving predators. The hypotheses are: (1) it is not possible to accurately predict the number of seeds inside an endocarp only by its size, and (2) the predictability of the number of seeds affects seed predation. We compared this strategy with a bluffing game and considered some factors to determine if this trait is an evolutionarily stable strategy.

METHODS

STUDY SITE.—The Pantanal is a seasonal floodplain located in western Brazil, close to the geographic center of South America, about 100 m asl. The weather is partly humid tropical, with an average annual temperature of 25°C (Calheiros & Fonseca 1996). This study was conducted during May 2002 on Nhumirim and Porto Alegre Ranches (18°59' S, 56°37' W; Corumbá, Mato Grosso do Sul, Brazil). These ranches comprise a mosaic of flooded grasslands, savannas, scrub savannas, forests, and several permanent and temporary ponds.

STUDY SPECIES.—The palm *A. phalerata* (Arecaceae) occurs in Bolivia, Peru, Brazil, and Paraguay in low dry open areas, disturbed forests and rainforests (Henderson *et al.* 1995). It grows abundantly in the Pantanal forests, sometimes in monospecific formations known locally as *acurizais* (Pott & Pott 1994). One plant may produce 8–12 infructescences at a time, with 350–500 fruits each (Quiroga-Castor & Roldan 2001), which drop in winter (May–September; Pott & Pott 1994). Fruits within the same plant have one to five or six seeds, depending on population location (Pott & Pott 1994, Quiroga-Castor & Roldan 2001).

Hyacinth macaws (*Anodorhynchus hyacinthinus*; Guedes & Harper 1995), bruchid beetles (*e.g.*, *Pachymerus cardo*; Quiroga-Castor & Roldan 2001), and spiny rats such as *T. pachyurus* and *C. laticeps* (Nascimento *et al.* 2004) are the few animals reportedly feeding on seeds from *A. phalerata* palms. We have also observed the Neotropical red squirrel *Sciurus eastuans* feeding on *A. phalerata* seeds, although this species is uncommon in the study site. Hyacinth macaws crack open endocarps in the center, destroying all the seeds, while rodents and bruchids destroy each seed individually.

Clyomys laticeps is a highly fossorial species that lives in colonies in savanna environments (Eisenberg & Redford 1999). These rodents dig characteristic burrows (Lacher & Alho 1989), which are found throughout the study area. *Thrichomys* spp. are generally associated with rocky outcrops (Eisenberg & Redford 1999), although *T. pachyurus* was observed in areas of sandy soils without rocks (Lacher & Alho 1989). There are no reports of fossorial habits for this species. In the Pantanal, both species occur in savannas and forest edges (Lacher & Alho 1989) and use *A. phalerata* fruits as an important food resource (Pott & Pott 1994).

DATA COLLECTION.—We demarcated 20 strips, each 0.25 × 10 m in the vicinity of adult palms and caught all the intact *A. phalerata*

endocarps falling within the transect. All the pulp had already been removed by frugivores, but the endocarps were not attacked by spiny rats. They were clean and intact. We measured the length and diameter of each endocarp and then broke it open to count the seeds it contained.

We located 20 *C. laticeps* burrows at least 200 m away from each other. At the entrance to each burrow we collected up to 10 gnawed endocarps that were probably discarded when the spiny rats cleaned their burrows. To compare the strategies of rats living in different habitats, half the samples we collected came from forest patches and the other half from shrub-savannas. We counted the number of seeds eaten in each endocarp and scarifications indicating unsuccessful attempts to eat a seed. The sum of successful and unsuccessful attempts indicated the intensity of predation. To estimate endocarp length and diameter, we rebuilt them with clay, then measured them and broke them open to count the seeds. We set up Sherman live traps at burrow entrances to ascertain which species of rodents were active in the field under study.

DATA ANALYSIS.—The size of endocarps collected by spiny rats and endocarps caught in the vicinity of the palms was compared by analysis of variance (ANOVA) to test the hypothesis that rats selected larger endocarps. A graph analysis suggested a correlation between endocarp size and the number of seeds it contained, albeit with considerable variability (Fig. 1). Therefore, we used logistic regression to model the probability of there being one (P_{x_1}), two (P_{x_2}), three (P_{x_3}), four (P_{x_4}), or five seeds (P_{x_5}), according to endocarp size. The logistic regression analysis detected no differences in size between four and five-seeded fruits ($t_{4,676} = -0.684$, $P = 0.494$), hence we pooled together the probability of there being four or five seeds (P_{x_4+5}).

