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Authors: Mourthé, Ítalo M. C., Strier, Karen B., and Boubli, Jean P.

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ARTICLES

SEED PREDATION OF *MABEA FISTULIFERA* (EUPHORBIACEAE) BY NORTHERN MURIQUIS (*BRACHYTELES HYPOXANTHUS*)Ítalo M. C. Mourthé^{1,2}, Karen B. Strier³ and Jean P. Boubli^{4,5}¹ Dept. of Zoology, Universidade Federal de Minas Gerais, Brazil² Departamento de Ecologia, Instituto Nacional de Pesquisas da Amazônia, Brazil, email: <imourthe@gmail.com>³ Dept. of Anthropology, University of Wisconsin-Madison, USA⁴ Dept. of Anthropology, University of Auckland, New Zealand⁵ Conservation and Research for Endangered Species of the Zoological Society of San Diego, USA**Abstract**

Seeds are staple foods in the diets of primates with morphological and behavioral specializations for seed predation, but are considered a less important resource for most other primates. Here we report the first observation of seed predation by northern muriquis (*Brachyteles hypoxanthus*). Twenty-four *Mabea fistulifera* (Euphorbiaceae) seed eating events were observed during a systematic study of two groups of northern muriquis in an Atlantic forest fragment in southeastern Brazil in July 2003, accounting for 2.9% of 836 feeding records during this month. Only unripe seeds were consumed in all records. The absence of *Mabea fistulifera* seeds in any of the 102 fecal samples examined suggests that the seeds were predated. Analyses of 47 fruits of *Mabea fistulifera* collected in different stages of ripeness in June 2004 indicated that fruits at earlier stages of ripeness were significantly softer than ones of later stages, implying that fruit hardness made their seeds unprofitable to these non-specialized seed predator monkeys.

Key Words: Plant-herbivore interaction; seed predation; food choice; fruit hardness.

Resumen

Las semillas son un alimento esencial en la dieta de los primates con adaptaciones morfológicas y comportamentales para la predación de estas, pero son consideradas un recurso alimentario menos importante por la mayoría de otros primates. Reportamos aquí la primera observación de predación de semillas por muriquís del norte (*Brachyteles hypoxanthus*). Veinticuatro eventos de consumo de semillas de *Mabea fistulifera* (Euphorbiaceae) fueron observados durante un estudio sistemático de dos grupos de muriquís del norte, en dos fragmentos de bosque Atlántico del suroeste de Brasil en Julio de 2003, correspondiendo estos al 2.9% de 836 registros de alimentación durante este mes. Solamente fueron consumidas semillas inmaduras durante los registros de alimentación. La ausencia de semillas de *Mabea fistulifera* en cualquiera de las 102 muestras de deposiciones de *B. hypoxanthus* examinadas sugiere que las semillas fueron predadas. Análisis de 47 frutos de *Mabea fistulifera* colectados en diferente grado de maduración durante Julio de 2004, mostraron que estos son significativamente más blandos durante las etapas más tempranas de maduración, que durante una etapa de maduración avanzada, implicando que la dureza de los frutos imposibilita el aprovechamiento de las semillas por parte de estos primates no especializados para tal fin.

Palabras Clave: Interacciones planta-herbívoro; predación de semillas; selección de alimento; dureza de fruto.

Introduction

Compared to ripe fruit, seeds are valuable resources in terms of their nutritional content and their relative abundance in space and time (Norconk *et al.*, 1998). Fruits are generally rich in calories, moderate in fiber and low in protein and secondary compounds (Milton, 1993). Seeds, by contrast, are relatively low in water soluble carbohydrates, highly variable in protein, and high in fat, fiber and secondary compounds (Kinzey and Norconk, 1993). To protect their seeds from predation, plants often invest in mechanical defenses such as increasing fruit hardness or toughness (Lucas *et al.*, 2000). Primates are regarded as seed predators when they destroy the seeds by masticating and digesting them (van Roosmalen *et al.*, 1988; Gautier-Hion *et al.*, 1993). Occasional seed predators, such as brown capuchin monkeys (*Cebus apella*: Peres, 1991) or gray woolly monkeys (*Lagothrix lagotricha cana*: Peres, 1994) incorporate small proportions of seeds from a few plant species into their diets, while other primates, such as Pitheciines (van Roosmalen *et al.*, 1988; Kinzey and Norconk, 1993;

