DIET AND ACTIVITY PATTERNS OF BLACK HOWLER MONKEYS *ALOUATTA CARAYA* (HUMBOLDT, 1812, PRIMATES, ATELIDAE) IN ECOTONE CERRADO-PANTANAL IN THE LEFT BANK OF AQUIDAUANA RIVER, MATO GROSSO DO SUL, BRAZIL

José Rímoli[1, 2,3]*, Rodrigo dos Santos Nantes[1]& Antônio Édson Lázaro Júnior[1]

[1] Universidade Federal de Mato Grosso do Sul (UFMS), Licenciatura em Ciências Biológicas, Campus de Aquidauana, Aquidauana, Mato Grosso do Sul, MS, Brasil, Caixa Postal: 135, Av. Oscar Trindade de Barros 740, CEP: 79.200-000 - Bairro da Serraria.

[2] Programa de Pós-Graduação, Mestrado em Biologia Animal, Universidade Federal de Mato Grosso do Sul (UFMS), Campus de Campo Grande, Campo Grande, Mato Grosso do Sul, MS, Brasil. Caixa Postal: 549, Av. Costa e Silva s/n, CEP: 79070-900.

[3] Geopark Bodoquena-Pantanal, FUNDECT, Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul, Rua São Paulo, 1436, CEP 79.010-050.

E-mail: jsrimoli@terra.com.br, rodrigolinguadeboi@hotmail.com, to_saulo@yahoo.com.br

ABSTRACT

The diet and activity patterns of a group of black howler monkeys (*Alouatta caraya*) were monitored on the left bank of the Aquidauana river over 11 months, from September 2008 to July 2009. The group was composed of eight individuals, two adult males, three females and three immature including subadults and infants. Quantitative data were collected using scan sampling method for 5 minutes with an interval of 15 minutes. The general activities budget (n = 6434 records) was 64.7% rest, 18.5% travel, 10.1% feeding, 4.4% for social behavior and 2.3% for miscellaneous behaviors. The level of rest was similar to patterns of genus (64.7%). The diet (n = 606 records) was composed mainly of leaves (72.8%) and flowers (14.8%) and supplemented by fruits (8.2%) and buds (4.2%). The consumption of reproductive parts of plants, especially flowers, was relatively high by the standards of southerly populations of the species. Members of the group rested significantly less than feed during the rainy season. The diet was marked by the consumption of leaves throughout the study. The consumption was higher in the dry at flowers (17.8%) and fruits in the rainy season (12.9%). It also registered a substantial difference in the behavior of adults and immature individuals, where the first rested significantly more, but spent less time in other categories: food, travel and social interactions. Given this, it's likely that the general budget was under the influence of group's composition, where there was a predominance of mature members, a typical pattern in the genus. The results indicate patterns of behavior and diet that are typical to the genus but marginal for the species. The contrasts can be related mainly to the geographic location of the area of the study, the ecotone Cerrado-Pantanal, and concomitant ecological differences. There is a clear need to continue the studies of *A. caraya* in the Bororo region, not only for a more systematic assessment of their ecological patterns, but also to contribute to the development of conservation strategies.

Keywords: black-howler-monkeys; animal biology; behavioral ecology; activity patterns.

RESUMO

DIETA E PADRÕES DE ATIVIDADES DE BUGIOS-PRETOS (*ALOUATTA CARAYA,* HUMBOLDT, 1812, PRIMATES, ATELIDAE) NO ECÓTONO CERRADO-PANTANAL NA MARGEM ESQUERDA DO RIO AQUIDAUANA, MATO GROSSO DO SUL, BRASIL. A dieta e o orçamento de atividades de um grupo de bugios-pretos (*Alouatta caraya)* foram monitorados na margem esquerda do rio Aquidauana ao longo de 11 meses, de setembro de 2008 a julho de 2009. O grupo era composto por oito indivíduos, dois machos adultos, três fêmeas adultas e três imaturos entre subadultos, jovens e filhotes. Dados quantitativos foram coletados em varreduras de 5 minutos, com intervalo de 15 minutos. O orçamento geral de atividades

(n = 6434 registros) foi de 64,7% para o descanso, 18,5% para o deslocamento, 10.1% para alimentação, 4,4% para o comportamento social e 2,3% para comportamentos não mutuamente exclusivos. O nível de descanso foi similar aos padrões do gênero (64,7%). A dieta (n = 606 registros) foi composta, principalmente por folhas (72,8%) e flores (14,8%) e completada por frutos (8,2%) e brotos (4,2%). O consumo de partes reprodutivas de plantas, principalmente flores, foi relativamente alto para os padrões das populações mais meridionais da espécie. Os membros do grupo descansaram significativamente mais e se alimentaram menos na estação chuvosa em relação à seca. A dieta foi marcada pelo consumo de folhas ao longo do estudo. A ingestão de flores foi significativamente maior na estação seca (17,8%) e a de frutos na chuvosa (12,9%). Foi registrada, também, uma diferença considerável no padrão comportamental de adultos e imaturos onde os primeiros descansaram significativamente mais, mas gastaram menos tempo nas demais categorias: alimentação, deslocamento e interações sociais. Frente a esta situação, parece provável que o orçamento geral sofreu a influência da composição do grupo, onde predominaram os membros adultos, um padrão típico no gênero. Os resultados indicam padrões de comportamento e dieta típicos do gênero, embora marginais para a espécie. Os contrastes podem estar relacionados principalmente em relação à localização geográfica da área de estudo uma área de ecótono Cerrado-Pantanal e diferenças ecológicas concomitantes. É clara a necessidade de dar continuidade aos estudos de *A. caraya* na região Bororo, não somente para uma avaliação mais sistemática de seus padrões ecológicos, como também contribuir para o desenvolvimento de estratégias de conservação.

Palavras-chave: bugios-pretos; biologia animal; ecologia comportamental; padrões de atividades.

RESUMEN

DIETAS Y PATRONES DE ACTIVIDAD DE LOS MONOS CARAYÁ NEGROS (*Allouatta caraya*, Humboldt, 1812, Primates Atelidae) EN EL ECOTONO CERRADO-PANTANAL EN EL MARGEN IZQUIERDO DEL RÍO AQUIDAUANA, MATO GROSSO DEL SUR, BRASIL. La dieta y los patrones de actividad de un grupo de monos carayá negros (*Allouatta caraya*) fue monitoreado en el banco izquierdo del río Aquidauana durante un periodo de 11 meses, desde septiembre de 2008 hasta julio de 2009. El grupo estaba compuesto por ocho individuos, dos machos adultos, tres hembras y tres individuos inmaduros, incluyendo sub-adultos e infantes. Los datos cuantitativos fueron colectados usando el método de observación rápida por 5 minutos con intervalos de 15 minutos. El patrón general de actividades (n = 6434 registros) fue 64,7% descansando; 18,5% en desplazamiento, 10,1% en alimentación, 4,4% en actividades sociales y 2,3% en comportamientos misceláneos. La dieta (n= 606 registros) estuvo compuesta principalmente por hojas (72,8%) y flores (14,8%) y complementada con frutas (8,2%) y yemas (4,2%). El consumo de partes reproductivas de las plantas, principalmente flores, fue relativamente alto en comparación con los estándares de las poblaciones más meridionales de la especie. Los miembros del grupo descansaron significativamente más y se alimentaron menos en la estación lluviosa en comparación con el periodo seco. La dieta estuvo marcada por el consumo de hojas durante todo el periodo de estudio. La ingestión de flores fue significativamente mayor en la época seca (17,8%) y la de frutos en la época lluviosa (12,9%). Se registró también una diferencia considerable en el patrón de comportamiento de los adultos en comparación con los inmaduros. Los primeros descansaron significativamente más, pero invirtieron menos tiempo en las demás categorías: alimentación, desplazamiento e interacciones sociales. Frente a esta situación, parece probable que el patrón general sufrió una influencia de la composición del grupo, en el que predominaron los miembros adultos, una característica típica del género. Los resultados indican patrones de comportamiento y dieta típicos del género, aunque marginales para la especie. Los contrastes pueden estar relacionados principalmente con la localización geográfica del área de estudio en un ecotono Cerrado-Pantanal con las consecuentes diferencias ecológicas. Es clara la necesidad de dar continuidad a los estudios de *A. caraya* en la región Bororo, no solamente para una evaluación más sistemática de sus patrones ecológicos sino también para contribuir al desarrollo de estrategias de conservación.

Palabras clave: carayá negros, biología animal, ecología comportamental, patrones de actividades.