We used ANCOVA to analyze if spiny rats attacked larger endocarps more intensively and if the intensity of predation by forest and savanna rats differed. To check for the assumption of

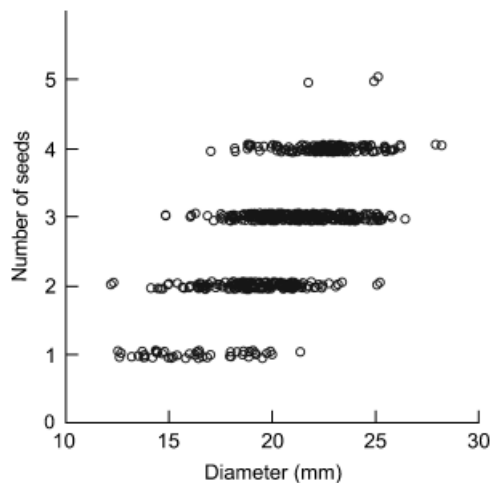


FIGURE 1. Relation between size and number of seeds of *Attalea phalerata* endocarps, collected during May 2002 in Brazilian Pantanal. There is a tendency for larger endocarps containing more seeds, albeit with a considerable overlap.

homogeneity of slopes, we tested a preliminary model including the term of interaction between the independent variables (Wilkinson 2004). Because this term was not significant ($F_{3,320} = 1.21$, $P = 0.272$), we proceeded to the ANCOVA model.

We conducted a binary logistic regression to analyze if multi-seeded endocarps were more likely to escape predation and which of the habitats contained more viable diaspores.

MARGINAL VALUE THEOREM MODEL.—To test our hypothesis, we built a model based on the Marginal Value Theorem (Charnov 1976), which explains the use of patchy habitats by an optimal predator. Briefly, the theory predicts the behavior of a predator that encounters food items within a patch, but spends time traveling between patches. When the predator is in a patch, it reduces the availability of food so the food intake rate decreases over time. The model calculates the ideal time for the predator to leave its present patch, even if food is still available, and move to another one to maximize the net rate of energy intake. We considered each endocarp a foraging ‘patch’ containing food (seeds). There were several patch types of different sizes.

Adapted from the Marginal Value Theorem, our equation is as follows:

$$\{S_i(s) \times G - [1 - S_i(s)] \times C\} < \{(\Sigma(P_i \times H_i) - L) / (\Sigma(P_i \times R_i) + L)\}.$$

The first term quantifies the energy assimilated by a predator while attacking an endocarp, while the second term quantifies the energy available in the habitat. When the first term is lower than the second term, the equation indicates when a predator should stop attacking the endocarp and search for another.

The model has the following variables: $P(i)$, proportion of endocarps of size i ; $S_i(s)$, proportion of endocarps of size i that have s seeds; $G = 1$, net gain of energy from eating a seed; C , energy cost per unit of scarification (this value is proportional to the net energy gained from eating a seed [$G = 1$] and is calculated by iteration. We tested values between 0.01 and 0.9 and calculated the difference between observed and expected values, selecting the one that minimized the sum of the squared residuals. This cost is related to the energy and time spent in unsuccessful attempts to eat a seed.); $E_i(s) = S_i(s) \times G - [1 - S_i(s)] \times C$, assimilated energy when scarifying an endocarp of size i 1, 2, 3 or 4 times (s); $CE_i(s) = \Sigma E_i(s)$, cumulative assimilated energy when scarifying an endocarp of size i 1, 2, 3 or 4 times (s); H_i , highest $CE_i(s)$ for each endocarp of size i ; R_i , optimal number of scarifications according to H_i for each endocarp of size i ; L , cost of searching for endocarps (this is calculated by iteration and is proportional to the energy gained from eating a seed [$= 1$]). This value varies according to habitat type and is calculated as C , above. This cost represents the energy and time spent searching for endocarps. It also involves endocarp availability); $AR = L + \Sigma(P_i \times R_i)$, average optimal scarifications; $AE = \Sigma(P_i \times H_i)$, average assimilated energy when applying the optimal number of scarifications R_i ; and $Eh = (AE - L)/AR$, average energy of the habitat (indicates the average amount of energy a predator can assimilate from each seed).

To maximize its energy intake, a predator should attack the next seed of the same endocarp if the probability of available energy is higher than Eh . When E_i falls below Eh , an optimal predator should attack another endocarp. The point where $E_i = Eh$ indicates the optimal average number of scarifications for an endocarp of size i .

Using the logistic regression model, which estimated the probability of having 1, 2, 3 or 4+5 seeds per endocarp size, we simulated two sets of populations with less variation in diameter for each number of seeds. To simulate the new data sets, we generated normal random distributions having the same mean diameter of sampled endocarps with 1, 2, 3 or 4+5 seeds. The simulated populations had the same original means, but the first set was computed to have 50 percent of the standard deviation and the second 25 percent of the original standard deviation.

