



Socioecology of wild bearded capuchin monkeys (*Sapajus libidinosus*): an analysis of social relationships among female primates that use tools in feeding

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Abstract

Socioecology considers that the features of food sources affect female social relationships in group-living species. Among primates, the tests of socioecological models are largely focused on Old World species and do not evaluate if the use of feeding tools affects the competitive regime over food and females' relations in wild populations. We studied female social relationships among a wild population of bearded capuchin monkeys (*Sapajus libidinosus*) that use percussive tools (stones) to crack encased foods, in a semi-arid habitat in Brazil. Females fed mainly on clumped, high quality resources, indicating that the habitat provides a high quality diet year-round. Females experienced contest competition within and between-groups. As predicted by socioecological models, females' social relationships were characterized by philopatry, linear dominance hierarchies, coalitions, and tolerance in feeding bouts. Females spent a small proportion of their feeding time using tools. Nevertheless, tool sites generated high rates of contest competition and lower indices of tolerance among females. Although the social structure of our study population did not differ significantly from the pattern observed in wild populations of *Sapajus* that do not use tools, tool use increased within-group contest competition and apparently contributed to the linearity of the dominance hierarchies established among females. We predict that when tool use results in usurpable food resources, it will increase contest competition within group-living species.

Keywords

socioecology, tool use, food competition, female social relationships, *Sapajus*.

1. Introduction

Socioecology intends to explain the evolution of social behavior as the collective result of individual adaptive strategies to deal with factors influencing individual fitness, particularly the distribution of risks and resources in the environment (Kappeler & van Schaik, 2002), controlling for the effects of phylogenetic inertia (Rendall & Di Fiore, 2007). One key aspect that affects individual strategies is sex, since males and females differ in reproductive physiology and investment in offspring, thus being limited by different factors (Trivers, 1972). Because females' reproductive success is affected by quantity and quality of food intake (Wrangham, 1980), socioecological models of primate social systems assume that females distribute themselves in the environment in relation to risks (predation and infanticide) and resources (key foods), whereas males distribute themselves in relation to the distribution of receptive females (Altmann, 1990). Group-living imposes costs to individuals that live together, especially increasing competition for limited resources among group members (Rubenstein & Wrangham, 1986). Feeding competition is considered the major cost of group-living for primate females (van Schaik, 1989; Isbell, 1991). Thus, the models assume that quality, distribution, and patch size of food sources determine the form and the intensity of food competition faced by females in a given population. The competitive regime, in turn, affects the pattern of social relationship established among them (Wrangham, 1980; Isbell, 1991; but see Sterck et al., 1997 for additional factors affecting females social relationships).

According to socioecological models, females can compete directly (contest competition) or indirectly (scramble competition) for food, both within and between groups (van Schaik, 1989). Within-group contest competition should prevail when females rely mainly on usurpable foods (*sensu* Isbell & Pruettz, 1998: i.e., if it can be taken from a lower-ranking individual). This occurs when foods are spatially clumped in the habitat and of intermediate size relative to group size, so that not all group members can feed in it at the same time (van Schaik, 1989; Janson, 1990; Isbell et al., 1998; Pruettz & Isbell, 2000; Chancellor & Isbell, 2009). Foods that take an intermediate length to deplete are usually more usurpable than foods that are depleted quickly or slowly because intermediate residence times increase the chances of one or some individuals excluding others from accessing the resource (Isbell & Van Vuren, 1996; Isbell et al., 1998). Thus, usurpability is considered to

promote agonistic interactions within groups. Within-group scramble competition should prevail when females rely mainly on foods that are evenly distributed, highly dispersed in the habitat or very large relative to group size. These foods do not need or cannot be usurped, either because they are found in all parts of the environment, or because they are small or too large to be defended respectively, so that no individual can exclude others. Between-group contest and scramble competition depend on the abundance of food resources and the population density in the habitat (Janson & van Schaik, 1988), but scramble competition between groups is not considered to affect female social relationships in group-living primates (van Schaik, 1989).

The combination of the modes and intensity of food competition experienced by female primates should lead to specific patterns of social relationships among them (Sterck et al., 1997). Thus, in the face of scramble competition or no competition, females are expected to establish egalitarian relations and may transfer from their natal group. In the face of contest competition between groups, females are expected to establish egalitarian relations with each other and remain in their natal group to help relatives in disputes between groups. In the face of contest competition within groups, females are expected to establish nepotistic relationships, linear dominance hierarchy, and remain in their natal groups to avoid losing the support of allies in contest competition within groups. When contest competition within groups is associated with contest competition between groups, dominant females are expected to be tolerant towards subordinate ones (allowing them to have regular access to key foods; van Schaik, 1989) to prevent losing their support during disputes between groups (Sterck et al., 1997). Females may transfer when within-group contest competition is low because there would be few benefits from establishing dominance hierarchies or using coalitions to compete for food. But females may also transfer from their natal group due to other factors, such as increased food competition (Isbell & Van Vuren, 1996), infanticide risk (Sterck et al., 1997; Jack & Fedigan, 2009), or when their chances of reproductive success within that group are lower than in another group (Isbell & Van Vuren, 1996).

In spite of some discrepancies between the socioecological models and actual field data, particularly concerning the predictions of female social relationships as categorical systems that do not account for the great diversity observed among living primates (Strier, 2009) and the assumption that folivorous primates do not face the effects of contest competition over food (e.g.,

Harris, 2006; Snaith & Chapman, 2007), the link between the features of food resources, competitive regimes and social relationships among females have been supported by several field studies, primarily for cercopithecoids (e.g., Nakagawa, 2008; Teichroeb & Sicotte, 2009) and lemurs (e.g., White et al., 2007; Dammhahn & Kappeler, 2009). However, the extent to which between-group contest competition affects the social relationships among primate females remains unclear, since only few studies support this prediction (Koenig, 2000; Lu et al., 2008). Moreover, the tests of socioecological models concern primates that do not use tools. Thus, to our knowledge, no studies have analyzed the features of feeding tool sites and whether tool use impacts competitive regimes and female social relationships.

In this context, tufted capuchin monkeys (genus *Sapajus*, Lynch Alfaro et al., 2012a, b) are suitable subjects to test socioecological models because they have a wide geographic distribution, occupying different ecosystems, and present variable and complex social organization and social structure. To date, systematically socioecological studies are restricted to wild populations living in forest habitats (e.g., Amazon: Izawa, 1980; Janson, 1985; Spironello, 2001; Atlantic Forest: Izar, 2004; Lynch Alfaro, 2007; and semi-deciduous forest of South America: Di Bitetti, 2001). Although studies of wild populations inhabiting savannah-like environments, such as *Cerrado* and *Caatinga*, have just begun, they are revealing striking features of these populations, particularly, the spontaneous use of tools to access and process embedded foods as a widespread behaviour among wild bearded capuchin monkeys (*S. libidinosus*) (Ottoni & Izar, 2008). Considering that studies of capuchins in forest habitats have found variability in the pattern of group cohesion, in female social relationships, and female dispersal (Izar, 2004; Lynch Alfaro, 2007), investigating the ecology and social behavior of tool-using capuchins in savannah-like environments can provide an interesting new test of socioecological models relating food resources and tool use to social relationships among females.

