A PRIMATOLOGIA NO BRASIL - 9
Rímoli, J., K.B. Strier & S.F. Ferrari, 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*: A Primatologia no Brasil - 9 (S.F. Ferrari & J. Rímoli, Eds.) Aracaju, Sociedade Brasileira de Primatologia, Biologia Geral e Experimental – UFS.

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

José Rímoli[1]
Karen B. Strier[2]
Stephen F. Ferrari[3]

Abstract. The behavior of the members of a group of black tufted capuchins (*Cebus nigritus*), with 24-29 individuals, was monitored at the Caratinga Biological Station in the Brazilian state of Minas Gerais. Data were collected in 5-minute scan samples at intervals of 10 minutes continuously throughout the day, in monthly sessions between June 1995 and August 1996, resulting in the collection of 13,825 individual behavioral records. The general activity budget was 37.99% feed, 26.12% travel, 25.93% forage, 5.23% rest, 3.59% social behavior and 1.14% miscellaneous. The diet was composed of three main items: non-reproductive plant parts, NRPPs (36.07% of feeding records), reproductive parts (20.27%), animal prey (23.51%), as well as sugarcane and maize from local plantations (20.16%). The home range was approximately 268 ha, with daily path lengths varying from 550 to 3,000 m. Significant seasonal differences were recorded in both diet and behavior patterns. During dry season months, the consumption of fruit declined significantly, while that of animal prey and NRPPs increased proportionately. Concomitantly, foraging behavior not only increased significantly, but also shifted to manual searching, often involving the destruction of substrates in which hymenopteran larvae were found. These results indicate that the subjects adopted an "energy-maximizing" strategy in response to resource scarcity. Significant differences were also observed between years, and appeared to be related to long-term fluctuations in different resources, as well as changes in group composition. Overall, the study indicated that the considerable behavioral flexibility of the capuchins enabled them to deal with both habitat fragmentation and seasonal and longitudinal changes in the distribution of resources.

Key words: activity budget, behavior, seasonality, capuchin monkey, *Cebus nigritus*, Atlantic Forest.

[1]Department of Biosciences, Fundação Universidade Federal de Mato Grosso do Sul, Campus de Aquidauana, Rua Oscar Trindade de Barros Serra s/n, 79.200-000 Aquidauana – MS, Brazil; e-mail: jsrimoli@ucdb.br;
[2]Department of Anthropology, University of Wisconsin, Madison, USA;
[3]Departamento de Biologia, Universidade Federal de Sergipe, São Cristóvão – SE, Brazil.

Resumo. O comportamento dos membros de um grupo de macacos-pregos-pretos (*Cebus nigritus*), com 24-29 indivíduos, foi monitorado na Estação Biológica de Caratinga em Minas Gerais. Os dados foram coletados em amostras de varredura de 5 minutos a intervalos de 10 minutos continuamente durante todo o dia, em sessões mensais entre junho 1995 e agosto 1996, tendo por resultado a coleção de 13.825 registros comportamentais individuais. O orçamento geral de atividades foi de 37,99% alimentação, 26,12% deslocamento, 25,93% forrageio, 5,23% descanso, 3,59% comportamento social e 1,14% outros. A dieta tinha três itens principais: partes não reprodutivas de plantas (NPPs: 36,07%), partes reprodutivas (20,27%) e presas animais (23,51%), além de cana-de-açúcar e milho das plantações locais (20,16%). A área de vida foi de 268 ha, com percursos diários variando de 550 a 3000 m. Variação sazonal significativa foi registrada na dieta e padrão comportamental. Na estação seca, o consumo de fruto diminuiu significativamente, enquanto o de presas e de NPPs aumentou proporcionalmente. Ao mesmo tempo, o comportamento de forrageio não somente aumentou significativamente, mas também mudou para a busca manual, envolvendo freqüentemente a destruição de substratos que contêm larvas de himenópteros. Os resultados apontam a adoção de uma estratégia de "maximização de energia" em resposta à escassez de recursos. Diferenças significativas também foram observadas entre anos, e pareciam ser relacionadas a flutuações longitudinais em diferentes recursos, além de mudanças na composição do grupo. De modo geral, o estudo mostrou que a flexibilidade comportamental considerável dos macacos-prego os habilitaram a lidar tanto com a fragmentação de habitat como a variação sazonal e longitudinal na distribuição de recursos.

Palavras-chave: orçamento de atividades, comportamento, sazonalidade, macaco-prego, *Cebus nigritus*, Floresta Atlântica.

INTRODUCTION

Resource seasonality is a primary determinant of behavior patterns in free-ranging primates (Stevenson *et al.*, 1998; White, 1998; Wrangham *et* al., 1998; Siemers, 2000). The reproductive phenology of plants is influenced primarily by climatic factors, in particular precipitation and temperature, and to a lesser extent daylight periodicity (Rathcke & Lacey, 1985), resulting in often severe fluctuations in the availability of both reproductive parts and leaves. Extremes of resource scarcity may be especially important selective pressures influencing the evolution of a primate species' behavior.

