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Differential primate handling on fruits of *Brosimum alicastrum* and its effect on the available offer for secondary mammal consumers

Manipulación diferencial de frutos de *Brosimum alicastrum* por parte de primates y su efecto sobre la oferta para mamíferos consumidores secundarios

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Abstract

Despite their importance, little is known about the effect that flashing massive production of fruits has on primary and secondary consumers. A series of experiments were conducted at Palo Verde, Costa Rica, in order to analyze: 1) the explosive fruit production of a tree of *Brosimum alicastrum* (Moraceae); 2) fruit handling by: mantled howler monkeys (*Alouatta palliata*) and white-faced capuchins (*Cebus capucinus*); and 3) visitation of fruits on the ground by potential mammalian secondary consumers. In three days fruits of *B. alicastrum* available on the branches fell from 10.000 to 1000. We documented a differential primate handling of *Brosimum* fruits, represented by a significantly greater proportion of naked seeds (F=2.83; *p* =0.049) dropped by *A. palliata*; and a significantly greater proportion of complete and partially consumed fruits (F=20.65; p=0.000918) dropped by *C. capucinus*. Treatments, consisting of footprint traps with naked seeds and complete fruits used as bait, were explored by four mammalian potential secondary consumers: white tail deer, *Odocoileus virginianus*; collared peccary *,Tayassu tajacu*, white nosed coati, *Nasua narica*, and the agouti, *Dasyprocta punctata*. *Tayassu tajacu* had the greater number of footprint tracks on both types of fruits offered; on the other hand, footprints of *N. narica* were only recorded in treatments with complete fruits, while footprints of *O. virginianus* were only recorded on treatments with naked seeds.

Keywords: *Brosimum;* Costa Rica; Dispersal; Primates.

Resumen

A pesar de su importancia, poco se conoce sobre el efecto que eventos esporádicos de producción masiva de frutos tiene sobre los consumidores primarios y secundario. En la Estación Biológica Palo Verde en Costa Rica, se realizó una serie de experimentos con el fin de analizar: 1) la producción explosiva de frutos en un árbol de *Brosimum alicastrum* (Moraceae); 2) el manejo de frutos por dos especies de primates: monos aulladores negros (*Alouatta palliata*) y capuchinos cariblancos (*Cebus capucinus*); y 3) la visita de frutos en el suelo por parte de mamíferos identificados como potenciales consumidores secundarios. En tres días, el número de frutos de *B. alicastrum* disponibles en las ramas cayó de 10.000 a 1000. Documentamos un manejo diferencial de frutos por parte de los primates representado por una significativamente mayor proporción de semillas desnudas (F=2.83; p=0.049) arrojadas por *A. palliata* y una significativamente mayor proporción de frutos enteros y parcialmente consumidos (F=20.65; *p* =0.000918) arrojados por *C. capucinus*. Los tratamientos que consistieron en trampas de huellas con semillas desnudas y frutos enteros como cebo, revelaron la exploración por parte de cuatro especies de mamíferos identificadas como potenciales consumidores secundarios: venado de cola blanca, *Odocoileus virginianus*; pecarí de collar, *Tayassu tajacu*, coatí de nariz blanca, *Nasua narica*, y el agutí, *Dasyprocta punctata*. *Tayassu tajacu* tuvo el mayor número de huellas en tratamientos con los dos tipos de frutos ofrecidos; de otra parte las huellas de *N. narica* solo se registraron en tratamientos con frutos completos, mientras que huellas de *O. virginianus* solo en tratamientos con semillas desnudas.

Palabras clave: *Brosimum;* Costa Rica; Dispersión; Primates.

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Introduction

Competition for dispersers is one of the most important aspects of plant evolution (Janzen 1967). In tropical forests, 75% of tree species produce fruits adapted for bird and mammals consumption and presumably they rely on them for seed dispersal (Howe 1980). Among the variety of strategies developed by plants to guarantee dispersal is the production of explosive amounts of fruits in extremely short periods of time, usually not longer than few days (van Shaik *et al.* 1993). The short duration of these episodes makes difficult to evaluate the effect they may have on the mammal community of primary and secondary consumers. *Brosimum alicastrum* (Moraceae) is a plant species typical of Central America with crops distributed through the year and fruits available for primary and secondary consumers for only few days (Cordero and Boshier 2003).