Here we analyzed two years of data on feeding behaviour, food sources size, competitive regimes and female social relationships of a tool-using population of *S. libidinosus*. We aimed at investigating if the features of food sources and of tool sites affect the competitive regime and social relationships among females in the directions predicted by the socioecological model (Sterck et al., 1997). Capuchin monkeys in this population routinely use stones (hammers) to pound open nuts placed on anvils (Fragaszy et al.,

2004). Although a tool site is not itself a food resource, we hypothesized that the tool sites could generate competition among females within a group in the same way as a clumped food source. Previous studies suggested that the tool sites (i.e., sandstone or wooden anvils and a stone tool used as hammer) in the study area have a clumped distribution (Visalberghi et al., 2007; details are presented in Methods). Thus, we predicted that tool sites could be usurpable food sites and, as a consequence, would cause contest competition. Alternatively, because tool use might be valuable to others in the group besides the tool user (e.g., immatures not yet proficient at using tools), through distribution of food (Otoni & Izar, 2008), and through positive social support for learning (Coussi-Korbel & Frigaszy, 1995; van Schaik et al., 1999), it is possible that the tool sites, even if usurpable, do not promote contest competition as do other usurpable food sources. Because there is substantial evidence that primate diet changes in accordance to seasonality of climatic variables affecting food availability (e.g., Chapman, 1987; Garber, 1993; van Doorn et al., 2010), which might lead to variation in food competition (e.g., Koenig, 2000), and because in our study site there is a severe seasonality in rainfall distribution (see Methods), we conducted all analyses considering the effect of season.

2. Methods

2.1. Study site

The study was carried out at Fazenda Boa Vista (hereafter FBV), a flat open woodland area located in the northeastern Brazilian state of Piauí (9°39'S, 45°25'W), within a transition zone between Cerrado and Caatinga habitats (Oliveira & Marquis, 2002). The region has a highly seasonal rainfall distribution with a clear dry season (lasting from May to September) and a wet season (lasting from October to April) (Viana et al., 2010). During the study period (from May 2006 to April 2008) the average annual rainfall was 1289 mm (24.5 mm in the dry season and 1265 mm in the wet season) and mean daily temperature was 27°C (26.7°C in the dry season and 27.5°C in the wet season) (for details see Spagnoletti et al., 2012). The vegetation is a mosaic of physiognomies comprising sandy plains, marshes, cliffs and plateaus, mostly composed by small (3–5 m tall) xeromorphic and scleromorphic trees (for details, see Visalberghi et al., 2007). Palms of *Attalea barreirensis*, *Astrocaryum campestre*, *Attalea* sp. and *Orbignya* sp. are

abundant in sandy plains (see below) and are an important food source for capuchin monkeys in FBV (Visalberghi et al., 2008). Monkeys consume the mesocarp of the palm nuts without tools, and access the endosperm with stone tools.

Based on a monthly census conducted during the study period, population density of *S. libidinosus* in the study site was estimated at 2.3 individuals/km² and four species of potential predators of primates were identified: two carnivores (*Puma concolor* and *Eyra barbara*), one large aerial raptor (*Gernoaethus* sp.) and one constrictor snake (*Boa* sp.) (Verderane, 2010).

2.2. Study group and observation period

We studied 12 females (9 adults and 3 juveniles up to 4 years old) from two wild groups of *S. libidinosus* (5 from ZA group and 7 from CH group). The size of ZA ranged from 8 to 14 individuals (4–5 adults, 0–4 subadult males, 2–4 juveniles and 2–3 infants) and the size of CH group from 17 to 19 individuals (6–8 adults, 4 subadult males, 4–5 juveniles and 3–5 infants). During the study period CH was provisioned (for 39 of 75 days of observation) with fresh fruits, vegetables and water in a selected area (field laboratory), for an average of 3082 ± 908 kcal/day of provision (about 197 ± 56 kcal/day per individual; Spagnoletti et al., 2012). Nevertheless, CH mainly fed on naturally available items (Verderane, 2010).

ZA was followed from May 2006 to April 2008, totalling 1466 h of group follows, and CH was followed from February 2007 to April 2008, totalling 542 h of group follows. Each group was followed daily from dawn to dusk, 4–17 days per month. Capuchins were fully habituated to human observers and individually recognized.

2.3. Data collection and measures

2.3.1. Feeding behaviour and diet

Data on time allocated by females to feeding (including searching, manipulating and ingesting) on different food items were recorded using scan sampling (Altmann, 1974) of 10 min with 10 min between the end of one sample and the start of the next. Females' diet was summarized as the mean monthly proportion of scans per individual devoted to consumption of pulp of fruits (including mesocarp of palm nuts), seeds, flowers, nectar, endosperm (foods

obtained with tools, mainly endosperm of palm nuts), leaves (the base of bromeliad leaves and grass), roots, invertebrates, vertebrates and provisioned foods (for CH). Each female was sampled in at least 44% of 5139 scans recorded for ZA and in 53% of 2140 scans recorded for CH. Because the vegetation in FBV is low and sparse and the study groups were cohesive and habituated to observers, for most of the study period M.P. Verderane (hereafter MPV) and two field assistants were able to conduct observations at a very close distance (1–10 m) from the animals and to move freely around them during scan samples.

2.3.2. Features of food sources

We measured the size of three types of food sources: (1) trees (where the monkeys fed on pulp of fruit, seed, nectar and flower); (2) palms (where the monkeys fed on pulp of nuts [mesocarp] and drank water [liquid endosperm]); and (3) tool sites (a stone or wood surface [anvil] with at least one hammer stone present, where encased fruits are processed). These food sources were considered to be potentially clumped or patchy because on the one hand they could be contested (e.g., Wrangham, 1980; Chancellor & Isbell, 2009) and on the other hand they could be shared by at least two group members (Boinski et al., 2002), as opposed to dispersed and evenly distributed sources that could not support two individuals at a time (insects, vertebrates, grass leaves, and roots). A potentially clumped food source was additionally defined as an area where the animals could feed and move continuously (White & Wrangham, 1988). Thus, two or more trees or palms of the same species were considered a unique food source if their canopies were united. Tool sites separated by less than 30 cm were also considered as a single tool site, since a monkey could move from a tool site to another in a single jump. However, we also recorded if the group was split and feeding in more than one potentially clumped food source (trees, palms or tool sites) at the same time and labelled this as simultaneous feeding (hereafter simultaneous, see below). The mean monthly density of palms with nuts in FBV was estimated as 21.5 ± 9.5 individuals/ha (Verderane, 2010, see Izar et al., 2012 for methodology description of palm phenology) and the most important species for capuchin monkeys have a subterranean stem and usually produce a single cluster of nuts at ground level (except *Mauritia flexuosa*). The mean density of tool sites was calculated as 1.82 tool sites/ha, with mean

size 1.89 m², and 1.1 hammer stones available per anvil (Visalberghi et al., 2007).