The southern Brazilian Atlantic Forest is an interesting environment in this context, given its considerable seasonal variation in climate and resource availability. This is reflected in the behavior patterns of a wide variety of native primates, from small-bodied marmosets, such as *Callithrix aurita* and *Callithrix flaviceps* (Corrêa *et al.*, 2000) to the large-bodied muriquis, *Brachyteles hypoxanthus* (Strier, 1999). Intermediate in body size, the capuchins, *Cebus* spp., present arguably the most complex and flexible behavior of any platyrrhine, which is reflected in their ability to occupy a wide variety of habitats (Fragaszy *et al.*, 1990, 2004; Perry, 1996; Manson *et al.*, 1999). In the Atlantic Forest, the genus is

represented by at least three species of tufted capuchins– *Cebus libidinosus*, *Cebus nigritus*, and *Cebus xanthrosternos* (cf. Rylands *et al*., 2000) – although their behavior and ecology is still poorly known.

The study of activity budgets in primates is an indirect approach to the problem of understanding their behavioral strategies for the optimization of foraging tactics and nutritional intake (Coelho *et al*., 1976; Clutton-Brock & Harvey, 1977; Strier, 1987). Considering this, the present study analyzed the variation in the behavior of the members of a group of *C. nigritus* that inhabits a large fragment of southern Atlantic Forest in the context of seasonal and long-term fluctuations in the spatial-temporal distribution of their dietary resources.

While *C. nigritus* is widespread in southern Brazil (Hirsch *et al*., 2002), which has suffered high levels of deforestation in recent decades, it has been the subject of very few field studies (but see Siemers, 2000; Izar, 2004; Lynch Alfaro, 2007). Understanding behavioral and ecological patterns in this species will not only contribute to the growing body of knowledge on the cognitive abilities of the capuchins (e.g. Visalberghi *et al*., 2005; Galvão & Barros, this volume), but also be essential to the development of effective conservation strategies for the remaining populations of *C. nigritus*.

METHODS

Study Site

The study was conducted in the Matão valley of the Caratinga Biological Station (EBC), an isolated, 1.040 hectare fragment (Veado *et* al., 1999) of the Brazilian Atlantic forest located on the Fazenda Montes Claros, in the state of Minas Gerais. The EBC – currently known as the RPPN Feliciano Miguel Abdalla – is located in the Serra da Mantiqueira (19°50'S, 41°50'W), 300 km north of Rio de Janeiro. Protected for more than 60 years by the late Sr. Feliciano Abdalla, the EBC was recently transformed by his family into an officially protected area (*Reserva Particular do Patrimônio Natural*).

The fragment is a mosaic of primary forest (submontane rainforest: Rizzini, 1979; Whitmore, 1990) and habitat in various stages of regeneration, with altitudes ranging from 318 to 682 m above sea level. In contrast with the more humid coastal habitats of the Atlantic Forest biome, the vegetation is characterized by a large proportion of semideciduous species. Mean annual precipitation is approximately 1200 mm (Strier, 1996), and there is a marked dry season between April and September, when less than a fifth of the annual

precipitation is recorded. During this period, many plants lose some or all of their leaves, allowing increased penetration of sunlight through the canopy (Lopes & Andrade, 1986; Ferrari, 1988). By contrast, the wet season is characterized by abundant leaf budding and growth, and greatly increased fruit production.

Typical climatic variation was recorded during the period of the present study, from June 1995 to August 1996 (Figure 1), although the second half of the wet season was relatively dry in comparison with long-term means (Strier, 1996). August 1996 was an exceptionally cold month. Absolute maximum and minimum temperatures were 33.0°C and 7.5°C, respectively. The study period was divided into dry (June-September 1995 and April-August 1996) and wet season (October 1995-March 1996) samples.

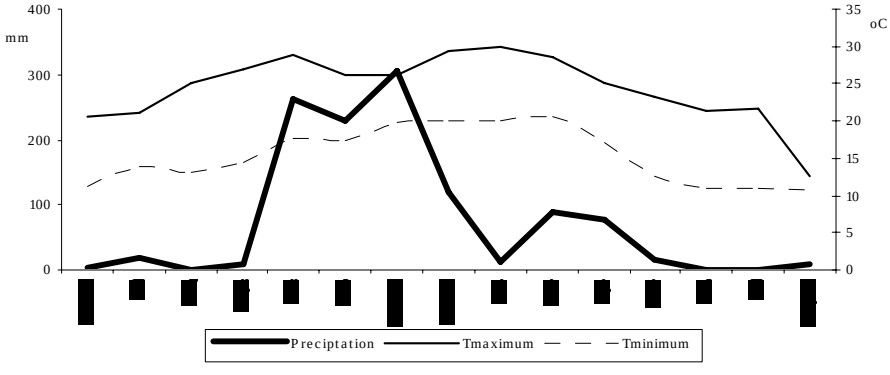

Figure 1. Monthly preciptation, and mean monthly minimum and maximum temperatures recorded at EBC between June 1995 and August 1996 (Rímoli, 2001).