Peres, 1994; Boubli, 1999; Peetz, 2001; Norconk, 2007), colobines (McKey, 1978), and cercopithecines (Lambert *et al.*, 2004), make a living from eating seeds, which account for up to 75% of their feeding time. Primates that include a wide variety of seeds in their diet have specialized adaptations for seed mastication, including robust canines, procumbent incisors, low relief molars, crenulated enamel, and strong jaw muscles (Kinzey, 1992). Most atelid monkeys, however, exploit ripe fruit pulp instead of seeds, and ingested seeds are usually defecated intact, which may help in the seeds' dispersal (Julliot, 1996; Vieira and Izar, 1999; Stevenson, 2000; Martins, 2006). Furthermore, this group of primates does not possess any specialized adaptations to exploit hard fruits routinely in their diet.

The northern muriqui (*Brachyteles hypoxanthus*) is considered a folivore-frugivore species, with a strong preference for ripe fruits (Strier, 1991). In addition to leaves and fruit, the diet of muriquis often includes flowers, as well as less commonly eaten items such as bark, nectar and seeds. The nectar of *Mabea fistulifera* is known to be an important seasonal resource for both, southern (Torres de Assumpção, 1981) and northern muriquis (Ferrari and Strier, 1992), as well as other vertebrates, particularly during periods of fruit shortage (Vieira *et al.*, 1992; Vieira and Carvalho-Okano, 1996; Passos and Kim, 1999; Olmos and Boulhosa, 2000; Miranda and de Faria, 2001). The consumption of seeds of the genus *Mabea* has been reported in *Cebus nigritus*, which occurs sympatrically with both southern (Torres de Assumpção, 1981) and northern muriquis (Rímoli, 2001), as well as in other primates such as *Cebus capucinus* (Oppenheimer, 1982) and *Cebus apella* (Peres, 1993), some birds (*Leptotila verreauxi* and *Crypturellus* sp.: Vieira *et al.*, 1992), and several ant species (*Megalomyrmex* sp. and *Pheidole* sp.: Peternelli *et al.*, 2004) in other areas. However, muriquis have not previously been observed to eat the seeds of this species.

We first observed seed consumption of *Mabea fistulifera* by northern muriquis in July 2002, when two seed predation events were recorded on different days, but fruit ripeness was not determined. A subsequent predation event was observed in June 2003, when fruit could be visibly determined as being in an early stage of ripeness. In this paper we report systematic records of northern muriquis eating seeds of *Mabea fistulifera*, and investigate fruit puncture resistance as a basis for fruit and seed choice by this species.

Methods

The study was conducted at the RPPN Feliciano Miguel Abdala, hereafter Reserve (previously known as Estação Biológica de Caratinga; 19° 50' S, 41° 50' W). The Reserve is a forest fragment of 957 ha of sub-montane semideciduous Atlantic forest, most of it in advanced stages of succession and has been described in detail elsewhere (Strier and Boubli, 2006). Seed predation on *Mabea fistulifera* was systematically recorded in July 2003 during

200 observation hours on two habituated groups, which were followed from dawn until dusk on alternate days over 21 days. The study groups, Jaó and Nadir, included about 60 and 40 individuals, respectively, utilizing partially overlapping home ranges in the northern part of the forest (Jaó valley; Boubli *et al.*, *in prep.*). All feeding records (FRs) in which monkeys were seen eating any food item were noted following methods employed by Boubli (1999). Feeding bout focal samples (FBFS) were also conducted opportunistically as soon as an individual entered and began feeding in a *Mabea fistulifera* tree (Strier, 1989; Mourthé, 2006). During FBFS, the times the animal entered and left the tree were recorded, and the items consumed were noted. As seed ingestion of *Mabea fistulifera* occurred rarely, we calculated the relative importance of seeds as a proportion of diet by summing the seed eating records and dividing by the total number of feeding records obtained during the same study period in July 2003 (N=836). A total of 102 fecal samples, collected while the groups were being followed during this period, were later washed and examined closely for any traces of *Mabea fistulifera* seeds.