INTRODUCTION

Activity budgets provide an indirect measure of the strategies primates follow to balance their energy requirements (Altmann 1980, Strier, 1987). Energetic demands vary considerably, not only between species, but also among populations of the same species, due to a range of factors, including body size (Coelho *et al.* 1976, McNab 1978, 1980), group size (Aguiar *et. al.* 2009), and differences among age-sex classes, reproductive states of females and sexual dimorphism (Clutton-Brock & Harvey 1977, Richard 1985, Strier 1987, Dunbar 1988).

The genus *Alouatta* is composed of ten species with twenty subspecies (Gregorin 2006). The species are: *Alouatta caraya*, *Alouatta sara*, *Alouatta nigerrima*, *Alouatta belzebul*, *Alouatta discolor*, *Alouatta palliata*, *Alouatta coibensis*, *Alouatta guariba*, *Alouatta seniculus* and *Alouatta pigra* (Rylands *et al.* 1997, Gregorin 2006). In Brazil, we find nine species: *A. seniculus*, *A. macconelli*, *A. juara*, *A. nigerrima* in the Amazon (Neville *et al.* 1988, Rylands *et al.* 1997, Gregorin 2006), *A. discolor* in the Mato Grosso part of the Amazon (Pinto 2002, Pinto & Setz 2004), *A. belzebul*, *A. ululata*, in the northeast of the Atlantic Forest and the Amazon (Pina 1999), *A. guariba* in the Atlantic Forest from Bahia to Rio Grande do Sul (Mendes 1985), and finally *Alouatta caraya* in the Cerrado and Pantanal regions (Santini 1985, Odalia-Rímoli *et al.* 2008) and in southern limits of the species geographical distribution (Bicca-Marques 1991, Ludwig 2006, Ludwig *et al.* 2008, Miranda 2009, Aguiar 2010).

The howler monkeys (*Alouatta* spp.) are among the largest platyrrhines (Bonvicino *et al.* 2001) and have, together with *Cebus* spp., the widest geographical distribution (Neville *et al.* 1988). The black howler monkey, *A. caraya* (Humboldt 1812) is found mainly in Brazil, has a large geographic distribution, the largest of the genus, occurring throughout the Cerrado and Pantanal regions (Santini 1985, Odalia-Rímoli *et al.* 2008) and the southern limits of their distribution in Atlantic Forest/Cerrado regions (Ludwig 2006, Aguiar *et al.* 2007, Passos *et al.* 2007, Ludwig *et al.* 2008, Miranda 2009, Aguiar 2010) the southern Atlantic Forest (Bicca-Marques 1991), and in adjacent areas of Bolivia, Paraguay and

Argentina (Agoramoorthy & Lohmann 1999, Bravo & Sallenave 2003). Along with *A. guariba clamitans*, they are the only taxon for *Alouatta* sexually dimorphic in coloration. Thus, one of the features of the species is their sexual dichromatism: adult males are completely black and females and juveniles are yellowish.

The behavior of howler monkeys is reasonably known (Zunino 1986, 1987, Crockett & Eisenberg 1987, Bicca-Marques 2003, Di Fiore & Campbell 2007). The social organization and behavior of the genus *Alouatta* can be characterized mainly by polygyny, low activity rates and high levels of folivory in most populations (Bicca-Marques 2003, Miranda & Passos 2004, Ludwig *et al.* 2008). *Alouatta caraya* follows this general pattern, although there are only some ecological data available for the species, most of which were obtained from studies in the extreme south of the species geographical distribution (Rumiz *et al.* 1986, Rumiz 1990, Bicca-Marques 1991, Agoramoorthy & Lohmann 1999, Bravo & Sallenave 2003). Until the present study, only two (Nantes & Rímoli 2008, Odalia-Rímoli *et al.* 2008) were available and provided ecological data of the contact zone of the Cerrado and Pantanal biomes, the region known as Bororo (Coimbra-Filho 1982), and one in the Atlantic Forest/Cerrado contact zone (Ludwig 2006).

In order to contribute to the knowledge of the species the main objective of the research was to study the diet and activity patterns of *A. caraya* in wet landscape at Cerrado-Pantanal ecotone. In the *Alouatta* genus adult individuals are larger and heavier than the juveniles and subadults and occupy a dominant social position which implies differences in their energy needs and priority access to food sources. Conversely, reproduction imposes metabolic requirements to females that increase their energy needs significantly. Thus, dominants males and females can forage in different ways depending on their energy requirements and to avoid competition for resources with the juveniles and subadults (Milton 1980, Glander 1980, Richard 1985). Thus, we proposed the hypothesis in which the howlers differ in relation to adults and young subadults in the frequency presented to the different behavioral categories: rest, feed, travel and social interactions. In

this case, it was expected that adult animals behaved, due to their hierarchical positions and because of their sizes differently than juveniles and subadults. For instance, juveniles and subadults (the immatures) devote more time to social activities and less time to rest than adults, and move more in search of food than adults.

We also proposed the following hypothesis, the activity budgets of the members of the study group will vary according to the temporal distribution of the main items of their diet, leaves, fruits and flowers. For the study group, it was assumed that variations in the temporal distribution of the major food resources, that is, leaves, fruits and flowers, directly influence their behavioral strategies. In this context, the basic hypothesis is that the patterns of activities vary systematically between seasons. More specifically, in the period of greatest food shortages, in the dry season, it was expected that: (a): the animals spend more time in locomotion behavior and less time to rest and to perform social interactions; and (b): the composition of the diet would change significantly between seasons.

Although *A. caraya* is not endangered, the populations are declining throughout most of their range due to the continuous expansion of farming and the fragmentation of natural habitats. In addition to evaluating the ecological and behavioral patterns of the species in the Bororo region on the left bank of the Aquidauana river, Mato Grosso do Sul, Brazil, this study also aimed to provide a database for planning conservation initiatives and management for the species and their habitats in this region.

METHODS

STUDY AREA

The survey was conducted in an urban fragment of Cerrado-Pantanal located on the left bank of the Aquidauana river, municipality of Anastacio, Mato Grosso do Sul, Brazil (20°29'01''S, 55°47'88''W), in the period from September 2008 to July 2009. The area is situated next to Unit I of the Fundação Universidade Federal de Mato Grosso do Sul (UFMS). Its space was established a stronghold of vegetation subject to flooding (from January to

March), reflecting variations in the water regime of the Aquidauana river (Figure 1). Its vegetation, characteristic of the Cerrado-Pantanal ecotone, is formed by riparian forest distributed over an area exceeding 40 hectares. For temperature and rainfall information the study used data from the weather station of EMBRAPA (Embrapa 2010).
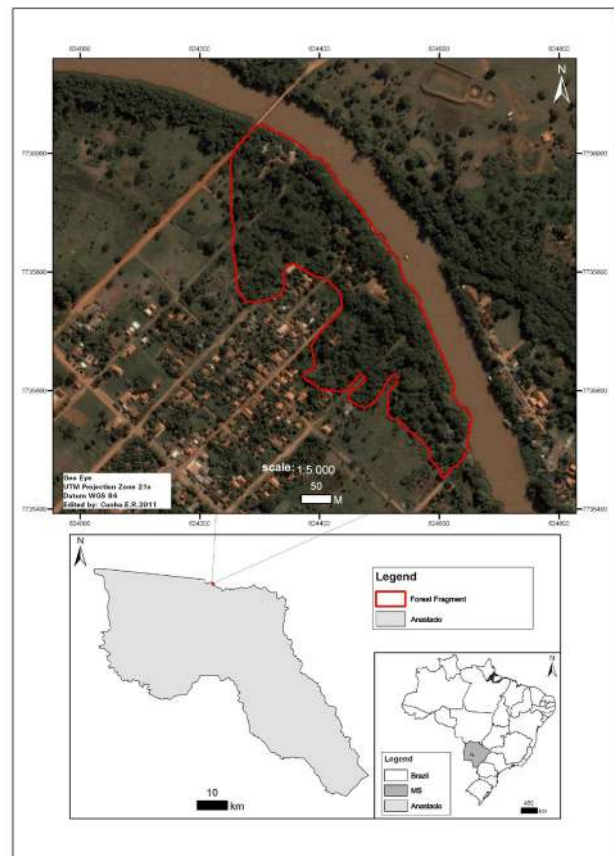

Figure 1. Home range of black howler monkeys group on the left bank of the Aquidauana river, in the municipality of Anastacio. Note that the area is inserted in urban fragment of Riparian Forest (image by E. R. Cunha). *Figura 1. Área de uso do grupo de bugios-pretos da margem esquerda do rio Aquidauana, no município de Anastácio. Notar que a área está inserida em um fragmento urbano de Mata Ciliar inundável (imagem por E. R. Cunha).*

STUDY GROUP

During the months of July and August, 2008, the riparian forests along the Aquidauana river were explored intensively in order to look for groups of monkeys; after this period, one group was found and followed in the left bank. The selected group (Figure 2, below) was already habituated, result of intense human activity in the area with strong anthropogenic pressure.