Using the parameters found for predation in the forest, we applied the model to the two simulated populations to verify how predation intensity would change if the uncertainty about the number of seeds were reduced.

Considering rats as optimal predators, we used the expected average scarification function, which was obtained through the Marginal Value Theorem applied to each simulated population, to calculate the proportion of diaspores surviving predation according to the simulated conditions (see example in Fig. 2A). For example, an optimal predator that scarified 20 mm diam endocarps on average 2.23 times would scarify all the endocarps at least twice and 23 percent of them three times. Therefore, all one and two-seeded endocarps of that size would be attacked, 77 percent of three-seeded endocarps would have one seed not attacked, and all four and five-seeded endocarps would have one or more seeds viable. Considering their relative proportions in the endocarp population, we would thus determine the proportion of total endocarps predated after the attack.

RESULTS

At the time of our study, we did not capture any *C. laticeps*, although we found endocarps inside their burrows. We only caught three individuals of *T. pachyurus* with the Sherman traps, two in forest habitat and one in the savanna.

We collected 356 intact endocarps and 320 predated ones, making a total of 676. Seven percent of all the diaspores were one-seeded, 26 percent were two-seeded, 45 percent were three-seeded, 22 percent were four-seeded and only three endocarps were five-seeded. Size distribution had normal shape with mean 20.7 ± 2.7 mm.

According to ANOVA, spiny rats did not select endocarps according to size ($F_{2,676} = 2.08$, $P = 0.126$; Fig. 3). Although logistic regression showed that larger endocarps contain more seeds ($\chi^2 = 349$, $df = 3$, $P < 0.001$), endocarps with different seed counts showed a certain extent of overlapping size distribution. For example, 60 percent of the endocarps of intermediate diameter (21.5 mm) contained three seeds, but 15 percent had fewer and 25 percent held more than three seeds (see Fig. 4A).

ANCOVA indicated that the frequency of attacks by spiny rats was directly correlated to the size of endocarps ($F_{2,320} = 47.1$, $P < 0.001$). Savanna rats attempted to attack seeds more frequently

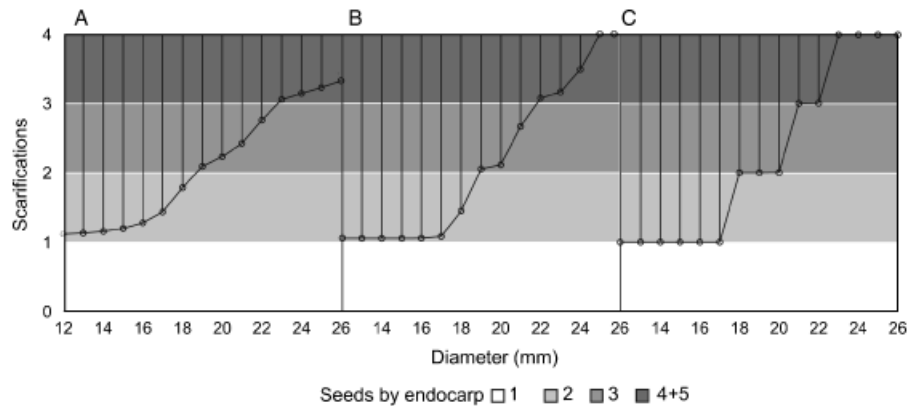


FIGURE 2. Relation between calculated scarification per endocarp size and viable diaspores in (A) the original sample collected during May 2002 in the Brazilian Pantanal, and in two simulated populations with (B) 50 percent and (C) 75 percent less variation in the number of seeds per size, respectively. The area above the expected average scarification curve (area with vertical lines) indicates the percentage of viable diaspores after predation, e.g., when rats scarify 20 mm diam endocarps on average 2.23 times, they predate 100 percent of the one- and two-seeded endocarps, 23 percent of the three-seeded endocarps and 0 percent of the four-seeded endocarps.

than forest rats ($F_{2,320} = 10.2$, $P = 0.002$). According to binary logistic regression, endocarp viability was positively correlated with the number of seeds they contained ($t = 5.79$, $N = 320$, $P < 0.001$) and with habitat ($t = -2.91$, $N = 320$, $P = 0.004$).

Applying the Marginal Value Theorem, the energy cost per unit of scarification was $C = 0.5$ in both forest and savanna. The cost of search was $L = 0.01$ in forest and $L = 0.2$ in savanna. When higher cost values were applied, the model indicated that endocarps would be attacked more intensely, while the opposite applied to lower values, albeit in the same proportion for each size. Graphically, only the point of origin changed, while the shape of the curve

remained the same. When the probability of assimilating energy decreased to $Eh = 0.81$ in forest and to $Eh = 0.70$ in savanna, an optimal predator would search for a new endocarp (Fig. 5).