Study Group

The study group had between 24 and 29 members during the course of the study period, with three to five adult males, and six or seven adult females. Identification of subjects was made possible by the considerable variation in pelage coloration and facial characteristics, as well as body size and behavior. Five births were recorded, in October, January and February. In May, three adults (two males, including the alpha, and a female) emigrated, and three infants died (Rímoli, 2001) returning the group to its original size.

Data Collection

Quantitative data were collected monthly throughout the study period, using instantaneous scan sampling (Martin & Bateson, 1993). Given the size of the study group and observation conditions, 5-minute samples were used, with a 15-minute interval, following Zhang (1995). Sampling was conducted continuously throughout the daily activity period. Each subject (group member) observed during a sample was identified and its activity state was recorded. Activity was classified in six main categories: travel, forage, rest, feed, social interaction and miscellaneous (for details, see Rímoli, 2001). These categories were adapted from previous studies of *Cebus* (Robinson, 1988; Janson, 1990; Spironelo, 1991), modified in accordance with specific patterns recorded at the study site. Additional information, such as the height of the subject in the forest and its spatial relationship with other group members, was recorded, but will be presented elsewhere. The information collected for a subject during a scan sample is referred to here as a record.

The use of horizontal space was evaluated using the scan sample records. Each record was plotted on a 1:10,000 scale map of the study area, over which a grid of 1-hectare squares was superimposed. Most records were mapped directly onto the trail system, whereas those located outside this system were mapped according to their orientation and distance to the nearest reference point on the trails. Home range and seasonal ranges were estimated by the number of grid squares visited at least once during the respective period. Daily paths were estimated by the length of the line drawn though all the consecutive records collected on a given day.

Data Analysis

Data were processed using Microsoft Excel 7.0 spreadsheets, and organized by day, month and season. Activity budgets were calculated using the frequency method, in which the time dedicated to each category is estimated according to its proportion of scan sample records.

For the analysis of seasonal variation, samples were separated into wet and dry season samples, as defined above. Longitudinal variation was evaluated on the basis of the comparison of the three-month period (July through August) for which data are available for the two years. Differences between seasons and years were evaluated statistically using binomial *z* scores, in which categories were analyzed separately. For category *i*, $z = x\text{-}m/\sqrt{(N.p.q)}$, where x = number of records of category *i* collected during the first period, N = total number of records of *i* collected, p = proportion of records of all categories collected during the first period, q = proportion of all records collected during the second period,

and $m = N.p$. In order to avoid "false positive" errors (type 1: Martin & Bateson, 1993) in the interpretation of results, a $p = 0.01$ level of significance (critical value of $z = 2.58$) was adopted, following Lima & Ferrari (2003). For the analysis of longitudinal patterns, the data for the equivalent months (June to August) of the two dry seasons were used. For parameters such as daily path, the *t* test was used for comparisons between periods.

RESULTS

General Activity Patterns

A total of 13,825 scan sample records were collected during 138 field days, including 84 "complete" days in which the group was monitored continuously for more than eight hours. The number of records collected in a given scan varied from one to 16, with an overall mean of 3.9±2.6 records per valid scan (i.e. in which at least one record was collected). Monthly means varied from 2.8±1.9 in June 1995 to 4.7±2.8 in October, but did not vary systematically in relation to season or the size of the study group.

Group members typically spent most of their day on the move, foraging intensively for prey in between visits to plant resources. Rest periods were rare and brief, even during the middle of the day, when most other platyrrhines generally engage in a prolonged "siesta".

Overall, study group members dedicated a relatively large proportion of activity time to the acquisition and ingestion of food items (Figure 2). The proportion of time spent feeding – 37.99% – is one of the largest recorded for a capuchin species, although in some studies, such as Terborgh (1983) and Miller (1997), this category is underestimated relative the present study by overlap with the forage category. In the present study, the latter category refers exclusively to the activities of searching for, capturing and manipulating items. As foraging and traveling each occupied slightly more than a quarter of the subjects' activity time, other activities such as rest and social behavior together accounted for less than 10% of the activity budget.

High rates of foraging and traveling are typical of all capuchins (*Cebus* spp.), although such a large proportion of time spent feeding is relatively unusual, not only for capuchins, but for most other primates, except, perhaps, pitheciines (see Peetz, 2001; Veiga, 2007). Interestingly, the most similar values have been recorded in two studies of *Cebus olivaceus*, both in semideciduous forests in Venezuela, where Robinson (1986) and Miller (1996) recorded 43.2% and 34.2% of time spent feeding, respectively. It is unclear, however, whether these rates were influenced specifically by the type of habitat, or other factors, such as positive observational bias.