The size of potentially clumped food sources was estimated according to (1) food site residence time (hereafter residence time; cf., Chancellor & Isbell, 2009), and (2) feeding unit size during feeding bouts in potentially clumped sources recorded by feeding tree focal sampling method (Strier, 1989). Residence time was measured as the interval between when the first individual started and when the last individual stopped feeding in a given clumped food source, subtracting the amount of time in which the monkeys did not feed (cf., Vogel & Janson, 2007). Each record of residence time in a given source was considered a feeding bout for analysis purposes. Feeding unit size was measured as the number of individuals that fed simultaneously at the same food source (cf., Izar, 2004). All group members were considered in these measurements. If monkeys fed at the same food source at different turns in the same day, we summed the duration of each bout and considered them as a single episode. In simultaneous feeding in clumped food sources (as defined above), we calculated the residence time and the feeding unit size for the entire set of trees, palms or tool sites exploited at the same time. Thus, we were able to record the actual proportion of group members that could feed at the same time on a given potentially clumped source or in simultaneous clumped sources, and the proportion of group members effectively excluded from these resources. These data were used to verify whether these sources could actually be considered clumped, and of intermediate size relatively to group size, the features relevant to the models' predictions. These episodes were recorded by two observers (MPV and one field assistant), that were able to record up to two food sources each, thus, together were able to record up to four food sources for a simultaneous episode. Specifically, each observer used a notebook to note the time and identification of the first group member to arrive at the source and the identification of each successive arrival, and the time of the last departure. The two field assistants that helped in this data collection were trained by MPV over four months until inter-observer reliability reached 85%. During this phase, inter-observer reliability was checked every day on individual recognition, time spent on a food source, and on behavioural categories. Because the vegetation in FBV is low and sparse and most trees present relatively open canopies (even in the wet season), the observers were able to collect detailed episodes of feeding in clumped food sources.

2.3.3. Competitive regime and female social relationships

The rate of food-related agonistic interactions among females is the most important index to access the intensity of contest competition over foods, within and between groups (Isbell, 1991). Thus, in order to verify if females in FBV faced contest competition within their group, we recorded ‘all occurrences’ (Altmann, 1974) of dyadic agonistic interactions involving females that included (1) physical aggression (biting, slapping, fur or tail-pulling), (2) chases (pursuing another), (3) nonphysical threats (facial threats and body displays) and (4) displacements (moving away when another is approaching or taking the place of another). The chance of missing an agonistic event was low since visibility conditions at the study site were excellent, the study groups were highly cohesive at all times, and agonistic behaviours were conspicuous, including vocalizations that attracted the attention of the observers (for further details, see Izar et al., 2012). Whenever possible the identity of participants, the context, and the results of aggressive interactions were recorded. The agonistic interactions were considered to be food-related when at least the loser participant was engaged in feeding or foraging at the onset of the interaction (cf., Pruett & Isbell, 2000). Whenever possible we recorded the food item contested. The hierarchical dominance relationships among females were determined on the basis of direction of agonistic dyadic interactions in which we could determine a clear aggressor and a clear receiver of the threat. We calculated the degree of linearity and the percentage of reversals against the hierarchy (i.e., interactions below the diagonal of the dominance matrix) of the hierarchical dominances using the directional consistency index (hereafter directional index) (van Hooff & Wensing, 1987), which is considered particularly appropriate for group samples smaller than six members (e.g., Chancellor & Isbell, 2009). Directional index ranges from 0 to 1 (where 0 is a completely nonlinear system and 1 is completely linear) and was calculated by $(H - L)/(H + L)$, where H is the total number of agonistic interactions in the direction of higher frequency and L is the total number of agonistic interactions in the direction of lower frequency (cf., Chancellor & Isbell, 2009). Coalitions involving females (when an individual actively supported another in an agonistic interaction with a third party) were collected using all occurrences method.

In this study we adopted the notion that feeding at the same time in the same potentially clumped food source is indicative of tolerance among females (van Schaik, 1989; Sterck et al., 1997; Belisle & Chapais, 2001;

Boinski et al., 2002). As Belisle & Chapais (2001), we considered that if contest competition regulates access to food, when a food can be usurped from one individual by another, co-feeding is evidence of tolerance. Therefore, we evaluated tolerance among females during episodes of feeding on potentially clumped food sources using the Simple Ratio association index ($SR_{XY} = a/a + b + c$, where $a = N$ episodes in which X and Y were feeding together at the same food source; $b = N$ episodes in which X was feeding on a potentially clumped food source and Y was not; and $c = N$ episodes in which Y was feeding on a potentially clumped food source and X was not) (Cairns & Schwager, 1987). The Simple Ratio association index (hereafter association index) was calculated for each pair of females in the three types of potentially clumped food sources. The closer the index is to 1.0, the greater the tolerance. In order to investigate if dominant females were tolerant to subordinate females in feeding sources, we classified females of each group as (1) high rank (ZA: $N = 2$; CH: $N = 2$), (2) middle rank (ZA: $N = 2$; CH: $N = 2$) or (3) low rank (ZA: $N = 1$; CH: $N = 3$) and compared the mean association index of high rank–high rank dyads; high rank–middle rank, high rank–low rank, middle rank–middle rank; middle rank–low rank, and low rank–low rank dyads in each type of potentially clumped source.

To test if females in FBV faced contest competition between groups we recorded all occurrences of agonistic encounters between ZA and CH and between these groups and other groups of *S. libidinosus*, noting the location, behavior of the animals and the outcome of each encounters.

The location of the study groups was recorded at 20-min intervals using a GPS device (Garmin e-Trex) in order to calculate daily travel distance used to evaluate if females in FBV experienced within-group scramble competition. Daily travel distances were calculated as the sum of distances between each pair of consecutive points the animals crossed in one day. The mean monthly daily distances were calculated using the data from days in which the observers had the monkeys in view for the entire day (179 days for ZA and 126 days for CH). Within-group scramble competition was also evaluated as per capita individual minutes of feeding (PCIM = IM (individual minutes)/group size; IM = residence time \times feeding unit size) (Janson, 1988). For each group, data were summarized as mean monthly PCIM and IM in the three types of potentially clumped sources.