Based on the Marginal Value Theorem, our model fit the observed data (Fig. 6). The model indicated that, after predation, 46 percent of diaspores remained viable under forest conditions and 31 percent under savanna conditions. This is close to the recorded findings of 47 percent and 35 percent of surviving diaspores found in the forest and savanna, respectively. When we simulated two data sets with less variability (see Fig. 4) under forest conditions, our model indicated that viable diaspores after 'predation' decreased to 36 and 15 percent, respectively (Fig. 2).

DISCUSSION

According to the Marginal Value Theorem, predator choices are based on the time elapsed between prey captures. The main difference of our model is that predator choices are based on the probability of capture. Our model can therefore be compared with a bluffing game, whose strategy is based on the probability of eating several seeds, the bluffing capacity of the other player (variation in seed number) and the risk that the player may assume (available energy of the habitat). The probability of finding an edible seed depends on the variation in the number of seeds according to endocarp size. Although larger endocarps usually contained more seeds, the palm bluffed with some uncertainty about the correct number of seeds. Thus, optimal predators have to play with the probabilities. The chance of finding a seed must be balanced against the cost of spending time and energy. According to the model, after the predator has successfully consumed a seed, it should attempt to consume another seed from the same endocarp only if the possible resulting net energy gain is higher than the average energy available in the habitat. This statement leads to two consequences: first, larger endocarps should be attacked more intensely because, on

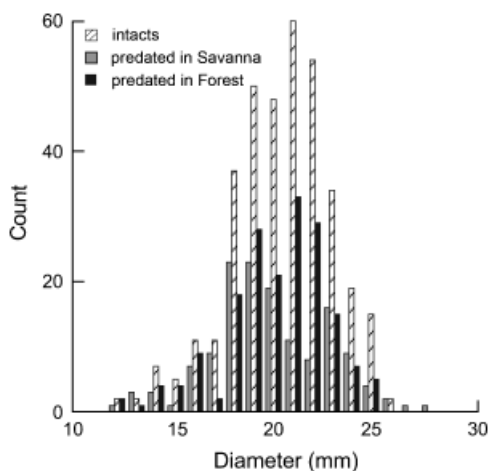


FIGURE 3. Size distribution of three *Attalea phalerata* endocarp samples collected during May 2002 in Brazilian Pantanal. The samples correspond to intact endocarps collected in the vicinity of the parent palms, predated endocarps collected in savanna and predated endocarps collected in forest. The three samples have the same size distribution.

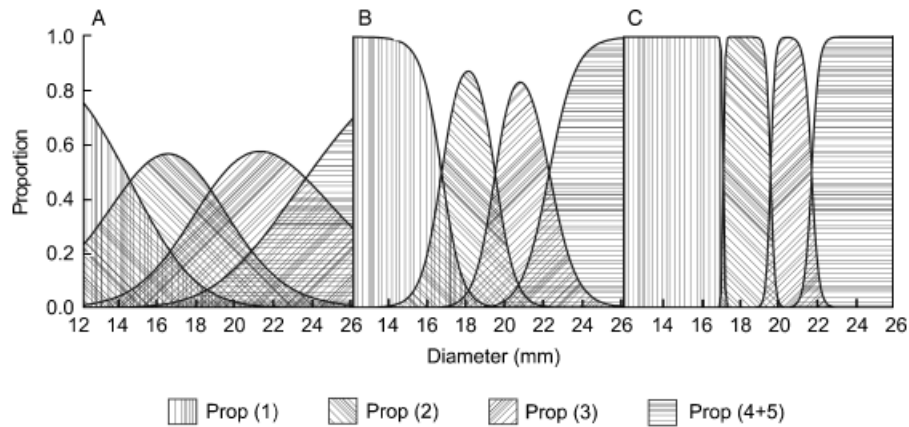


FIGURE 4. Proportion (Prop) of endocarps with 1, 2, 3 and 4+5 seeds per size in (A) the original sample collected during May 2002 in the Brazilian Pantanal, and in two simulated populations with (B) 50 percent and (C) 75 percent less variation in the number of seeds per size, respectively.