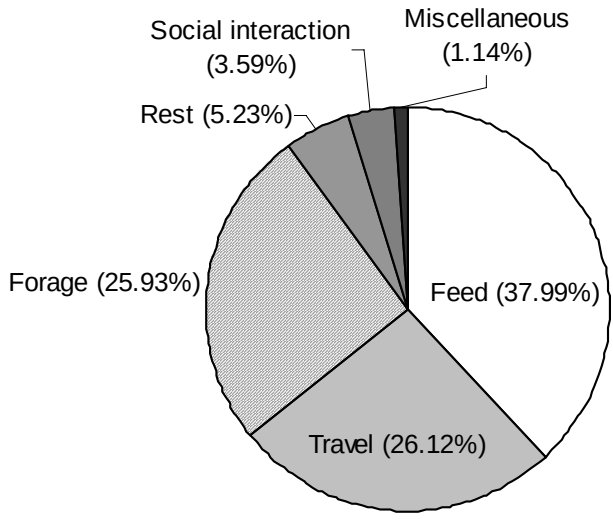

Figure 2. General activity budget of the *C. nigritus* study group at the EBC between June 1995 and August 1996 (n = 13,825 scan sample records).

An additional factor in the present study is the dietary importance of two exotic plant species (sugar-cane, *Saccharum officinarum*, and maize, *Zhea mays*) in the study group's diet. Overall, a fifth of feeding records were attributed to these two species (Figure 3), which were obtained from plantations adjoining the EBC forest. Exploitation of these exotic species has also been recorded in other studies of tufted capuchins in Atlantic Forest fragments (Galetti & Pedroni, 1994; Siemers, 2000), but did not appear to influence feeding rates.

Other items provided similar proportions of the diet (Figure 3), with the exception of nonreproductive plant parts (NPPs), which was the most important category overall. This category included the pith of palm leaves (*Euterpe edulis*), leaf stems of *Apuleia leiocarpa* and woody parts of species of the family Flacourtiaceae. Animal prey was typical of the genus *Cebus*, with a predomination of immature Isoptera (termites) and Hymenoptera (ants, bees, and wasps).

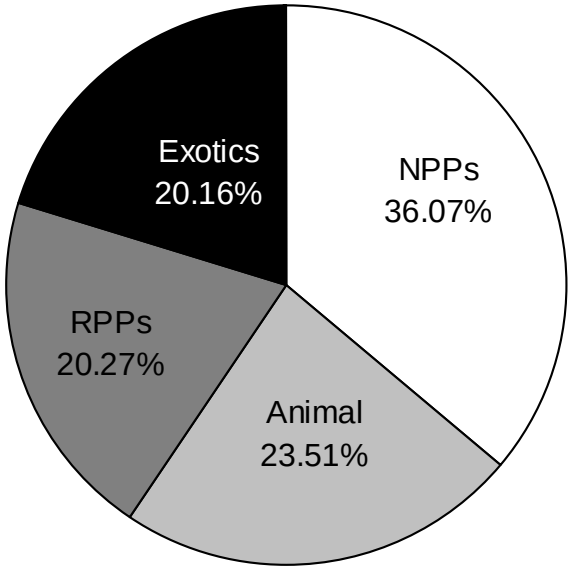

Figure 3. Composition of the diet of the *C. nigritus* study group at the EBC between June 1995 and August 1996 (n = 5,373 records). RPP = Reproductive Plant Parts, NPP = Non-reproductive Plant Parts.

The home range recorded during the present study was 268 hectares, which is relatively small in absolute terms (see Spironelo, 1988; Zhang, 1995a), but is consistent with ranges recorded for *C. nigritus* in continuous forest in Argentina (Di Bitteti, 2001) and, in particular, in fragments (Aguiar *et al.*, 2002; Freitas *et al.*, 2005). Daily ranging were evaluated on the basis of 76 days during which the group was monitored continuously for at least 11 hours. For this sample, mean daily path length was 1605.0±488.7 m (range 550-3000 m), while mean day range was 14.4±5.4 ha (range 2.5-31.5 ha).

Seasonal Variation

A comparison between seasons (Table 1) revealed both similarities and differences. Whereas group members spent effectively the same proportion of their time feeding and traveling in the two seasons, they spent significantly more time foraging during the dry season, while rest and social behavior declined accordingly. The dry season increase in foraging was due to the subjects spending twice as much time in manipulative searches, in which they investigated substrates manually, frequently in a destructive fashion, e.g. breaking

open hollow branches to reach insect larvae. Whereas this type of foraging accounted for only 6.07% of activity time (or 26.46% of foraging time) during the wet season, it rose to 12.70% (43.76% of foraging) in the dry season (z = -1.554, p = 0.1202). By contrast, the second foraging category (scanning visually for signs of prey) was virtually stable, with 16.87% of records during the wet season, and 15.78% during the dry.

Table 1. Activity budget of the *C. nigritus* study group by season, and binomial z scores for comparisons between seasons. For this analysis, miscellaneous activities were allocated to an appropriate category: e.g. "carry sugarcane" was included in Forage, "drink water" was included in Feed, and "scratch self" was included in Rest.

