

Seasonal variation of consumption of the species used as fruit source by brown howler monkeys (*Alouatta clamitans*) in southern Brazil

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Abstract: Considering the seasonal variation of fruits availability in seasonal semideciduous forests, this study analyzed whether the richness of fruit species exploited by *Alouatta clamitans* is higher in the rainy period rather than the dry one. Plant species consumed were investigated by visualization and feces analysis, from July 2005 to June 2006, in a seasonal semideciduous forest fragment in Paraná state, Brazil. Ten species of fruits were consumed during the rainy period and 13 during the dry period: three were consumed exclusively during the rainy period; six exclusively during the dry period; and seven in months that covered both dry and rainy periods. The number of fruit species consumed during the rainy period was considerably lower than the expected richness. Moreover, among fruit species consumed during the rainy period, only four bear fruits mainly in this period of the year, the other species bear fruits in great part of it. Therefore, the selectivity of *A. clamitans* was mainly directed to species capable of providing fruits along the year, prioritizing these species even when other fruit sources are available.

Keywords: diet, frugivory, fruiting phenology, guariba, seasonal semideciduous forests.

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Resumo: Em face da variação sazonal na disponibilidade de frutos nas florestas estacionais semidecíduais, este trabalho analisou se a riqueza de espécies de frutos exploradas por *Alouatta clamitans* é maior no período chuvoso do que no seco. As espécies vegetais consumidas foram investigadas por visualização e análise de fezes, entre julho de 2005 e junho de 2006, em um fragmento de floresta estacional semidecidual no estado do Paraná, Brasil. Dez espécies de frutos foram consumidas durante o período chuvoso e 13 durante o período seco: três foram consumidas exclusivamente durante o período chuvoso; seis exclusivamente durante o período seco; e sete em meses que abrangeram tanto o período seco quanto o chuvoso. O número de espécies de frutos consumidas durante o período chuvoso foi consideravelmente menor do que a riqueza esperada. Além disso, entre as espécies de frutos consumidas durante o período chuvoso, apenas quatro apresentam frutos principalmente nesse período do ano, as outras espécies apresentam frutos em grande parte do ano. Assim sendo, a seletividade de *A. clamitans* foi direcionada principalmente para espécies capazes de fornecer frutos ao longo do ano, priorizando essas espécies mesmo quando outras opções de frutos estão disponíveis.

Palavras-chave: dieta, frugivoria, fenologia da frutificação, guariba, floresta estacional semidecidual.

Introduction

The primates of genus *Alouatta* Lacépède, 1799 (howler monkeys) are the most folivorous in the Neotropics (Strier 1992). Nevertheless, they are characterized as folivorous-frugivorous (Crockett & Eisenberg 1987), due to an important contribution to their diet of ripe and unripe fruits, besides young and mature leaves. To a lesser extent, they also ingest petioles, buds, flowers, seeds and stems (Neville et al. 1988). Their diet is seasonally variable, with constant consumption of mature leaves, and consumption of fruits, flowers and young leaves according to environmental availability (Bicca-Marques & Calegari-Marques 1995, Queiroz 1995). In fact, fruit intake may reach more than half the consumption during the greatest abundance period of this resource (Prates et al. 1990, Aguiar et al. 2003).

Since the resource distribution and supply in forests affect the abundance, displacement (Levey 1994) and reproductive success of many vertebrates (Powlesland et al. 1997), maintaining the resource supply throughout the year is essential to the conservation of these species (Reys et al. 2005, França et al. 2009). The concern with the resources provision must be even higher in fragmented landscapes, such as the northern region of Paraná state, Brazil. Although howlers are known for their ability to persist in both conserved and disturbed conditions, they are negatively affected by high levels of habitat loss, fragmentation and degradation. Patch size appears to be the main factor constraining populations in fragmented habitats, probably because patch size is positively related to food availability, and negatively related to anthropogenic pressures, physiological stress and parasite loads. In general, food availability decreases with patch size, not only due to habitat loss, but also because the density of big trees, plant species richness and howlers' home range size are lower in smaller patches, where howlers' population densities are commonly higher (Arroyo-Rodríguez & Dias 2010).