average, they contain more seeds; second, intensity of predation should be greater in habitats with less available energy. In fact, we observed that larger endocarps were attacked more often than smaller ones and that predation was more intense in the savanna. This suggests that the rats' behavior was close to optimal and that the Marginal Value Theorem can be applied to test predation by spiny rats in simulated endocarp populations. The calculated cost of scarifying remained the same in both habitats, but the cost of searching was greater in savanna than in forest. Savanna predators are not as close to seed sources as forest predators, because they depend on palms distributed sparsely in the savanna and on small numbers of endocarps occasionally dispersed by large animals such

as cattle (Soriano *et al.* 1994) and feral pigs (Galetti *et al.* 2003, Donatti *et al.* 2005). Therefore, it is probable that more time and energy is spent searching in this habitat than in forest. Consequently, there is less energy available in savannas and predators from this habitat may assume higher costs than predators from forest, attacking endocarps more intensely (see Fig. 5). However, this study involved two species of rodents. We detected *C. laticeps* because of its characteristic burrows, but only *T. pachyurus* were caught in the traps. In previous studies we noted that both species feed on *A. phalerata* seeds but we could not distinguish differences in their gnawing marks. We did not study each species separately, and although we do not know if predation intensity differs among species, we do know that the two species forage in both habitats, hence our findings involve combined data of the two species. The savanna held few viable diaspores after predation, due to the more intense predation in this habitat. Nevertheless, about one third and one half of the diaspores predated, respectively, in savanna and forest, were still able to generate seedlings, particularly multiseeded endocarps.

The proportion of viable diaspores would probably be much lower if the variability were reduced, as in the simulated data. Doing an analogy to a bluffing game, when the number of seeds is

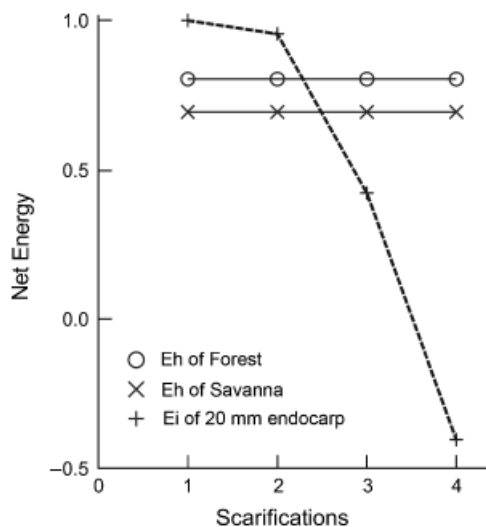


FIGURE 5. Optimal average number of scarifications for a 20 mm diam endocarp as a function of habitat. Horizontal lines indicate the average energy available per endocarp in forest and savanna relative to the energy from one seed (= 1). The dashed line indicates assimilated energy when a 20 mm diameter endocarp is scarified 1–4 times. The point where lines intersect indicates the optimal number of scarifications for that endocarp size.

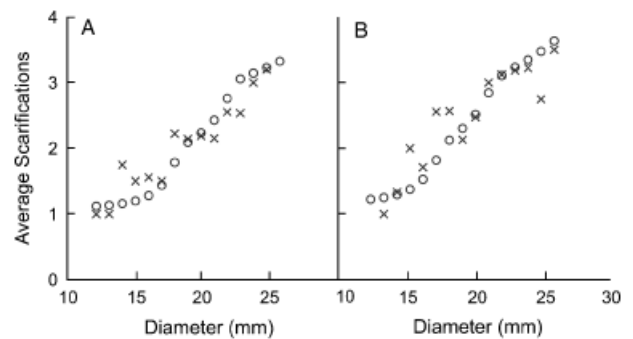


FIGURE 6. Comparison of average scarifications observed (×) per endocarp size and optimal (o) average scarifications calculated by the Marginal Value Theorem, for (A) forest and (B) savanna predators.

not unpredictable (prey players cannot bluff), predators are able to know how many seeds there are inside an endocarp (predators know what cards are dealt) and how many scarifications they should attempt (what they should go after). Scarification would be more correlated to the number of seeds and fewer diaspores would survive predation.

Dispersal ability and competition among siblings are strong factors that promote brood reduction. However, predation plays a major role in determining patterns in life history, and traits that affect the ability to avoid predation should therefore be under strong selection (Abrams 2000). Earlier studies have generally reported that the main predators of *Attalea* spp. are bruchid beetles, although they are only pre-dispersal predators (Janzen 1971a, Wilson & Janzen 1972, Bradford & Smith 1977, Forget *et al.* 1994) that attack endocarps clustered in palm forests. Fragoso (1997) observed that post-dispersed *Attalea* spp. seeds, free of bruchid predation and of competition with the parent palm, are more likely to generate a new plant than nondispersed seeds. If seeds dispersed in savannas have more impact on the palms' fitness, savanna spiny rats will probably have a stronger effect on palm strategies to avoid seed predation than forest spiny rats. Because predators from the savanna attack endocarps intensely, palms should respond with more seeds per fruit.

