American Journal of Primatology 73:1–17 (2011)

RESEARCH ARTICLE

Flexible and Conservative Features of Social Systems in Tufted Capuchin Monkeys: Comparing the Socioecology of *Sapajus libidinosus* and *Sapajus nigritus*

PATRÍCIA IZAR[1]*, MICHELE P. VERDERANE[1], LUCAS PETERNELLI-DOS-SANTOS[1], OLÍVIA MENDONÇA-FURTADO[1], ANDRÉA PRESOTTO[1], MARCOS TOKUDA[1], ELISABETTA VISALBERGHI[2], AND DOROTHY FRAGASZY[3]
[1] *Department of Experimental Psychology, Institute of Psychology, University of São Paulo, São Paulo, Brazil*
[2] *Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy*
[3] *Psychology Department, University of Georgia, Athens, Greece*

Socioecological models assume that primates adapt their social behavior to ecological conditions, and predict that food availability and distribution, predation risk and risk of infanticide by males affect patterns of social organization, social structure and mating system of primates. However, adaptability and variation of social behavior may be constrained by conservative adaptations and by phylogenetic inertia. The comparative study of closely related species can help to identify the relative contribution of ecological and of genetic determinants to primate social systems. We compared ecological features and social behavior of two species of the genus *Sapajus*, *S. nigritus* in Carlos Botelho State Park, an area of Atlantic Forest in São Paulo state, and *S. libidinosus* in Fazenda Boa Vista, a semi-arid habitat in Piauí state, Brazil. *S. libidinosus* perceived higher predation risk and fed on clumped, high quality, and usurpable resources (fruits) all year round, whereas *S. nigritus* perceived lower predation risk and relied on evenly distributed, low-quality food sources (leaves) during periods of fruit shortage. As predicted by socioecology models, *S. libidinosus* females were philopatric and established linear and stable dominance hierarchies, coalitions, and grooming relationships. *S. nigritus* females competed less often, and could transfer between groups, which might explain the lack of coalitions and grooming bonds among them. Both populations presented similar group size and composition and the same polygynous mating system. The species differed from each other in accordance with differences in the characteristics of their main food sources, as predicted by socioecological models, suggesting that phylogenetic inertia does not constrain social relationships established among female *Sapajus*. The similarity in mating systems indicates that this element of the social system is not affected by ecological variables and thus, is a more conservative behavioral feature of the genus *Sapajus*. Am. J. Primatol. 73:1–17, 2011. © 2011 Wiley-Liss, Inc.

Key words: food competition; predation risk; phylogenetic inertia; adaptability; *Cebus*; *Sapajus*

INTRODUCTION

Primate socioecology comprehends primate social systems as evolved species-specific traits, the adaptive outcome of individual behavioral decisions to deal with selective pressures such as the distribution of risks and of limiting resources [reviewed in Janson, 2000]. By means of hypothetic deductive models derived from evolutionary theory, different causal factors have been associated with three fundamental elements of social systems: the social organization (the number, sex ratio, and spatial cohesion of conspecific individuals that typically live together), the social structure (the set of non-reproductive social relationships among these individuals), and the mating system (the pattern of mating relationships) [reviewed in Kappeler & van Schaik, 2002].

In socioecological models, food competition among females plays a central role in all the above aspects of primate social systems. As female reproductive success is limited by food intake (due to the costs of high parental investment [Trivers, 1972]), the number of females in a group is expected to be limited by food competition [Isbell, 1991; Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980]. In contrast, male reproductive success is limited by access to sexually receptive females, so the number of

---

Contract grant sponsor: FAPESP; Contract grant numbers: 06/51577-2; 06/56059-0; 08/55684-3; Contract grant sponsor: CNPq; Contract grant number: 420038/2005-1; Contract grant sponsors: National Geographic Society; Leakey Foundation; IBAMA; CNPq.

*Correspondence to: Patrícia Izar, Av. Prof. Mello Moraes, 1721, CEP: 05508-030, São Paulo, SP, Brazil. E-mail: patrizar@usp.br

Received 15 November 2010; revised 28 March 2011; revision accepted 23 April 2011

DOI 10.1002/ajp.20968

males in a group is expected to be a function of the spatial (number) and temporal (estrous synchrony) distribution of reproductive females [Clutton-Brock, 2004; Lindenfors et al., 2004]. Thus, food competition limits group size, because larger groups deplete food sources faster and need to travel to find other sources, increasing daily travel costs [e.g. Chapman & Chapman, 2000; Isbell, 1991; Izar, 2004; Snaith & Chapman, 2007; Strier, 1989; Teichroeb & Sicotte, 2008], and decreasing female reproductive success [e.g. Borries et al., 2008; Ryan et al., 2008; van Belle & Estrada, 2008]. Besides affecting social organization, food competition affects mating systems because the capacity of individual males to monopolize sexually receptive females is correlated with the size and degree of overlap of females' range [Komers & Brotherton, 1997] and with the number of males in a group [Kutsukake & Nunn, 2006]. Food competition also affects female social relationships. Females might compete directly for patchy usurpable foods, and indirectly for evenly distributed foods, within group and between groups [reviewed in Isbell & Young, 2002]. According to the most recent model [Sterck et al., 1997], the combination of the level of the four types of food competition leads to four behavioral syndromes of female social relationships, in regards to their tendency to remain in the natal group, and to establish dominance relationships and kin-biased affiliative relationships.

Predation risk is considered the ultimate cause of group living in diurnal primates [van Schaik, 1983; but see Rasoloarison et al., 1995]. At the proximate level, it is expected to affect social organization and mating system, by limiting minimum group size [Dunbar, 1996; but see Boinski et al., 2003; McGraw & Zuberbühler, 2008] and increasing group cohesion [Boesch & Boesch-Achermann, 2000; Sterck et al., 1997], and there is evidence that the extra-number of males in a group (expected by number of females) is correlated with predation risk [Hill & Lee, 1998; Stanford, 2002; van Schaik & Hörstermann, 1994].

Sexual conflict is also expected to affect primate social systems. In this view, mating patterns might reflect female strategies to confound (e.g. promiscuous mating) or to concentrate paternity, counteracting male strategies like harassment and infanticide [Nunn & van Schaik, 2000]. As a consequence, species showing the same social organization might present different mating systems according to female behavioral strategies [Izar et al., 2009] and reproductive synchrony [Ostner et al., 2008]. In addition, female dispersal might be a response to risk of infanticide by males [Jack & Fedigan, 2009; Robbins et al., 2009], that can limit the number of females in a group, as has been shown for howler monkeys [Crockett & Janson, 2000].

Socioecological models have been criticized due to some discrepancies between predictions of the models and patterns of social systems actually observed in field studies, and because most field tests were based on Old World species [e.g. Chapman & Rothman, 2009; Strier, 1994, 2003, 2009; Thierry, 2008], indicating that more studies are necessary to improve the models, especially incorporating the less investigated New World primate species [Janson, 2000; Kappeler & van Schaik, 2002; Strier, 1994]. More research is also necessary to address the question of how flexible and how conservative primate social systems are. The focus of behavioral ecology is on adaptation, but it is assumed that selection act(ed) on individual strategies, or decision rules, so that organisms behave as fitness maximizers. Indeed, tests of the models are based ''on the current fit of an organism's behavior to local environmental conditions'' [Rendall & Di Fiore, 2007, p 509] and thus behavior should vary according to local and current environment conditions, within the limits of social trajectories or behavioral syndromes [Cahan et al., 2002; Sih et al., 2004]. One method to identify what behavioral features vary along with variation in ecological factors is to study behavioral variation among populations or sister species, on the assumption that there is little or no biological difference among them [e.g. Barton et al., 1996].

Tufted capuchin monkeys are particularly suitable for this kind of study. According to recent reviews based on morphological [Oliveira & Langguth, 2006; Silva, 2001] and molecular evidence [Lynch-Alfaro et al., submitted], this is a group of eight species of the Neotropical genus *Sapajus* (*S. apella*, *S. macrocephalus*, *S. libidinosus*, *S. cay*, *S. nigritus*, *S. robustus*, *S. xanthosternos*, and *S. flavius*), formerly classified as the robust forms of the Neotropical genus *Cebus* (that now, according to these reviews, includes only the gracile forms *C. albifrons*, *C. olivaceus*, and *C. capucinus*). The genus *Sapajus* has a wide distribution, occupying very different habitats, including evergreen tropical forests, mangrove forests, the semi-arid *Caatinga* and *Cerrado* in northeast and central Brazil, and dry seasonal forests [Fragaszy et al., 2004a]. These habitats vary widely in ecological features, including food availability and predation risk. It has been argued that capuchins' capacity to adapt to these different environments is related to their great behavioral flexibility, particularly with respect to feeding behavior, including tool use [Fragaszy et al., 2004b; Visalberghi et al., 2005]. Whether these species present heritable differences in social behavior is still unknown, but the fact that in captivity they hybridize and individuals interact naturally, forming stable social groups, provides some evidence against this argument. Moreover, most captive studies report a similar pattern of social system, characterized by a dominance hierarchy among males and among females, a male that is dominant over all other group members, a female mate choice biased toward the dominant male, and grooming down the hierarchy [reviewed in Fragaszy et al., 2004b].

In order to test predictions of the socioecological models, here we present a direct comparison of two tufted capuchin species, the bearded capuchin monkey *S. libidinosus*, living in an area of Cerrado-Caatinga transition, the Fazenda Boa Vista (FBV), in northeastern Brazil, and the black-horned capuchin *S. nigritus*, living in an area of Atlantic Forest, Carlos Botelho State Park (PECB), in southeastern Brazil. For these two populations, we compare data on predation risk, food availability, feeding behavior, competitive regimes, group size, sex ratio, mating behavior, dispersal, and female social relationships. For the purpose of this comparison, we reanalyze data on mating behavior of *S. nigritus* presented by Izar et al. [2009], on group cohesion presented by Nakai and Izar [in review], and on food availability, feeding behavior, competitive regimes, dispersal, and female social relationships of *S. libidinosus* presented by Verderane et al. [in review], who studied the impact of tool use on female social relationships.