Most tropical forest communities, especially those in seasonal environments, display seasonal variation in the presence of young leaves, flowers, and fruits (Van Schaik et al. 1993). In seasonal semideciduous forests in Paraná state the availability of zoochorous fruits is higher during the rainy period in comparison to the dry period (Carmo & Morellato 2000, Novaes 2007, Perina 2011). Due to the seasonal variation of resource availability, this study aimed to analyze the species' fruiting period and consumption by brown howler monkey, *A. clamitans* Cabrera, 1940, in a forest fragment in northern Paraná state and to test the hypothesis that the richness of fruit-producing species exploited by *A. clamitans* is higher during the rainy period rather than the dry period.

Material and Methods

The study was conducted in Doralice Farm (23° 16'S and 51° 03'W – farm headquarters) located in the municipality of Ibiporã, Paraná state, Brazil. The farm is adjacent to the Tibagi River at 484 m of altitude. Approximately 100 ha are covered by continuous forest vegetation classified as seasonal semideciduous forest (Soares-Silva et al. 1992), surrounded by pastures, and by palm and soybean cultivation, bordering the Tibagi river on south and east.

The climate is humid subtropical (Köppen climate classification *Cfa*). The average annual temperature is 21.9 °C and the average pluvial precipitation is 1570 mm. There is a drop in temperature and precipitation from March to September, characterizing the autumn and winter as a colder and drier period (Soares-Silva et al. 1992), July being the coldest month and February the hottest month (Costa et al. 2011). During dry period 20 to 50% of the trees drop totally or partially their leaves (Instituto... 1992) and flowers and zoochorous fruits become less available (Carmo & Morellato 2000, Novaes 2007, Perina 2011).

The fieldwork took place from July 2005 to June 2006, counting with direct observations totalizing 24 hours per month in the autumn and winter and 27 hours in spring and summer, corresponding to two days from sunrise to sunset. The group of *A. clamitans* observed had five individuals at the beginning of the work (one adult male, one subadult male, two adult females and one juvenile I) and three at the end (one adult male and two adult females) (according to age and sex classification proposed by Mendes 1989).

The fruit species consumed were observed directly (visualization) and indirectly (fecal analyzes).

During direct observations the species consumed were recorded *ad libitum*. Infrutescences, and immature and mature fruits were generically called as "fruits". Plant material was collected, herborized, identified by experts, and deposited in the Herbarium of Universidade Estadual de Londrina - FUEL. The species and name spelling of corresponding authors are in accordance with the species list of Brazil's flora (<http://floradobrasil.jbrj.gov.br/>).

Indirect observations consisted of feces collection during or after the direct observations or during the animal search. Feces collected were washed in running water over a network mesh of 0.5 mm, placed on absorbent paper to dry and screened with tweezers and magnifying glass, for further seeds identification with the assistance of experts. The difference in the number of species per fecal sample among seasons was compared with the Kruskal-Wallis test, using the BioEstat 4.0 software with significance level of 5%.

Rarefaction curves were generated by EstimateS 9.1.0 software (Colwell 2013), after 100 randomizations on the sampling order with 95% confidence intervals in order to examine whether the species richness observed was greater than, equal to, or lower than the species richness estimated by nonparametric richness estimators ICE and Chao2.

Information about species fruiting period in the region was gathered from the literature (Barneby 1975, Carmo & Morellato 2000, Mikich & Silva 2001, Emmerick 2007, Novaes 2007, Pereira et al. 2007, Perina 2011), and from personal observation during the fieldwork.

Results

Sixteen plant species were identified as fruit source for *A. clamitans*: eleven were identified through visualization and fecal analyses, whereas five were found only in feces (Table 1). In addition to those, six seed species found in feces could not be identified.

Forty-six fecal samples were collected, of which 15 were collected in the winter, 10 in the spring, 9 in the summer and 12 in the autumn. Seeds were found in 82.6% of fecal samples; in the remaining fecal samples only vegetable fibers were found. The species number per fecal sample ranged from zero to six, with an average of 1.8, with no difference among seasons ($H = 3.1726$, $p = 0.3658$).