Figure 2. Some individuals of the *Alouatta caraya* study group. On left side dominant adult male and at right adult female with your infant (photo by Oscar Fernandes Júnior).

Figura 2*. Alguns indivíduos do grupo de estudo de Alouatta caraya. À esquerda o macho adulto dominante e à direita, uma fêmea adulta com seu filhote (fotografia de Oscar Fernandes Júnior).*

At the beginning of the study in September 2008, the group consisted of eight animals: two adult males, three adult females, and three subadults of different ages. In April 2009, with a birth and an emigration of one adult male the group composition remained with eight individuals. Table 1, presents the age-sex composition of study group.

Table 1. Composition of the black howlers monkeys group (*Alouatta caraya*) on the left bank of the River Aquidauana throughout the study period (2008/2009). Include immature infants (≤ 1 year), juveniles 1 and 2 (J1 = 1-2 years, J2 = 2-3 years) and subadults (3-4 years) and adults (≥ 4 years).

Tabela 1*. Composição do grupo de bugios-pretos (Alouatta caraya) da margem esquerda do rio Aquidauana através do período de estudo (2008/2009). Incluem-se filhotes (≤ 1 ano), jovens 1 e 2 (J1 = 1-2 anos, J2 = 2-3 anos), subadultos (3-4 anos) e adultos (≥ 4 anos).*

Classes	2008	2009
Adult Males	2	1
Adult Females	3	3
Subadults Males	0	0
Subadult Females	1	1
Juveniles Males	0	0
Juveniles Females	0	1
Infants Males	1	2
Infants Females	1	0
Total	**8**	**8**

*Note: In April 2009, occurred the birth of one infant and the emigration of one adult male.

ACTIVITY BUDGETS

The activity patterns were investigated during eleven consecutive months of field work, from September 2008 to July 2009. During this period the animals were observed in 11 monthly sessions, generating 1723 scans of 5 minutes each, which resulted in 6434 records in total.

DATA COLLECTION

The basic patterns of the daily activities of the group members were registered by instantaneous scan-sampling (Altmann 1974, Martin & Bateson 1993). The method is suitable for the collection of reliable quantitative data on the social behavior of arboreal primates, which have a number of issues of visibility and observational bias (Ferrari & Rylands 1994). We used a sampling scheme for 5 minutes with an interval of 15 minutes between scans, similar to other studies on *A. caraya* (Santini 1985, Bicca-Marques 1991, Nantes & Rímoli 2008, Odalia-Rímoli *et al.* 2008).

Scans were performed continuously throughout the period of daily activity in the study group, from dawn to dusk during the sample period of five consecutive days per month. In each scan we recorded: (a) the time and location of the group relative to the tracks; and, for each visible member during scanning we recorded: (b) identity, (c) behavior (second pre-defined ethogram), (d) posture (sitting, lying down, grabbed, suspended by the tail and limbs), (e) neighbors observed within a 10m radius, (f) distance (s) between observed animal and other (s) neighbor (s) member (s) of the group (g) height above the ground according to the categories (soil, ≤ 5m, 6-10m; 11-20m; ≥ 20m), (h) animal-observer distance, (i) other information considered relevant.

The behavioral categories were considered as follows: feeding: when the animal was observed biting, chewing and ingesting any item such as new leaves, mature leaves, fruits and seeds, buds and flowers; rest: when the animal was at rest while observed (inactive), and when lying down or sitting asleep; travel: when the animal was observed moving over great distances or even short paths in the same tree or between trees; and socialization: when the animal was observed engaged in social interactions with other individual(s).

For the analysis of the general activity budgets we used the data gathered during all the months of observation (see Table 2). However, within the context surrounding the general pattern of activities of the study group, a seasonal analysis was based in the rainy and dry period. The dry season was characterized by less rainfall and lower temperatures and the rainy season is the opposite table (Embrapa 2010). Thus, for this analysis, data were grouped seasonally, except for September 2008, rainy season (between October 2008 and March 2009) and dry season (from April to July 2009). The differences between the seasons were analyzed using the binomial z test (Pina 1999), whereas the significance level was α = 0.05 (Martin & Bateson 1993). The behaviors were calculated for the group as a whole and separately for the group members, adults and immature, to evaluate possible differences in the pattern of behavior related to the subject's age. Diet composition was calculated similarly, dividing the number of records of each item by the total number of feeding records collected during the study period.

RESULTS

The general activity budget for behaviors of the study group (Table 2) was typical of the genus with a predominance of rest periods and low levels of social interaction. The budget is, however, very different in terms of time spent in motion (18.5%), the value is almost half of that obtained for *A. caraya* (29.9%) living in gallery forests in Terenos (MS) (Odalia-Rímoli *et al.* 2008), the highest value recorded for a species of the genus (Di Fiore & Campbell 2007), and inferior to the other of *A. caraya* (25.4%) group studied in the central part of Aquidauana (MS) town between 2007 and 2008 (Nantes & Rímoli 2008).

Table 2. Activity budgets observed for some species of the genus *Alouatta* (% of records).
Tabela 2. Orçamentos de atividades observados para algumas espécies do gênero Alouatta (% dos registros).

Species	Rest	Feed	Travel	Source
A. caraya	64.7	10.1	18.5	**This study**
	48.3	24.1	25.4	Nantes & Rímoli (2008)
	50.9	14.7	29.9	Odalia-Rímoli *et al.* (2008)
	56.5	14.9	23.4	Prates & Bicca-Marques (2008)
	77.4	15.2	2.4	Zunino (1986)
	63.0	14.9	17.1	Bicca-Marques (1991)
	57.0	19.0	16.0	Bravo & Sallenave (2003)
A. belzebul	58.7	13.7	23.1	Pina (1999)
	55.9	7.5	19.3	Bonvicino (1989)
A. discolor	58.7	20.0	14.2	Pinto (2002)
A. guariba	56.0	12.0	24.0	Kock & Bicca-Marques (2007)
	71.8	17.3	11.0	Mendes (1985)
	67.0	10.0	12.0	Martins (1997)
	57.6	19.0	18.8	Marques (1996)
	63.7	18.7	13.2	Chiarello (1993)
A. palliata	65.5	16.2	13.4	Milton (1980)
	79.7	17.3	2.2	Estrada *et al.* (1999)
	57.0	13.6	27.4	Williams-Guillén (2003)
A. pigra	61.9	24.4	9.8	Silver *et al.* (1998)
A. seniculus	78.5	12.7	6.2	Gaulin & Gaulin (1982)
	76.3	6.0	16.0	Queiroz (1995)

Figure 3 shows the behavior of the study group by comparing the seasons. The general pattern of behavior in terms of different categories was recorded in dry and rainy seasons.

The analysis presents the results of principal activities correlated with the seasons. While the indices obtained for social behavior (z = 0.04, p > 0.05, n = 264) were stable, the members of the group spent significantly more time resting in the rainy season (z = - 2.29, p < 0.05, n = 3884), and both the feeding behavior (z = 2.23, p < 0.05, n = 606) and the travelling over de home range (z = 2.57, p < 0.05, n = 1110) were higher during the dry season.

The overall diet of the study group was similar to other species of genus, there was a predominance of leaves (72.8%), but fruit (8.2%) and especially flowers and plant material (stems and petioles and budding leaves and flowers) were well representative, with 14.9% and 4.0% respectively (Figure 4).
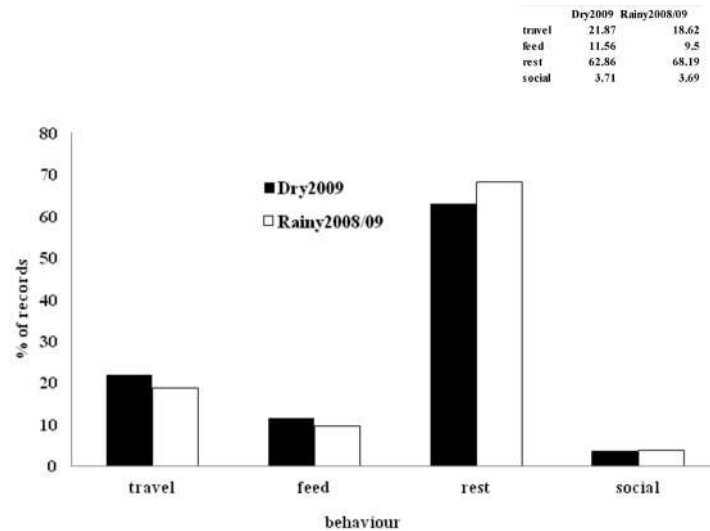
	Dry2009	Rainy2008/09
travel	21.87	18.62
feed	11.56	9.5
rest	62.86	68.19
social	3.71	3.69

