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Seed toughness in Persea americana (Lauraceae) and Dioclea reflexa (Papilionaceae) and feeding behavior in agoutis (Dasyprocta punctata)

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Seed toughness in *Persea americana* (Lauraceae) and *Dioclea reflexa* (Papilionaceae) and feeding behavior in agoutis (*Dasyprocta punctata*)

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Abstract

Agoutis are a common study subject because of their caching behavior and for their role in seed dispersal in the tropics (Wainwright 2002). This study examined the relationship between the hardness of seed coats and their rate of consumption by conducting trials at eight known agouti territories in Monteverde, Costa Rica using softened and untreated seeds. Trials were conducted separately for each seed species. A significant difference was found between the number of hard and soft seeds of *Persea americana* and *Dioclea reflexa* left behind at the sites. According to statistical tests, agoutis seem to prefer softer seeds of *P. americana* over hard seeds (Wilcoxon Matched Pairs test, $p = 0.0858$) and no preference in *D. reflexa* (Wilcoxon Matched Pairs test, $p = 0.715$). This difference can be explained by the much more noticeable softening of *P. Americana* when compared to *D. reflexa*, which may have allowed a shorter seed handling time.

Resúmen

Las guatusas son objeto común de estudio por su comportamiento de almacenamiento de semillas y porque cumplen un rol importante en la dispersión de semillas en los trópicos (Wainwright 2002). Este estudio examinó la relación entre la dureza de las semillas y su tasa de consumo haciendo pruebas en ocho sitios en Monteverde, Costa Rica, usando semillas suavizadas y no tratadas. Se hicieron pruebas separadas para cada especie de semillas. Se encontró una diferencia significativa entre el número de semillas duras y suavizadas de *Persea americana* y *Dioclea reflexa* en los sitios. Las guatusas parecen tener una preferencia para las semillas suavizadas de *P. americana* y no presentan preferencia en *D. reflexa.* Esta diferencia se puede explicar porque la suavidad es más notoria en *P. americana* que en *D. reflexa*, lo que puede tener un efecto en el tiempo de manejo de la semilla.

Introduction

Seed dispersal is a challenge for many tropical trees and plants, which must utilize creative ways to make sure their seeds are spread around the forest. One common dispersal mechanism for plants that fruit and bear large seeds is the relationship with the agouti (*Dasyproctus punctata*), which exhibits a scatter-hoarding behavior (Wainwright 2002). Agoutis are diurnal mammals that are exclusively ground-dwelling and feed on an assortment of food items, including fruits, seeds, fungi, insects, and crabs (Wainwright 2002). They are most active during the late afternoon and prefer to inhabit forested areas with dense undergrowth (Emmons 1997). They tend to cache extra seeds throughout the rainy season when food is plentiful so that they will have a sufficient amount when food is scarce (Wainwright 2002). They also have been known to eat the sweet fruit of some trees when ripe, but cache the hard seed which is sometimes initially inedible (Smythe 1970). Agoutis locate their caches through visual and olfactory cues, but usually do not recover all of their caches and therefore help distribute seeds of many tree species, including those of *Persea americana* and some *Dioclea reflexa* species (Murie 1977).

Plant species have evolved different mechanisms to deal with seed predation, including toxic compounds and tough seed coats (Janzen 1971). Previous studies indicate that seed preference may be based on these deterrents or other factors including nutritional content or handling time (Meiners 1997). In this study I will examine if agoutis show a preference in the seed toughness of *P. americana* and *D. reflexa*. I expected that there would be a difference in the number of normal versus softened seeds that were eaten. Based on previous research, it is my prediction that agoutis will eat more of the seeds that have been softened. They will prefer softer seeds because of the shorter handling time and the higher effectiveness of caching hard seeds, which will be less prone to decay than softened seeds.

Materials and Methods

This study was conducted from mid-July to early August of 2007 for two weeks in the area of Monteverde and Santa Elena in Costa Rica. Eight known territories of *D. punctata* located in this area were used to conduct experimental trials. These territories were mostly located on forest edges in fairly open areas, although two were located in closed forest. Both *Dioclea reflexa* and *Persea americana* were used in separate trials. In order to test the effect of seed toughness, half of the seeds to be used in the upcoming trial were soaked for 48 hours in water prior to use in a trial. Three trials were conducted using *P. americana* while two trials were conducted with *D. reflexa*. For each of the eight *D. punctata* territories, ten control seeds and ten soaked seeds of *P. americana* were placed in two separate piles about one meter apart from each other with untreated seeds placed on the left and softened seeds placed on the right. The same procedure was used for the *D. reflexa* trials, with the exception that five control and five soaked seeds were used at each site. The sites were checked after 48 hours to inventory the number of seeds that were uneaten (Appendix 1). After recording how many seeds remained, new seeds were placed of either *P. americana* or *D. reflexa*, such that the trials alternated between each seed species. Statistical analysis included non-parametric Wilcoxon Matched Pairs tests, used to determine if there was a significant difference between the types of seeds eaten or left at the sites. Seeds were assumed to be either eaten or cached if removed from the site.