According to phenology data seven species present fruits all year: *Ficus eximia*, *F. guaranitica*, *F. insipida*, *Guarea kunthiana*, *Cecropia glaziovi*, *Syagrus romanzoffiana* and *Euterpe edulis*; four mainly in the rainy period (spring and summer): *Annona sylvatica*, *Jacaratia spinosa*, *Maclura tinctoria* and *Phytolacca dioica*; three mainly in the dry period (autumn and winter): *Pereskia aculeata*, *Ocotea silvestris* and *Psidium sartorianum*; and one in the end of the rainy period and in the early dry period: *Hyperbaena domingensis* (Table 1). A phenological study of *F. trigonata* has not been found for the region, however, it can be inferred from *A. clamitans* feeding data that the species presents fruits in the dry period. Considering the main period of fruiting, the same number of species provides fruits in both rainy and dry periods. However, 13 species present fruits in

at least one month of the rainy period and 15 species present fruits in at least one month of the dry period (Table 1).

Three fruit species were consumed exclusively during the rainy period: *A. sylvatica*, *J. spinosa* and *P. dioica*; six exclusively during the dry period: *E. edulis*, *P. aculeata*, *O. silvestris*, *P. sartorianum*, *H. domingensis* and *F. trigonata*; and seven in months covering both the dry and the rainy period: *F. eximia*, *F. guaranitica*, *F. insipida*, *G. kunthiana*, *C. glaziovii*, *S. romanzoffiana* and *M. tinctoria* (Table 1). In total, 10 species were consumed during the rainy period and 13 during the dry period.

The rarefaction curves depicted in Figure 1 reflect the richness of fruit species consumed in rainy and dry periods. The number of fruit species consumed during the dry period was close to that expected by ICE and Chao2 estimators, whereas the number of fruit species consumed during the rainy period was considerably lower than the estimated richness.

The fruit species consumed in most months were *F. eximia* (whose fruits were consumed in eight months of the year), *F. guaranitica* and *F. insipida* (whose fruits were consumed in five months of the year). Most fruit species were consumed only during one or two months.

Table 1. Presence of fruits (light gray) or dispersal (dark gray) for the species with a record in the region, and consumption of fruits by *Alouatta clamitans* in the forest fragment of Doralice Farm (Ibiporã, Paraná, Brazil) from July/2005 to June/2006, according to the information source (V = visualization; F = feces analysis). R = record in the Herbarium FUEL. Autumn: April, May and June; Winter: July, August and September; Spring: October, November and December; Summer: January, February and March. ¹Perina (2011); ²Mikich & Silva (2001); ³Emmerick (2007); ⁴Pereira et al. (2007).

Species	R	Autumn			Winter			Spring			Summer		
		A	M	J	Jl	Au	S	O	N	D	J	F	M
<i>Ficus eximia</i> Schott ³	41865	F	F	-	V/F	V/F	F	-	-	F	F	-	V/F
<i>F. guaranitica</i> Chodat ⁴	41861	V/F	-	-	-	V/F	-	F	-	-	V/F	-	F
<i>F. insipida</i> Willd. ³	41863	F	V/F	F	F	-	-	V/F	-	-	-	-	-
<i>Guarea kunthiana</i> A. Juss. ¹	41882	-	-	-	-	F	F	F	-	-	-	-	-
<i>Cecropia glaziovii</i> Sneathl. ²	41862	-	-	V	-	-	-	-	F	-	-	-	-
<i>Syagrus romanzoffiana</i> (Cham.) Glassman ¹	41870	-	F	F	-	F	-	-	-	-	-	-	F
<i>Euterpe edulis</i> Mart. ¹	41869	F	-	-	-	-	-	-	-	-	-	-	-
<i>Annona sylvatica</i> A.St.-Hil. ¹	41221	-	-	-	-	-	-	-	-	-	-	-	V/F
<i>Jacaratia spinosa</i> (Aubl.) A. DC. ¹	41220	-	-	-	-	-	-	-	-	-	-	-	V/F
<i>Maclura tinctoria</i> (L.) D. Don ex Steud ²	41886	F	-	-	-	-	-	-	V/F	-	-	-	-
<i>Phytolacca dioica</i> L. ²	41880	-	-	-	-	-	-	-	F	-	-	-	-
<i>Pereskia aculeata</i> Mill. ²	41894	-	-	V/F	-	-	-	-	-	-	-	-	-
<i>Ocotea silvestris</i> Vattimo-Gil ²	41887	-	-	-	V/F	F	-	-	-	-	-	-	-
<i>Psidium sartorianum</i> (O. Berg) Nied.	41889	-	-	F	V/F	V/F	-	-	-	-	-	-	-
<i>Hyperbaena domingensis</i> (DC.) Benth.	41878	-	-	F	-	-	-	-	-	-	-	-	-
<i>F. trigonata</i> L.	41864	-	-	F	V	-	-	-	-	-	-	-	-