Our study was carried out in a habitat mosaic, with patches of palm forests surrounded by savanna. These palm populations are more subject to savanna predators than palms forming large forests. In future studies, it would be interesting to compare the production of multiseeded fruits by palm populations from these different habitats. It would be reasonable to expect to find more multiseeded fruits in patchy habitats than in large forests. Further studies about the role of predation in the maintenance of multiseeded fruits in *Attalea* spp. populations must consider bruchid beetle predation, but we believe the same logic can be applied to them. Various studies found that bruchids usually lay one egg on each endocarp (Wilson & Janzen 1972, Bradford & Smith 1977); however, we observed several endocarps predated by more than one bruchid larva. Palms may also be playing a bluffing game with bruchids.

Finally, does this bluffing game have a winner? Palms that are preyed upon will succeed if they are able to maintain variation in the population, therefore keeping seed predation at the same levels they have already achieved. In other words, is variation an evolutionarily stable strategy? Our results showed that multiseeded endocarps have a selective advantage, because each additional seed increases the probability of surviving predation. Therefore, palms producing multiseeded endocarps may have a selective advantage. In our sample, we found one to five seeds per endocarp, with three seeds on average. In *ad hoc* observations of *A. phalerata* populations in the southern Amazon, we found one to six seeds per endocarp. Other populations in the Beni Biological Station, Bolivia, also contain up to six seeds per endocarp (Quiroga-Castor & Roldan 2001). If seed predation is driving *A. phalerata* populations to produce more multiseeded endocarps, this interaction may lead to a Red Queen Strategy (Van Valen 1973), an ongoing process of reciprocal coadaptation, in which the evolving parties continually respond and counterrespond to the selection pressures imposed by each other (Lythgoe & Read 1998). Red Queen assumes that the

more extreme a phenotypic trait is, the better it is, and that there are no constraints on the growth of such a phenotypic trait value. If there are no constraints in increasing the number of seeds per fruit, species will reach an equilibrium at which they all continually evolve to neutralize each other's improved counteradaptations, and their ecological relationships remain fixed (Rosenzweig *et al.* 1987), *i.e.*, variation in the number of seeds per fruit is maintained. However, it is more realistic to assume that there is a biological limit to the number of seeds per fruit. In that case, the bluffing strategy would only be stable if other forces rendered the production of few-seeded fruits advantageous. This may occur, for example, when there is a tradeoff between the production of large quantities of fruits and multiseeded fruits. If the survival of each individual seed increases when more endocarps are available (predator satiation hypothesis; Janzen 1971b, Kelly & Sork 2002), the production of large numbers of few-seeded fruits is also selectively advantageous and variation is maintained. Otherwise, there is a tendency for more multiseeded rather than few-seeded fruits to be produced until the limit is reached, reducing the variability in the number of seeds per fruit and increasing its predictability. The strategy will thus fail and predators will have more seeds available to them, thereby winning the bluffing game.

ACKNOWLEDGMENTS

We thank Embrapa/Pantanal for logistic support and CNPq/Peld (n 520056/98-1) for financial support. William Magnusson made many useful suggestions and Arnaud Desbiez and Dustin Chase Perry improved the English of the draft manuscript.

LITERATURE CITED

- ABRAMS, P. A. 2000. The evolution of predator-prey interactions: Theory and evidence. *Annu. Rev. Ecol. Syst.* 31: 79–105.
- ADAMS, M. W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, *Phaseolus vulgaris*. *Crop. Sci.* 7: 505–510.
- AKHAKATSI, M., M. PFAUTH, AND C. L. CALVIN. 1999. Structural aspects of ovule and seed development and nonrandom abortion in *Melilotus officinalis* (Fabaceae). *Protoplasma* 208: 211–223.
- ARATHI, H. S., K. N. GANESHAIAH, R. UMA SHAANKER, AND S. G. HEGDE. 1996. Factors affecting embryo abortion in *Syzygium cuminii* (L.) Skeels (Myrtaceae). *Int. J. Plant. Sci.* 157: 49–52.
- ARATHI, H. S., K. N. GANESHAIAH, R. UMA SHAANKER, AND S. G. HEGDE. 1999. Seed abortion in *Pongamia pinnata* (fabaceae). *Am. J. Bot.* 86: 659–662.
- AUGSPURGER, C. K. 1986. Double- and single-seeded indehiscent legumes of *Platypodium elegans*: Consequences for wind dispersal and seedling growth and survival. *Biotropica* 18: 45–50.
- BRADFORD, D. F., AND C. C. SMITH. 1977. Seed predation and seed number in *Scheelea* palm fruits. *Ecology* 58: 667–673.
- BRONSTEIN, J. L. 1988. Limits to fruit production in a monoecious fig: Consequences of an obligate mutualism. *Ecology* 69: 207–214.
- CALHEIROS, D. F., AND W. C. JR. FONSECA. 1996. Perspectivas de estudos ecológicos sobre o Pantanal. EMBRAPA-CPAP, Documentos 18. Brazilian Agricultural Research Corporation, Corumbá, MS, Brazil.
- CASPER, B. B. 1990. Seedling establishment from one- and two-seeded fruits of *Cryptantha flava*: A test of parent-offspring conflict. *Am. Nat.* 136: 167–177.
- CASPER, B. B., S. B. HEARD, AND V. APANIUS. 1992. Ecological correlates of single-seededness in a woody tropical flora. *Oecologia* 90: 212–217.