Figure 3. Comparison of behavioral patterns in dry and rainy seasons to *Alouatta caraya* study group (n = 2454, dry season; n = 3549, rainy season) in the left bank of Aquidauana river.
Figura 3. *Comparação dos padrões comportamentais do grupo de estudo de Alouatta caraya, nas estações seca e chuvosa (n = 2454, estação seca e n = 3549, estação chuvosa) na margem esquerda do rio Aquidauana.*
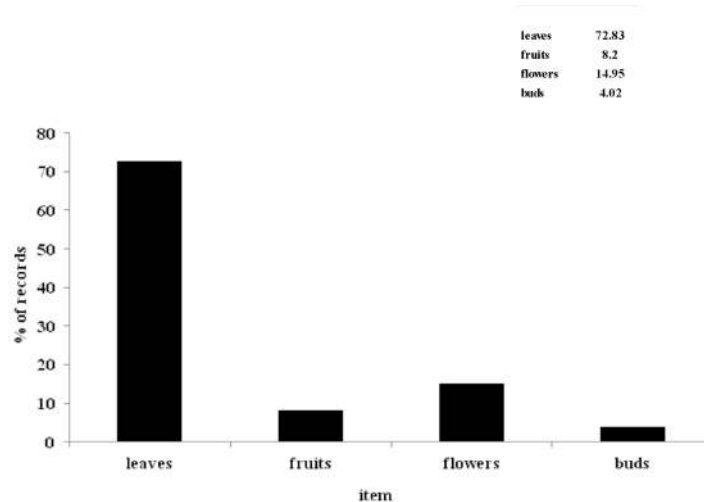
leaves	72.83
fruits	8.2
flowers	14.95
buds	4.02

Figure 4. Diet for different feeding resources of *Alouatta caraya* (n = 606) in left bank of Aquidauana river.
Figura 4. *Dieta para os diferentes recursos alimentares de Alouatta caraya (n = 606) na margem esquerda do rio Aquidauana.*

The general diet for three different feeding items of the study group, that is, leaves, fruits and flowers, is presented in Table 3, which also showed the comparison between the use of these different items for species of the *Alouatta* spp. The feeding items, and the diet, were typical of the genus with a predominance of leaves, but items other than fruits and flowers were consumed in significant proportions.

Table 3. Comparison between main feed items in the diet of *Alouatta caraya* (% of feeding records) and other howler species.
Tabela 3. Comparação entre os principais itens alimentares da dieta de Alouatta caraya (% dos registros alimentares) e outras espécies de bugios.

Species	Leaves	Fruits	Flowers	Source
A. caraya	72.8	8.2	14.9	**this study**
	78.3	6.8	14.8	Nantes & Rímoli (2008)
	47.5	35.5	12.9	Odalia-Rímoli *et al.* (2008)
	82.4	12.3	2.7	Prates & Bicca-Marques (2008)
	74.2	23.6	2.2	Zunino (1986)
	60.9	28.9	2.7	Bicca-Marques (1991)
	68.0	19.0	12.0	Bravo & Sallenave (2003)
	65.0	24.0	10.0	Ludwig *et. al.* (2008)[1]
	49.0	46.0	5.0	Ludwig *et. al* (2008)[2]
A. belzebul	13.3	59.0	27.6	Bonvicino (1989)
	61.5	31.8	0.3	Pina (1999)
A. díscolor	24.8	55.6	5.7	Pinto (2002)
A. guariba	66.0	19.0	4.0	Kock & Bicca-Marques (2007)
	76.0	15.6	8.4	Mendes (1985)
	76.0	19.0	3.0	Martins (1997)
	73.0	5.2	11.7	Chiarello (1993)
	50.3	47.9	1.4	Aguiar *et al.* (2003)
	57.0	41.0	1.7	Miranda & Passos (2004)
A. palliata	48.2	42.1	9.6	Milton (1980)
	54.4	40.6	0.7	Estrada *et al.* (1999)
	55.8	34.8	7.9	Williams-Guillén (2003)
A. pigra	45.1	40.8	10.6	Silver *et al.* (1998)
A. seniculus	52.1	42.3	5.4	Gaulin & Gaulin (1982)
	57.0	25.5	12.6	Julliot & Sabatier (1993)
	45.5	47.3	1.5	Queiroz (1995)

[1,2]Ludwig *et. al.* 2008, (1) island group and (2) mainland group, both in upper Paraná River.
[1,2]Ludwig et. al. 2008, (1) grupo da ilha e (2) grupo da terra firme, ambos no alto rio Paraná.

The leaves were used throughout the study period (Figure 5), varying little between the rainy season, 77.0% and the dry season, 75.5%, although this item has been replaced by flowers (17.8%) in the dry season.

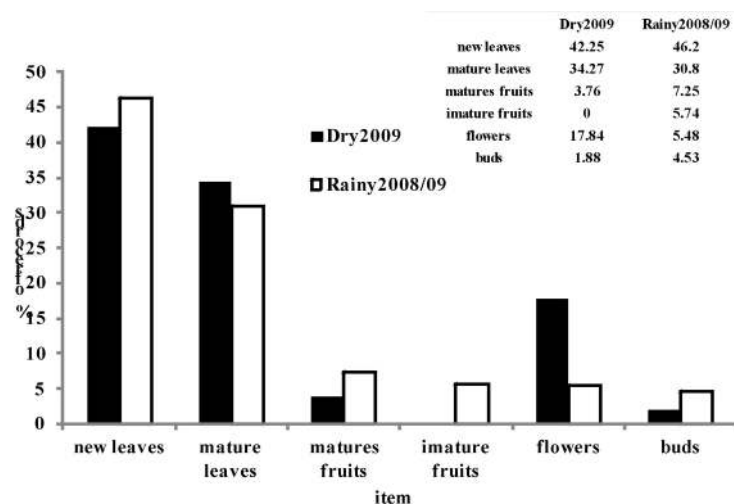|	Dry2009	Rainy2008/09
new leaves	42.25	46.2
mature leaves	34.27	30.8
matures fruits	3.76	7.25
imature fruits	0	5.74
flowers	17.84	5.48
buds	1.88	4.53

Figure 5. Comparison of the diet of *Alouatta caraya* study group between dry and rainy seasons, 2008 and 2009.
Figura 5. Comparação da dieta do grupo de estudo de Alouatta caraya entre as estações seca e chuvosa, 2008 e 2009.

The analysis of the seasonal pattern in the diet shows that there was an increase in the consumption of fruits (12.9%) and new leaves in the rainy season (46.2%). Howlers consumed more fruits in the rainy season and flowers in the dry season (z = 4.10, p < 0.05). The sharp increase in frugivory recorded during the rainy season was entirely due to the consumption of genipaps (*Genipa americana*) and the fruits of a large fig (*Ficus enormis*), in which the group 'camping out' for long periods in this species. The frugivory was more observed during the rainy season (12.9%) when compared the dry one (3.7%) (z = -4.45, p < 0.05). There were also significant differences between adult group members and immature (Figure 6). Considering that adults spend more of their time resting in shifts (78.8%) than immature individuals (59.3%), these, in turn, devoted more time to all the other categories (solitary play were only observed at this age-sex class).
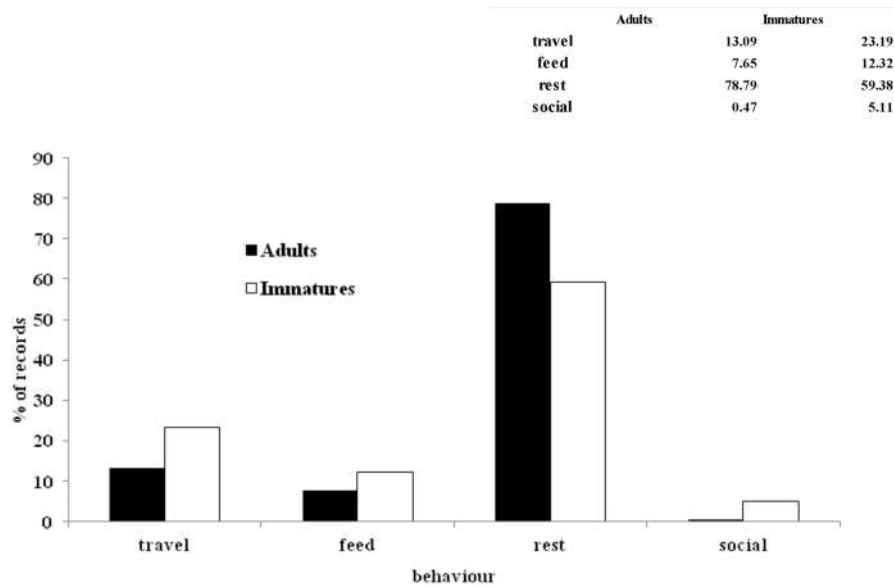
	Adults	Immatures
travel	13.09	23.19
feed	7.65	12.32
rest	78.79	59.38
social	0.47	5.11

Figure 6. Comparison between adults and immature individuals in relation to the activity budget of the black howler monkeys study group in the left bank of Aquidauana river.
Figura 6. Comparação entre indivíduos adultos e imaturos em relação ao orçamento de atividades do grupo de estudo de bugios-pretos na margem esquerda do rio Aquidauana.