	Scan sample records (% of the total) collected during the:			
Category	Dry season	Wet season	*z*	*p*
Feed	3130 (37.54)	2040 (37.10)	0.349	0.3632
Travel	2206 (26.46)	1483 (27.02)	-0.626	0.2676
Forage	2453 (29.02)	1283 (22.94)	6.689	<0.0001
Rest	348 (4.13)	391 (7.05)	-7.341	<0.0001
Social interaction	200 (2.85)	291 (5.30)	-8.863	<0.0001
Total	8337 (100.00)	5488 (100.00)		

While group members spent a similar proportion of their time traveling in the two periods, they ranged over a slightly wider area, on average, each day in the wet season, with a mean daily path of 1746.5±603.9 m (n = 21) and range of 16.5±5.8 ha, in comparison with 1559.4±426.6 m (n = 55) and 13.1±4.6 ha, respectively, in the dry season. While these differences were not statistically significant, they do indicate that the group ranged more widely during wet season months.

These behavior patterns appear to be linked primarily to shifts in the group's resource base (Table 2). Whereas reproductive plant parts (primarily fruit) constituted the main component of the subjects' diet during the wet season, the emphasis shifted significantly to non-reproductive parts and animal material during the dry season. Crops contributed approximately a fifth of records in each period. As in most other tropical forests, fruit is relatively abundant during the wet season at Caratinga (Strier, 1986; Ferrari, 1988; Rímoli, 2001), so the increase in the consumption of non-reproductive parts in the dry season is a predictable shift in the group's resource base.

Table 2. Seasonal variation in the diet of the *C. nigritus* study group, and binomial *z* scores for comparisons between seasons.

	Scan sample records (%of feeding records):			
Item	Dry season	Wet season	*z*	*p*
Non-reproductive	1424 (40.29)	340 (18.49)	7.149	<0.0001
Reproductive	506 (14.32)	583 (31.70)	-13.430	<0.0001
Animal	923 (26.12)	514 (18.49)	5.473	<0.0001
Exotics	681 (19.27)	402 (21.86)	-2.006	0.0448
Total	3534 (100.00)	1839 (100.00)		

Arthropods also tend to be more abundant in the wet season (Ferrari, 1988; Rímoli, 2001), which apparently contradicts the dry season increase in prey feeding. However, the wet season peak in abundance refers to mature arthropods, whereas the dry season increase in feeding was due to a shift to immature prey, such as hymenopteran larvae. Thus, while the contribution of mature prey to the group's diet declined during the dry season to 5.29% of feeding records, from 8.79% in the wet season, that of immature prey increased considerably, from 9.70% in the wet season, to 20.83% in the dry. This shift in the prey resource base matches the significant increase in manipulative foraging observed during the dry season (see above).

These results indicate a clear seasonal shift in the foraging strategy of the subjects, with the dry season scarcity of fruit and mature insects being compensated for by the exploitation of non-reproductive parts, while the lack of easily-obtainable mature insects was offset by a significant increase in foraging behavior directed at the capture of immature arthropods, the ingestion of which increased considerably. As non-reproductive plant parts are generally less nutritious than fruit, the apparent increase in the consumption of animal material – a relatively rich source of nutrients – would also have offset, in part, the reduction in the availability of fruit.

Longitudinal Variation

The comparison of the same dry season period (July through August) for which data are available from both study years reveal wide-ranging differences in behavior patterns (Table 3). The only category for which the difference between years was not significant was rest. There are consistencies with the general seasonal pattern identified above, such as the emphasis on manipulative foraging. However, the difference between years – in particular the considerable increase in foraging in the second year and the concomitant

reduction in feeding – indicates that, while the subjects maintained an "energy-maximizing" foraging strategy during this period of maximum resource scarcity, the strategy was less effective in 1996.

Table 3. Longitudinal variation in the activity budget of the *C. nigritus* study group during the late dry season (June to August), and binomial *z* scores for comparisons between years.

	Scan sample records (% of the total) in June-August of:			
Category	1995	1996	*z*	*p*
Feed	1513 (42.29)	624 (35.82)	3.491	0.0004
Travel	979 (27.36)	394 (22.62)	3.196	0.0014
Visual forage	334 (9.33)	231 (13.26)	-4.123	<0.0001
Manual forage	480 (13.41)	323 (18.54)	-4.516	<0.0001
Rest	184 (5.15)	81 (4.65)	0.755	0.4502
Social interaction	56 (1.56)	57 (3.27)	-4.008	<0.0001
Miscellaneous	32 (0.90)	32 (1.84)	-2.941	0.0032
Total	3578 (100.00)	1742 (100.00)		

Despite the significant reduction in time spent traveling in 1996, the mean daily path was significantly longer (1209.6±414.4 *vs.* 1806.8± 473.7: $t = -4{,}30$, $p < 0{,}0001$, g.l. = 40), and mean day range was larger (11.4±4.5 ha *vs.* 14.8±4.6 ha: $z = -5.09$, $p < 0.0001$). This difference may, however, have been at least partly related to changes in group composition and the pattern of range use (monitoring of neighboring groups).

The feeding data (Table 4) indicate that these changes in behavior patterns may have been related to a significant shift in the group's diet. In particular, while the consumption of fruit was higher than average (Figure 3) during 1995, it was minimal in 1996. An inverse pattern was recorded for crops, primarily sugarcane. The consumption of vegetative items also increased in the second year, whereas feeding on animal material declined slightly, despite the increase in foraging behavior.