FBV is a seasonally dry area of open woodland with mostly small (3–5 m tall) xeromorphic and scleromorphic trees, whereas PECB is an area covered by dense tall evergreen trees, with no dry season. Based on these general habitat features, first we expected that predation risk at FBV would be higher than in PECB due to the differences in vegetation features, in particular less canopy cover at FBV, since reports of avian attacks on Neotropical primates in forest habitats indicate that they always occur when the monkeys are in open areas, unprotected by foliage [Boinski et al., 2003; Eason, 1981]. The difference between sites in predation risk would lead to more cohesive groups [Sterck et al., 1997] in FBV than in PECB, with a higher proportion of males, because males are more involved than females in defense against predators [Hill & Lee, 1998; Stanford, 2002; van Schaik & Hörstermann, 1994]. The higher proportion of males in a group would lead to a more promiscuous mating system in FBV, either due to a female strategy against the risk of infanticide or to a lower capacity of the dominant male to monopolize females.

Second, due to the vegetation features and the severe dry season, we expected that fleshy fruits would be less available to the capuchins in FBV than in PECB [e.g. Batalha & Martins, 2004], and fruit sources would be small, not usurpable, and complemented with evenly dispersed foods in FBV, and of intermediate size to large, and usurpable, in PECB. According to the socioecological model [Sterck et al., 1997], based on these features of food sources, we expected that females would experience indirect food competition within groups in FBV and direct food competition within groups in PECB. Food competition between groups is considered a function of population density [Sterck et al., 1997], or a negative function of food abundance [Isbell, 1991]. Population density is the same in both sites (2.3 inds/km^2) and considered low in comparison with other sites [Izar, 2004; Verderane et al., in review]. According to Sterck et al. [1997], we expected higher contest competition between groups in PECB than in FBV, and according to Isbell [1991] we expected higher food competition in FBV than in PECB. Owing to the different regimes of food competition between sites, we expected that females in PECB would remain in their natal groups, establishing linear dominance relationships, with coalitions and grooming relationships, whereas females in FBV could disperse, and develop more egalitarian relationships with no coalitions and grooming relationships among them.

Finally, current human interference in the environment is apparently greater in FBV than in PECB. Human interference is thought to reduce the risk of predation because predators are eliminated, which could reduce the number of males in a group. It is also thought to alter the food availability due to the introduction of patches of highly productive unnatural vegetation (such as fruit orchards and crops), thus increasing contest competition for food [reviewed in Sterck, 1999]. If human interference alters the primate habitat in FBV in these directions, then we expect similar social systems in both populations.

METHODS

Study Groups and Sampling Methods

Sapajus libidinosus

The data were collected by M.P.V. and one field assistant, trained until 85% of concordance, on one habituated individually recognized wild and nonprovisioned group (ZA) of 8–14 individuals (one adult male, three adult females, 2–0 subadult males, three juvenile males, three juvenile females, and 0–3 infants), in FBV, Gilbués, Piauí state (9°00′S, 45°00′W), from May 2006 through April 2008, totaling 1,932 hr of observation. The site is described in Visalberghi et al. [2007]. Data on fruit availability, size of food sources, ranging behavior and female agonistic, coalitionary and grooming relationships given for *S. libidinosus* in this report are taken from Verderane et al. [in review].

We calculated a Human Interference Index following Bishop et al. [1981]. The index is an average of four measures that range between 1(minimum interference) and 4: (a) human alteration of the habitat (1 = undisturbed, 2 = moderately disturbed, 3 = mosaic of human-made areas and type 1 or 2 areas, 4 = urban); (b) harassment of animals (1 = animals undisturbed, 2 = minimal harassment, 3 = occasion-specific harassment, 4 = daily harassment), (c) habituation to humans at start of study (1 = wild, 2 = semihabituated, 3 = habituated, 4 = habituated and comensal), and (d) the presence of predators (1 = full complement of predators, 2 = partial complement of predators, 3 = impoverished complement of predators, 4 = no predators).

To estimate predation risk, we recorded ''all-occurrences'' [Altmann, 1974] of alarm calls (and the cause, whenever possible) and encounters of the studied group with potential predators.

Fruit availability was estimated combining two methods. (1) One hundred fruit traps were placed at 30-m intervals, 1-m off the side of a 3-km trail crossing the different physiognomies of the study area. The content of the traps was collected and weighed every 2 weeks. (2) Palm trees of the species *Attalea barreirensis* ($N = 136$) and *Orbignya* sp ($N = 118$) selected along the same 3-km trail were observed. Every month the researcher noted the presence/absence of fruits in these palms. This second method was employed because most palm species eaten by the capuchins at FBV have subterraneous stems and clusters emerge from the soil [Fragaszy et al., 2004c], so that palm fruits would not fall into the fruit traps. Because the method of fruit traps, although indicated for comparison of fruit abundance between habitats, presents several potential biases [Chapman et al., 1994], we also analyzed tufted capuchin capuchins behavioral correlates of fruit availability (activity budget, diet composition, and ranging area; e.g. Terborgh [1983]). Data on activity budget and diet were collected through 10-minute scan samples [Altmann, 1974] for 6–10 complete days (from dawn to dusk) each month. Coordinate locations of the animals were collected at every scan using a GPS device. Coordinate points were plotted using ArcGis 9.1, and monthly range area was calculated by connecting the most external points.

The size of patchy food sources was evaluated according to (1) food site depletion time, using the ''feeding tree focal sample'' (FTFS) method [Strier, 1989], which is the interval between when the first individual entered and when the last individual left a food tree, subtracting the amount of time in which the monkeys did not feed (cf. Vogel and Janson [2007]), and (2) feeding unit size, which is the number of individuals that fed simultaneously in the same tree. According to Isbell et al. [1998], food site depletion time is the relevant feature of food sources affecting female social relationships because it is correlated to the usurpability of a source. A short depletion time indicates a small not usurpable food source. Moreover, since the animals could feed in the same trees several times, FTFS is a more accurate measure of variation in fruit productivity of the same tree than is crown volume. According to Boinski et al. [2002], feeding unit size that indicates if a food patch can be shared by group members, which is a condition for contest competition within groups to cause female nepotism and philopatry.

To estimate contest food competition and female relationships, we recorded ''all-occurrences'' of conspicuous agonistic interactions within and between groups (aggressive physical contact, chasing, and aggressive display), coalitions (the intervention of a third party during a conflict between two individuals, clearly supporting one participant, cf. Ferreira et al. [2006]), and grooming relationships, including the context, the participants, and the direction of the behavior whenever visible (used to analyze dominance relationships). Missing an event of the above behaviors by using ''all-occurrences'' method was considered unlikely because, with the exception of grooming, they are all conspicuous and associated with typical vocalization and noises that attract the attention of the observers. The group was generally cohesive and observations were conducted at close distance (1–10 m) from the animals most of the time by two observers, the researcher and the field assistant. Grooming, although discrete, occurs during resting when the group is very cohesive and all individuals can be easily observed in a small area.

As in Izar [2004], ranging behavior was used as a measure of scramble competition for food, since correlation between group size and daily travel distances indicates scramble competition within group, and correlation between group size and home range is an indicative of scramble competition between groups [Chapman & Chapman, 2000; Isbell, 1991]. Data reported on scramble competition are taken from Verderane et al. [in review].

We included two additional years of data on ZA group and on a second group of habituated individually recognized monkeys (CH) for analysis of group size, sexual ratio, and mating behavior. Following Fragaszy et al. [2004b], we considered adult and subadult males for the calculus of sexual ratio. The additional 2 years of data collection were conducted by two observers and by field assistants trained by MPV. Data on mating behavior were recorded on an ''all-occurrences'' basis.

Sapajus nigritus

The data were collected in Carlos Botelho State Park (PECB), São Paulo state (24°00′ to 24°15′S, 47°45′ to 48°10′W), by six observers each trained by the preceding main researcher (until 85% of concordance) to recognize the individuals and to collect behavioral data, aided by the same trained field assistant. The site is described in Presotto and Izar [2010]. Data were collected on one group (Pimenta) of which all adult individuals were recognized (and some of the immatures) from February 2004 to March 2006 and from March 2007 to August 2008, totaling 1,576 hr of observation. The group varied from 21, in 2004–2006, to 14 individuals (2-1 adult males, 2-1 subadult males, 7-3 adult females, 8-7 juveniles, and two infants). The methods were the same as described for *S. libidinosus*, except that we recorded the animals' behavior at 5-min (rather than 10-min) scan sampling, and we estimated fruit availability using fruit traps only (we placed 153 traps at 50 m intervals along a 7-km trail crossing the three landforms of the study area). Palm trees in this area produce fruit clusters in the crown, so availability of palm fruits is adequately measured by the trap method. As argued for FBV, we considered that the probability of missing an event recorded through "all-occurrences" method was low. During periods of high fission–fusion dynamics (see Results), we were able to follow only one subgroup at a time, but observations were not biased to particular individuals since changing subgroup membership is habitual in this population. Visibility conditions of the animals in PECB are generally lower than in FBV due to the denser forest canopy. However, observations were always conducted beneath the monkeys, from a distance varying from 5 to 30 m (depending on their height in the trees), by the researcher and the field assistant. Moreover, before comparing rates of behaviors between populations, we verified whether rates of the behaviors recorded through all-occurrences could differ between the two populations due to different observation conditions. We compared the frequency of total agonistic events recorded in each site with the frequency of these events in which the context and the participants were identified by the observers. No difference was found: in FBV, context and participants were identified in 56% of the events ($N = 525$ of 944), and in PECB, in 62% of the events ($N = 133$ of 213, $\chi^2 = 0.88$, $P = 0.35$). Data on group size, sex ratio, and mating behavior included two additional years (2002 and 2009), three other social groups, and data reported in Izar et al. [2009]. Data on group cohesion are reported in Nakai and Izar [in review]. Data reported on scramble competition are taken from Izar [2004].

The research in both sites complied with protocols approved by the Animal Research Ethics Committee of Institute of Psychology of University of São Paulo and adhered to the Brazilian legal requirements, and to the American Society of Primatologists principles for the ethical treatment of primates.

Statistical Analysis

Using GLM tests performed with the statistical package SPSS 13.0, we compared between sites and seasons: (1) monthly fruit biomass; (2) monthly proportion of scans devoted to foraging (feeding included), to traveling, to resting, and to other activities (including vigilance and social behavior); (3) monthly proportion of foraging scans devoted to fruits, flowers, invertebrates, leaves and to other items; (4) monthly group ranging area and monthly individual range area (range area divided by group size); (5) monthly rate (events/hr of observation) of alarm calls; (6) mean monthly FTFS and feeding unit size; and (7) monthly rate of agonistic interactions, and of coalitions. Although there is no actual dry season in PECB, rainfall is lower between April and September (the dry season in FBV) than between October and March (the rainy season). Data were tested for normality before conducting the GLM analysis using Kolmogorov–Smirnov and Shapiro–Wilk tests. Significance level was set to 0.05. Effect sizes were determined by partial eta squared (η). We also compared FTFS and feeding unit size between both populations using the whole sample of feeding trees (that is, the trees the monkeys fed in) recorded in each study site. Because these last data deviated from normal distribution, we made the comparisons using the nonparametric Mann–Whitney test and we ran Monte Carlo estimates of the exact P-values based on 10,000 sampled tables. We compared the frequency of grooming and of coalition between female–female dyads in relation to total occurrence of these behaviors between FBV and PECB using χ^2 tests. Following Chancellor and Isbell [2009], due to the small size of our groups of females (<6), we assessed linearity of female dominance hierarchies using the directional consistency (DC) index: $DC = (H–L)/(H+L)$, where $H =$ number of agonistic interactions in the direction of higher frequency and $L =$ number of agonistic interactions in the direction of lower frequency.