The differences between age-sex classes were significant at p = 0.05. Although this analysis is relatively simple, it does indicate that the general activity budgets (Figure 6) may have been influenced significantly by the composition of the study group, which dominates mature members (62.5% of total). The comparison between adults and immature individuals for the general categories of behavior showed significant differences. With a tendency for adults; in relation to the activities budget categories, presented significantly differences for rest (z = 8.9, p < 0.05), travel (z = 8.6, p < 0.05) and feed (z = 5.41, p < 0.05). However, the immature individuals were more active in social activities such as play behavior and affiliative interactions such as grooming (z = -9.61, p < 0.05).

DISCUSSION

During the observations, the Aquidauana river monkeys spent 64.7% of their time inactive, 10.1% feeding, 18.5% traveling, 4.4% in social activities, and 2.3% involved in other miscellaneous behaviors. The study group is a typical primate group of howler monkeys, showing high levels of inactivity, normally associated with a highly folivorous diet. For the activity pattern of the studied group of black howler monkeys, the behavioral category "resting" was more frequently observed. In this context, some authors confirm the rest as a useful strategy for sparing energy for the genus *Alouatta*. For *A. caraya* at other southern sites (Zunino 1986, Bicca-Marques 1991) and Cerrado-Pantanal sites in the similar region of the

study group (Nantes & Rímoli 2008) or other areas of the Atlantic Forest (Odalia-Rímoli *et al*. 2008, Ludwig 2006, Ludwig *et al*. 2008) this strategy is also confirmed.

In most cases, the howlers *Alouatta* spp. spend less than 10% of their time traveling, and rarely more than 20%, although Williams-Guillén (2003) reported a very high value (27.4%) for *Alouatta palliata*. However, the time budget is very different in terms of time spent in traveling (18.5%), the value is almost half of that obtained for *A. caraya* (29.9%) living in gallery forests in Terenos (MS) (Odalia-Rímoli *et al*. 2008), the highest value recorded for a species of the genus (Di Fiore & Campbell 2007), and inferior to the others groups of the *A. caraya* (25.4%) studied in central part of Aquidauana (MS) (Nantes & Rímoli 2008) and in Alegrete (Rio Grande do Sul, Brazil) with 23.4% of their time traveling (Prates & Bicca-Marques 2008). In the southern geographic distribution of *A. caraya*, Zunino (1986) showed a value of only 2.4% while Bicca-Marques (1991) registered 17.1%.

The rest tends to be higher in the middle of the day, in periods where temperatures are relatively higher in warmer seasons (rainy seasons) and during longer periods when temperatures are low, in colder seasons (dry seasons). The high rates of rest for *Alouatta* species may be related to a strategy for minimizing energy expenditure, considering the standard folivory in the diet of these animals, i.e., high rates of inactivity seem to be a compensation (trade-off) for feeding behavior based on poor resources (Milton 1980, Neville *et al*. 1988, Bicca-Marques 1993, 2003).

Thus, the behavioral pattern observed in the study group was very similar to those observed in previous studies with other species of the genus (Table 2), in which invariably the predominant periods of inactivity or rest are invariable. Although the values for rest, feed and travel were similar, respectively, for the genus, it is important to remember the wide range of methodological factors that can influence any direct comparison between studies (Ferrari & Rylands 1994).

We also had proposed the hypothesis in which the activity budgets of the members of the study group would vary according to the temporal distribution of the main items of their diet, leaves, fruits and flowers. For the study group, it was assumed that

variations in the temporal distribution of the major food resources, leaves, fruits and flowers, directly influence their behavioral strategies. In this context, the basic hypothesis is that the patterns of activities vary systematically between climatic seasons. More specifically, in the period of greatest food shortages, the dry season it was expected that: (a): the animals spend more time in locomotion behavior, and less time to rest and to social interactions; and (b): the composition of the diet would change significantly between seasons. The analysis confirmed this hypothesis in part, the results of principal activities correlated with the seasons indicated that social behavior were stable (p > 0.05) and that the members of the group spent significantly more time resting in the rainy season (p < 0.05), and both, the feeding behavior (p < 0.05) and the travelling over de home range (p < 0.05) were higher during the dry season. The howlers maintain the proportion of time for activities in different seasons, but this does not mean that the total times allocated are the same. They respond to seasonal, generally by altering the activity period. This is evident, for example, at rest and sleep. In the wet it was higher than the dry season, a difference that may be have to do with the extended temporal dimension of rainy season.

To obtain a satisfactory amount of food, primates have to deal in their foraging behavior, with the space-temporal features of the habitats that they occupy. Factors such as the spatial and temporal distribution, quality and abundance of resources are identified as determinants of social organization in primates, both in evolutionary level as at the level of immediate adjustments to the environment (Clutton-Brock & Harvey 1977, Milton 1980, Jolly 1985, Oates 1987, Dunbar 1988).

The diet of howlers is a reflection of basic needs determined by body size, anatomical specializations (size and structure of the gastrointestinal tract) and the ability to switch large periods of rest. These adaptations make the howlers able to draw energy from food theoretically lower energy content, where the leaves (Milton 1980, Glander 1981, Mendes 1985, Bicca-Marques 1991, Chiarello 1993), in this case leaves reflect of certain basic needs. In general there is a predominance of leaves in the diet, found they eating leaves in a ratio greater than others items. But this characteristic in the diet does not think that

the leaves are only the most important goal of the foraging behavior of howlers, fruit, a more energetic item, seems to have a preponderant role in the diet of most species where the fruits were in abundance in rainy seasons (see examples in Pina 1999 - *A. belzebul*, Pinto 2002, Pinto & Setz 2004 - *A. discolor* and Ludwig *et al.* 2008 - *A. caraya*).

For the study group, the diet consisted predominantly by plant material, especially leaves (Figure 4), a pattern typical of the genus *Alouatta* spp. (Di Fiore & Campbell 2007). The use of leaves had a relatively similar diet in comparison with most of other related studies with howlers monkeys (Table 3), including *A. caraya* (Bicca-Marques 1991, Sallenave & Bravo 2003). In contrast, both the consumption of fruits and flowers were relatively large, while the consumption of fruits has been lower than the values reported in other studies *A. caraya*, but similar to a sympatric group that lived in the proximity in Aquidauana between 2007 and 2008 (Nantes & Rímoli 2008). Flowers were appreciated resources in the dry season (April-July 2009) and its consumption was higher (see Table 4) than in other groups of *A. caraya* (Zunino 1986, 1987, Bicca-Marques 1991, Bravo & Sallenave 2003).

In the case of howlers, the analysis of the seasonal pattern in the diet, demonstrated that there was an increased on consumption of the fruits (12.9%) and new leaves in the rainy season (46.2%), they are consuming more fruits in rainy season and flowers in dry season (p < 0.05). The frugivory was marked during the rainy season (12.9%) when compared to dry (3.7%) (p < 0.05).

Despite that not obtain independent measures of resource availability, howlers seem to consume these items according to availability for the seasons. The analysis of the seasonal pattern in the diet, increased consumption of the new leaves in the rainy season is in accordance with the productivity of the period (Takahasi & Fina 2004, Lehn 2008, Ferreira *et al.* 2010), the same can be said of the consumption of fruits, since this period is characterized by a relative abundance of fruit in the majority of the other study sites (Pinto & Setz 2004). A similar pattern can be seen in case of leaves, where folivory predominates in most but not all species of the genus (Table 3). Although we find that there is also some species

selectivity for off season as was the case with the consumption of genipaps (*Genipa americana*) and the fruits of a large fig (*Ficus enormis*), in which the group 'camping out' for long periods in this species, regardless of the season.

Regarding seasonal differences, howler monkeys are capable of adjusting to the availability of resources, the consumption of leaves is balanced between seasons (77.0% and 75.5% in the rainy and dry seasons respectively) but flowers and fruits are consumed according to availability station, fruits in rainy and flowers in dry season. Similarly the consumption of leaves, fruits are an important resource with 8.2% of consumption and occupy a significant fraction of the activity in the study.