Results

For the duration of the study, a total of 480 *P. americana* seeds and 160 *D. reflexa* seeds were placed at the eight sites. Overall, the removal of softened seeds was more prevalent for *P. americana* than for *D. reflexa* (Wilcoxon Matched Pairs tests). There was a tendency for the agoutis to leave behind fewer softened seeds than tough seeds in *P. americana* (Wilcoxon Matched Pairs test, $p = 0.0858$, $n = 24$, $df = 22$). There was no difference in preference between softened and untreated *D. reflexa* seeds (Wilcoxon Matched Pairs test, $p = 0.715$, $n = 16$, $df = 14$). While neither p-values were significant for either seed species, it can be seen from Figures 1 and 2 that there was a definite difference between the number of softened seeds and hard seeds left of *P. americana*. With further trials or the addition of more seeds, a significant difference may be found for the seed type preferred by agoutis in *P. americana*.

Discussion

Agoutis appeared to prefer softer seeds to the hard seeds for *P. americana* because they became softer in 48 hours of soaking in water than *D. reflexa*. The entire seed became much easier to crack open in addition to the meat of the seed itself becoming softer, as observed during the trials that were conducted. Further research could be done to determine exactly why the softer seeds are preferred. It could be a difference in the handling time or even something as simple as a change in the palatability of the seed, as noted in previous studies (Meiners 1997). A shorter handling time would be preferred by agoutis because it would expose them to less predation by shortening the amount of time they would need to spend sitting in one place and chewing a seed or fruit (Meiners 1997). A softer seed, or a seed that has been softened naturally by rain or other conditions, would decrease the amount of time necessary for seed consumption and thus might be preferred over tougher seeds.

In contrast to *P. americana*, there was shown to be no difference between the number of untreated and soft seeds of *D. reflexa* left at each site. It was observed during the experiment that the soaking of *D. reflexa* seeds did not soften them as much as *P. americana*. The *D. reflexa* seeds had a much tougher exocarp, which made them less permeable to water. The fact that there was not a difference between the untreated seeds and the soaked seeds is shown by the fact that the agoutis did not appear to distinguish between the two types (Figure 2). *D. reflexa* seeds appeared to have been chosen either randomly or without preference with regards to seed softness. Another factor that may have had an effect on the number of seeds consumed at each site was the decreased amount of seeds placed at the sites when compared to the amounts left of *P. americana* (Tables 1 and 2). As seen in the tables, some of the sites had all of the seeds removed of both types, which may have skewed the results. More trials or the use of more seeds may confirm or reject the idea that agoutis have no preference for seed toughness in *D. reflexa*.

These results show that the agoutis may be choosing the food they eat based on its seed toughness, among other factors. Their scatter-hoarding behavior has often been studied due to its effect on seed survival rates and plant redistribution (Wainwright 2002), so studies on preference with regards to seed toughness may illuminate more aspects of this behavior. For instance, agoutis may choose to cache seeds with harder seed coats because they are able to remain fresher than seeds with thin seed coats, which might decay rapidly (Janzen 1971). If this were the case, it should be common to find varieties of soft seeds more prone to predation immediately after falling from the tree or after many days of rain, which would soften some seeds further. Further studies could be conducted regarding caching behavior that would examine the seed toughness of the cached seeds in relation to seeds that are eaten at a site.