RESULTS

Comparisons between the two populations are summarized in Table I. The average index of human disturbance in FBV is higher than in PECB. In FBV, the habitat is a mosaic of undisturbed areas and areas disturbed by human exploitation; the capuchins might be occasionally harassed when invading crops; they avoid human contact probably due to hunting in the past, and natural predators are represented by few individuals of the major species. PECB is covered mainly by undisturbed forest, contact with humans is rare and the monkeys are not harassed, they vary in their reaction to human contact but generally just move away, and natural predators also occur in low density but are more protected than in FBV.

In spite of this, we assume that the two sites do not differ in predation rate, since in both sites no event of predation was observed. However, the perception of predation risk measured by monthly rates of alarm calls varied significantly between sites ($F = 13.37$; $df = 1$; $P = 0.01$; $\eta = 0.29$; obs. power $= 0.94$), with higher rates in FBV ($\text{mean} \pm SD = 0.24 \pm 0.14$ alarms/hr) than in PECB (0.06 ± 0.13 alarms/hr). Alarm calls in both sites were emitted mainly to aerial predators, and other large birds, but in FBV 38% of the alarm calls

TABLE I. Ecological and Behavioral Comparisons Between a Population of *Sapajus libidinosus* at Boa Vista (FBV) and a Population of *Sapajus nigritus* at Carlos Botelho State Park (PECB)

Characteristic	FBV	PECB
Human influence index[a]	2.25	1.50
Human alteration of habitat	3	1
Harassment of animals	2	1
Habituation to humans at start	1	2
Presence of predators	3	2
Perception of predation risk	24 alarms/100 hr (no predation events observed in ~2,000 hr)	6 alarms/100 hr (no predation events observed in ~2,500 hr)
Fruit availability (mean total annual biomass)	3,818±1,079 kg/ha ($N = 2$ years)	2,682±949 kg/ha ($N = 5$ years)
Home range (average)	300.0±50.0 ha ($N = 2$ groups)	484.5±24.5 ha ($N = 2$ groups)
Group size and cohesion	8–19; cohesive groups ($N = 2$)	13–20; variable degree of cohesiveness according to food availability[b] ($N = 4$)
Male–female ratio	0.58	0.65
Mating system; mating bias toward dominant male	Polygyny; 71[c] –95%[d]	Polygyny; 75[e] –100[f]%[g]
IBI (months)	22.2±1.48 ($N = 4$ females)	30.22±6.43 ($N = 10$ females)[g]
Activity budget (monthly mean percentage of scans)		
Foraging	46±7%	58±12%
Travelling	32±11%	36±11%
Resting	8±5%	4±4%
Others	4±1%	2±3%
Diet (monthly mean percentage of foraging scans)		
Fruit	47±13%	35±16%
Flower	4±7%	2±4%
Invertebrate	31±9%	22±14%
Leaves	4±2%	36±23%
Others	12±7%	5±6%
Mean food patch depletion time (minutes)	17±3[h]	9±2
Feeding unit size (mean number of group members sharing a patchy food source)	4±0.4 individuals[h]	3±0.5 individuals
Within-group contest competition for food	Yes; 35 events/100 hr[h]	Yes; 8 events/100 hr
Female participation (percentage of events)	52.6%[h]	18.6%
Formal dominance hierarchy	Yes[h], linear	No
Coalition between females	2.6 times the expected by number of available partners[h]	No
Between-group contest competition for food	Yes; 1.1 events/100 hr[h]	Yes; 1.4 events/100 hr
Female participation in intergroup encounters	Yes[h]	No
Within-group indirect competition for food	No, daily travel distance not correlated to group size[h]	Yes, daily travel distance correlated to group size[i]
Between-group indirect competition for food	No, home range not correlated to group size[h]	Yes, home range correlated to group size[i]
Grooming between females	16% of total frequency within group, 2 times more frequent than the expected by number of available partners	1.4% of total frequency within group, 65% of the frequency expected by the number of available partners
Female transfer	No[h]	Yes

[a] cf. Bishop et al. [1981], see text for definition of indexes.
[b] Nakai and Izar [submitted].
[c] Data for group CH.
[d] Data for group ZA.
[e] Data for period of high fission–fusion.
[f] Data for period of high-group cohesiveness.
[g] Izar et al. [2009].
[h] Verderane et al. [submitted].
[i] Izar [2004].

were emitted due to human disturbance (including domestic animals), versus none in PECB.

Mean total annual fruit biomass was higher in FBV than in PECB (Table I), and there was a tendency toward a significant difference in monthly fruit biomass between sites (FBV = 314 ± 296 kg/ha; PECB = 235 ± 162 kg/ha; $F = 2.96$; df = 1; $P = 0.09$; $\eta = 0.03$; obs. power = 0.40) (Fig. 1). In both sites, fruit availability tended to be higher during the rainy season (FBV: rainy = 348 ± 345 kg/ha, dry = 283 ± 248 kg/ha; PECB: rainy = 280 ± 179 kg/ha, dry = 192 ± 133 kg/ha; $F = 1.97$; df = 3; $P = 0.12$; $\eta = 0.06$; obs. power = 0.49). Palm fruits were available throughout the year in FBV, with a peak during the dry season (Fig. 1).

The home range was 1.6 times larger in PECB than in FBV (Table I). This difference was stronger when comparing mean monthly range area (115 ± 53 vs. 58 ± 30 ha; $F = 21.48$; df = 1; $P < 0.001$; $\eta = 0.30$; obs. power = 0.99; Fig. 2), and held true when dividing range area by group size (12 ± 6 vs. 7 ± 3 ha; $F = 14.49$; df = 1; $P < 0.001$; $\eta = 0.23$; obs. power = 0.96).

Group sizes were similar in the two populations. Groups in FBV were highly cohesive during all activities throughout the day, across months and years while Nakai and Izar [in review] report that in PECB group cohesion varied across months and years and that the groups were cohesive in periods when large food sources were available and split into subgroups containing few group members when the monkeys were feeding mainly on small food sources. Groups in FBV had a slightly lower proportion of adult males to adult females in relation to groups in PECB (Table I).

In both populations, females were strongly biased for to exhibit proceptive behavior toward the dominant male (Table I). In PECB, females solicited the dominant male in 75% of 16 proceptive episodes [Izar et al., 2009]. In FBV, females solicited the dominant male in 71% of seven proceptive estrous episodes observed in group CH and in 95% of 19 estrous proceptive episodes observed in group ZA. Females' choice was not caused by dominant male coercion, since we did not observe aggression or interference toward proceptive females by males in either population. Interbirth interval in PECB was 8 months longer than in FBV for females whose previous infant was still alive (Table I).

Feeding Behavior and Feeding Sources Size

The activity budget and diet varied between sites ($F = 94.40$; df = 9; $P < 0.001$; $\eta = 0.94$; obs. power = 1.00) and seasons ($F = 5.20$; df = 9; $P < 0.001$; $\eta = 0.45$; obs. power = 0.99) and there was a significant effect of interaction between site and season ($F = 3.85$; df = 9; $P < 0.005$; $\eta = 0.38$; obs. power = 0.97). The capuchins from PECB foraged more ($F = 18.52$; df = 1; $P < 0.001$; $\eta = 0.22$; obs. power = 0.99), and traveled more ($F = 35.31$; df = 1; $P < 0.001$; $\eta = 0.35$; obs. power = 1.00) than the capuchins from FBV. In FBV, the capuchins rested more ($F = 9.08$; df = 1; $P < 0.005$; $\eta = 0.12$; obs. power = 0.84) and performed other activities more ($F = 14.80$; df = 1; $P < 0.001$; $\eta = 0.19$; obs. power = 0.97) than in PECB (Fig. 3, Table I). The capuchins foraged more during the dry season ($F = 14.54$; df = 1; $P < 0.001$; $\eta = 0.18$; obs. power = 0.96), but the seasonal difference was significant only for

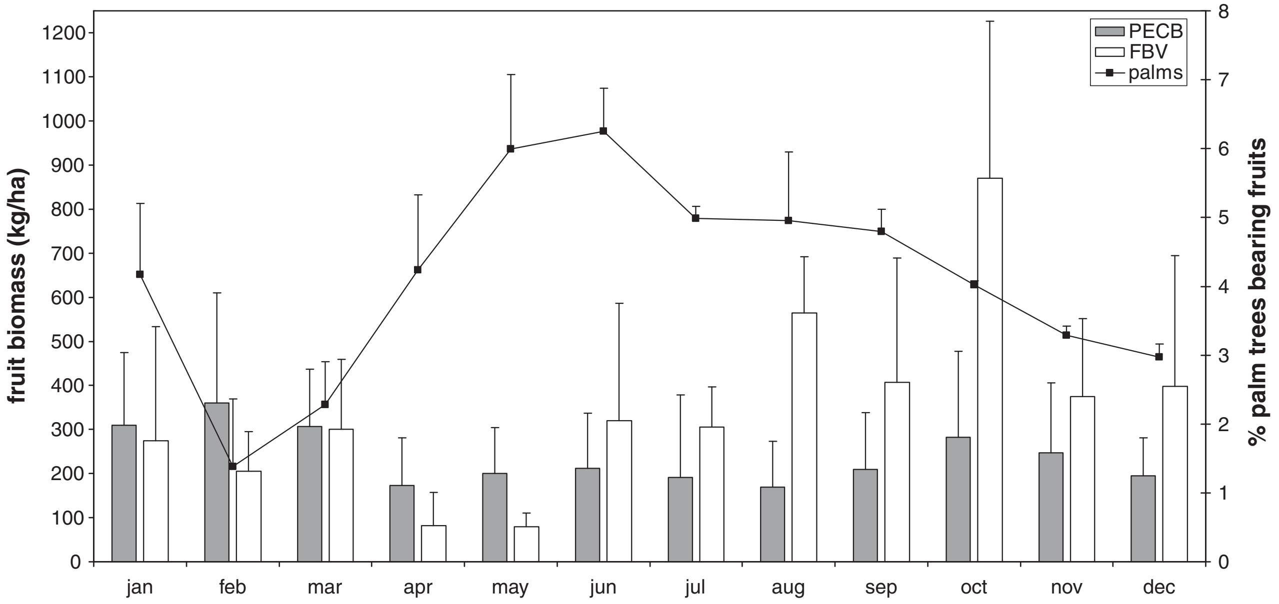

Fig. 1. Mean monthly variation in fruit biomass in PECB ($N = 5$ years) and FBV ($N = 2$ years), and mean proportion of sampled palm nuts bearing fruit in FBV. Line = palms. Bar = fruit biomass.