- CHARNOV, E. L. 1976. Optimal foraging, the marginal value theorem. *Theor. Pop. Biol.* 9: 129–136.
- DONATTI, C., M. GALETTI, AND M. PIZO. 2005. Fruits and Frugivores in the Pantanal. In M. E. W. Chandler and P. Johansson (Eds.): *The Pantanal Conservation Research Initiative, Annual Report 2005*. pp. 15–20. Earthwatch Institute's Conservation Research Initiatives CRIs, Maynard, Massachusetts. Available at http://www.earthwatch.org/images/Pdfs/AboutUs/Conservation/CRI_ANNUAL_REPORT_PANTANAL_2005.PDF (accessed on August 1, 2008).
- DOWNHOWER, J. F., AND C. H. RACINE. 1976. Darwin's finches and *Croton Soculeri*: An analysis of the consequences of seed predation. *Biotropica* 8: 66–70.
- EHRLEN, J. 1992. Proximate limits to seed production in a herbaceous perennial legume, *Lathyrus Vernus*. *Ecology* 73: 1820–1831.
- EISENBERG, J. F., AND K. H. REDFORD. 1999. *Mammals of the Neotropics, Volume 3, The central neotropics: Ecuador, Peru, Bolivia, Brazil*. The University of Chicago Press, Chicago, Illinois.
- FORGET, P. M., E. MUNOZ, AND E. G. , JR. LEIGH. 1994. Predation by rodents and bruchids beetles on seeds of *Scheelea* palms on Barro Colorado Island, Panama. *Biotropica* 26: 420–426.
- FRAGOSO, J. M. V. 1997. Tapir-generated seed shadows: Scale-dependent patchiness in the Amazon rain forest. *J. Ecol.* 85: 519–529.
- GALETTI, M., M. A. PIZO, AND C. DONATTI. 2003. Keystone Fruits and Frugivores in the Pantanal. In D. P. Eaton and A. Keuroghlian (Eds.): *The Pantanal Conservation Research Initiative, Annual Report 2003*. pp. 31–34. Earthwatch Institute's Conservation Research Initiatives CRIs, Maynard, Massachusetts. Available at http://www.earthwatch.org/images/Pdfs/AboutUs/Conservation/pantanal_03.pdf (accessed on August 1, 2008).
- GARRISON, W. J., AND C. K. AUGSPURGER. 1983. Double and single-seeded acorns of Bur Oak *Quercus macrocarpa* frequency and some ecological consequences. *Bull. Torrey. Bot. Club.* 110: 154–160.
- GORCHOV, D. L. 1988. Effects of pollen and resources on seed number and other fitness components in *Amelanchier arborea* (Rosaceae: Maloideae). *Am. J. Bot.* 75: 1275–1285.
- GUEDES, N. M. R., AND L. H. HARPER. 1995. Hyacinth macaws in the Pantanal. In J. Abramson, B. L. Speer, and J. B. Thomsen (Eds.): *The large macaws: Their care, breeding and conservation*. pp. 163–174. Raintree Publications, Fort Bragg, California.
- HEITHAUS, E. R., E. STASHKO, AND P. K. ANDERSON. 1982. Cumulative effects of plant-animal interactions on seed production by *Bauhinia Ungulata*, a neotropical legume. *Ecology* 63: 1294–1302.
- HENDERSON, A., G. GALEANO, AND R. BERNAL. 1995. *Field guide to the palms of the Americas*. Princeton University Press, Princeton, New Jersey.
- JANZEN, D. H. 1971a. The fate of *Scheelea rostrata* fruits beneath the parent tree: Predispersal attack by bruchids. *Principes* 15: 89–101.
- JANZEN, D. H. 1971b. Seed predation by animals. *Annu. Rev. Ecol. Syst.* 2: 465–492.
- KELLY, D., AND V. L. SORK. 2002. Mast seeding in perennial plants: Why, how, where? *Annu. Rev. Ecol. Syst.* 33: 427–447.
- LACHER, T. E. , JR., AND C. J. R. ALHO. 1989. Microhabitat use among small mammals in the Brazilian Pantanal. *J. Mammal.* 70: 396–401.