Variations in phenological patterns of *B. alicastrum* in Central America are mainly driven by its response to local precipitation regimes (Cordero and Boshier 2003). *Brosimum alicastrum* trees produce yellow berries of 2 to 2.5 cm in diameter with a thick orange pericarp sweet in flavor and a large edible seed primarily dispersed by birds and mammals. Primates are considered among primary dispersers of specific fruit species (Gautier-Hion *et al.* 1993, Juliot 1996) and they are likely to differ not only in their role as primary dispersers but also in the way that post-dispersal fate of seeds may be affected. *Alouatta palliata* and *Cebus capucinus* are the most widespread primate species in Costa Rica, and can be generally found foraging together and using the same fruit resources (Glander 1975, Wehncke *et al.* 2001, 2004). It is well known that seed processing and handling behavior differ among Neotropical primates affecting visitation by secondary consumers (Terborgh 1983, Terborgh 1986).

Figure 1. Palo Verde Field Biological Station, Province of Guanacaste, in northwestern Costa Rica.

In the present work, a series of experiments were conducted in order to analyze: 1) an explosive and massive episode of fruit production of a tree of *Brosimum alicastrum* (Moraceae); 2) fruit handling and fruit products dropped on the ground by mantled howler monkeys (*A. palliata*) and white-faced capuchins (*C. capucinus*); and 3) the way in which differences in primates fruit handling may affects visitation by potential mammal secondary consumers.

Methods

The herein reported preliminary observations correspond to an explosive episode of fruit production of a *B. alicastrum* tree during three days (July 25 to 28 2001) within the little summer season («veranillo») at Palo Verde Field Biological Station, Guanacaste, northwestern Costa Rica (10° 21' N, 85° 21' W) (Figure 1).

Quantification of fruits. We visually estimated the number of fruits in a tree by direct counts on discrete area units of the crown. We selected five 1 m^3 areas of the crown on an *ad libitum* basis, and counted the number of fruits on each. The average number of fruits counted in the five selected areas was then multiplied by the total number of units estimated in fructifying branches (See details in Chapman *et al.* 1992, p. 528).

Fruit handling. In order to analyze the effect of primate handling on the type of *B. alicastrum* fruit resources dropped on the ground, we recorded fruit consumption of *B. alicastrum* by both species during 36 hours

of focal observations, consisting on 10-minutes intervals, separated from each other by five-minutes of no observations to guarantee independence. The number and type of fruit products dropped by the primates was estimated in different ways for *A. palliata* (fruit traps), and *C. capucinus* (direct counting).

Fruit traps consisted in five pieces of fabric of 4 m^2 distributed randomly under the tree canopy. We checked the traps every fifteen minutes during four daily sampling hours (5:30-9:30), and counted the number of fruits, also registering the characteristics of their handling in two categories: 1) naked seeds: seeds without pericarp; and 2) complete fruits (which also included partially consumed fruits). The time frame selected corresponded to that of major feeding activity reported in the literature for the primates.

Since visitation of *C. capucinus* to the studied *B. alicastrum* tree was sporadic (three hours in total), we avoided the use fruit traps to quantify and qualify capuchins handling; instead, fruit handling was recorded by focal observations in ten minutes intervals. On the other hand, fruit products dropped on the ground by *C. capucinus* were quantified by direct collection.

Same fruit handling categories used for *A. palliata* were considered. Differences in fruit products dropped by the primates were statistically assessed by an F-Test.

Identification of potential mammalian secondary consumers. In order to document the visitation of mammalian potential secondary consumers and their exploration on the two types of fruit products dropped by the primates (complete fruits and naked seeds), five footprints traps were randomly set under the studied tree. Traps consisted on five 9 m^2 areas cleaned of litter with a rake and delimited with 30 cm fluorescent powder stripes. Inside each area, two inner squares of 1 m^2 were also delimited with 30 cm stripes of fluorescent powder of different colors. Inside one of the squares, placed in the center, a pile of ten naked seeds was used as bait; while in the other square a pile of ten complete fruits was used as bait. Seeds and fruits used were marked with an ink-marker dot. A scaled diagram of the traps is presented in Figure 2. The areas out of the traps were maintained in their natural stage. Traps were checked twice a day, in intervals of 12 hours, starting at 8:30. Footprints on each inner square were measured and compared with mammalian footprints drawings in Reid (1997). Independent tracks were identified using as criteria: 1) color of powder, 2) size of independent footprints (length and wide); and 3) spacing.