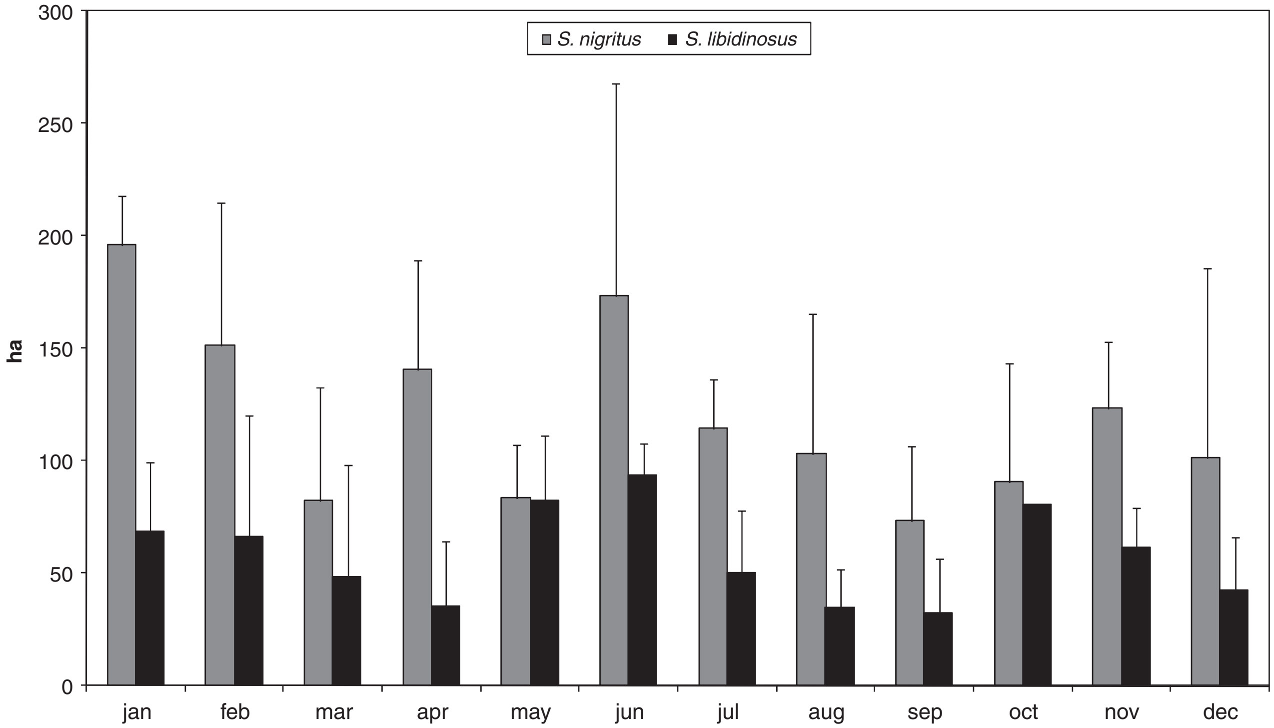

Fig. 2. Mean monthly range used by a group of *Sapajus nigritus* in PECB and by a group of *Sapajus libidinosus* in FBV. FBV, Fazenda. Boa Vista.

PECB ($F = 10.18$; df = 1; $P < 0.005$; $\eta = 0.13$; obs. power = 0.88).

Regarding the diet, capuchins from PECB spent less time than capuchins from FBV foraging for fruits ($F = 8.73$; df = 1; $P < 0.005$; $\eta = 0.19$; obs. power = 0.83), flowers ($F = 4.31$; df = 1; $P < 0.05$; $\eta = 0.06$; obs. power = 0.53), invertebrates ($F = 7.81$; df = 1; $P < 0.01$; $\eta = 0.11$; obs. power = 0.79), and other food items ($F = 18.16$; df = 1; $P < 0.001$; $\eta = 0.22$; obs. power = 0.99), and spent more time foraging for leaves ($F = 46.16$; df = 1; $P < 0.001$; $\eta = 0.41$; obs. power = 1.00) than capuchins from FBV (Table I, Fig. 4). Season affected foraging for fruits ($F = 4.33$; df = 1; $P < 0.05$; $\eta = 0.06$; obs. power = 0.54) and flowers ($F = 11.37$; df = 1; $P < 0.01$; $\eta = 0.15$; obs. power = 0.91), so that the monkeys spent more time foraging for fruits during the rainy season (mean difference ± SD = 8 ± 4% of scans) and more time foraging for flowers during the dry season (mean difference ± SD = 4 ± 1), but this last difference occurred only in FBV ($F = 6.86$; df = 1; $P < 0.05$; $\eta = 0.10$; obs. power = 0.73).

The size of patchy food sources, estimated as depletion time (FTFS) and feeding unit size, varied according to site ($F = 24.22$; df = 2; $P < 0.001$; $\eta = 0.70$; obs. power = 1.00). Mean monthly depletion time at PECB was smaller than at FBV (9 ± 2 vs. 17 ± 3 min; $F = 50.74$; df = 1; $P < 0.001$; $\eta = 0.70$; obs. power = 1.00; Fig. 5), as well as mean monthly feeding unit size (3 ± 0.5 vs. 4 ± 0.4 individuals; $F = 5.79$; df = 1; $P < 0.05$; $\eta = 0.21$; obs. power = 0.63; Fig. 6). These differences hold true when we compared all the trees in which the animals were recorded feeding for each site (depletion time: Mann–Whitney $Z = -12.36$; $P < 0.001$; Monte-Carlo $P < 0.001$; PECB median = 5.00 min, IQR = 7.50; FBV median = 10.00 min, IQR = 15.7; feeding unit size: Mann–Whitney $Z = -3.50$; $P < 0.001$; PECB median = 3.00 individuals, IQR = 2.00; FBV median = 3.00, IQR = 3.00, $N = 1{,}734$ trees for PECB and 1,355 trees for FBV).

Competitive Regimes and Social Relationships

Monthly rates of food-related aggression involving females were significantly higher in FBV in comparison with PECB (0.20 ± 0.11 events/hr vs. 0.03 ± 0.05; $F = 60.56$; $P < 0.001$; $\eta = 0.51$; obs. power = 1.00. Verderane et al. [in review] reported that females at FBV participated in 53% of the observed agonistic interactions, being the aggressors in 70% of the events. Conflicts at PECB occurred at a low rate, 0.15 agonistic interactions/hr ($N = 213$) and in those for which we were able to identify the individuals involved ($N = 133$), females participated in only 19%. Females were the aggressors in 93% of the events in which they did participate, mainly against juveniles.

In FBV, it was possible to order group females into a linear dominance hierarchy [Verderane et al.,

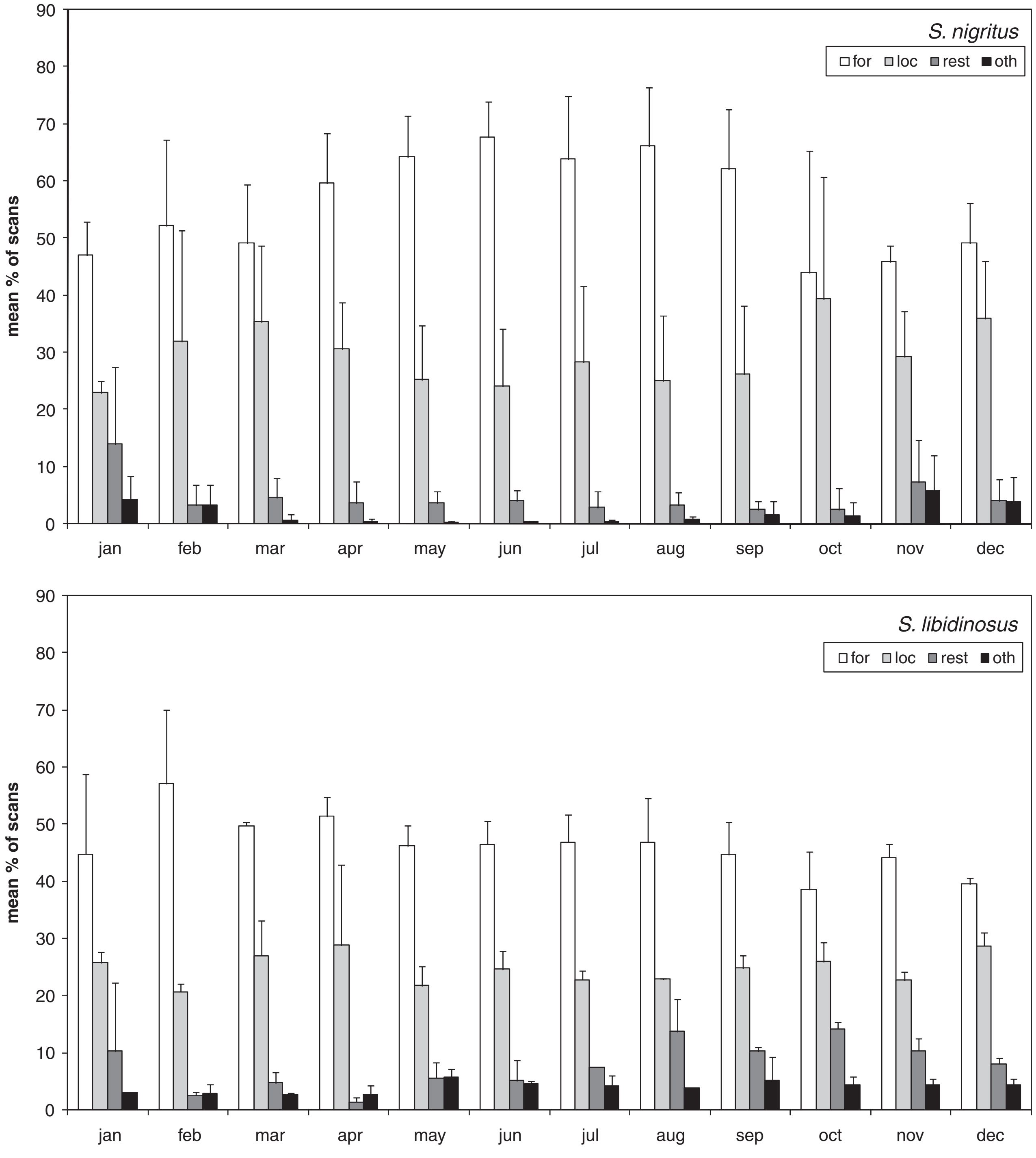

Fig. 3. Time allocation to foraging (for), resting (rest), traveling (loc), and other activities (oth) by a group of *Sapajus nigritus* in PECB and a group of *Sapajus libidinosus* in FBV. Bars represent the mean monthly proportion of scans of 4 years for PECB and of 2 years for FBV. FBV, Fazenda Boa Vista.

in review] (Table II). Agonistic interactions among females were unidirectional, with no reversals (DC index = 1.00). It was not possible to identify dominance relationships between females at PECB due to the lack of agonistic interactions among them (Table III).