In June 2004, 47 *Mabea fistulifera* fruit samples at different stages of ripeness were collected. The length and width of each fruit and seed was measured to the nearest mm with a steel caliper. Resistance to puncture was assessed with a Macro-line [0-20 Kg] Spring Scale Pesola® adapted with pressure accessories (pin 5 mm width). Fruit hardness was sampled in a way that mimics muriqui feeding behavior (e.g., monkeys were often seen biting the side of *Mabea fistulifera* fruits and usually bit a fruit only once before discarding it or open it). Resistance to puncture was defined as the maximum pressure applied immediately prior to fracturing the fruit husk, and was measured by slowly and continuously submitting the side of a whole fruit to the penetrometer pin until the husk fractured (Kinzey and Norconk, 1990). Each fruit was tested only once because it was destroyed in the process of measuring its resistance. Resistance to puncture was measured in megapascals (MPa), based on the following formula: $MPa = ((F * G) / area) / 1,000,000$ (A. Marques, *pers. comm.*), where F is the force (kg) needed to break the fruit husk; G , is the gravity acceleration (e.g., 9.80665 m/s^2); and $area$, is the point of the pin surface (m^2). A Pascal is equivalent to one Newton per square meter, and it is a proper SI unit of pressure measurement (Lucas *et al.*, 2000). Fruit volume was calculated as a sphere. Because *Mabea fistulifera* is a dehiscent species (disperse their seeds explosively), the process of fruit maturation is complex and fruit color or size alone were not reliable indicators of fruit ripeness. Specifically, we observed that ripe fruits lost water and this promotes a small but noticeable size reduction (e.g., really ripe fruits are smaller than unripe ones). Fruit color also changed somewhat from reddish-green husks when unripe to reddish-brown husks when ripe. As muriquis were never seen eating ripe fruits of *Mabea fistulifera*, this stage was not collected or processed in this study and all fruits, and consequently seeds, consumed and tested in our sample

were considered as unripe. We distinguished two types of unripe fruits, early and late, based on the presence of a thin brown coat covering the seeds in the late unripe stage. During this study period, the first fruits appeared in the beginning of June, becoming abundant from the end of June through the middle of July, which corresponds to the peak dry season at this site (Strier, 1991).

Results

A total of 24 records of predation on *Mabea fistulifera* seeds were observed during July 2003, representing 2.9% of the 836 FRs obtained during this month. In all records, unripe seeds were consumed by adult individuals. Northern muriquis spent on average 4.8 ± 2.9 min (Mean \pm SD; range 1-9 min; N=5) consuming seeds from *Mabea fistulifera* trees. No intact seeds of *Mabea fistulifera* were found in examinations of any of the 102 fecal samples collected during the same period. *Mabea fistulifera* fruits are hard, dry, spherical dehiscent cocci, containing an average of 3.0 ± 0.28 (N=47) small seeds (seed length = 7.7 ± 0.89 mm; seed width = 5.4 ± 0.42 mm; wet weight per seed = 0.12 ± 0.02 g; N=28 seeds). Whole fruits had an average length of 17.8 ± 1.49 mm and an average width of 17.0 ± 1.92 mm, and weighed 2.99 ± 0.79 g (N=42 fruits). Fruit volume was significantly greater in the late stage (38.7 ± 2.15 mm³; range 34.6-41.2 mm³; N=12) than early stage of ripeness (35.1 ± 3.57 mm³; range 29.6-40.2 mm³; N=32; Wilcoxon rank sum test $W=79$, $p < 0.01$). Fruits in the late stage were also significantly harder (6.34 ± 2.51 MPa; median = 7.19 MPa; range 0.40-9.20 MPa; N=12) than fruits in an earlier stage of ripeness (1.86 ± 1.89 MPa; median = 1.87 MPa; range 0.32-6.50 MPa; N=33; $W=40$, $p < 0.001$; Figure 1).