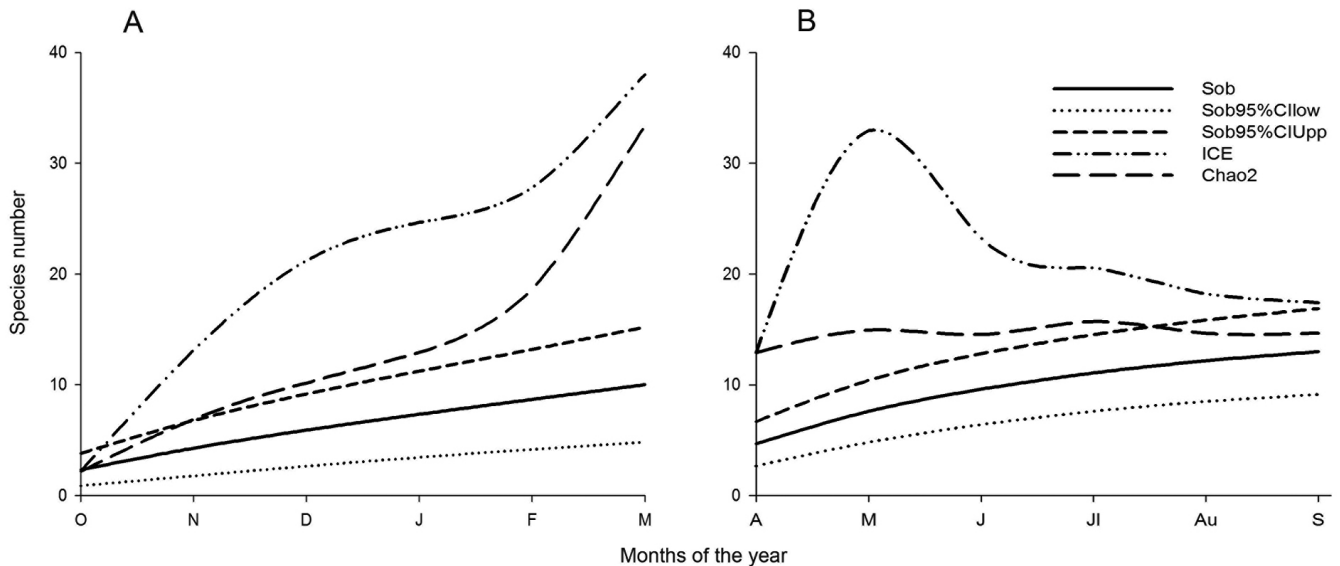


Figure 1. Number of fruit species consumed by *Alouatta clamitans* in the forest fragment of Doralice Farm (Ibiporã, Paraná, Brazil) from July/2005 to June/2006. Rarefaction curves for species richness observed (Sob) during (A) rainy period (October to March) and (B) dry period (April to September) with 95% confidence intervals and species richness estimated by nonparametric richness estimators ICE and Chao2.

Discussion

Feces collection was extremely important, since one third of fruit sources was exclusively known by this method, in addition to six seed species not identified. Although the sampling effort has remained the same throughout the year, the number of fecal samples collected was lower in the spring and summer because the incidence of rain dismantled the feces. Difference in the number of fecal samples probably did not affect the results because the proportion between species consumed in each period remains the same considering both methods or only species found exclusively in the feces.