Accessibility. In order to analyze how ground coverage affects the foraging for fruit products, we recorded consumption in a set of four separate combinations of piles including: a) naked seeds in open areas; b) naked seeds in covered areas; c) complete fruits in open areas; and d) complete fruits in covered areas. This experiment had three replicates. A χ^2 test was performed to determine deviations from an equal removal.

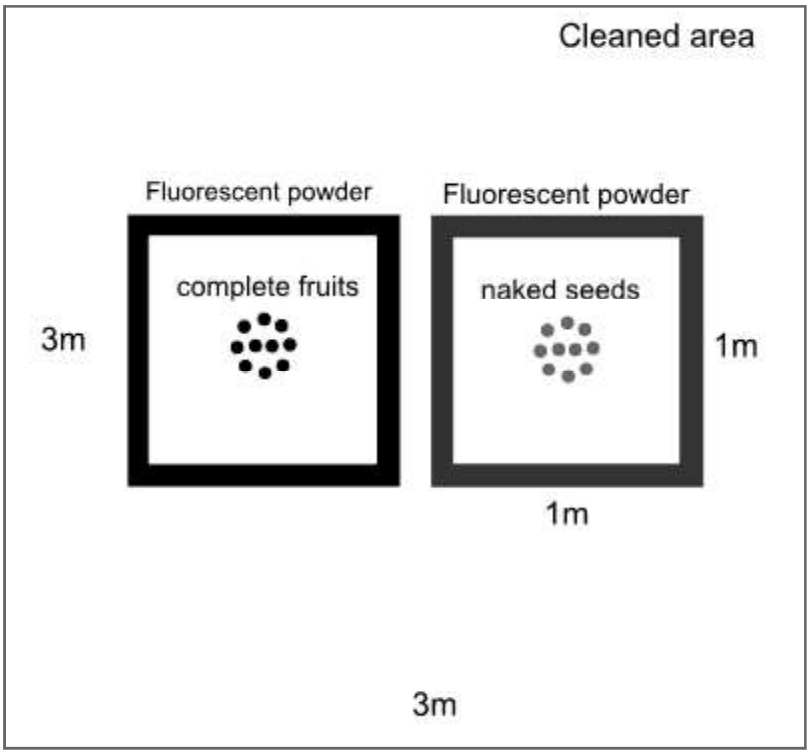

Figure 2. Example of a footprint trap used in this work. Five plots of 3 x 3 m, were cleaned of litter with a rake and in its center two squares were delimited by color fluorescent powder. In the center of each inner square delimited with different color powder a pile of complete fruits and naked seeds were placed.

Results

Quantification of fruits on the tree. There was a clear declining in the number of fruits available on the branches during our sample. During our first day, the estimate of crop production was 10.000 fruits approximately; whereas the estimate during the final sampling day was 1000 fruits approximately.

Quantification of dropped fruit products. The herein presented data correspond to one group of mantled howler monkeys consisting of 15 individuals (12 adults and three juveniles) and a group of white faced capuchins of at least nine adult primates (the little amount of time that the *C. capucinus* troop spent on the tree prevented us to provide a total number of individuals in the group). The howler group was present at the *B. alicastrum* tree during the whole observations time, using the tree as sleeping site. The feeding activity on *B. alicastrum* by the howlers was concentrated early in the morning between 6:00 and 8:00 h. On the other hand, we recorded only two visits by the capuchins troop, accounting for a total of three hours divided in two days (two and one hour, respectively). Visits of the capuchins occurred between 9:30 and 11:30, the first day; and between 10:30 and 11:30 the second day.

The proportion of naked seeds dropped by *A. palliata* was higher and statistically significant than the proportion of complete or partially consumed fruits (F=2.83; p=0.049) (Figure 3). In contrast, *C. capucinus* dropped a higher and statistically significant proportion of complete fruits than the proportion of naked seeds (F=20.65; p=0.000918; Figure 4).