Discussion

Our results indicate that northern muriquis opened the cocci of *Mabea fistulifera* and consumed their seeds at a relatively early stage of ripeness, presumably because the fruit husks become increasingly tough as the fruit matures, increasing the difficulty of processing them and inhibiting seed consumption at late stages of ripeness. *Mabea fistulifera* is one of the hardest fruits opened by northern muriquis at our study site. As northern muriquis lack the morphological specializations required to deal with hard fruits, they should be consuming only the early unripe, and consequently softer, fruits of this species. During this study, the northern muriquis were seen biting and discarding several unopened fruits of *Mabea fistulifera* before finally opening one and ingesting their small seeds, discarding the dry exocarp. Monkeys often took fruit bunches in their hands and bit several fruits at the same bunch one by one, breaking fruit husks by the teeth only, although we could not determine whether they were sampling and puncturing with their canines or premolars or both. By means of this behavior, northern muriquis appeared to be sampling for fruits that could be easily opened to extract their seeds, all of which were probably at early stages of ripeness. This behavior suggests that puncture resistance dictates northern muriqui food choices while consuming the seeds of this species.

Considering the muriquis' large body size, it is possible that although they may be capable of breaking the hard husks of *Mabea fistulifera* fruits in late stages of ripeness, they avoided doing so because of the high costs/benefit ratio of handling time versus energy gain for such small

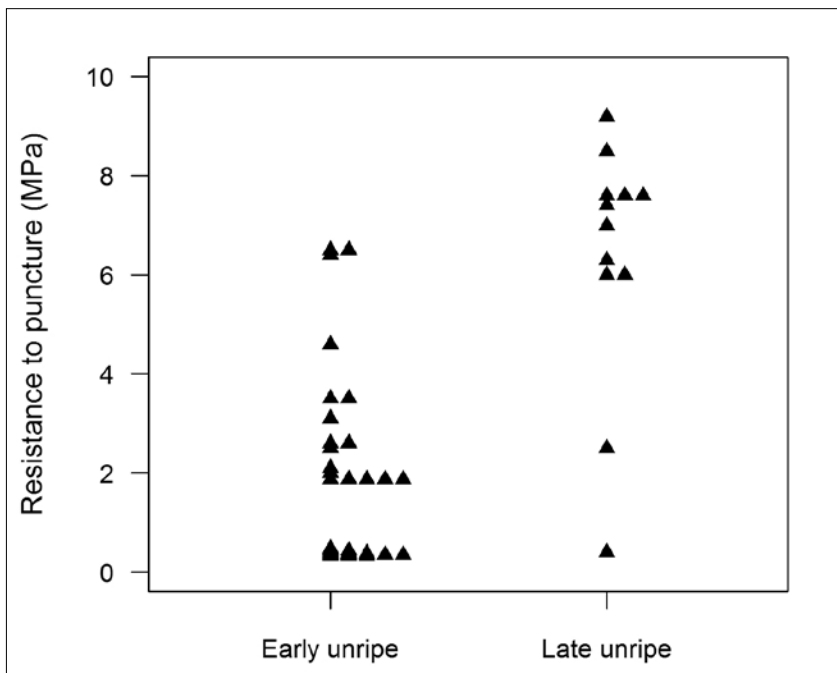


Figure 1. Resistance to puncturing of earlier (N = 28) and late unripe (N = 12) *Mabea fistulifera* fruits.

seeds (Charnov, 1976). Northern muriquis may be capable of opening late unripe fruits, but it may not be profitable for them to do so. In a previous study, Martins (2007) found that the southern muriqui, *Brachyteles arachnoides*, selects unripe seeds of fleshy/protected as well as dry fruits based on the availability of these types in her study area. Unfortunately, we do not have systematic measures of *Mabea fistulifera* seed availability during our study, but northern muriquis appeared to consume their unripe seeds during the period when they were most abundant and also when the majority of fruits were at earlier stages of maturity (from end of June to middle of July). By mid-July, the husks of the fruits become much harder as the fruits ripen. Thus, there appears to be a fairly narrow window of time during which *Mabea fistulifera* fruits are soft enough for northern muriquis to break open and ingest their seeds. Muriqui seed predation could thus be considered as a seasonal phenomenon, similar to that described for *Lagothrix lagotricha cana* in the Amazon (Peres, 1994).