The frequency of agonistic events that involved coalitionary behavior did not differ between populations ($\chi^2 = 2.15$, $P = 0.42$), but participation of females in coalitions was significantly different between sites ($\chi^2 = 43.4$, $P < 0.001$). At FBV, females participated in 78% of coalitions ($N = 122$) [Verderane et al., in

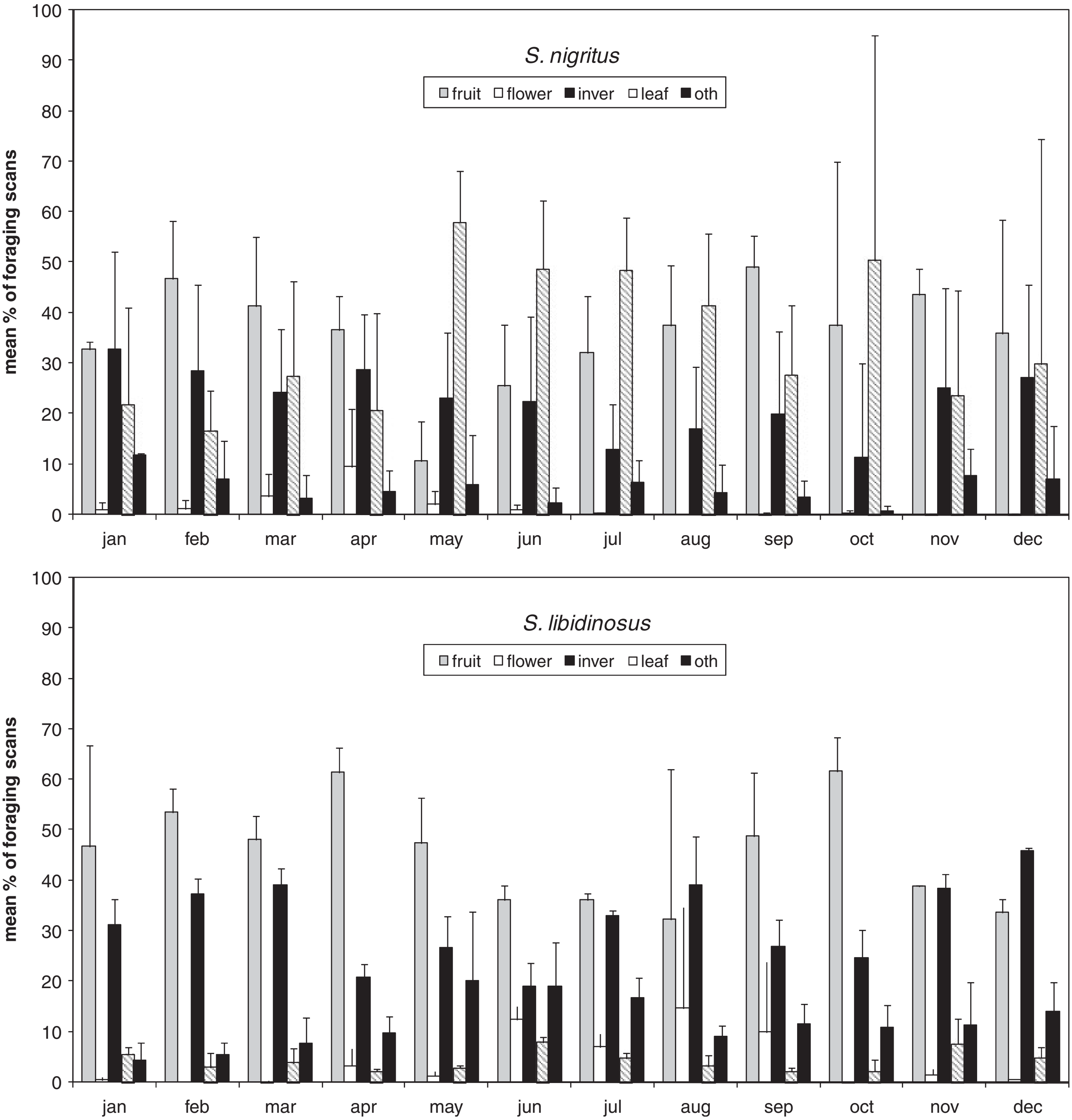

Fig. 4. Allocation of foraging activity to fruits, flowers, invertebrates, leaves, and other items by a group of *Sapajus nigritus* in PECB and a group of *Sapajus libidinosus* in FBV. Bars represent the mean monthly proportion of foraging scans of 4 years for PECB and of 2 years for FBV. FBV, Fazenda Boa Vista.

review], and coalitions between female–female dyads were 2.6 times more frequent than the expected by the number of possible dyads of each age/sex class between group members. Coalitions between females and the dominant male were 3.4 times higher than expected, and coalitions between females and juveniles were 1.9 times higher than expected. At PECB, a female participated in just one of the 21 coalitions recorded, supporting the dominant male. In all the other coalitions, the dominant male supported a juvenile against another group member (Table I).

Group encounters occurred at a similar monthly rates in both sites (Table I). In both sites, members of different groups behaved aggressively against each other. However, at FBV, females actively participated in these conflicts while at PECB the dominant males performed most of the aggression. Indeed, at PECB, one female of our study group disappeared

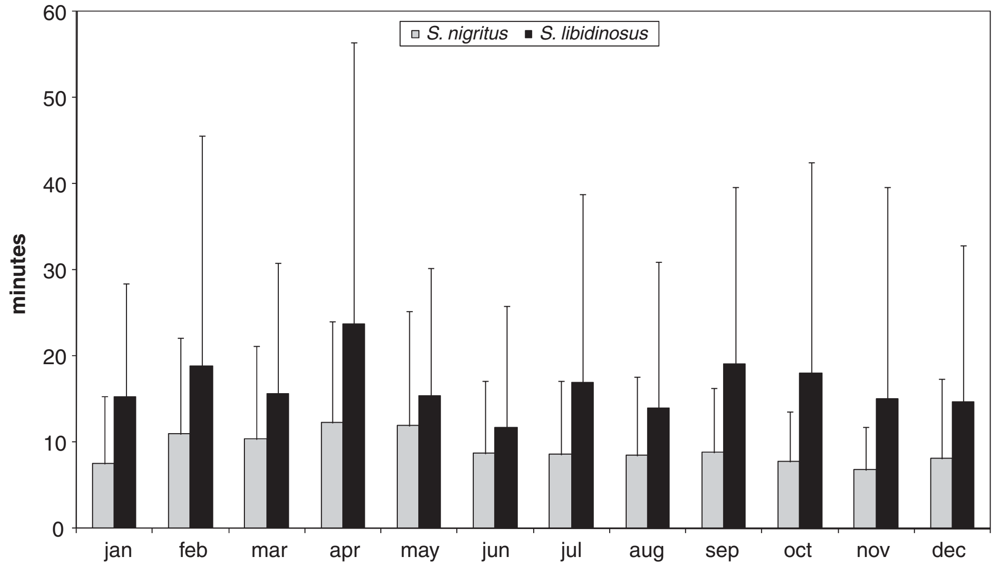

Fig. 5. Mean monthly depletion time (FTFS) of patchy food sources of a group of *Sapajus nigritus* in PECB and a group of *Sapajus libidinosus* in FBV. FBV, Fazenda Boa Vista; FTFS, feeding tree focal sample.

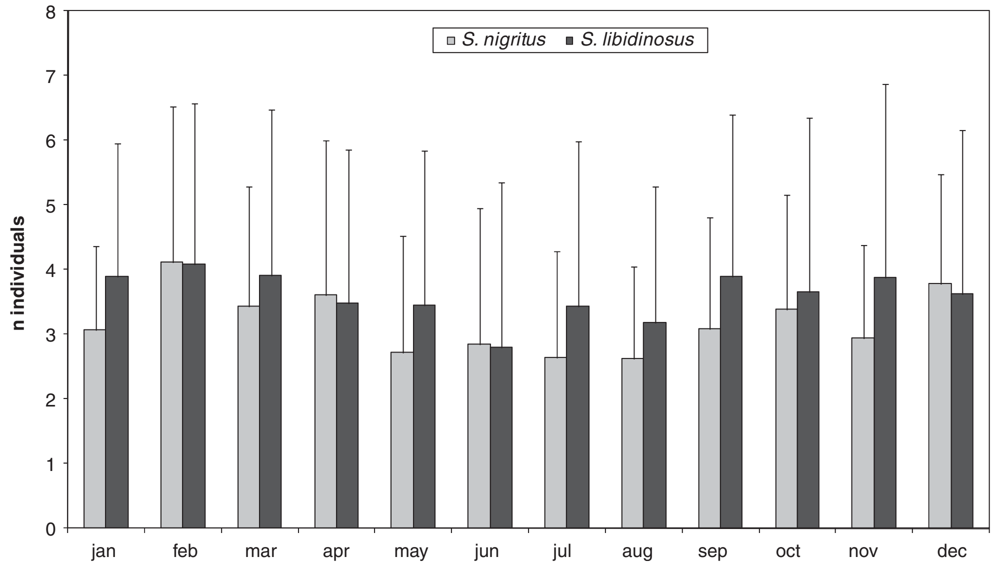

Fig. 6. Mean monthly feeding unit size of patchy food sources of a group of *Sapajus nigritus* in PECB and a group of *Sapajus libidinosus* in FBV. FBV, Fazenda Boa Vista.