- LYTHGOE, K. A., AND A. F. READ. 1998. Catching the Red Queen? The advice of the Rose. *Trends Ecol. Evol.* 13: 473–474.
- MARSHALL, D. L., D. A. LEVIN, AND N. L. FOWLER. 1985. Plasticity in yield components in natural populations of three species of *Sesbania*. *Ecology* 66: 753–761.
- MCDADE, L. A., AND P. DAVIDAR. 1984. Determinants of fruit and seed set in *Pavonia dasypetala* (Malvaceae). *Oecologia* 64: 61–67.
- NASCIMENTO, V. L. A., L. L. SOUZA, J. A. FERREIRA, W. M. TOMAS, P. A. N. BORGES, A. DESBIEZ, AND A. TAKAHASI. 2004. Utilização de frutos de acuri (*Attalea phalerata* Mart. ex Spreng.) por cutias *Dasyprocta azarae* no Pantanal da Nhecolândia. IV simpósio sobre recursos Naturais e Sócio-econômicos do Pantanal, Corumbá/MS, Brazil. Available at <http://www.cpap.embrapa.br/agencia/simpan/sumario/artigos/asperctos/pdf/bioticos/645RB-Acúri%20cutia-OKVisto.pdf>
- PIMENTEL, D. S., AND M. TABARELLI. 2004. Seed Dispersal of the Palm *Attalea oleifera* in a Remnant of the Brazilian Atlantic Forest. *Biotropica* 36: 74–84.
- POTT, A., AND V. J. POTT. 1994. *Plantas do Pantanal*. Brazilian Agricultural Research Corporation EMBRAPA-SPI, Corumbá, MS, Brazil.
- PRIMACK, R. B. 1978. Regulation of seed yield in *Plantago*. *J. Ecol.* 66: 835–847.
- QUIROGA-CASTOR, V. D., AND A. I. ROLDAN. 2001. The fate of *Attalea phalerata* Palmae seeds dispersed to a tapir latrine. *Biotropica* 33: 472–477.
- ROSENZWEIG, M. L., J. S. BROWN, AND T. L. VINCENT. 1987. Red Queens and ESS: The coevolution of evolutionary rates. *Evol. Ecol.* 1: 59–94.
- SASSAKI, R. M., AND G. M. FELIPPE. 1999. Single-seeded fruits and seedling establishment in *Dalbergia miscolobium* Benth. (Papilionaceae). *Biotropica* 31: 591–597.
- SILVIUS, K. M. 2002. Spatio-temporal patterns of palm endocarp use by three Amazonian forest mammals: Granivory or “grubivory”? *J. Trop. Ecol.* 18: 707–723.
- SILVIUS, K. M., AND J. M. V. FRAGOSO. 2002. Pulp handling by vertebrate seed dispersers increases palm seed predation by bruchid beetles in the northern Amazon. *J. Ecol.* 90: 1024–1032.
- SORIANO, B. M. A., H. OLIVEIRA, J. B. CATTO, J. A. COMASTRI-FILHO, S. GALDINO, AND S. M. SALIS. 1994. *Plano de Manejo da Estação Ecológica Nhumirim*. EMBRAPA-CPAP Documentos 12 - Brazilian Agricultural Research Corporation, Corumbá, MS, Brazil
- STEPHENSON, A. G. 1981. Flower and fruit abortion: Proximate causes and ultimate functions. *Annu. Rev. Ecol. Syst.* 12: 253–279.
- UMA SHAANKER, R., K. N. GANESHIAH, AND K. S. BAWA. 1988. Parent-offspring conflict, sibling rivalry, and brood size patterns in plants. *Annu. Rev. Ecol. Syst.* 19: 177–205.
- VAN VALEN, L. 1973. A new evolutionary law. *Evol Theory* 1: 1–30.
- WILKINSON, L. 2004. SYSTAT—Systems for Statistics. Version 11. Systat Software Inc, Chicago, Illinois.
- WILSON, D. E., AND D. H. JANZEN. 1972. Predation on *Scheelea* palm seeds by bruchid beetles: Seed density and distance from the parent palm. *Ecology* 53: 954–959.
- WRIGHT, S. J. 1983. The dispersion of eggs by a bruchid beetle among *Scheelea* palm seeds and the effect of distance to the parent palm. *Ecology* 64: 1016–1021.