In addition to fruit hardness, other characteristics, such as nutrient content and palatability, could account for the northern muriquis' selection of early unripe *Mabea fistulifera* fruits. Indeed, because the muriquis' are known to consume nectar from the inflorescences of this species between late April and May at this site (Ferrari and Strier, 1992; Mourthé, 2006), they would be familiar with resource, and primed to exploit it for other items, such as seeds. There is evidence that the mid-dry season, when they consumed these seeds, is a period of food shortage at our study site (Strier, 1991). *Mabea fistulifera* seeds are very rich in oil (Vieira *et al.*, 1992), which could provide an important source of energy when other fruits that are easier to process are scarce. Indeed, the seasonal inclusion of seeds in the diets of other primates is thought to compensate for seasonal fruit shortages (Norconk, 2007). Even small seeds can be valuable sources of protein and lipids, as in the case of three other Euphorbiaceae species (*Maprounea guianensis*, *Sapium aubletianum* and *Actinostemon schomburgkii*), which are known to have high lipid and protein levels (Norconk and Conklin-Brittain, 2004).

Palatability is strongly influenced by the percentage of secondary compounds stored in plant parts. However, the concentrations of these toxic metabolites are known to be lower in the leaves of fast-growing trees (Coley *et al.*, 1985). *Mabea fistulifera* is considered to be a pioneer species (Olmos and Boulhosa, 2000; Peternelli *et al.*, 2004), and as such, may be similar to other fast-growing trees that invest less in the production of chemical defenses and therefore have few, if any, secondary metabolites stored in their seeds. Moreover, Norconk and Conklin-Brittain (2004) found no differences in tannin levels between plant parts eaten and not eaten by Venezuelan white-faced sakis (*Pithecia pithecia*). Monkeys could accept a trade-off for foods that are high in antifeedants but also high in nutrients (Kinzey and Norconk, 1993; Norconk and Conklin-Brittain, 2004). Therefore, whatever chemical compounds

may be present in *Mabea fistulifera* seeds may not be as efficient in deterring a primate that deals on a daily basis with the detoxification of a great amount of plant secondary compounds abundant in mature leaves (Kinzey and Norconk, 1990) such as northern muriquis do. The impact of secondary compounds on herbivores' diets is very difficult to assess (Janzen, 1978), and analyses of the chemical and nutritional properties of *Mabea fistulifera* seeds are needed to evaluate how they might interact with fruit hardness and ripeness to influence the stage at which muriquis consume them. For instance, black colobus monkeys (*Colobus satanas*) consume high levels of secondary compounds in seeds, but ignore leaves with similar concentrations of these chemicals because of the great reward in nutrients they are able to get on seeds (McKey, 1978).

Northern muriquis were also seen feeding but not destroying seeds from other plant species (e.g., *Aspidosperma* sp., *Cabralea canjerana*, *Carpotroche brasiliensis*, *Clusia* sp., *Copaifera langsdorffii*, *Gomidesia crocea*, *Hymenaea courbaril*, *Mucuna* sp., *Nectandra rigida*, *Ocotea* sp., *Phyllostemonodaphne geminiflora*, *Phyllostemonodaphne* sp., *Rheedia gardneriana*, *Symphonia globulifera* and *Virola oleifera*) in the southern part of the Reserve (Strier, 1991; Rímoli, 2001). For instance, northern muriquis feed heavily on fruits of *Carpotroche brasiliensis* when they are available during the driest months of the year (June-August), and the seeds are later found intact in their feces or masticated, indicating that northern muriquis can serve as both seed dispersers and predators (Strier, 1986). Although we were able to find seeds of other species as small as 2 mm in our present analyses of muriqui fecal samples, no intact seeds of *Mabea fistulifera* were found, implying that these seeds were chewed up and digested, consistent with seed predation practices observed in other primates (Gautier-Hion *et al.*, 1993). We guess that these small seeds are being completely destroyed because they are the only reward of *Mabea fistulifera* dry fruits. However, it is important to keep in mind that the low abundance of *Mabea fistulifera* seeds in northern muriqui diet could reduce the chances of finding them in the fecal samples.

Several studies have examined the hardness of foods ingested by primates relative to their morphological and behavioral adaptations (Kinzey and Norconk, 1990, 1993; Peres, 1993; Norconk *et al.*, 1997; Lambert *et al.*, 2004), but few have evaluated fruit hardness relative to the nutritional content and palatability of other foods available at the times of year during which seeds are predated (Kinzey and Norconk, 1993; Norconk and Conklin-Brittain, 2004). More studies of this type are needed to help us better understand the relationship between primate food choices and the characteristics of the fruits that they eat.

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