

Testing the quick meal hypothesis: The effect of pulp on hoarding and seed predation of *Hymenaea courbaril* by red-rumped agoutis (*Dasyprocta leporina*)

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Abstract: Red-rumped agoutis (*Dasyprocta leporina*) are important seed dispersers/predators of Neotropical large-seeded plants. Several species of seeds cached by agoutis have an edible reward, in contrast to temperate rodent-dispersed diaspores. The quick meal hypothesis states that the presence of a reward such as edible pulp will enhance the efficiency of rodents as seed dispersers by satiating the animal and, consequently, reducing seed predation and enhancing hoarding. In this study, this hypothesis was tested using as the reference system the pulp and seeds of *Hymenaea courbaril*. Seeds with and without pulp were offered to agoutis and the behaviour of each individual was recorded. Since the probability of predation and hoarding were complementary, we used the probability of predation. The proportion of agoutis that preyed on at least one seed was similar for seeds with (42.8% of individuals) and without (40.0% of individuals) pulp. In agoutis that preyed upon at least one seed, the probability that they killed a seed did not differ between seeds with (0.17 ± 0.03) and without (0.20 ± 0.08) pulp. Hence, these results do not support the 'quick meal hypothesis'.

Key words: Atlantic forest, caching, Caviomorpha, food hoarding, seed predation.

INTRODUCTION

The fate of seeds is an important aspect of plant population ecology (Harper 1977; Vander Wall 1994). The interactions of animals with seeds and diaspores can lead to many possible outcomes for plant fitness (Smith 1975). Animals can reduce plant fitness by preying upon seeds or seedlings (Janzen 1969, 1971), or enhance fitness by cleaning or dispersing seeds (Howe & Smallwood 1982; Guimarães & Cogni 2002). Alternatively, they may have no effect at all on plant recruitment (Larson & Howe 1987).

Some seed predators, such as rodents, cause seed dispersal by scatterhoarding seeds and nuts for later consumption (Vander Wall 1990). Hoards are usually sites that are safe from other seed predators and may lead to seed germination and seedling recruitment (Vander Wall 1994). Scatterhoarding rodents do not always retrieve all of their hoarded seeds, and this

failure in retrieval can enhance seed dispersal (Smith & Reichman 1984; Vander Wall 1990). As a consequence, a single species of scatterhoarding rodent can reduce (by seed predation) or increase (by hoarding) seed survival, and rodent foraging behaviour is a key predictor of the probability of seed survival.

Rodent behaviour is affected by characteristics not directly related to plant diaspores, such as the density of conspecifics in the area, season, and the animal's energy needs (reviewed by Vander Wall 1990). The probability of seed dispersal is also affected by diaspore characteristics, such as seed mass (Jansen *et al.* 2002, 2004), presence of reward (Guimarães *et al.* 2005) and the presence of secondary compounds in the seeds (Guimarães *et al.* 2003). Since the interaction with rodents influences plant fitness, understanding how diaspore characteristics affect rodent feeding behaviour is of fundamental importance.

The seeds of some plants, such as the Brazil-nut tree *Bertholletia excelsa* and other Lecythidaceae species (including *Lecythis* spp.), have traits convergent with temperate rodent-dispersed nuts, such as large seeds

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Accepted for publication July 2005.

with no edible tissue. However, several large-seeded genera dispersed by rodents have edible pulp, including palms such as *Acrocomia* (P. Guimarães, pers. obs. 1999), and legume trees such as *Hymenaea* (Asquith *et al.* 1999). The presence of pulp in these large-seeded fruits may be an adaptation to promote hoarder satiation (Smythe 1970; Smith 1975; but see Guimarães *et al.* 2005), an anachronism (Janzen & Martin 1982), a defence against insect predation (Silvius & Fragoso 2002), or simply a trait related to seed dispersal by mammals.

Agoutis (*Dasyprocta* spp. Caviomorpha) are large, terrestrial rodents that occur from the cerrado (savanna-like vegetation) to evergreen forests of Central and South America (Emmons & Feer 1997). Agoutis are mainly frugivorous and granivorous (Henry 1999), and feed on large-seeded fleshy fruits and pulpless seeds, for which they can act as dispersers (Forget 1990, 1992; Peres & Baider 1997; Peres *et al.* 1997; Asquith *et al.* 1999; but see Larson & Howe 1987). Several studies have indicated that agoutis are key dispersers of some plant species, such as *Hymenaea courbaril* (Hallwachs 1986; Asquith *et al.* 1999), but little is known about how diaspore characteristics influence foraging behaviour in *Dasyprocta* spp. (Smythe 1970, 1978).