2.3.4. *Statistical analyses*

Because the study groups differed in relation to provision of food (provisioned *vs* non-provisioned) and period of data collection (24 months for ZA and 15 months for CH), data on feeding behaviour, potentially clumped food sources size, contest and scramble competition, and female social relationships they were analyzed separately. According to the Shapiro–Wilk test, with significance set at 0.05, all data presented here have a normal distribution.

GLM tests were used to verify the effect of season on (1) mean monthly residence time, feeding unit size, individual minutes of feeding (measured as IM), per capita individual minutes of feeding (measured as PCIM), and the rate of feeding bouts in the three types of potentially clumped food sources, (2) monthly rate of agonistic interactions involving adult females, (3) monthly daily travel distance (for this last analysis, we also used data collected by N. Spagnoletti, so these analyses account for the period July 2006–April 2008) and (4) mean association index obtained for each female in each type of potentially clumped food source. GLM test was also used to verify if there was difference in the proportion of females' feeding scans devoted to the consumption of clumped *vs* evenly distributed or dispersed resources. GLMM test was employed to verify if the proportion of females' feeding scans devoted to different food items varied between-seasons. In this analysis, we used females and food items as random factors, season as independent variables and proportion of feeding scans spent in each kind of food item as the response variable (dependent variable).

Chi square tests were used to examine (1) if the frequency of within group food-related aggression involving females differed from the expected calculated by the percentage of time spent feeding on each food item and (2) if the frequency of coalition bouts between females and other age/sex class differed from the expected by the number of available partners in the group. Because females in FVB are philopatric and males disperse from their natal groups (Izar et al., 2012), we assume that relatedness between females is greater than between females and males and between males. Thus, if females are nepotistic, we expect higher frequency of coalition between females than between other age/sex classes.

We used Pearson correlations to verify if residence time was correlated to feeding unit size in each type of clumped food sources. All statistical analyses were conducted using SPSS 13 for Windows, except for GLMM

analyses that was conducted using SAS 9.0 for Windows, and significance for all tests was set at $\alpha = 0.05$. For GLM analyses the effect sizes were determined by partial eta squared. Bonferroni post hoc tests were used when data presented homogeneity of variances and Games–Howell when variances were not homogeneous.

3. Results

3.1. Feeding behaviour

Food items were identified in 91% of feeding scan samples recorded for ZA and in 89% recorded for CH. Females from both groups fed mainly on fruits and invertebrates, but spent a small proportion of their feeding time consuming endosperm extracted with tools (Table 1). Females' diet differed between seasons in both groups ($F = 114.19$, $p < 0.001$), so that they consumed more fruits and invertebrates in the wet than in the dry season, and more seeds in the dry than in the wet season. Additionally, in the dry season, females of ZA fed more on flowers and nectar, while females of CH fed more on provisioned foods (Table 1).

Overall, females fed significantly more on potentially clumped (ZA = $58.5 \pm 11.3\%$ of feeding time; CH = $63.9 \pm 11.2\%$ of feeding time) than on evenly distributed or dispersed resources (ZA = $41.5 \pm 11.3\%$ of feeding time; $F = 14.6$; $df = 47$; $p < 0.001$; $\eta^2 = 0.25$; power = 0.96; CH = $36.1 \pm 11.2\%$ of feeding time; $F = 36.6$; $df = 29$; $p < 0.001$; $\eta^2 = 0.58$; obs. power = 1.0) in both seasons.

3.2. Food sources size

We recorded 1548 bouts of feeding in potentially clumped food sources for ZA and 670 for CH. Simultaneous episodes (i.e., group members were feeding on more than one potentially clumped food source at the same time) represented 20% ($N = 314$) of feeding bouts recorded for ZA and 31.5% ($N = 212$) recorded for CH. In ZA, but not in CH, residence time differed according to the food source type ($F = 16.8$; $df = 2$; $p < 0.001$; $\eta^2 = 0.02$; obs. power = 1.0), so that palms had longer residence time than trees ($p < 0.001$) and tool sites ($p < 0.001$), and trees had longer residence time than tool sites ($p < 0.01$) (Table 2). In contrast, feeding unit size differed according to the food source type in both groups (ZA: $F = 45.9$; $df = 2$; $p < 0.001$; $\eta^2 = 0.06$; obs. power = 1.0; CH: $F = 8.8$; $df = 2$; $p < 0.001$;

Table 1. Mean proportion ± SD of feeding time (eating + foraging) allocated to exploitation of different food items by females of ZA and CH in all study period, in the dry and the wet seasons.

Group	Period	Sd	Fr	Nc	Fl	In	Rt	Lv	Ed ^a	Vt	Pv
ZA	All	14.8 ± 15.0	36.3 ± 14.7**	3.5 ± 7.1	1.2 ± 3.6	34.6 ± 10.4*	1.5 ± 2.1	4.6 ± 3.0	2.7 ± 2.3	0.8 ± 0.9	–
CH		11.9 ± 11.3	27.9 ± 19.4**	1.7 ± 3.8	0.5 ± 1.2	28.1 ± 9.6*	1.4 ± 2.0	6.3 ± 5.7	5.1 ± 3.5	0.3 ± 0.4	16.8 ± 16.5
ZA	Dry	20.7 ± 12.8**	26.0 ± 13.0**	7.6 ± 9.7**	2.6 ± 5.3*	31.2 ± 9.5**	2.8 ± 2.8	5.4 ± 3.0	3.4 ± 1.7	0.4 ± 0.4	–
	Wet	10.6 ± 15.5**	43.6 ± 11.2**	0.6 ± 1.6**	0.2 ± 0.5*	37.1 ± 10.6**	0.6 ± 0.8	4.0 ± 3.0	2.3 ± 2.6	1.1 ± 1.1	–
CH	Dry	21.0 ± 13.9**	11.6 ± 11.9**	1.9 ± 2.6	1.3 ± 2.0	21.4 ± 4.8**	2.3 ± 2.9	4.0 ± 3.1	6.0 ± 3.0	0.4 ± 0.3	30.1 ± 13.1**
	Wet	7.3 ± 6.4**	36.1 ± 17.2**	1.6 ± 4.5	0.1 ± 0.3	31.4 ± 9.8**	0.9 ± 1.4	7.4 ± 6.5	4.7 ± 3.8	0.2 ± 0.4	10.2 ± 14.2**

Sd, seed; Fr, fruit; Nc, nectar; Fl, flower; In, invertebrate; Rt, root; Lv, leaves; Ed, endosperm; Vt, vertebrate; Pv, provisioned foods.

^aFoods extracted with tools.

* $p < 0.05$; ** $p < 0.001$, statistic significance in GLMM comparisons between ZA and CH considering all study period and between the dry and wet seasons for both groups.