As precipitation is often minimal during the late dry season at the study site, as it was during bother periods here (Figure 1), the rainfall during the preceding wet season may have a more pronounced effect on the availability of resources during the dry season (Ferrari *et al*., 1996). This pattern was upheld in the present case, even though it contradicts the feeding data. Fruit was more abundant in the 1996 dry season (Rímoli, 2001), which

following a relatively humid wet season (total precipitation: 1017.5 mm) in comparison with 1995 (720.0 mm). However, the overall abundance of fruit does not necessarily reflect the availability of this resource to a given primate species, given that many species may be inedible or inaccessible.

Much of the difference between years is in fact due to a major reproductive peak of a single species, *Mabea fistulifera* (Euphorbiaceae), in 1995. The nectar of this species is exploited intensively by other primates at the same site (Ferrari & Strier, 1992), although in the case of *C. nigritus*, the fruit (ripe and immature) and latex were also consumed.

Table 4. Longitudinal variation in the diet of the *C. nigritus* study group, and binomial *z* scores for comparisons between years.

	Scan sample records (% of feeding records):			
Item	1995	1996	*z*	*p*
Non-reproductive	638 (41.53)	609 (46.07)	1.36	0,08
Reproductive	344 (22.40)	75 (5.67)	11.64	0,00003
Animal	454 (29.56)	356 (26.93)	-1.82	0,03
Exotics	100 (6.51)	282 (21.33)	-10.80	0,00003
Total	1536 (100.00)	1322 (100.00)		

DISCUSSION

Overall, the behavior patterns recorded in the present study were broadly similar to those recorded for capuchins at other sites (e.g. Terborgh, 1983; Robinson, 1986; Zhang, 1995; Miller, 1998), with the subjects spending a large proportion of their time foraging and feeding, while a relatively small amount of time was dedicated to rest and social interactions. Significant seasonal and longitudinal variations in these patterns were found, and in most cases, they appeared to be linked systematically to fluctuations in the abundance of resources.

A primary seasonal pattern was a significant shift in the composition of the group's diet, and concomitant changes in foraging patterns. While feeding on fruit declined significantly during the dry season, foraging not only increased significantly, but shifted to manual searching for hidden prey such as hymenopteran larvae. These patterns are consistent with an "energy-maximizing" foraging strategy (Schoener, 1971), in which the animals invested more time and energy in the quest for a high-quality resource (arthropods) as a

means of compensating for the seasonal decline in the availability of fruit. Interestingly, this strategy contrasts with the "time-minimizing" adopted by the other insectivorous primate present at the study site, the buffy-headed marmoset, *Callithrix flaviceps* (Ferrari, 1988). Rather than increasing foraging time, the small-bodied marmosets – which are approximately a tenth of the size (body weight) of a capuchin – reduced activity time and rested more.

An additional pattern was the increased exploitation of non-reproductive plant parts during the dry season, in particular the pith of palm leaves (*Euterpe edulis*). This strategy was also seen in Argentinian *C. nigritus* (Brown *et al*., 1986; Brown & Zunino, 1990), where the primary resource was the leaf bases of bromeliads. Robinson (1986) also recorded the intensive exploitation of stems and petioles during the dry season by *C. olivaceus* in Venezuela. In the specific case of the present study, it is perhaps surprising that crop-raiding did not also increase during this period, although of course, the availability and quality of this resource also declines considerably during the dry season, in line with the prevailing climatic conditions.

Considerable variation was found when comparing the same period of the late dry season between consecutive years, although most of the observed patterns are consistent with the standard adoption of an "energy-maximizing" strategy during periods when resources – in particular arthropod prey – were scarce. However, a major shift in the abundance of a single resource – *Mabea fistulifera* – had a major effect on the composition of the group's diet and associated behavior patterns. Changes in group composition and inter-group relationships also appeared to play a role in longitudinal patterns.

The results of the present study re-emphasize the behavioral and ecological flexibility of *C. nigritus*, which is characteristic of the genus (Fragaszy *et* al., 2004), and its ability to cope with the effects of habitat fragmentation. The systematic exploitation of sugarcane and maize plantations, which has never been observed in the other primates present at the study site, appeared to be an important component of the group's ecology. While this behavior may contribute significantly to the group's survival, it also raises tensions between *C. nigritus* and the local human population, and needs to be taken into consideration in the planning of long-term conservation strategies.

Acknowledgements This paper is dedicated to the memory of Sr. Feliciano Miguel Abdalla, Dona Raimunda and Cláudio Pereira Nogueira. JR was supported by a graduate stipend from CAPES, and the Liz Claybourne and Art Ortenberger Foundation, and SFF received a research grant from CNPq (process no. 307506/2003-7).

REFERENCES

Aguiar, L.M., N.R. Reis, V.J. Rocha & G. Ludwig, 2002. Área de uso de *Cebus apella* (Linnaeus, 1758) no remanescente florestal Mata Doralice, Ibiporã-Paraná. **Livro de Resumos do XI Congresso Brasileiro de Primatologia** p. 100.