Phenology and fruit consumption data show that there is a complementation between the fruiting periods in this community. The studied fragment provides fruits along the year, even during the dry period, when there is typically less resource supply for wildlife. The zoochorous fruits availability along the year is important for nutritional and energetic balance of *A. clamitans*, as well as other animals, especially those predominantly frugivorous that depend on this item to survive. Therefore, the forest fragment of Doralice Farm, though relatively small and having a proportionally large area occupied by edges - due to its elongated shape - preserves important features for wildlife maintenance. This complementation between fruiting periods was observed for the ornithocoric species in seasonal semideciduous forest in the state of São Paulo, although the fruit species consumed by primates *Sapajus nigritus* (Goldfuss 1809) (capuchin monkey) and *A. clamitans* showed no marked pattern of sequential fruiting (Galetti 1992).

The fruit consumption of *Ficus* spp. by *A. clamitans* during several months of the year was also reported by Prates et al. (1990) and Aguiar et al. (2003), not surprisingly, due to its known intraspecific asynchronous fruiting pattern (Milton 1991, Bicca-Marques 2003, Tweheyo & Lye 2003, Emmerick 2007). However *Ocotea* Aubl. (Miranda & Passos 2004), *S. romanzoffiana*, and *Coussapoa microcarpa* (Schott) Rizzini (Prates et al. 1990) were similarly pointed as fruit sources present in the diet of *A. clamitans* most of the year. In southern Amazon rainforest *Dialium guianense* (Aubl.) Sandwith was the main fruit source for *A. discolor* (Spix, 1823) (red-handed howler), used during six months of the year (Pinto & Setz 2004).

The consumption of most fruit species only during one or two months was also reported by Pinto & Setz (2004) for *A. discolor* and by Aguiar et al. (2003) for *A. clamitans*.

Although producing fruits during a long period, some species were consumed within a few months. However, it is possible to notice in these cases that consumption occurred mainly during the months when fruits are ripe and ready for dispersal. For instance, *E. edulis* produces fruits almost the whole year, but the fruits were only consumed in April, one of the months in which the species dispersal occurs (Perina 2011); *G. kunthiana* bears fruits all year, but its fruits were consumed only from August to October, the species dispersal period (Perina 2011); *P. dioica* bears fruits from August to March, but its fruits were only consumed in December, one of the months in which dispersal occurs (Mikich & Silva 2001).

According to Carmo & Morellato (2000), although there are zoochorous species producing ripe fruit along the year in the riparian forests of the Tibagi river, there is a higher number of species fruiting during the rainy period. Therefore, a higher number of fruit species consumed during the spring and summer was expected compared to autumn and winter. Contrary to the expectations, *A. clamitans* exploited a relatively low number of fruit species during the rainy period. In similar proportions with the present study, Ludwig et al. (2008) reported that most sources of fruits - five species - consumed by black-and-gold howler monkeys, *A. caraya* (Humboldt 1812), in riparian forest in the Upper Paraná River (mainland) were used both

in the rainy and dry period, whereas three were consumed exclusively during dry period and one exclusively in the rainy period.

Differently from our findings, Ludwig et al. (2008) studying *A. caraya* in an island in the Upper Paraná river, and Aguiar et al. (2003) studying *A. clamitans* in Doralice Farm, reported a higher richness of fruit species consumed exclusively during the rainy period, in comparison to species consumed exclusively in the dry period or those consumed in both periods. Prates et al. (1990) studying *A. clamitans* in Parque Estadual de Itapuã, southern Brazil, reported that about a half of fruit species was consumed exclusively during the rainy period, the remaining fruit species were consumed in both periods, and none was consumed exclusively in the dry period. They dismembered the fruit supplying plants into three groups: preferred perennial species - fruit throughout the year and are always consumed; preferred annual species - fruit only during certain times of the year but are widely exploited during these periods; and alternative species - plants with a long-term bearing periods, but from which fruits are eaten only occasionally. Most of the fruit species consumed by the group they studied was "preferred annual species", all fruiting and being consumed in the rainy period. These reports suggest that howlers exploit fruit species available during the dry period but expand fruit sources when there are more options to choose.