The climatic seasons, of course, differ in photoperiod and temperature as both variables are smaller in dry season. Thus, for efficiency, assuming that the animals were defending a minimum consumption of food, they should move in the season more frequently with less time available, in this case, the dry. Thus, animals should be more efficient in dry season. There is a great tendency in this direction, howlers are moving more and engaging in food major shifts.

In the present case, in addition to other potential variables, such as habitat type, floristic composition and biome, the age-sex class composition of mature group members may have had an important influence on the general results. In fact, the activity budget was much more similar to those recorded for *A. caraya* by Zunino (1986), Bicca-Marques (1991) and Bravo & Sallenave (2003). For *A. caraya* in Upper Paraná River, for example, a combination of environmental, social, phylogenetic and ecological factors may all influence group size and composition (Ludwig *et al.* 2008, Aguiar *et. al.* 2009). The differences between age-sex classes were significant at p = 0.05 (Figure 6). Although this analysis is relatively simple, it does indicate that the general budget of activities may have been influenced significantly by the composition of the study group, which dominates mature members (62.5% of total). Obviously, the comparative analysis of age classes presented here was tentative considering, among other questions, the marked difference between males and females in this species, as well as the heterogeneity of age-sex class composition for the immatures.

Nevertheless, this analysis indicates clearly that a more systematic approach is needed for the comparative analysis of different studies, one which should include the standardization of sampling procedures, the age-sex composition of study groups, and the study period, all of which may influence recorded values considerably. In *Alouatta*, there is often as much variation within species as there is between species (Table 2). In addition to possible methodological issues, differences may reflect the influence of site (habitats and biomes, for example) at the population level (Aguiar *et al*. 2009), or even individual factors, making identification almost impossible at interspecific patterns (Odalia-Rímoli *et al*. 2008).

It seems possible that methodological factors may be less important here, and indeed, there seems to be much less intraspecific variation (Odalia-Rímoli *et al*. 2008). Overall, folivory seems to be more pronounced in populations at higher latitudes, especially those of species howler monkeys that *A. guariba* (Miranda & Passos 2005) and *A. caraya* (Aguiar *et al*. 2008), compared with species whose populations are located closer to the equator in the Amazon region, such as *A. belzebul* (Pina 1999), *A. seniculus* (Julliot & Sabatier 1993) and *A. discolor* (Pinto 2002, Pinto & Setz 2004). This may reflect both productivity levels (Aguiar *et al*. 2008) and, especially, the less pronounced seasonality of the equatorial ecosystems (Odalia-Rímoli *et al*. 2008).

The highest consumption of leaves and reduced folivory of reproductive plant parts such as flowers and partly fruits, recorded for the study group compared to other populations of *A. caraya*, located in southern Brazil (Bicca-Marques & Callegaro Marques 1994, 1995), and northern Argentina (Zunino 1986, 1987), would be consistent with this hypothesis, the intraspecific level when the availability of fruits is significant directs their efforts in diet for the consumption of this item (Odalia Rímoli *et al*. 2008). For example, the diet of the red-handed howlers (*A. discolor*) (Pinto & Setz 2004) have complements the high frugivory observed in *A. belzebul* (Pina 1999). Although intraspecific variation in howler diets is high and new studies with highly folivorous species have shown higher frugivory, *A. belzebul* seems to be the most consistently frugivorous howler species (Pina

1999), in spite of its wide geographic distribution and sympatry with *Ateles chamek*, a highly frugivorous primate (Pinto & Setz 2004).

Also, reduced by resting periods would be consistent with a diet frugivorous (Coelho *et al*. 1976, McNab 1978, 1980), as observed in other atelidae such as *Ateles* spp. (Chapman 1988, Di Fiore & Campbell 2007) and *Brachyteles* spp. (Strier 1987, 1992), although such behavior patterns for black howler monkeys, *A. caraya* require that these interpretations are made with some caution when considering the possible influence of methodological issues described above.

According Pinto & Setz (2004) howler studies evidence great variation of dietary specific richness, mostly due to differences in vegetation richness among habitats and study duration, and confirms high frugivory for several primate species commonly exhibit dietary changes following seasonal variation in fruit availability (Milton 1980, Terborgh 1983, Strier 1987, 1992, Odalia-Rímoli *et al*. 2008, Rímoli *et al*. 2008). Therefore, is expected that howlers would consume less fruit in the dry season in Cerrado/Pantanal (Takahasi & Fina 2004, Lehn 2008, Barbosa-Filho & Araújo 2009, Ferreira *et al*. 2010), when there is a shortage of fruit production, the same seems to be the norm in other biomes as Amazon (Terborgh 1983, Setz 1993, Peres 1994, Pina 1999, Pinto 2002, Pinto & Setz 2004), and Atlantic forest (Rylands 1984, Strier 1987, 1992, Passos 1992, Rímoli 2001).

The results of this study showed activity patterns and feeding behavior typical of the genus *Alouatta*, while pointing to possible intra and interspecific differences, encouraging the idea of developing more systematic research on the species. Obviously, there is a clear need for additional studies performed by *A. caraya* in the Cerrado-Pantanal region, not only to provide further information on the ecological patterns, but also to contribute to the development of strategies for the conservation of species and their habitats.

REFERENCES

AGORAMOORTHY, G. & LOHMANN, R. 1999. Population and conservation status of the black-and-gold howler monkeys, *Alouatta caraya*, along the rio Riachuelo, Argentina. *Neotropical Primates,* 7: 43-44.

AGUIAR, L.M. 2010. Sistema social de grupos mistos de espécies de bugios (*Alouatta caraya* e *Alouatta clamitans*) e potenciais híbridos no alto rio Paraná, sul do Brasil. *Tese de Doutorado*. Universidade Federal do Paraná. Curitiba, PR, Brasil. 252p.

AGUIAR, L.M.; LUDWIG, G. & PASSOS, F.C. 2009. Group size and composition of black-and-gold howler monkeys (*Alouatta caraya*) on the Upper Paraná River, Southern Brazil. *Primates,* 50: 74-77. http://dx.doi.org/10.1007/s10329-008-0115-0

AGUIAR, L.M.; MELLEK, D.M.; ABREU, K.C.; BOSCARATO, T.G.; BERNARDI, I.P.; MIRANDA, J.M.D. & PASSOS, F.C. 2007. Sympatry between *Alouatta caraya* and *Alouatta clamitans* and the rediscovery of free-ranging potential hybrids in Southern Brazil. *Primates,* 48: 245-248. http://dx.doi.org/10.1007/s10329-007-0039-0

AGUIAR, L.M.; PIE, M.R. & PASSOS, F.C. 2008. Wild mixed groups of howler species (*Alouatta caraya* and *Alouatta clamitans*) and new evidence for their hybridization. *Primates,* 49: 149-152. http://dx.doi.org/10.1007/s10329-007-0065-y

ALTMANN, J. 1974. Observational study of behavior sampling methods. *Behaviour*, 49: 227-267. http://dx.doi.org/10.1163/156853974X00534

ALTMANN, J. 1980. *Baboon, Mothers and Infants*. Harvard University Press, Cambridge, MA. 272p.

BARBOSA-FILHO, G.B. & ARAÚJO, A. C., 2009. Fenologia de floração e síndromes de polinização na Serra de Maracaju, Mato Grosso do Sul. *Anais do Encontro de Iniciação Científica*, ENIC, 1: n°1(5).

BICCA-MARQUES, J.C. & CALEGARO-MARQUES, C. 1994. Feeding behavior of the black howler monkey (*Alouatta caraya*) in a seminatural Forest. *Acta Biologica Leopoldensia,* 16: 69-84.

BICCA-MARQUES, J.C. & CALEGARO-MARQUES, C. 1995. Ecologia alimentar do gênero *Alouatta* LACÉPEDE, 1799 (Primates, Cebidae). *Cadernos UFAC*, 3*:* 23-49.

BICCA-MARQUES, J.C. 1991. Ecologia e comportamento de um grupo de bugios-pretos *Alouatta caraya* (Primates, Cebidae) em Alegrete, RS, Brasil. *Dissertação de Mestrado*. Universidade de Brasília. Brasília, DF, Brasil. 200p.

BICCA-MARQUES, J.C. 1993. Padrão de atividades diárias do bugio-preto *Alouatta caraya* (Primates, Cebidae): Uma análise temporal e bioenergética, Pp. 35-49. *In:* M.E. Yamamoto & M.B.C. Sousa (eds.). A Primatologia no Brasil vol. 4. Sociedade Brasileira de Primatologia, Natal, RN, Brasil. 212p.

BICCA-MARQUES, J.C. 2003. How do howler monkeys cope with habitat fragmentation? Pp. 283-303. *In*: L.K. Marsh (Ed.). Primates in Fragments: Ecology and Conservation. Kluwer Academic/Plenum Publishers, New York, NY. 428p.