Brown, A.D., S.C. Chalukian, L.M. Malmierca & O.J. Collias, 1986. Habitat structure and feeeding behavior of *Cebus apella* (Cebidae) in El Rey National Park, Argentina pp. 137-151. *In*: **Current Perspectives in Primate Social Dynamics** (D.M. Taub & F.A. King, Eds.) Van Nostrand Reinhold, New York**.**

Brown, A. & G.E. Zunino, 1990. Dietary Variability in *Cebus apella* in Extreme Habitats: Evidence for Adaptability. **Folia Primatologica** 54: 187-195.

Clutton-Brock, T.H. & P.H. Harvey, 1977. Species differences in feeding and ranging behaviour in primates pp.557-583. *In*: **Primate Ecology** (T.H. Clutton-Brock, Ed) Academic Press, New York.

Coelho, A.M., C.A. Bramblett, L.B. Quick & S.S. Bramblett, 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.

Corrêa, H.K.M., P.E.G. Coutinho & S.F. Ferrari, 2000. Between-year differences in the feeding ecology of highland marmosets (*Callithrix aurita* and *Callithrix flaviceps*) in southeastern Brazil. **Journal of Zoology** 252: 421-427.

Di Bitteti, M.S. 2001. Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. **Journal of Zoology** 253: 33-45.

Ferrari, S.F. 1988. The Behaviour and Ecology of the Buffy-Headed Marmoset, *Callithrix flaviceps* (O Thomas, 1903). **PhD Thesis**, University College London.

Ferrari, S. F. & K.B. Strier, 1992. Explotation of *Mabea fistulifera* nectar by marmosets (*Callithrix flaviceps*) and muriquis (*Brachyteles arachnoides*) in south-east Brazil. **Journal of Tropical Ecology** 8: 225 - 239.

Ferrari, S.F., H.K.M. Corrêa & P.E.G. Coutinho, 1996. Ecology of the "southern" marmosets (*Callithrix aurita* and *Callithrix flaviceps*) pp. 151-171. *In*: **Adaptive Radiations of Neotropical Primates** (M.A. Norconk, A.L. Rosenberger & P.A. Garber, Eds.). Plenum Press, **N**ew York.

Fragaszy, D., E. Visalberghi & J.G. Robinson, 1990. Variability and adaptability in the genus *Cebus*. **Folia Primatologica** 54: 114-118.

Fragaszy, D.M., L.M. Fedigan & E. Visalberghi, 2004. **The Complete Capuchin.** Cambridge University Press, New York.

Freitas, C.H., E.Z.F. Setz & N. Gobbi, 2005. Área de vida de *Cebus apella* em fragmentos florestais no município de Franca–SP. **Livro de Resumos do XI Congresso Brasileiro de Primatologia** p. 103.

Galetti, M. & F. Pedroni, 1994. Seasonal diet of capuchin monkeys (*Cebus apella*) in a semideciduous forest in south-east Brazil. **Journal of Tropical Ecology** 10: 27-39.

Galvão, O.F. & R.S. Barros, 2008. Uma abordagem para o estudo da cognição em primates pp. 57-66 *In*: **A Primatologia no Brasil – 9** (S.F. Ferrari & J. Rímoli, Eds.) Sociedade Brasileira de Primatologia, Biologia Geral e Experimental-UFS, Aracaju.

Hirsch, A., L.G. Dias, L.O. Martins, R.F. Campos, N.A.T. Resende & E.C. Landau, 2002. Database of georeferenced occurrence localities of Neotropical primates. Departamento de Zoologia, UFMG, Belo Horizonte. http://www.icb.ufmg.br / ~primatas / home_bdgeoprim.htm Accessed in 13/09/2007.

Izar, P. 2004. Female relationships of *Cebus apella nigritus* in a southeastern Atlantic forest: an analysis through ecological models of primate social evolution. **Behaviour** 141: 71-99.

Janson, C.H. 1990. Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. **Animal Behaviour** 40: 922-934.

Lima, E.M. & S.F. Ferrari, 2003. Diet of a free-ranging group of squirrel monkeys (*Saimiri sciureus*) in eastern Brazilian Amazonia. **Folia Primatologica**, 74: 36-44.

Lopes, M.A. & P. Andrade, 1986. Inventário das espécies vegetais da Fazenda Montes Claros. **Unpublished report**, Departamento de Botânica, UFMG, Belo Horizonte.

Lynch Alfaro, J.W. 2007 Subgrouping patterns in a group of wild *Cebus apella nigritus*. **International Journal of Primatology** 28: 271-289.

Manson, J.H., L.M. Rose, S. Perry & J. Gros-Louis, 1999. Dynamics of female-female relationships in wild *Cebus capucinus*: data from two Costa Rican sites. **International Journal of Primatology** 20: 679-706.

Martin, P & P. Bateson, 1993. **Measuring Behaviour: an Introductory Guide**. Cambridge University Press, Cambridge.

Miller, L.E. 1996. The behavioral ecology of wedge-capped capuchin monkeys (*Cebus olivaceus*) pp. 271-287. *In*: **Adaptive Radiations of Neotropical Primates** (M.A. Norconk, A.L. Rosenberger & P.A. Garber, Eds.) Plenum Press, new York.