Identification of footprints. We identified four mammalian species (presumably secondary consumers) on the plots: white tail deer, *Odocoileus virginianus*; collared peccary, *Tayassu tajacu*, white nosed coati, *Nasua narica*, and the agouti, *Dasyprocta punctata*. The proportion of footprints in each inner square for each potential secondary consumer was different. The most active species in the plots was *T. tajacu* with 176 tracks representing the eighty percent of the independent tracks; followed by *O. virginianus* (N=22; 10%); *D. punctata* (N=16; 7%); and *N. narica* (N=2; 1%). We were not able to identify four tracks (2%; Table 1). In our first day of sampling, we did not register any removal of com-

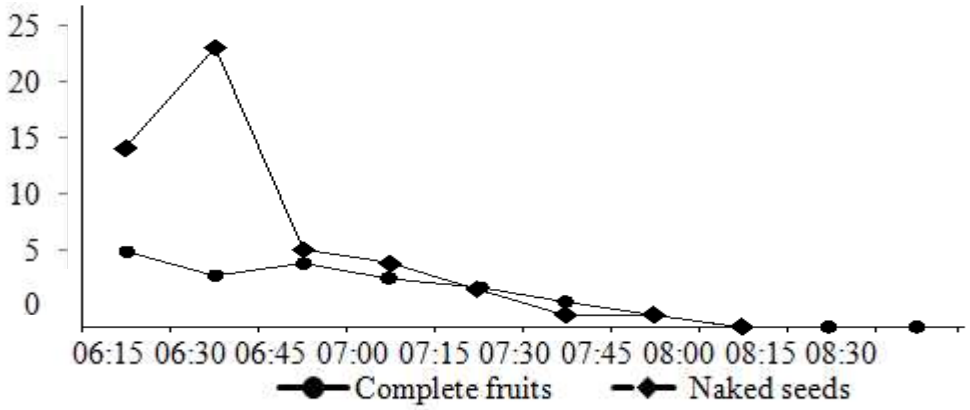

Figure 3. Number of *Brosimum alicastrum* fruits dropped by *Alouatta palliata*.

Table 1. Percentages of footprints of mammalian potential secondary consumers of *B. alicastrum* in Palo Verde, Costa Rica.

Secondary consumers	Traps	Number of footprints	Total %	Number of foot prints	
				Naked seeds	Complete fruits
Odocoileus virginianus	1,2	22	10,1	14	8
Tayassu tajacu	1,2,3,4	176	80,7	97	79
Dasyprocta punctata	2,4	16	7,3	16	0
Nasua narica	1,2	2	0,9	0	2
Undetermined	3,4	4	1,8	1	3
Total		220		128	92

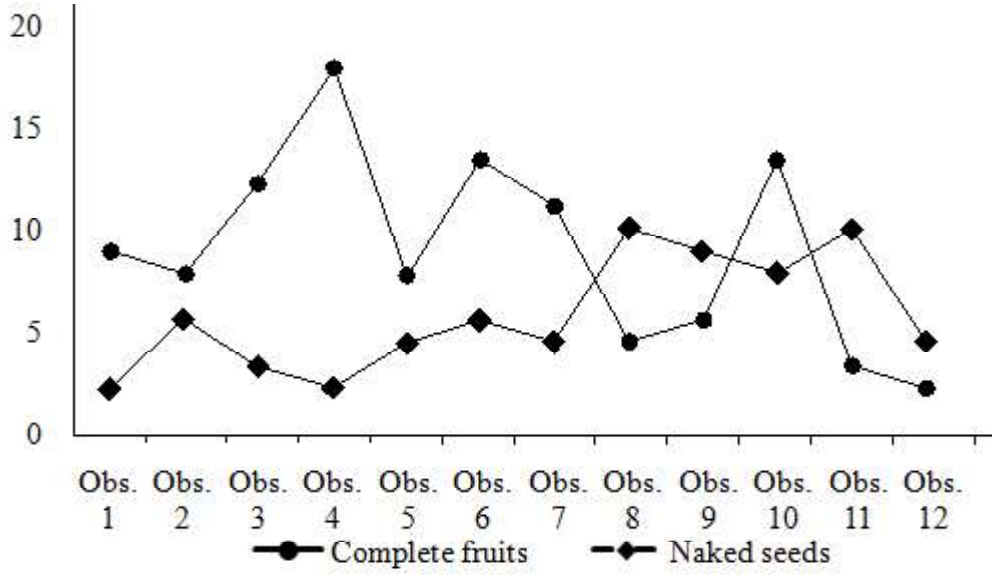

Figure 4. Number of complete fruits and naked seeds dropped on the ground by *Cebus capucinus* recorded in observation intervals of 15 minutes (Obs.). Data presented here correspond to two visits that accounted for a total of three hours divided in two days (day one: two hours; day two: one hour). Observations are presented in chronological order.

Table 2. Percentage of fruit products removed from treatments in our experiment on accessibility in Palo Verde, Costa Rica.