Table 2.

Total episodes, rate of feeding bouts, mean residence time \pm SD, and mean feeding unit size \pm SD for the three types of clumped food sources exploited in 24 months by ZA and in 15 months by CH.

	ZA			CH		
	Tree	Palm	Tool site	Tree	Palm	Tool site
Episodes (<i>N</i>)	1114	242	192	481	89	100
Rate of feeding bouts/h	1.1	0.21	0.15	1.5	0.25	0.26
Simultaneous episodes (<i>N</i>)	255	42	17	156	23	33
Residence time (min)	15.5 \pm 19.1	20.9 \pm 27.4	10.1 \pm 11.8	16.6 \pm 15.2	19.6 \pm 21.4	16.7 \pm 17.9
Feeding unit size (ind)	3.5 \pm 2.4	4.2 \pm 2.7	2.1 \pm 1.4	5.1 \pm 3.6	5.6 \pm 4.1	3.2 \pm 2.3

$\eta^2 = 0.03$; obs. power = 1.0). In ZA, feeding units were larger in palms than in trees ($p < 0.001$) and tool sites ($p < 0.001$) and larger in trees than in tool sites ($p < 0.001$). On average, $44.3 \pm 27.9\%$ of group members were able to feed in palm sources, $37.4 \pm 25.8\%$ in tree sources and $20.3 \pm 12.7\%$ in tool sites. For CH, feeding units were larger in trees ($p < 0.001$) and palms ($p < 0.001$) than in tool sites (Table 2). On average, $32.0 \pm 23.4\%$ of group members were able to feed in palm sources, $29.1 \pm 20.1\%$ in tree sources, and $18.2 \pm 13.2\%$ in tool sites.

In ZA, but not in CH, feeding unit size of trees, palms and tool sites differed between seasons ($F = 8.6$; $df = 2$; $p < 0.001$; $\eta^2 = 0.01$; obs. power = 0.97), so that feeding unit size of trees was higher in the wet than in the dry season, while feeding unit size of palms and tool sites was higher in the dry than in the wet season (Table 3).

In both groups, residence time was positively correlated with feeding unit size in the three kinds of potentially clumped food sources: trees (ZA: $r = 0.664$; $p < 0.001$; CH: $r = 0.715$; $p < 0.001$), tool sites (ZA: $r = 0.682$; $p < 0.001$; CH: $r = 0.680$; $p < 0.001$) and palms (ZA: $r = 0.607$; $p < 0.001$; CH: $r = 0.737$; $p < 0.001$).

3.3. Contest competition

Agonistic interactions occurred at a rate of 0.6 episodes/hour of observation within ZA ($N = 944$) and at a rate of 2.2 episodes/hour of observation

Table 3.

Mean residence time \pm SD and mean feeding unit size \pm SD for the three types of clumped food sources exploited by ZA and CH in the dry and the wet seasons.

	ZA			CH		
	Tree	Palm	Tool site	Tree	Palm	Tool site
Residence time (min)						
Dry	14.1 \pm 17.1	23.7 \pm 32.6	12.1 \pm 14.3	14.5 \pm 13.5	12.4 \pm 12.5	14.2 \pm 15.2
Wet	16.5 \pm 20.4	16.0 \pm 13.0	7.5 \pm 6.2	17.8 \pm 15.9	21.4 \pm 22.8	17.6 \pm 18.8
Feeding unit size (ind)						
Dry	3.1 \pm 2.3	4.6 \pm 2.9	2.2 \pm 1.6	4.3 \pm 3.2	4.4 \pm 3.7	3.1 \pm 2.7
Wet	3.8 \pm 2.5	3.5 \pm 2.1	1.9 \pm 1.2	5.5 \pm 3.8	5.9 \pm 4.2	3.2 \pm 2.1

within CH ($N = 1177$). In both groups the rate of aggression did not vary between the dry (ZA = 0.6 episodes/h; CH = 2.6 episodes/h) and the wet season (ZA = 0.7 episodes/h; CH = 2.0 episodes/h). It was possible to determine the identity of individuals involved in agonistic interactions in 64.0% of episodes recorded for ZA and in 75.0% of episodes recorded for CH. Females participated as aggressor and/or victim in 63.5% ($N = 385$) of agonistic interactions of ZA and in 52.5% ($N = 467$) of CH. In ZA, 62% of episodes were disputes among females, 14% were disputes in which a female threatened, chased or displaced a male, and 24% were disputes in which a female was threatened, chased or displaced by a male. In CH, 21% of episodes were disputes among females, 48% were disputes in which a female threatened, chased or displaced a male, and 31% were disputes in which a female were threatened, chased or displaced by a male.

The context of agonistic interactions involving females was determined in 88.0% ($N = 339$) of episodes recorded for ZA and in 92% ($N = 430$) of episodes recorded for CH. In both groups, agonistic interactions occurred mainly as food-related disputes (ZA: 67% of agonistic episodes involving females; CH: 75.5% of agonistic episodes involving females). Pulp of fruits and provisioned foods (in the case of CH) were the primary foods contested by females (Figure 1). The frequency of disputes over each type of food differed from that expected from the time that females spent feeding on each item. Overall, disputes over invertebrates occurred less often than expected, while disputes over provisioned food occurred more often than expected in CH. The adjusted residuals of χ^2 revealed that, in both groups, tool sites were

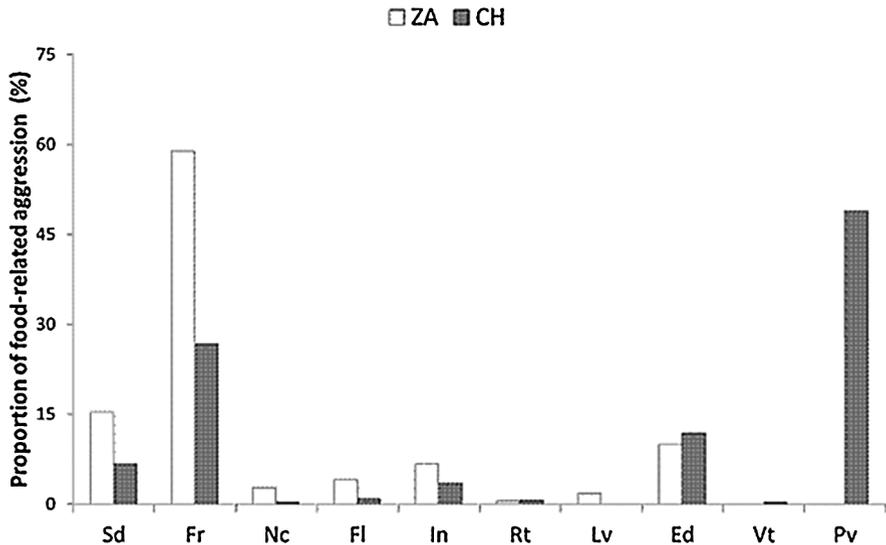


Figure 1. Proportion of food-related disputes over different food items involving females of ZA and CH. Sd, seed; Fr, fruit; Nc, nectar; Fl, flower; In, invertebrate; Rt, root; Lv, leaves; Ed, endosperm extracted with tools; Vt, vertebrate; Pv, provisioned foods.

the second feeding context in frequency of aggression among females (Table 4), although the foods obtained with tools were the sixth-most consumed food item both by ZA-females (out of 9 food items) and by CH-females (out of 10 food items).