Miller, L.E. 1997. Methods of assessing dietary intake: a case study from wedge-capped capuchins in Venezuela. **Neotropical Primates** 5: 107-108.

Miller, L.E. 1998. Dietary choices in *Cebus olivaceus*: a comparison of data from Hato Piñero and Hato Masaguaral, Venezuela. **Primate Conservation** 18: 42-50.

Peetz, A. 2001. Ecology and social organization of the bearded saki, *Chiropotes satanas chiropotes* (Primates: Pitheciinae) in Venezuela. **Monographs in Tropical Ecology** 1: 1-170.

Perry, S. 1996. Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). **International Journal of Primatology** 17: 309-330.

Rathcke, B. & E.P. Lacey, 1985. Phenological patterns of terrestrial plants. *Annual* **Review of Ecological Systems** 16: 179-214.

Rímoli, J. 2001 Ecologia de macacos-prego (*Cebus apella nigritus*, Goldfuss, 1809) na Estação Biológica de Caratinga (MG): Implicações para a conservação de fragmentos de Mata Atlântica. **Ph.D thesis**, UFPa/MPEG, Belém.

Rizzini, C.T. 1979. **Tratado de Fitogeografia do Brasil**. Vol. 2. Editoras Hucitec e USP, São Paulo.

Robinson, J.G. 1986. Seasonal variation in the use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: implications for foraging theory. **Smithsonian Contributions to Zoology** 431: 1-60.

Robinson, J.G. 1988. Group size in wedge-capped capuchin monkeys *Cebus olivaceus*. **Behavioural Ecology and Sociobiology** 23: 187-189.

Rylands, A.B., H. Schneider, A. Langguth, R.A. Mittermeier, C.P. Groves & E. Rodriguez-Luna, 2000. An assessment of the diversity of New World primates. **Neotropical Primates** 8: 61-93.

Schoener, T.W. 1971. Theory of feeding strategies. **Annual Review of Ecology and Systematics** 2: 369-404.

Siemers, B.M. 2000. Seasonal variation in food resource and forest strata use by brown capuchin monkeys (*Cebus apella*) in a disturbed forest fragment. **Folia Primatologica** 71: 181-184.

Spironelo, W.R. 1991. Importância dos frutos de palmeiras (Palmae) na dieta de um grupo de *Cebus apella* (Cebidae, Primates) na Amazônia Central pp. 285-296. *In*: **A Primatologia no Brasil – 3** (A.B. Rylands & A.T. Bernardes, Eds.) Sociedade Brasileira de Primatologia, Belo Horizonte.

Stevenson, P.R., M.J. Quiñones & J.A. Ahumada, 1998. Effects of fruit patch availability on feeding subgroup size and spacing patterns in four primate species at Tinigua National Park, Colombia. **International Journal of Primatology** 19: 313-326.

Strier, K. B. 1986. The Behavior and Ecology of Woolly Spider Monkeys, or Muriquis (*Brachyteles arachnoides*). **Doctoral dissertation**, Harvard University..

Strier, K.B. 1987. Activity budgets of woolly spider monkeys or muriqui (*Brachyteles arachnoides*). **American Journal of Primatology** 13: 385-395.

Strier, K.B. 1996. Reproductive ecology of female muriquis (*Brachyteles arachnoides*) pp. 511-532. *In*: **Adaptive Radiations of Neotropical Primates** (M.A. Norconk, A.L. Rosenberger & P.A. Garber, Eds.). Plenum Press, new York.

Strier, K.B. 1999 **Faces in the Forest: the Endangered Muriqui Monkeys of Brazil.** Harvard University Press, Cambridge.

Terborgh, J. 1983. **Five New World Primates, a Study in comparative Ecology.** Princeton University Press, Princeton.

Veiga, L.M. 2007. Ecologia e comportamento do cuxiú-preto (Chiropotes satanas) na paisagem fragmentada da Amazônia oriental. **Ph.D thesis**, Universidade Federal do Pará, Belém.

Veado, E.M.V., A.M. Bragança & R. Abdalla. 1999. A recuperação de áreas pertubadas: "corredores ecológicos" na Fazenda Montes Claros/Estação Biológica de Caratinga. **Resumos do IX Congresso Brasileiro de Primatologia** pp. 47-48.

Visalberghi, E., D.M. Fragaszy, P. Izar & E.B. Ottoni, 2005. Terrestriality and tool use. **Science** 308 (5724): 951.

White, F.J. 1998. The importance of seasonality in primatology. **International Journal of Primatology** 19: 925-927.

Wrangham, R.W., N.L. Conklin-Brittain & K.D. Hunt, 1998. Dietary response of chimpazees and cercopithecines to seasonal variation in fruit abundance. I. antifeedants. **International Journal of Primatology** 19: 949-970.

Zhang, S.Y. 1995. Activity and ranging patterns in relation to fruit utilization by brown capuchins (*Cebus apella*) in French Guiana. **International Journal of Primatology** 16: 489- 507.