Smith (1975) proposed the 'quick-meal hypothesis' (Smith & Reichman 1984), which states that the presence of a reward, such as an edible pulp layer in some Neotropical, rodent-dispersed diaspores, is an adaptation to enhance hoarding by promoting temporary satiation (see also Smythe 1970; Smith & Reichman 1984). The quick meal hypothesis predicts that (i) the probability of hoarding will be higher in fruits with pulp than in fruits without pulp; and (ii) the probability of seed predation will be lower in fruits with pulp than in fruits without pulp. In this study, we examined the influence of the presence of edible pulp on the feeding behaviour of red-rumped agoutis (*Dasyprocta leporina*). Specifically, we assessed whether there was any influence of the presence of pulp on the extent of diaspore manipulation, hoarding and seed predation by these animals.

METHODS

The studies were done from September 2004 to October 2004 in the Bosque dos Jequitibás (hereafter BJ), a 10-ha forest fragment/urban park in Campinas, São Paulo, Brazil (Matthes 1980). The area is home to more than 60 tamed agoutis whose behaviour can be observed at close range (see detailed description of study site in Guimarães *et al.* 2003). To test the quick meal hypothesis, we offered seeds of *H. courbaril* with and without a pulp layer. *Hymenaea courbaril*, locally known as 'jatobá', is a large-seeded tree that is wide-

spread throughout the savannas and forests of Brazil (Lorenzi 1997). The plant produces large pods (50–200 g) with one to eight seeds (de Souza *et al.* 1996). The pulp inside the pods is farinaceous and covers all of the seeds. The seeds represent about 18% of fruit weight, while the farinaceous pulp represents about 20% of the fruit weight (de Souza *et al.* 1996). We used two groups of seeds. In the first group (hereafter referred to as cleaned seeds), the pulp layers were completely removed from the seeds, while in the second group (hereafter referred to as seeds with pulp), the pulp mass of each fruit was broken into pieces, with each piece containing one seed. Using this approach, we were able to maintain the natural proportion of pulp per seed found in the fruits.

Once individual agoutis had been located for the experimental trials, 10 seeds from the same group (cleaned seeds or seeds with pulp) were placed on the forest floor and the behaviour of the agoutis was monitored individually by direct observation for 40 min. The group of seeds (seeds with pulp or cleaned seeds) was randomly assigned to the agouti. Any agouti that removed less than five seeds was excluded from the analysis. We used agoutis as units because the fates of seeds at such stations are not independent (Jansen *et al.* 2002). The seeds suffered one of two fates: (i) predation, in which the seed was at least partially consumed by the animal; and (ii) hoarding, in which the seed was buried in the forest floor (see Smythe 1978). Since these two probabilities were complementary, we chose to analyse only the probability of predation. We estimated the mean probability of seed predation for both seed groups. Bootstrapping procedures (10 000 randomizations) were used to generate a 95% confidence interval for the observed mean probability of seed predation. The confidence limits were determined using the percentile method (Manly 1997). We investigated two effects of the presence of pulp on agouti behaviour. First, we used binary logistic regression to assess whether the presence of pulp affected the probability of at least one seed being predated by an agouti. Second, we used ANOVA to assess whether the presence of pulp affected the probability of a seed being predated by an agouti that preyed on at least one seed. This latter probability was angular transformed to improve normality. Binary logistic regression and ANOVA analyses were performed using the JMP software (SAS Institute, Cary, USA).

RESULTS

Twenty-nine agoutis removed more than five seeds and were used in the analysis: 14 manipulated seeds with pulp and 15 manipulated cleaned seeds. Agoutis often cleaned the seeds with pulp before caching or preying upon them. However, sometimes the animal

did not eat the pulp and discarded it on the forest floor. The probability of predation was small and similar for seeds with pulp (0.029–0.075–0.121, lower confidence limit–mean–upper confidence limit) and for cleaned seeds (0.028–0.079–0.136). The low mean probabilities of seed predation reflected two aspects of agouti behaviour: (i) the occurrence of agoutis that did not prey upon a single seed; and (ii) the occurrence of agoutis that preyed upon seeds but only in low quantities. The proportion of agoutis that preyed on at least one seed was similar for seeds with (42.8% of individuals) and without pulp (40.0% of individuals, binary logistic regression, d.f. = 1, $\chi^2 = 0.024$, $P = 0.876$). In agoutis that preyed on at least one seed, the probability of a seed being predated did not differ between seeds with (0.17 ± 0.03) and without (0.20 ± 0.08 , ANOVA, d.f. = 11, $F = 0.268$, $P = 0.616$) pulp.