	Number of seeds removed			
Replicate	**Naked exposed**	**Complete exposed**	**Naked non-exposed**	**Complete non-exoposed**
1	10	8	6	3
2	5	4	7	4
3	10	4	6	4
	25	16	19	11

plete fruits or naked seeds in any of the footprint traps. In the second day, the traps were checked at 20:30 hrs and both naked seeds and complete fruits were removed from plots one and two. In plot number three all naked seeds were removed, while only two complete fruits were left. In the third day at 5:30, naked seeds and fruits of trap four were totally removed. No fruits or seeds were removed from trap five.

Accesibility. A greater proportion of naked seeds than complete fruits was removed from our treatments of removal. No statistical differences were found in terms of removal of exposed versus non-exposed fruit products (χ^2=0.04; p=0.83) (Table 2).

Discussion

Phenological patterns in tropical areas are mainly determined by precipitation regimes, with a general overall fruit production tied to the rainy seasons and fruit scarcity associated with dry seasons (Janzen 1967, van Schaik *et al.* 1993). However, modifications from the general pattern have been selected in some plants, in order to avoid competition for fruit dispersal by primary and secondary consumers (Lobo *et al.* 2003). The region of Guanacaste (Figure 1), presents a marked seasonality (Hagnauer 1980) where crops of *B. alicastrum* have been observed between March and June (Martínez 2010). A main peak of production in the study area is reported within the «veranillo» or «canícula» (Chavarria, pers comm 2001), a weather phenomenon that occurs in Central America during what is traditionally known as the «rainy season» («*invierno*», locally in Costa Rica). It is basically an interruption of the rainy season for about a month, starting around solstice on June 21

(CATIE 1982). The reduction of precipitation at this time has a strong effect on the general production of fruits in the area, and just few species of plants with crops, such as *B. alicastrum,* are presumably available for the frugivore community (Chavarria, pers comm 2001, Martínez 2010). During our observation time a large amount of fruits of *B. alicastrum* was available on the branches for few days and then production fell down drastically. That may explain the concentration of primary and secondary consumers on the tree. Trees with a long-term range of production distribute the attention of primary and secondary consumers in time (van Shaik *et al.* 1993). The massive production of fruits of *B. alicastrum* within this period attracts at least six frugivore mammals, including: the two primate species present in Palo Verde (*A. palliata* and *C. capucinus*). Although *A. palliata* has been considered primarily as a folivorous species, studies on their feeding behavior have shown the importance of fruit fraction in their diet (Milton 1980, 1981, Terborgh 1983, 1986, Silver *et al.* 1998). During our samples, howlers used the *B. alicastrum* tree as their sleeping site, spending a significant portion of their feeding time to selection and handling of fruits. These primates dropped a greater proportion of naked seeds than complete or partially consumed fruits. In contrast, the short periods of exploration of *C. capucinus* at the tree, conditioned a sloppy use of fruit resources offered by *B. alicastrum*, as inferred by the larger proportion of complete fruits in apparent good conditions and partially consumed fruits dropped on the ground by these primates. Fruits on the ground attracted four species of mammals identified as potential secondary consumers including two ungulates (*O. virginianus* and *T. tajacu*), a carnivore (*N. narica*), and a rodent (*D. punctata*). Some authors suggest that from the perspective of the frugivore community, the degree of association of resources in the space is one of the most important aspects that address the selection of specific patches of resources (Terborgh 1986). In our first sampling day approximately 10.000 fruits remained on the *B. alicastrum* tree branches, implying a low number of fruits on the ground. The same day, no seeds or complete fruits were removed from the traps. In day two and three, fruits available on the tree decreased one order of magnitude, most of them falling directly under the crown. Within the second and third sampling days, the majority of the fruits were removed from the traps. Although it is difficult to determine if exploration of the plots were actually accompanied by consumption, it is interesting that footprints of *D. punctata* were only documented on inner squares with naked seeds and tracks of *N. narica* were only registered on inner squares with complete fruits. The ungulates *O. virginianus* and *T. tajacu*, with the greater number of tracks, were the most active potential secondary consumers with most of their footprint tracks recorded on inner squares containing naked seeds. Although we were able to identify independent tracks of footprints, the nature of our experimental design prevented us to determine the actual number of individuals visiting the plots. It is known that the two ungulates documented forage in groups (Reid 1997). In contrast, *D. punctata* and males of *N. narica* are more likely to be solitary animals (Reid 1997). We expect that this preliminary data motivate further experiments on this phenomenon.

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