TABLE II. Agonistic Conflicts Between Members of a Group of *Sapajus libidinosus*

	Za	**Mb**	**Mc**	**Em**	ju	In
Za		6	5	4	85	34
Mb	0		**5**	**11**	43	4
Mc	0	**0**		**18**	63	3
Em	0	**0**	**0**		13	2
ju	0	0	19	11	66	21
in	0	0	0	0	1	4

Females in bold. ju, all juveniles; in, all infants; ZA, dominant male.

TABLE III. Agonistic Conflicts Between Members of a Group of *Sapajus nigritus*

	B1	Ce	**Ol**	**Ru**	**Pa**	ju	in
B1		11	0	1	0	11	0
Ce	1		0	0	0	9	0
Ol	0	0		**0**	**0**	2	0
Ru	0	0	**0**		**0**	11	1
Pa	0	0	**1**	**0**		0	0
ju	0	0	0	0	0	23	11
in	0	0	0	0	0	1	1

Females in bold. ju, all juveniles; in, all infants; B1, dominant male, Ce, subadult male.

right after an intergroup encounter and a few days later she was observed traveling with the other group [Peternelli-dos-Santos, pers. obs.], and never returned to the original group.

Home range and daily travel distances were correlated with group size in PECB but not in FBV (Table I).

The frequency of grooming between female–female dyads in relation to total grooming was significantly different between FBV and PECB ($\chi^2 = 21.14$, $P < 0.001$). We observed 405 events of grooming in FBV (0.28 events/hr) and 16% of these events were between female–female dyads, whereas in PECB we observed 143 events of grooming (0.15 events/hr) and only 1.4% of these events were between female–female dyads. At FBV, grooming interactions between females was 2.0 times higher than expected by the number of available partners of each age–sex class, and grooming between females and the dominant male were 3.3 times higher than expected. At PECB, grooming interactions between females was observed only during the periods when the group was cohesive, and even then less frequently than expected by the number of available partners. Grooming between females and the dominant male was 3.2 times higher than expected by the number of available partners (Table I).

Dispersal

At PECB, four adult females disappeared from the study group, two in 2003 and two in 2004. All these disappearances occurred after a period of several months (3–6) in which the female was rarely observed within the group, suggesting a gradual process of emigration. In 2007, a fifth adult female was observed transferring between groups, as described above. Two subadult females joined the study group, one in 2005 and one in 2007. Several attempts of male immigration were observed across the study period and two subadult males joined the group in 2004 in two separate events, one in February and one in September.

At FBV, no female transfer was observed during the study, nor in the 2 years after it ended. Four males, two subadult and two juveniles, emigrated from ZA group to CH group in a period of 2 months (two in parallel and the other two with an interval of weeks). Besides that, two attempts of male immigration (in one case, four males at the same time) and two successful immigrations (one individual at a time) were observed in group ZA.

DISCUSSION

Predation Risk

No successful attack by a predator was observed in either population. Nonetheless, capuchins in FBV emitted alarm calls four times as often as capuchins in PECB, indicating a higher perception of predation risk by capuchins in FBV. As pointed out by Hill and Dunbar [1998], the animals' perception of the likelihood of a predator attack is what represents the populations' history of predation and maintains the current antipredator strategies. Our findings support our prediction that predation risk would be higher in FBV than in PECB. The alternative hypothesis, that predation risk would be lower in FBV than in PECB due to the effects of higher human interference in FBV, can be dismissed. Contrary to what we expected, in FBV human interference probably enhanced the monkey's perception of predation risk, since more than one third of the alarm calls were due to human presence or presence of domestic animals, including dogs, than can fatally attack wild tufted capuchin monkeys [Oliveira et al., 2008].

We predicted that the difference in predation risk between the sites would lead to (1) more cohesive groups, with (2) a higher proportion of males in FBV than in PECB. The first prediction was met, since groups in PECB present high fission–fusion dynamics [cf. Aureli et al., 2008], whereas in FBV groups are constantly cohesive. Although low food availability seems to be the cause of low-group cohesion in PECB, [Nakai & Izar, in review; Izar, 2004], the low perception of predation risk might allow individuals to forage in small subgroups [Boinski et al., 2002; Izar, 2004]. The second prediction was not met, since both populations presented a similar sex ratio, within the values reported for populations of *S. nigritus* and *S. apella* compiled by Fragaszy et al. [2004b] that reveal a range of male/female proportion between 0.56 and 1.20. Results for FBV and PECB are similar to data for *S. nigritus* from Iguazú National Park, Argentina (0.56 males per female) and from Caratinga, Brazil (0.68 males per female), lower than the sex ratio reported for populations of *S. apella* from La Macarena, Colombia (1.0 male per female) and Cocha Cashu, Peru (1.2 males per female). Predation risk in those sites is not reported, and most data on group size and composition compiled by Fragaszy et al. [2004b] are based on only one group per species. Therefore, more studies are necessary to assess the effect of predation risk on sex ratio in groups of tufted capuchin monkeys.

Food Availability, Features of Food Sources, and Food Competition

We predicted that *S. nigritus* in PECB would either have higher fruit availability throughout the year in comparison with *S. libidinosus* in FBV or both populations would face a similar condition due to human interference in FBV. The results were the opposite. Data on fruit biomass, activity budget, feeding and ranging behavior indicated that capuchins in PECB face lower fruit availability than capuchins in FBV. The capuchins in FBV spent more time in resting and less time in foraging and traveling than capuchins in PECB, a pattern of activity budget that has been associated with higher food availability [e.g. Bronikowski & Altmann, 1996; Ferreira et al., 2008; Pazol & Cords, 2005]. More importantly, capuchins in PECB spent less time foraging for fruits and other high-quality foods and more time foraging for leaves than the capuchins in FBV. The leaves most commonly eaten by the capuchins in PECB were leaf base of bromeliads and petiole of palm leaves, both energetically poor but very abundant and evenly distributed resources [Brown & Zunino, 1990; Izar, 2004; Taira, 2007]. Moreover, groups in PECB had significantly larger ranging areas than groups in FBV. Several studies have shown a negative relationship between home range size and food availability in different populations of tufted capuchin monkeys [*S. apella*: Spironello, 2001; Zhang, 1995; *S. nigritus*: Izar, 2002; *S. libidinosus*: Sabbatini et al., 2008]. Finally, the longer interbirth interval in PECB than in FBV is evidence of low energetic income either due to scramble competition [Borries et al., 2008] or due to poor food quality [Pope, 2000]. Nutritional condition of female primates affects their ability to conceive [Koenig et al., 1997; Lee & Houser, 1998; Ziegler et al., 1997]. In fact, females in PECB have the longest interbirth interval reported for tufted capuchin monkeys [Izar et al., 2009].

Besides the low fruit availability of PECB, the fruit sources exploited by *S. nigritus* in PECB sustained fewer group members, for less time, than the fruit sources exploited by *S. libidinosus* in FBV. The competitive regimes faced by tufted capuchin females in both sites followed predictions of the socioecological model. The small, low-quality fruit patches found by females in PECB would not compensate the costs of engaging in contest competition to monopolize these food sources and within group scramble competition is prevalent (as indicated by the correlation of group size with daily travel distance). On the other hand, fruit sources found by females in FBV sustained more individuals for a longer time than food sources in PECB, but were small enough to allow some group members to monopolize them and exclude others by means of contest competition. Our results parallel those reported by Boinski et al. [2002] when comparing three species of the Neotropical genus *Saimiri* and by several authors studying cercopithecoids [e.g. Barton et al., 1996; Koenig, 2000; Pazol & Cords, 2005; Saito, 1996] and add further evidence that the type of within group food competition experienced by female primates is an effect of food distribution.

Our results also indicate that contest competition between groups for food is an effect of food distribution only, and does not reflect population density or food abundance. Female participation in food contest between groups was higher in FBV than in PECB in spite of similar population densities of *Sapajus* in both sites (contrary to the prediction based on Sterck et al. [1997]) and in spite of higher food availability in FBV (contrary to the prediction based on Isbell [1991]). The difference between FBV and PECB in scramble competition between groups (higher in PECB than in FBV) was in the opposite direction of contest competition (higher in FBV than in PECB), contrary to Isbell's [1991] prediction that both types of food competition co-vary.

Female Social Relationships

Females of *S. nigritus* in PECB were subject to high within group scramble competition and to low contest competition between groups for food. According to Sterck et al. [1997], under this competitive regime, females would transfer between groups and establish egalitarian relationships with no differentiated coalitionary and affiliative relationships among them. Females of *S. libidinosus* in FBV were subject to high within group contest competition and low contest competition between-groups for food. Under this competitive regime, Sterck et al. [1997] predict that females would remain in their natal group, and establish a linear dominance hierarchy, and coalitionary and grooming relationships among them. Our results fit the models' predictions quite exactly. Since the results reported here for PECB are based on a long-term study, the undetectability of dominance ranks among females is not the result of insufficient observation [Isbell & Young, 2002]. In a previous study on another social group, Izar [2004] identified a partial dominance hierarchy, but the conclusion was based on few instances of agonistic interactions between females (12 interactions among four females over 800 hr of observation). The rate of intragroup agonism reported for the group studied by Izar [2004] was much higher than that observed in the present study, which probably reflected a short period of exceptional high availability of large patchy food sources [Nakai & Izar, in review]. And even in that study, the main victims of females' aggressive interactions in food trees were juveniles, as in the present study.

It is important to provide a note of caution here about data on female dispersal for PECB: at present we cannot affirm if female dispersal is obligatory. We have observed several (10 successful, three attempts) events of female transfer between groups, including nulliparous females, but the majority were multiparous females. Females of all species of *Cebus* and *Sapajus* are generally philopatric and male dispersal, including *S. nigritus* in PECB [Izar, 2004], is the rule. However, female dispersal occurs not only in *S. nigritus* but also in *C. olivaceus* and *C. capucinus*, when females experience low food income and/or risk of infanticide by males [Jack & Fedigan, 2009]. These observations contradict predictions of Sterck et al.'s [1997] model with regard to female dispersal and favor Isbell's [2004] prediction that female dispersal will occur whenever the costs of remaining in the group outweigh the costs of dispersal, even in species in which females are normally philopatric.