DISCUSSION

Agoutis are the main seed dispersal vectors for some large-seeded Neotropical plants such as *H. courbaril* and *B. excelsa* (Hallwachs 1986; Forget 1990, 1992; Peres & Baider 1997; Peres *et al.* 1997; Asquith *et al.* 1999). As with other scatterhoarding animals, these rodents also prey upon seeds and are seed predators for some plant species (e.g. *Ormosia arborea*, Galetti 2002). However, few studies have investigated how diaspore characteristics affect seed choice by agoutis (Guimarães *et al.* 2003).

Smith (1975) proposed the quick-meal hypothesis in which the presence of edible tissue in large-seeded diaspores dispersed by scatterhoarding rodents was an adaptation to enhance the hoarding of seeds and reduce seed predation by satiating large rodents with pulp (Smith & Reichman 1984). Our results did not corroborate the idea of a reduction in predation and enhanced hoarding based on at least three aspects of feeding behaviour: (i) the probability of a seed being preyed upon; (ii) the probability of the agouti eating at least one seed; and (iii) the probability of a seed being preyed upon by agoutis that actually preyed on at least one seed. All these aspects of feeding behaviour were similar between seeds with and without pulp. Although our results may be influenced by pulp chemistry and internal physiological conditions of the agoutis, a brief overview of studies focusing on agouti-seed interactions leads to the conclusion that pulp is not necessary to higher rates of hoarding. Agoutis and other scatterhoarding rodents actively hoard large seeds without any edible pulp (e.g. *B. excelsa*, Lecythidaceae, Peres & Baider 1997), seeds of fruits in which the edible pulp was removed by arboreal mammals (e.g. *Dipterix panamensis*, Leguminosae, Forget 1993), and dry palm pyrenes (e.g. *Bactris acanthocarpa*, Arecaceae, Silva & Tabarelli 2001). Thus, our results

and the evidence derived from studies with phylogenetic unrelated plants that are actively or even exclusively dispersed by agoutis, suggest that pulp may not be an important factor conditioning hoarding rates.

Although our study did not support the quick-meal hypothesis, we observed an ecological pattern in the presence of rodent-dispersed fruits with edible pulp. Since temperate rodent-dispersed plants are usually dry nuts, the question 'What is the adaptive significance of the presence of pulp in Neotropical, rodent-dispersed plants?' remains an important question for understanding the evolution of seed dispersal systems. One possible answer is that the presence of edible pulp can affect other aspects of rodent-seed interactions. For example, Guimarães *et al.* (2005) demonstrated that the fleshy pulp of *Syagrus romanzoffiana* (Arecaceae) enhances the probability that a rodent will find a seed, that is, the pulp acts as an attractor of seed dispersing rodents.

An alternative hypothesis is that there is no adaptive significance of edible pulp related to dispersal by rodents. Cache-dispersed nuts of temperate regions include *Juglans*, *Carya*, *Quercus*, *Fagus*, *Castanae*, *Castanopsis*, *Lithocarpus*, *Corylus*, *Aesculus* and *Prunus* (Vander Wall 2001). Most of these genera appear to have evolved from ancestors with wind-dispersed seeds; the single exception is *Prunus*, which evolved from fleshy fruits (Vander Wall 2001). In contrast, many agouti-dispersed plants in the Neotropics evolved in families in which fruits with edible pulp are recorded, such as Arecaceae, Lecythidaceae, Leguminosae and Sapotaceae. Thus, it is possible that the presence of edible pulp in some Neotropical plants is solely a non-functional trait related to their phylogenetic origin. We recommend that future work should focus on the phylogenetic basis of fruit traits in rodent-dispersed plants, testing this non-adaptive hypothesis.

ACKNOWLEDGEMENTS

The authors thank G. Machado, P. M. Forget, P. P. Coltri, R. Cogni, S. B. Vander Wall and an anonymous reviewer for comments on an earlier version of the manuscript, and P. A. Jansen for criticisms and discussion. E. Santos, P. Anselmo, the staff of the Bosque Jequitibás and the Museu de História Natural (UNICAMP) provided logistical support. P. R. G. was supported by FAPESP, CAPES and CNPq, and M. G. was supported by FAPESP, the International Foundation for Science (IFS) and a fellowship from CNPq.

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