BONVICINO, C.R. 1989. Ecologia e comportamento de *Alouatta belzebul* (Primates: Cebidae) na Mata Atlântica. *Revista Nordestina de Biologia,* 6: 149-179.

BONVICINO, C.R.; LEMOS, B. & SEÚANEZ, H.C. 2001. Molecular philogenetics of howler Monkeys (*Alouatta*, Platyrrini): a comparison with karyotypic data. *Chromossoma,* 110: 241-246. http://dx.doi.org/10.1007/s004120000128

BRAVO, S.P. & SALLENAVE, A. 2003. Foraging behavior and activity patterns of *Alouatta caraya* in the northeastern argentinean flooded forest. *International Journal of Primatology,* 24: 825-846, doi: 0164-0291/03/0800-0825/0

CHAPMAN, C. 1988. Patterns of foraging and range use by three species of neotropical primates. *Primates,* 29: 177-194. http://dx.doi.org/10.1007/BF02381121

CHIARELLO, A.G. 1993. Home range of the brown howler monkey, *Alouatta fusca*, in a forest fragment of southeastern Brazil. *Folia Primatologica,* 60:173-5. http://dx.doi.org/10.1159/000156687

CLUTTON-BROCK, T.H. & HARVEY, P.H. 1977. Species differences in feeding and ranging behavior in Primates. Pp. 557-579. *In*: T.H. Clutton-Brock (ed.). Primate Ecology. Academic Press, New York, NY. 631p.

COELHO, A.M.; BRAMBLETT, C.A.; QUICK, L.B. & BRAMBLETT, S.S. 1976. Resource availability and population density in primates: a socio-bioenergetic analysis of the energy budgets of Guatemalan howler and spider monkeys. *Primates,* 17: 63–80. http://dx.doi.org/10.1007/BF02381567

COIMBRA-FILHO, A.F. 1982. Os primatas do Brasil, patrimônio a conservar. *Ciência Hoje*, 2: 62-69.

CROCKETT, C.M. & EISENBERG, J.F. 1987. Howlers: variations in group size and demography. Pp. 54–68. *In:* B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker (eds.). Primate Societies. University of Chicago Press, Chicago, IL. 585p.

DI FIORE, A. & CAMPBELL, C.J. 2007. The Atelines: variation in ecology, behavior, and social organization. Pp. 155-185. *In*: C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger & S.K. Bearder (eds.). Primates in Perspective. Oxford University Press, New York, NY. 736p.

DUNBAR, R.I.M. 1988. *Primate Social Systems*. Croom Helm Ltd., London, England. 373p.

EMBRAPA 2010. Relatório Anual das temperaturas máximas e mínimas e dados pluviométricos. *Relatório não publicado*. Campo Grande, MS, Brasil, 60p.

ESTRADA, A.; JUAN-SOLANO, S.; ORTÍIZ-MARTÍNEZ, T.J. & COATES-ESTRADA, R. 1999. Feeding and general activity patterns of a howler monkey (*Alouatta palliata*) troop living in a forest fragment at Los Tuxtlas, Mexico. *American Journal of Primatology,* 48: 167–183. http://dx.doi.org/10.1002/(SICI)1098-2345(1999)48:3<167::AID-AJP1>3.3.CO;2-Y

FERRARI, S.F. & RYLANDS, A.B. 1994. Activity budgets and differential visibility in field studies of three marmosets (*Callithrix* spp.). *Folia Primatologica*, 63: 78-83. http://dx.doi.org/10.1159/000156795

FERREIRA, K.R.; FINA, B.G.; KUSANO, D.M.; GONÇALVES DE REZENDE, M.P.; MONTEIRO DE OLIVEIRA, N.; RAMIRES, G.G. & CARDOSO, I.L. 2010. Comportamento Fenológico de *Erythroxylum suberosum* ST. Hil. (Erythroxylaceae) em uma área de Cerrado sensu stricto em Aquidauana, Mato Grosso do Sul. *Anais do Encontro de Iniciação Científica*, ENIC, 1(3).

GAULIN, S.J.C. & GAULIN, C.K. 1982. Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. *International Journal of Primatology,* 3: 1-32. http://dx.doi.org/10.1007/BF02693488

GLANDER, K.E. 1980. Reproduction and population growth in free-ranging howling monkeys. *American Journal of Primatology,* 53: 25-36.

GREGORIN, R. 2006. Taxonomia e variação geográfica das espécies do gênero *Alouatta* Lacépède (Primates/Atelidae) no Brasil. *Revista Brasileira de Zoologia,* 23: 64-144. http://dx.doi.org/10.1590/S0101-81752006000100005

JOLLY, A. 1985. *Evolution of Primate Behavior*. Macmillan Publishing Company, New York, NY. 416p.

JULLIOT, C. & SABATIER, D. 1993. Diet of red howler monkey (*Alouatta seniculus*) in French Guiana. *International Journal of Primatology,* 14: 527–550. http://dx.doi.org/10.1007/BF02215446

KOCH, F. & BICCA-MARQUES, J.C. 2007. Padrão de atividades e dieta de *Alouatta guariba clamitans* Cabrera, 1940: uma análise sexo-etária. Pp. 353-361. *In*: J.C. Bicca-Marques (ed.). A Primatologia no Brasil vol. 10. Sociedade Brasileira de Primatologia, Porto Alegre, RS, Brasil. 268p.

LEHN, C.R. 2008. Aspectos estruturais e fenológicos de uma população de *Danaea sellowiana* C.Presl (Marattiaceae) em uma floresta estacional semidecidual no Brasil Central. *Dissertação de Mestrado*. Universidade Federal de Mato Grosso do Sul. Campo Grande, MS, Brasil. 90p.

LUDWIG, G. 2006. Área de vida e uso do espaço por *Alouatta caraya* (HUMBOLDT, 1812) em ilha e continente do Alto Rio Paraná**,** 2006. *Dissertação de Mestrado*. Universidade Federal do Paraná. Curitiba, PR, Brasil. 88p.

LUDWIG, G.; AGUIAR, L.M.; SVOBODA, W.K.; HILST, C.L.S.; NAVARRO, I.T.; VITULEI, J.R.S. & PASSOS, F.C. 2008. Comparação da dieta de *Alouatta caraya* (Primates: Atelidae) em mata ciliar insular e continental na região do Alto rio Paraná, Sul do Brasil. *Revista Brasileira de Zoologia,* 25: 419-426. http://dx.doi.org/10.1590/S0101-81752008000300006

MARQUES, A.A.B. 1996. O bugio ruivo *Alouatta fusca clamitans* (Cabrera, 1940) (Primates, Cebidae) na Estação Ecológica de Aracuri, RS: variações sazonais de forrageamento. *Dissertação de Mestrado*. Pontifícia Universidade Católica do Rio Grande do Sul. Porto Alegre, RS, Brasil. 129p.

MARTIN, P. & BATESON, R. 1993. *Measuring Behaviour*. Cambridge University Press, Cambridge, MA. 238p. http://dx.doi.org/10.1017/CBO9781139168342

MARTINS, C.S. 1997. Uso de habitat pelo bugio, *Alouatta fusca clamitans*, em um fragmento florestal em lençóis Paulista- SP. *Dissertação de Mestrado*. Universidade Estadual de Campinas. Campinas, SP, Brasil. 87p.

MCNAB, B.K. 1978. Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on a ubiquitous food supply. Pp. 153-162. *In:* G.G. Montgomery (ed.). The Ecology of Arboreal Folivores. Smithsonian Press, Washington, WA. 574 p.

MCNAB, B.K. 1980. Foods habitats, energetics and the population biology of mammals. *American Naturalist,* 116: 106-124. http://dx.doi.org/10.1086/283614

MENDES, S.L. 1985. Uso do espaço, padrões de atividades diárias e organização social de *Alouatta fusca* (Primates, Cebidade) em Caratinga, MG. *Dissertação de Mestrado*. Universidade de Brasília. Brasília, DF, Brasil. 70p.

MILTON, K. 1980. *The Foraging Strategy of Howler Monkeys, a Study in Primate Economics*. Columbia University Press, New York, NY. 165p.