In both groups, frequency of agonism in potentially clumped sources varied from 0 to 5 events per feeding bout. Frequency of agonism increased with median residence time of the three types of potentially clumped food sources in both groups. We observed no agonism in potentially clumped food sources with the lowest and the highest residence times (Figure 2).

Intergroup encounters occurred at a rate of 0.9 episodes per 100 h of observation ($N = 25$), with a higher percentage (88%) during the rainy months. Encounters between ZA and CH were 80% of the observed episodes, whereas 20% were encounters between ZA and solitary males or small groups containing only males. We did not observe encounters between CH and other groups of capuchin monkeys besides ZA. In all episodes members of each group behaved aggressively towards members of the other group, mainly with vocal exchanges, facial threats and agonistic displays (including stone banging: individuals using stones to hit rock outcrops in a conspicuous

Table 4.

Proportion of food-related disputes in ZA and CH as a function of females' feeding time.

Food item	ZA			CH		
	Obs(<i>N</i>)	Exp(<i>N</i>)	<i>A_r</i>	Obs(<i>N</i>)	Exp(<i>N</i>)	<i>A_r</i>
Fruit	130	79.6	1.84	83	76.2	−0.78
Seed	34	31.3	0.11	21	33.6	−1.39
Endosperm ^a	22	0.9	0.84	37	7.1	0.04
Flower	9	2.6	0.26	3	1.6	−0.90
Nectar	6	7.1	−0.01	1	3.2	−0.10
Provisioned	–	–	–	152	52.9	2.25*
Leaves	4	9.7	−0.20	0	21.6	−1.70
Invertebrate	15	74.6	−2.37*	11	92.3	−3.68*
Root	1	2.8	−0.04	2	3.2	−0.96
Vertebrate	0	1.9	−0.04	1	0.6	−0.93

Obs, absolute frequency of food-related disputes; Exp, frequency of food-related disputes expected as a function of females' feeding time; *A_r*, χ^2 -adjusted residual. For ZA, $\chi^2 = 564.5$ ($p < 0.001^b$, $df = 9$); for CH, $\chi^2 = 418.9$ ($p < 0.001^b$, $df = 9$).

^aFoods extracted with tools.

^bSignificant after applying the Monte Carlo correction ($\alpha = 0.001$).

* $p < 0.05$, significant difference.

aggressive display; cf., Moura, 2007). Adult females participated in intergroup encounters in a prominent way, initiating threats and chasing. In fact, the only observed episode of actual physical aggression (biting, slapping, and fur-pulling) occurred during a conflict between females from ZA and females from CH. Nevertheless, all group members (including juveniles and infants) were observed participating in intergroup encounters. In spite of the aggressive nature of intergroup encounters, we also observed affiliative behaviours (affiliative facial displays and play) between members of ZA and CH, especially between adult and juvenile males. All encounters between CH and ZA resulted in CH evicting ZA irrespective of location and context in which the encounters occurred, and in the majority of these events ($N = 19$, 75% of total encounters) CH had privileged access to areas where high quality foods were available.

3.4. Scramble competition

The mean monthly daily traveled distances differed between groups ($F = 9.8$; $df = 303$; $p < 0.01$; $\eta^2 = 0.03$; obs. power = 0.88), so that ZA traveled

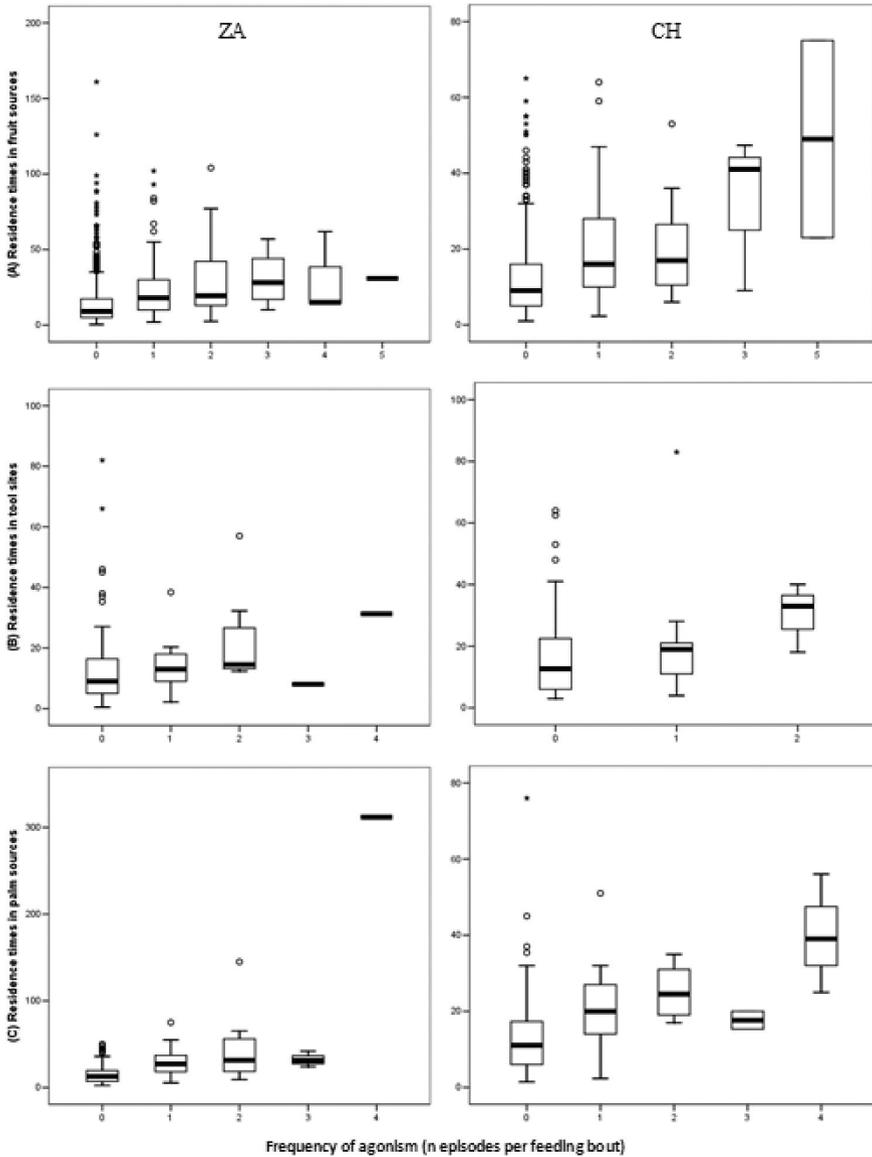


Figure 2. Frequency of agonism in relation to residence time of three kinds of clumped food sources. (A) Fruits, (B) tool sites and (C) palms.

longer distances (1.967 ± 0.608 m) than CH (1.729 ± 0.732 m), and between seasons ($F = 9.3$; $df = 303$; $p < 0.01$; $\eta^2 = 0.03$; obs. power = 0.86),

Table 5.