Among so many species that bear fruits during the rainy period, why only a few are present on the diet of *A. clamitans* in the forest fragment of Doralice Farm? Many consumers shift food preferences according to their environmental availability. When there is high food availability, consumers tend to focus on high-energy items and on sites with abundance. As a result, they consume fewer food options in greater quantity. In this way, they minimize time and energy spent in searching and maximize energy intake. When there is low food availability, search time is relatively high, leading the consumer to accept a higher number of species as food, even those which are not preferred food resources, rather than ignore them and continue its search for favorite items (Dajoz 2005, Begon et al. 2007). Despite the low number of fruit species consumed in the rainy period, the amount of fruits consumed did not show the same pattern. In the same period of study, summer was the season with the highest rate of fruit consumption and the only season in which time spent on fruit consumption exceeded time spent on leaves consumption (Santos 2007). Hence, the harvest of favorite fruits is probably sufficient during the rainy period, therefore *A. clamitans* does not search for other species; in the dry period, with no preferred fruits in sufficient quantity to supply its nutritional and energetic demands, a higher number of fruit species is exploited.

It is important to remember that howlers are folivorous-frugivorous (Crockett & Eisenberg 1987) and their diet is seasonally variable, with constant consumption of mature leaves, and consumption of fruits, flowers and young leaves according to environmental availability (Bicca-Marques & Calegari-Marques 1995, Queiroz 1995). Thus, in times of low food availability, when consumers tend to accept a higher number of species as food, even lower-quality items, howlers are expected to expand their diet including leaves sources, instead of continuing their search for fruits, which are scarce. The fact that *A. clamitans* expanded fruit sources during the period of low food availability is one more strong indication of the quality of the fragment where it lives.

Among the 10 fruit species consumed during the rainy period, only four bear fruits mainly in this period of the year, the other species bear fruits in great part of it. Even if the trend is the choice of a few species during the period of high food availability, *A. clamitans* could have selected other fruit species among the large number of options, different from those it uses during times of food scarcity.

Among so many species that bear fruits mainly during the rainy period, why only a few are chosen to be part of the diet of *A. clamitans* in this time of the year? In the midst of the tree species sampled in the forest fragment of Doralice Farm (Soares-Silva et al. 1992) there are more than 50 zoochorous species, among which about a third was identified as fruit sources for *A. clamitans*. According to Galetti et al. (2011) monkeys consume fruits of 41% of the 186 zoochorous species sampled in a lowland Atlantic rain forest of the Parque Estadual Intervales, southeast Brazil. Prates et al. (1990) observed that fruit species used for *A. clamitans* comprised only 15.3% of the potential food sources in an adjacent area with the same floristic formation of the Parque Estadual de Itapuã, highlighting its selective diet. The selectivity in the food choice by *Alouatta* is essential to obtain a nutritionally adequate diet (Nagy & Milton 1979). Moreover, using a limited number of plant species and individuals as food sources may allow *Alouatta* to specialize and be more efficient in the use of such resources (Serio-Silva et al. 2002). Differences in chemical and nutritional contents affect the selection of species, individuals, and feed items by *Alouatta* (Silver et al. 2000, Teaford et al. 2006, Welker et al. 2007, Behie & Pavelka 2012a, b, Luecke-Bridgeman 2012), but density, abundance and phenological patterns of plant species strongly influence food selection, since the permanent availability of resources offers the chance to use them intensively and meet their basic nutrient needs, rather than use ephemeral, nutrient-rich resources (Serio-Silva et al. 2002). It can be inferred that the selectivity of *A. clamitans* was mainly directed to species capable of providing fruits along the year, prioritizing these species even when other fruit sources are available.

According to our findings in the dry period several fruit species collaborated to nutritional and energetic balance of *A. clamitans*, whereas during the rainy period a relatively low number of fruit species was exploited, presumably those which could provide fruits in sufficient quantity to supply its nutritional and energetic demands without spending too much time and energy searching. The phenological patterns of plant species clearly influenced food choice, since *A. clamitans* prioritized species that bear fruits throughout the year instead species that bear fruits in a short period of the year.

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