The comparison between *S. nigritus* in PECB and *S. libidinosus* in FBV reveals that group cohesion, female dispersal, and female relationships vary in response to food availability and distribution, as predicted by socioecological models [Isbell, 2004; Sterck et al., 1997]. However, the observed covariation between social behavior and ecological features could be a mere coincidence if the social behavior patterns of each studied species were related to genetic differences reflecting past adaptation. Two arguments work against this possibility. First, *S. libidinosus* in FBV shares the observed pattern of social organization and social structure with other species of *Sapajus* studied in the wild [*S. apella*: Izawa, 1980; Janson, 1990; *S. nigritus*: Di Bitetti, 1997; Lynch-Alfaro, 2007; but see Pinha, 2007 for a report of low female–female agonism in *S. libidinosus*] and with most captive groups [reviewed in Fragaszy et al., 2004b]. This pattern is similar to that described for two species of the genus *Cebus* [*C. olivaceus*: O'Brien & Robinson, 1991; *C. capucinus*: Bergstrom & Fedigan, 2010; Perry, 1996]. Second, two other populations of *S. nigritus* studied in the wild [Estação Biológica de Caratinga, Minas Gerais, Brasil: Lynch-Alfaro, 2007; Iguazú National Park, Argentina: Di Bitetti, 1997] present the general pattern of female philopatry and dominance hierarchy observed here for *S. libidinosus*. Therefore, one cannot attribute the lack of female bonding observed in PECB to a genetic predisposition of *S. nigritus*. Although comparable data on fruit availability and distribution are not available for Caratinga and Iguazú, data on home range and group size (Caratinga: 268 ha, 24–29 individuals [Rímoli et al., 2008], Iguazú: 81–293 ha, 12.4 ± 7.0 to 16.8 ± 9.5 individuals [Di Bitetti, 2001]) in comparison with our results (see Table I) suggest that these sites present higher food availability than PECB. Moreover, patchy food sources are an important part of the diet of capuchins in both sites, such as reproductive parts of *Mabea fistulifera* in Caratinga [Rímoli et al., 2008], and the fruits of "very productive" fig and palm trees in Iguazú [Di Bitetti, 2001, p 38]. It is striking that subgrouping during foraging, as observed for *S. nigritus* in PECB, has been reported also for *S. nigritus* in Caratinga [Lynch-Alfaro, 2007], but not for any other species of tufted capuchins, which could indicate a species-specific pattern. Nonetheless, groups of *S. nigritus* in Iguazú are cohesive [Di Bitetti, 2001], suggesting that fission–fusion dynamics is another flexible aspect of tufted capuchin social system, as suggested by Aureli et al. [2008] for all primates.

The features of female social relationships (female dispersal, low-group cohesiveness, egalitarian relationships, lack of affiliative relationships) found for *S. nigritus* in PECB argue against phylogenetic inertia as determinant of the social system of *Cebus* and *Sapajus*. The argument of phylogenetic inertia as determinant of social systems was made by Di Fiore and Rendall [1994] to explain the similarity of social systems found within the family Cercopithecoidea, in spite of its great ecological diversity, contrary to predictions of the socioecological models. However, the similarity between our results for *S. libidinosus* in FBV, a semi-arid area of open woodland, and those reported for forest populations of *S. apella* and *S. nigritus* indicates that ecological diversity in terms of general habitat features does not necessarily translate in different regimes of competition for food, the relevant ecological feature for female social relationships according to socioecological models.

Mating System

In spite of the ecological and social differences, *S. nigritus* in PECB and *S. libidinosus* in FBV presented the same mating system. As described in other studies on tufted capuchin monkeys, regardless of the presence of other adult males in a group, females prefer to solicit and mate with the dominant male, characterizing a uni-male polygynous mating system [*S. apella*: Janson, 1986; *S. nigritus*: Di Bitetti & Janson, 2001; Lynch-Alfaro, 2005; for a review see Carosi et al., 2005]. This suggests that the mating system is quite conservative within the genus *Sapajus* and does not vary along with ecology.

In both the populations, the dominant male was the most frequent coalitionary and grooming partner of adult females. Females' preference for associating with the dominant male is a feature of all wild and captive groups of tufted capuchins already studied [e.g. Di Bitetti, 1997; Ferreira et al., 2006; Janson, 1986]. The fact that this aspect of social structure is invariant among different populations regardless of ecological variability favors the hypothesis that female preference for the dominant male as a social partner hinges on the mating system [Izar et al., 2009].

In conclusion, the comparison between *S. nigritus* and *S. libidinosus* reveals that many components of their social systems differ congruently with variation in ecological features as predicted by socioecological models. In particular, group cohesion, female dispersal, and female relationships varied in accordance with differences in food availability and distribution between PECB and FBV. In contrast, our data in comparison with data from the literature discussed above suggest that the mating system is quite conservative within the genus *Sapajus* and does not vary in response to ecological features.

ACKNOWLEDGMENTS

We thank the Instituto Florestal de São Paulo, especially José Carlos Maia, for permission to conduct the research at PECB, and Marino Gomes de Oliveira's family for permission to conduct the research at FBV. We thank Eraldo Vieira, Jozemar, Arizomar, and Marino Junior for their assistance in the field, and Noemi Spagnoletti, Mariana D. Fogaça, and Caio M. Moreira for sharing their data. Jessica Lynch Alfaro and two anonymous reviewers contributed helpful comments. Permission to work in Brazil was granted by IBAMA and CNPq to D.F. and E.V.

REFERENCES

Altmann J. 1974. Observational study of behaviour: sampling methods. Behaviour 49:223–265.

Aureli F, Schaffner C, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, DiFiore A, Dunbar RIM, Henzi PS, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, van Schaik CP. 2008. Fission–fusion dynamics: new research frameworks. Current Anthropology 49:627–654.

Barton RA, Byrne R, Whiten A. 1996. Ecology, feeding competition and social structure in baboons. Behavioral Ecology and Sociobiology 38:321–329.

Batalha MA, Martins FR. 2004. Reproductive phenology of the cerrado plant community in Emas National Park (central Brazil). Australian Journal of Botany 52:149–161.

Bergstrom ML, Fedigan LM. 2010. Dominance among female white-faced capuchin monkeys (*Cebus capucinus*): hierarchical linearity, nepotism, strength and stability. Behaviour 147: 899–931.

Bishop N, Hrdy SB, Teas J, Moore J. 1981. Measures of human influence in habitats of South Asian langurs. International Journal of Primatology 153–167.

Boesch C, Boesch-Achermann H. 2000. The chimpanzees of the Taï forest. Oxford: Oxford University Press.

Boinski S, Sughrue K, Selvaggi L, Quatrone R, Henry M, Cropp S. 2002. An expanded test of the ecological model of primate social evolution: competitive regimes and female bonding in three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*). Behaviour 139: 227–261.

Boinski S, Kauffman L, Westoll A, Stickler CM, Cropp S, Ehmke E. 2003. Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*). Behaviour 140:1421–1467.

Borries C, Larney E, Lu A, Ossi K, Koenig A. 2008. Costs of group size: lower developmental and reproductive rates in larger groups of leaf monkeys. Behavioral Ecology 19:1186–1194.

Bronikowski AM, Altmann J. 1996. Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. Behavioral Ecology and Sociobiology 39:11–25.

Brown AD, Zunino GE. 1990. Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. Folia Primatologica 54:187–195.

Cahan SH, Blumstein DT, Sundström L, Liebig J, Griffin A. 2002. Social trajectories and the evolution of social behavior. Oikos 96:206–216.

Carosi M, Linn GS, Visalberghi E. 2005. The sexual behavior and breeding system of tufted capuchin monkeys (*Cebus apella*). In: Slater PJB, Rosenblatt JS, Snowdon CT, Roper TJ, editors. Advances in the study of behavior. San Diego: Academic Press-Elsevier. p 105–149.

Chancellor RL, Isbell LA. 2009. Food site residence time and female competitive relationships in wild gray-cheeked mangabeys (*Lophocebus albigena*). Behavioral Ecology and Sociobiology 63:1447–1458.

Chapman CA, Chapman LJ. 2000. Determinants of group size in primates: the importance of travel costs. In: Boinski S, Garber PA, editors. On the move: how and why animals travel in groups. Chicago: University of Chicago Press. p 24–41.

Chapman CA, Rothman JM. 2009. Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. Primates 50:12–22.

Chapman CA, Wrangham R, Chapman LJ. 1994. Indices of habitat-wide fruit abundance in tropical forests. Biotropica 26:160–171.

Clutton-Brock TH. 2004. What is sexual selection? In: Kappeler PM, van Schaik CP, editors. Sexual selection in primates, new and comparative perspectives. Cambridge: Cambridge University Press. p 24–36.

Crockett CM, Janson CH. 2000. Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In: van Schaik CP, Janson CH, editors. Infanticide by males and its implications. Cambridge: Cambridge University Press. p 75–98.

Di Bitetti MS. 1997. Evidence for an important social role of grooming in a platyrrhine primate. Animal Behaviour 54: 199–211.

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

Di Bitetti MS, Janson CH. 2001. Reproductive socioecology of tufted capuchins (*Cebus apella nigritus*) in northeastern Argentina. International Journal of Primatology 22: 127–142.

Di Fiore A, Rendall D. 1994. Evolution of social organization: a reappraisal for primates by using phylogenetic methods. Proceedings of the National Academy of Sciences, USA 91: 9941–9945.

Dunbar RIM. 1996. Determinants of group size in primates: a general model. In: Maynard SJ, Runciman WG, Dunbar RIM, editors. Evolution of social behaviour patterns in primates and man. London: British Academy Press. p 33–57.

Eason P. 1981. Harpy eagle attempts predation on adult howler monkey. The Condor 91:469–470.

Ferreira RG, Izar P, Lee PC. 2006. Exchange, affiliation and protective interventions in semi-free ranging brown capuchin monkeys (*Cebus apella*). American Journal of Primatology 68:765–776.

Ferreira RG, Lee PC, Izar P. 2008. Food competition in a semi-free-ranging *Cebus apella* group. Folia Primatologica 79:463–475.

Fragaszy DM, Visalberghi E, Fedigan L, Rylands AB. 2004a. Taxonomy, distribution and conservation: where and what arethey, and how did they get there? In: Fragaszy D, Fedigan L, Visalberghi E, editors. The complete capuchin: the biology of the genus *Cebus*. Cambridge: Cambridge University Press. p 13–35.

Fragaszy DM, Visalberghi EM, Fedigan LM. 2004b. The complete capuchin: the biology of the genus *Cebus*. Cambridge: Cambridge University Press.