Mean individual minutes (IM) and per capita individual minutes (PCIM) for the three types of clumped food sources exploited by ZA in 24 months and by CH in 15 months.

	ZA			CH		
	Tree	Palm	Tool site	Tree	Palm	Tool site
IM	85 ± 170	133 ± 265	33 ± 69	124 ± 184	174 ± 299	80 ± 133
PCIM	9.1 ± 17.8	13.9 ± 27.1	3.0 ± 5.4	7.1 ± 10.5	4.6 ± 17.1	9.9 ± 7.5

with longer distances traveled by both groups during the wet season (ZA = 2.075 ± 0.698 ; CH = 1.822 ± 0.576 ; dry season: ZA = 1.819 ± 0.414 ; CH = 1.576 ± 0.258).

In ZA, but not in CH, the mean individual minutes of feeding (IM) and per capita individual minutes of feeding (PCIM) varied according to the type of potentially clumped food source, so that both IM ($F = 17.5$; $df = 29$; $p < 0.001$; $\eta^2 = 0.02$; obs. power = 1.0) and PCIM ($F = 19.1$; $df = 29$; $p < 0.001$; $\eta^2 = 0.02$; obs. power = 1.0) were higher in palms than in trees ($p < 0.05$) and in tool sites ($p < 0.001$), and higher in trees than in tool sites ($p < 0.001$) (Table 5). In both groups, IM and PCIM did not vary between the dry and wet seasons (Table 6). IM did not vary between groups. In contrast, PCIM differed between groups ($F = 4.1$; $df = 1580$; $p < 0.05$; $\eta^2 = 0.003$; obs. power = 0.52), so that PCIM of ZA was higher than CH.

Table 6.

Mean individual minutes (IM) and per capita individual minutes (PCIM) for the three types of clumped food sources exploited by ZA and CH in the dry and the wet seasons.

	ZA			CH		
	Tree	Palm	Tool site	Tree	Palm	Tool site
IM						
Dry	72 ± 145	165 ± 317	44 ± 88	93 ± 146	96 ± 156	79 ± 154
Wet	95 ± 185	75 ± 102	18 ± 24	141 ± 200	194 ± 323	81 ± 126
PCIM						
Dry	7.6 ± 15.1	16.8 ± 32.3	3.7 ± 6.7	5.4 ± 8.5	5.7 ± 9.2	4.6 ± 9.1
Wet	10.2 ± 19.5	8.7 ± 11.9	1.9 ± 2.6	7.9 ± 11.3	10.9 ± 18.5	4.6 ± 7.0

Table 7.

Mean association index between female dyads of different and similar dominance rank in the three kinds of clumped food sources.

	High–high ranking	High–middle ranking	High–low ranking	Middle–middle ranking	Middle–low ranking	Low–low ranking
Group ZA						
Trees	0.28	0.20	0.17	0.17	0.18	–
Palms	0.44	0.28	0.23	0.16	0.24	–
Tool sites	0.02	0.01	0.03	0.06	0.12	–
Group CH						
Trees	0.26	0.18	0.14	0.13	0.11	0.11
Palms	0.36	0.22	0.10	0.14	0.09	0.03
Tool sites	0.11	0.06	0.04	0	0.04	0

3.5. Female social relationships

Dominance relationships among females in FBV were well resolved and could be described as hierarchical, linear and stable. Agonistic interactions among females of both groups were strongly unidirectional (directional index: ZA = 0.99; CH = 0.97) and the number of reversals was low (ZA = 1%; CH = 2.5%), revealing that most interactions followed the direction of the hierarchy (ZA: Mb > Mc > Ema > Dun > Cat; CH: Pi > Di > Ch > Am > Tn = Ca = Dd). In all types of potentially clumped sources, high and middle-ranking-females were observed co-feeding with low-ranking females (Table 7). The association index showed that females from both groups were significantly more tolerant to each other during feeding on tree sources (mean association index: ZA = 0.22; CH = 0.14) and on palm sources (ZA = 0.29; CH = 0.13) than when they were using tool sites (ZA = 0.04; $F = 694.7$; $p < 0.001$, $\eta^2 = 0.96$; obs. power = 1.0; CH = 0.04; $F = 57.2$; $p < 0.001$, $\eta^2 = 0.98$; obs. power = 1.0). This result holds true even when we compared the dyads classified by their dominance rank (Table 7).

In ZA, coalitions occurred in 12% ($N = 115$) of the agonistic episodes in which participants were identified, at a rate of 0.08 coalitions/h. In CH, coalitions occurred in 25% ($N = 297$) of the agonistic episodes in which participants were identified, at a rate of 0.6 coalitions/hour. Females participated as intervener (supporting one of the two opponents in an aggressive conflict) or receiver (gets help in an aggressive conflict) in 95.5% of coalitions recorded for ZA and in 87.0% of coalitions recorded for CH. The context of

these coalitions was determined in 86.0% of the episodes recorded in ZA and 90.5% of the episodes recorded in CH. In both groups, most of the coalitions involving females took place during food-related disputes (ZA = 78.0% of episodes; CH = 74.5% of episodes; Verderane et al., in prep.). Coalitions between sex/age classes differed from the expected by the number of available partners in the groups (ZA: $\chi^2 = 138.4$; $df = 7$; $p < 0.001$; Monte Carlo $p = 0.001$; CH: $\chi^2 = 336.0$; $df = 13$; $p < 0.001$; Monte Carlo $p = 0.001$). The adjusted residual of χ^2 indicated that coalitions among adult females occurred 2.56 times above the expected in ZA and 1.38 times above the expected in CH. Coalitions between females and the dominant male in ZA and between females and adult males in CH were also higher than expected by the number of available adult males in the groups (ZA = 3.38 times higher; CH = 1.46 times higher).