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Figures

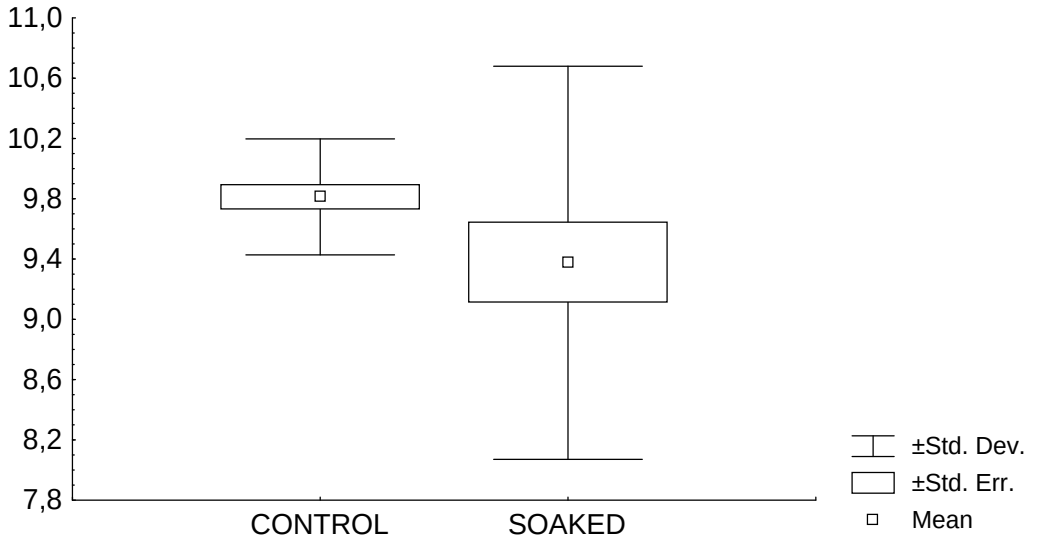

Figure 1. A Wilcoxon Matched Pairs Test comparing the amount of *Persea americana* seeds that remained uneaten over three trials at eight different agouti (*Dasyprocta punctata*) territories. For this test, p = 0.0858 which was almost significant, thus signifying a tendancy to leave behind less soaked seeds than control seeds. For these trials, n=24 and the degrees of freedom = 22. (T=8, Z=1.718).

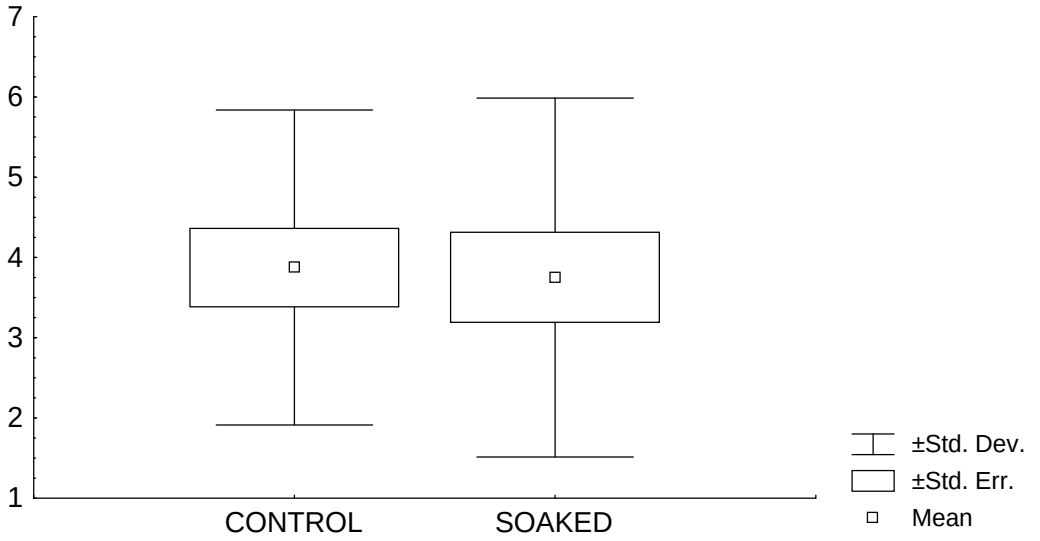

Figure 2. A Wilcoxon Matched Pairs Test comparing the amount of *Mucuna* sp. seeds that remained uneaten over two trials at eight different agouti (*Dasyprocta punctata*) territories. The p-value for this test was 0.715, which indicates that there is no statistical difference between the amount of control or soaked seeds that remained uneaten. For these trials, n = 16 and the degrees of freedom = 14. (T = 4, Z = 0.365).

Appendix 1

Table 1. The data collected from each of the eight agouti sites for *Persea americana* for three separate trials. The number of seeds left after 48 hours out of the ten seeds placed at the beginning of each trial was recorded for both the untreated seeds and the seeds that had been soaked for 48 hours previously.

site	control (7/21)	soaked (7/21)	control (7/26)	soaked (7/26)	control (7/30)	soaked (7/30)
Station	10	6	10	10	10	10
Turid Forsyth	10	9	10	10	10	10
Bruce Young	10	10	10	10	10	10
Bajo del Tigre	9	10	9.5	10	10	10
Bob Law	10	8.5	9	10	10	10
Frank Joyce	10	10	10	9	10	10
John Trostle	10	10	10	10	10	10
Conservation Association	9	6	9	6.5	10	10

Table 2. The data collected from each of the eight agouti sites for Mucuna sp. for two separate trials. The number of seeds left after 48 hours out of ten seeds placed at the beginning of each trial was recorded for both the untreated seeds and the seeds that had been soaked for 48 hours previously.

site	control (7/23)	soaked (7/23)	control (7/28)	soaked (7/28)
Station	5	5	5	5
Turid Forsyth	5	5	0	0
Bruce Young	5	5	5	5
Bajo del Tigre	4	5	5	5
Bob Law	0	0	0	0
Frank Joyce	5	5	4	5
John Trostle	5	5	5	0
Conservation Association	4	5	5	5