MIRANDA, J.M.D. & PASSOS, F.C. 2004. Hábito alimentar de *Alouatta guariba* (Humboldt) (Primates, Atelidae) em Floresta de Araucária, Paraná, Brasil. *Revista Brasileira de Zoologia,* 21: 821-826. http://dx.doi.org/10.1590/S0101-81752004000400016

MIRANDA, J.M.D. & PASSOS, F.C. 2005. Composição e dinâmica de *Alouatta guariba clamitans* Cabrera (Primates, Atelidae) em floresta ombrófila mista no Estado do Paraná, Brasil. *Revista Brasileira de Zoologia,* 22: 99-106. http://dx.doi.org/10.1590/S0101-81752005000100013

MIRANDA, J.M.D. 2009. Comportamentos sociais, relações de dominância e confrontos intergrupais em *Alouatta caraya* (Humboldt, 1812) na Ilha Mutum, alto rio Paraná, Brasil. *Tese de Doutorado*. Universidade Federal do Paraná. Curitiba, PR, Brasil. 104p.

NANTES, R.S. & RÍMOLI, J. 2008. Ecologia e comportamento de bugios-pretos (*Alouatta caraya*, Primates, Atelidae) em fragmentos florestais em Aquidauana, Mato Grosso do Sul. *Relatório Final*, PIBIC/UFMS/CNPq. 21p.

NEVILLE, M.K.; GLANDER, K.E.; BRAZA, F. & RYLANDS, A.B. 1988. The Howling Monkeys, Genus *Alouatta*. Pp. 349-453. *In*: R.A. Mittermeier, A.B. Rylands, A.F. Coimbra-Filho & G.A.B Fonseca (eds.). Ecology and Behavior of Neotropical Primate Vol. 2. Editora Littera Maciel Ltda., Contagem, MG, Brasil. 612p.

OATES, J.F. 1987. Food distribution and foraging behavior. *In:* B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker (eds.). Primate Societies. University of Chicago Press, Chicago, IL. 585p.

ODALIA-RÍMOLI, A.; VALDIVINO, E.M.; RÍMOLI, J. & FERRARI, S.F. 2008. Behavior patterns of a group of black howler monkeys *Alouatta caraya* (Humboldt, 1812) in a forest fragment in Terenos, Mato Grosso do Sul: a seasonal analysis. Pp. 179-191. *In:* S.F. Ferrari & J. Rímoli (eds.). A Primatologia no Brasil vol. 9. Sociedade Brasileira de Primatologia, Aracaju, SE, Brasil. 201p.

PASSOS, F.C. 1992. Hábito alimentar do mico-leão-preto *Leontopithecus chrysopygus* (Mikan, 1823) (*Callitrichidae, Primates*) na Estação Ecológica de Caetetus, município de Gália, SP. *Dissertação de Mestrado*. Universidade Estadual de Campinas. Campinas, SP, Brasil. 99p.

PASSOS, F.C.; MIRANDA, J.M.D.; AGUIAR, L.M.; LUDWIG, G.; BERNARDI, I.P. & MORO-RIOS, R.F. 2007. Distribuição e ocorrência de Primatas no Estado do Paraná. *In:* J.C. Bicca-Marques (ed.). A Primatologia no Brasil vol. 10. Sociedade Brasileira de Primatologia, Porto Alegre, RS, Brasil. 268p.

PERES, C.A. 1994. Primate responses to phenological changes in an Amazonian terra firme forest. *Biotropica,* 26: 98–112. http://dx.doi.org/10.2307/2389114

PINA, A.L.C.B. 1999. Dinâmica socio-ecológica em uma população de guaribas-das-mãos-vermelhas (*Alouatta belzebul*) na Estação Científica Ferreira Penna, PA. *Dissertação de Mestrado*, Universidade Federal do Pará, PA, Brasil. 89p.

PINTO, L.P. & SETZ, E.Z.F. 2004. Diet of *Alouatta belzebul discolor* in an Amazonian Rain Forest of Northern Mato Grosso State, Brazil. *International Journal of Primatology*, 25: 1197-1211, doi: 0164-0291/04/1200-1197/0 C

PINTO, L.P. 2002. Dieta, padrão de atividades e área de vida de *Alouatta belzebul discolor* (Primates, Atelidae) em Paranaíta, Norte de Mato Grosso. *Dissertação de Mestrado*. Universidade Estadual de Campinas. Campinas, SP, Brasil. 116p.

PRATES, H.M. & BICCA-MARQUES, J.C. 2008. Age-Sex Analysis of Activity Budget, Diet, and Positional Behavior in *Alouatta caraya* in an Orchard Forest. *International Journal of Primatology,* 29:703-715. http://dx.doi.org/10.1007/s10764-008-9257-6

QUEIROZ, H.L. 1995. *Guaribas e Preguiças. Os mamíferos herbívoros arbóreos de Mamirauá.* Sociedade Civil Mamirauá, Brasília, DF.160p.

RICHARD, A.F. 1985. *Primates in Nature.* W. H. Freeman and Company, New York, NY. 586p.

RÍMOLI, J. 2001. Ecologia de macacos-pregos-pretos (*Cebus apella nigritus,* Goldfuss, 1809) na Estação Biológica de Caratinga (MG): implicações para a conservação de fragmentos de Floresta Atlântica. *Tese Doutorado*. Universidade Federal do Pará. Belém, PA, Brasil. 187p.

RÍMOLI, J.; STRIER, K. B. & FERRARI S.F. 2008. Seasonal and longitudinal variation in the behavior of free-ranging black tufted capuchins *Cebus nigritus* (Goldfuss, 1809) in a fragment of Atlantic Forest in Southeastern Brazil, Pp. 130-146. *In*: S.F. Ferrari & J. Rímoli (eds.). A Primatologia no Brasil vol. 9. Sociedade Brasileira de Primatologia, Aracaju, SE, Brasil. 201p.

RUMIZ, D.I. 1990. *Alouatta caraya:* population density and demography in northern Argentina. *American Journal of Primatology,* 21: 279-294. http://dx.doi.org/10.1002/ajp.1350210404

RUMIZ, D.I.; ZUNINO, G.E.; OBREGOZO, M.L. & RUIZ, J.C. 1986. *Alouatta caraya*: habitat and resource utilization in northern Argentina. Pp. 175–193. *In:* D.M. Taub & F.A. King (eds.). Current Perspectives in Primate Social Dynamics. Van Nostrand Reinhold, New York, NY. 530p.

RYLANDS, A.B. 1984. Exudate-eating and tree-gouging by marmosets (Callithrichidae, Primates). Pp. 155-168. *In:* A.C. Chadwick & S.L. Sutton (eds.). Tropical Rain Forest: The Leeds Symposium, Leeds Philosophical Society, Leeds, UK. 615p.

RYLANDS, A.B.; MITTERMEIER, R.A. & RODRÍGUEZ-LUNA, E. 1997. Conservation of neotropical primates: threatened species and an analysis of primate diversity by country and region. *Folia Primatologica*, 68: 134-160. http://dx.doi.org/10.1159/000157243

SANTINI, M.E.L. 1985. Alimentação e padrões de atividade de *Alouatta caraya* (Primates, Cebidae), reintroduzido no Parque Nacional de Brasília – DF. *Dissertação de Mestrado*. Universidade de Brasília. Brasília, DF, Brasil. 133p.

SILVER, S.C.; OSTRO, L.E.T.; YEAGER, C.P. & HORWICH, R. 1998. Feeding ecology of the black howler monkey (*Alouatta pigra*) in Northern Belize. *American Journal of Primatology*, 45: 263-279. http://dx.doi.org/10.1002/(SICI)1098-2345(1998)45:3<263::AID-AJP3>3.0.CO;2-U

STRIER, K.B. 1987. Activity budgets of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *American Journal of Primatology*, 13: 385-395. http://dx.doi.org/10.1002/ajp.1350130404

STRIER, K.B. 1992. Atelinae adaptations: behavioral strategies and ecological constraints. *American Journal of Physical Anthropology*, 88: 515-524. http://dx.doi.org/10.1002/ajpa.1330880407

TAKAHASI, A. & FINA, B.G. 2004. Síndromes de dispersão de sementes de uma área do Morro do Paxixi. *In:* Livro de Resumos do IV Simpósio sobre Recursos Naturais e Sócio-Econômicos do Pantanal, Corumbá, MS.

TERBORGH, J. 2003. *Five New World Primates, a study in comparative ecology.* Princeton University Press, Princeton, NJ. 260 p.

WILLIAMS-GUILLÉN, K. 2003. The behavioral ecology of mantled howling Monkeys (*Alouatta palliata*) living in a Nicaraguan shade coffee plantation. *Tese de PhD*. New York University. New York, NY, United States of America. 484p.

ZUNINO, G.E. 1986. Algunos aspectos de la ecología y etología del mono aullador negro (*Alouatta caraya*) en habitat fragmentado. *Tese de Doutorado*. Universidade de Buenos Aires, Buenos Aires, BA, Argentina. 152p.

ZUNINO, G.E. 1987. Nutricion em primates folivoros: la dieta de *Alouatta caraya* en vida silvestre. *Boletim Primatologico,* 5: 78-87.