Fragaszy D, Izar P, Visalberghi E, Ottoni EB, de Oliveira MG. 2004c. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. American Journal of Primatology 64:359–366.

Hill R, Dunbar RIM. 1998. An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. Behaviour 135:411–430.

Hill RA, Lee PC. 1998. Predation risk as an influence on group size in cercopithecoid primates: Implications for social structure. Journal of Zoology, London 245:447–456.

Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. Behavioral Ecology 2:143–155.

Isbell LA. 2004. Is there no place like home? Ecological bases of female dispersal and philopatry and their consequences for the formation of kin groups. In: Chapais B, Berman C, editors. Kinship and behavior in primates. New York: Oxford University Press. p 71–108.

Isbell LA, Young TP. 2002. Ecological models of female social relationships in primates: similarities,disparities,and some directions for future clarity. Behaviour 139:177–202.

Isbell LA, Pruetz JD, Young TP. 1998. Movements of adult female vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. Behavioral Ecology and Sociobiology 42:123–133.

Izar P. 2002. Estratégias de forrageamento em *Cebus apella*. In: Albuquerque FS, editor. org Anais XX Encontro Anual de Etologia. Natal: UFRN. p 51–63.

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

Izar P, Stone A, Carnegie SD, Nakai ES. 2009. Sexual selection, female choice and mating systems. In: Garber P, Estrada A, Bicca-Marques JC, Heymann E, Strier KB, editors. South American primates: testing new theories in the study of primate behavior, ecology, and conservation. New York: Springer Press. p 157–189.

Izawa K. 1980. Social behaviour of wild black-capped capuchin (*Cebus apella*). Primates 21:443–467.

Jack K, Fedigan LM. 2009. Female dispersal in a female-philopatric species, *Cebus capucinus*. Behaviour 146:471–497.

Janson CH. 1986. The mating system as a determinant of social evolution in capuchin monkeys (*Cebus*). In: Else J, Lee PC, editors. Primate ecology and conservation, Vol. 2. Cambridge: Cambridge University Press. p 169–180.

Janson CH. 1990. Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Animal Behaviour 40:910–921.

Janson CH. 2000. Primate socio-ecology: the end of a golden age. Evolutionary Anthropology 9:73–86.

Kappeler PM, van Schaik CP. 2002. Evolution of primate social systems. International Journal of Primatology 23: 707–740.

Koenig A. 2000. Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). Behavioral Ecology and Sociobiology 48:93–109.

Koenig A, Borries MK, Chalise M, Winkler P. 1997. Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). Journal of Zoology, London 243:215–235.

Komers PE, Brotherton NM. 1997. Female space use is the best predictor of monogamy in mammals. Proceedings of the Royal Society of London, B. Biological Sciences 264: 1261–1270.

Kutsukake N, Nunn C. 2006. Comparative tests of reproductive skew in male primates: the roles of demographic factors and incomplete control. Behavioral Ecology and Sociobiology 60: 695–706.

Lee PC, Houser MD. 1998. Long-term consequences of changes in territory quality on feeding and reproductive strategies of vervet monkeys. Journal of Animal Ecology 67: 347–358.

Lindenfors P, Froberg L, Nunn CL. 2004. Females drive primate social evolution. Proceedings of the Royal Society B: Biological Sciences 271:S101–S103.

Lynch-Alfaro JW. 2005. Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*). American Journal of Primatology 67: 313–328.

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

McGraw WS, Zuberbühler K. 2008. Socioecology, predation, and cognition in a community of West African monkeys. Evolutionary Anthropology 17:254–266.

Nunn CL, van Schaik CP. 2000. Social evolution in primates: the relative roles of ecology and intersexual conflict. In: van Schaik CP, Janson CH, editors. Infanticide by males and its implications. Cambridge: Cambridge University Press. p 388–412.

O'Brien TG, Robinson JG. 1991. Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness. Behaviour 119:31–50.

Oliveira MM, Langguth A. 2006. Rediscovery of Marcgrave's capuchin monkey and designation of a neotype for *Simia flavia* Schreber 1774 (Primates, Cebidae). Boletim do Museu Nacional, Rio de Janeiro: Zoologia 523:1–16.

Oliveira VB, Linares AM, Corrêa GLC, Chiarello AG. 2008. Predation on the black capuchin monkey *Cebus nigritus* (Primates: Cebidae) by domestic dogs *Canis lupus familiaris* (Carnivora: Canidae) in the Parque Estadual Serra do Brigadeiro, Minas Gerais, Brazil. Revista Brasileira de Zoologia 25:376–378.

Ostner J, Nunn CL, Schülke O. 2008. Female reproductive synchrony predicts skewed paternity across primates. Behavioral Ecology 19:1150–1158.

Pazol K, Cords M. 2005. Seasonal variation in feeding behavior, competition and female social relationships in a forest dwelling guenon, the blue monkey (*Cercopithecus mitis stuhlmanni*), in the Kakamega Forest, Kenya. Behavioral Ecology and Sociobiology 58:566–577.

Perry S. 1996. Female-female relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. American Journal of Primatology 40:167–182.

Pinha OS. 2007. Interações sociais em grupos de macacos-prego (*Cebus libidinosus*) no Parque Nacional de Brasília. Master Thesis, Universidade de Brasília, Brazil.

Pope TR. 2000. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). Behavioral Ecology and Sociobiology 48:253–267.

Presotto A, Izar P. 2010. Spatial reference of black capuchin monkeys in Brazilian Atlantic Forest: egocentric or allocentric? Animal Behaviour 80:125–132.

Rasoloarison RM, Rasolonandrasana B, Ganzhorn JU, Goodman SM. 1995. Predation on vertebrates in the Kirindy forest,Western Madagascar. Ecotropica 1:59–65.

Rendall D, Di Fiore AF. 2007. Homoplasy, homology, and the perceived special status of behavior in evolution. Journal of Human Evolution 52:504–521.

Rímoli J, Strier KB, Ferrari SF. 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. In: Ferrari SF, Rímoli J, editors. A Primatologia no Brasil 9. Aracaju: Sociedade Brasileira de Primatologia, Biologia Geral e Experimental–UFS. p 130–146.

Robbins AM, Stoinski TS, Fawcett KA, Robbins MM. 2009. Leave or conceive: natal dispersal and philopatry of female mountain gorillas in the Virunga volcano region. Animal Behaviour 77:831–838.

Ryan SJ, Starks PT, Milton K, Getz WM. 2008. Intersexual conflict and group size in mantled howler monkeys: a 23- year evaluation. International Journal of Primatology 29:405–420.

Sabbatini G, Stammati M, Tavares MCH, Visalberghi E. 2008. Behavioural flexibility of a group of capuchin monkeys (*Cebus libidinosus*) in the National Park of Brasília (Brazil): consequences of cohabitation with visitors. Brazilian Journal of Biology 68:685–693.

Saito C. 1996. Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: effects of food patch size and inter-patch distance. Animal Behaviour 51:967–980.

Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: an integrative overview. The Quarterly Review of Biology 79:241–277.

Silva Jr JS. 2001. Especiação nos macacos-prego e caiararas, gênero *Cebus* Erxleben, 1777 (Primates, Cebidae). Doctoral Thesis, Rio de Janeiro, Universidade Federal do Rio de Janeiro. 377p.

Snaith TV, Chapman CA. 2007. Primate group size and socioecological models: do folivores really play by different rules? Evolutionary Anthropology 16:94–106.

Spironello WR. 2001. The brown capuchin monkey (*Cebus apella*). Ecology and home range requirements in Central Amazonia. In: Bierregaard Jr RO, Gascon C, Lovejoy TE, Mesquita R, editors. Lessons from Amazonia: the ecology and conservation of a fragmented forest. New Haven & London: Yale University Press. p 271–283.

Stanford CB. 2002. Avoiding predators: expectations and evidence in primate antipredator behavior. International Journal of Primatology 23:741–757.

Sterck EHM. 1999.Variation in langur social organization in relation to the socioecological model, human habitat alteration, and phylogenetic constraints. Primates 40:199–213.

Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41:291–310.

Strier KB. 1989. Effects of patch size on feeding associations in muriquis (*Brachyteles arachnoides*). Folia Primatologica 52: 70–77.

Strier KB. 1994. Myth of the typical primate. Yearbk Phys Anthropol 37:233–271.

Strier KB. 2003. Primate behavioral ecology: from ethnography to ethology and back. Am Anthropol 105:16–27.

Strier KB. 2009. Seeing the forest through the seeds: mechanisms of primate behavioral diversity from individuals to populations and beyond. Current Anthropology 50: 213–228.

Taira JT. 2007. Consumo do palmito juçara (*Euterpe edulis*) por macacos-prego (*Cebus nigritus*): estratégia de forrageamento ótimo ou requinte de um gourmet? Master Thesis, Universidade de São Paulo, Brazil.

Teichroeb JE, Sicotte P. 2008. Test of the ecological-constraints model on ursine colobus monkeys (*Colobus vellerosus*) in Ghana. American Journal of Primatology 71:49–59.

Terborgh J. 1983. Five new world primates. A study in comparative ecology. Princeton, NJ: Princeton University Press.

Thierry B. 2008. Primate socioecology, the lost dream of ecological determinism. Evolutionary Anthropology 17: 93–96.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man. Chicago: Aldine. p 136–179.

van Belle S, Estrada A. 2008. Group size and composition influence male and female reproductive success in black howler monkeys *(Alouatta pigra*). American Journal of Primatology 70:613–619.

van Schaik CP. 1983. Why are diurnal primates living in groups? Behaviour 87:120–144.

van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley RA, editors. Comparative socioecology, Oxford: Blackwell. p 195–218.

van Schaik CP, Hörstermann M. 1994. Predation risk and the number of adult males in a primate group: a comparative test. Behavioral Ecology and Sociobiology 35: 261–272.

Visalberghi E, Fragaszy D, Izar P, Ottoni EB. 2005. Terrestriality and tool use. Science 308:951–952.

Visalberghi E, Fragaszy D, Ottoni EB, Izar P, Oliveira MG, Andrade FRD. 2007. Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. American Journal of Physical Anthropology 132:426–444.

Vogel ER, Janson C. 2007. Predicting the frequency of food-related agonism in white faced capuchin monkeys (*Cebus capucinus*) using a novel focal-tree method. American Journal of Primatology 69:533–550.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour 75:262–300.

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

Ziegler TE, Santos CV, Pissinatti A, Strier KB. 1997. Steroid excretion during the ovarian cycle in captive and wild muriquis, *Brachyteles arachnoides*. American Journal of Primatology 42:311–321.