During the study period, we did not observe any female transferring between groups, whereas four subadults males migrated from ZA to CH. Five attempts of male transfer were observed, in which unknown subadults males tried to transfer into ZA, without success.

4. Discussion

4.1. Features of food sources

Tufted capuchin females of FBV fed mainly on pulp of fruits and invertebrates, like forest-living tufted capuchin monkeys (Terborgh, 1983; Peres, 1993; Zhang, 1995; Di Bitetti, 2001; Spironello, 2001; Izar, 2004). Fruits consumed by female capuchins in FBV can be considered high-quality clumped food sources that enable one or some individuals to exclude other group members by means of contest competition, both in the wet and in the dry seasons. First, they are high-quality sources because many fruit species eaten by capuchins in FBV are rich in carbohydrates (Roesler et al., 2007; Silva et al., 2008; Guimarães & Silva, 2008) and/or lipids (Almeida, 1998; Carvalho et al., 2008), while alternative foods consumed in the dry season are rich in essential fats, starches and proteins (i.e., seeds) and soluble sugars (i.e., flowers and nectar: Janson & Chapman, 1999; Strier, 2007). Second, they could actually be considered clumped foods because in most feeding bouts in trees and palms, only one fruit tree or one palm tree was available in areas exploited by the groups, as revealed by the small proportion of simultaneous feeding bouts recorded for both groups along this study. Third, the

trees and palms species exploited by capuchins in our study site have a long residence time (cf., Izar, 2004), since monkeys normally spent more than 12 min feeding in a given tree or palm, both in the dry and in the wet season. The number of group members co-feeding at a clumped source was correlated to its residence time, and the mean size of feeding units was smaller than the group size, even in simultaneous clumped food sources. Thus, it is possible to conclude that females in FBV fed significantly more on clumped, high-quality foods than on evenly distributed resources, both in the wet and in the dry season.

4.2. *Competitive regime over food*

As predicted by Sterck et al. (1997) for groups that feed on spatially clumped, high-quality, and usurpable foods, females of *S. libidinosus* in FBV seem to face contest competition within and between groups for food. Agonistic interactions involving females occurred mainly as disputes about accessing clumped food sources, so that disputes were more frequent over fruits in ZA and over provisioned foods in CH than over other foods (controlled for time devoted to the consumption of each food item). This result is consistent with the argument that clumped foods elicit higher rates of within-group contest competition than do disperse and evenly distributed foods, as described for several primate species (e.g., *Saimiri* spp.: Boinski et al., 2002; *Cebus capucinus*: Vogel, 2005; *Macaca* spp.: Su & Birky, 2007; *Lemur catta*: White et al., 2007; *Gorilla beringei*: Robbins, 2008; *Erythrocebus patas*: Nakagawa, 2008; *Microcebus berthae* and *M. murinus*: Dammhahn & Kappeler, 2009). Moreover, in accordance with previous studies, we found that food sources of intermediate size generated more agonism, thus, were more usurpable, than food sources with shorter or longer residence times (Janson, 1990; Isbell et al., 1998; Chancellor & Isbell, 2009).

Inter-group encounters were characterized by consistent inter-group avoidances, threats, chases and physical aggression between members of different groups, so that it was possible to detect dominance relation between the two study groups in FBV. Moreover, ZA constantly monitored and avoided CH and, even though inter-group encounters were broadly distributed throughout the ZA's home range, all encounters between ZA and CH were won by CH. In particular, adult females participated prominently in almost all encounters, behaving aggressively toward members of the other group. In fact, the single episode with inter-group physical aggression occurred between adult and juvenile females. These behaviours reveal that

females from our study population also experienced between-group contest competition for food (Wrangham, 1980; Boinski et al., 2002; Harris, 2006), in addition to within-group contest competition.

Results about scramble competition within groups were not conclusive. On the one hand, data on per capita individual minutes on clumped sources revealed that, as expected by the models, females from the larger group experienced higher scramble competition than those from the smaller group (PCIM was higher for ZA than for CH). On the other hand, data on daily traveled distances, showing that the smaller group (ZA) travelled longer per day than the larger group, and not vice-versa as scramble competition would predict (Isbell, 1991), suggest that females on FBV were not facing the effects of scramble competition. A likely explanation for this inconsistency is the fact that the larger group (CH) received provisioned foods. So it is possible to argue that provisioning mitigated the effect of within-group scramble competition on energy intake and, consequently, on daily travelled distance. The fact that CH has been frequently observed spending several hours each day resting and foraging nearby the area where provisioned foods were available reinforce this argument.

4.3. Female social relationships

Female social relationships in FBV were in accordance with three of Sterck et al.'s (1997) predictions for primates experiencing contest competition within and between groups. First, since no female transferred between-groups occurred during the study period (or in the subsequent years, Izar et al., 2012), while several males transferred from ZA to CH (and from other groups to ZA in subsequent years, unpublished data), we conclude that females in FBV are philopatric. Second, females established linear (strongly unidirectional) and stable (low proportion of reversals, that is, lower-ranking females won in agonistic interactions with higher-ranking females: ZA = 1%; CH = 2.5%) dominance hierarchies, a result consistent with several comparative studies showing that more linear and formalized hierarchies are formed when female primates face high levels of within-group contest competition over food (i.e., *Macaca* spp.: Su & Birky, 2007; *Saimiri* spp.: Boinski et al., 2002; *Pan troglodytes*: Wittig & Boesch, 2003; *Semnopithecus entellus*: Koenig, 2000; Koenig et al., 1998; *Presbytis thomasi* and *M. fascicularis*: Sterck & Steenbeek, 1997; *E. patas* and *Cercopithecus aethiops*: Nakagawa, 2008). This is also the pattern found in several wild populations

of forest-living tufted capuchin monkeys (Izawa, 1980; Janson, 1990; Di Bitetti, 2001; Lynch Alfaro, 2007, see Izar et al., 2012 for a more comprehensive comparison). Another evidence that female' dominance relationships in FBV is well-decided is the fact that most of these agonistic interactions (81% in ZA and 77.5% in CH) were ritualised, with low aggressive potential, and involved just vocal and facial displays, threatening, and displacements, but not physical aggression.

Finally, in both groups, coalitions among females were more frequent than expected (by the number of females in each group) and occurred mainly in food-related disputes. This result follows the prediction that philopatric primate females should form coalitions to compete within their group for access to high quality clumped food sources when facing within-group contest competition (Sterck et al., 1997). In spite of showing linear dominance hierarchies and high rates of agonistic interactions, high-ranking females allowed the presence of middle and low-ranking females when feeding in clumped food sources, specifically in fruit trees and palms. Therefore, in accordance with several studies that define tolerance as a dominant individual allowing a subordinate one to co-feed at the same usurpable food source (e.g., van Schaik, 1989; Sterck et al., 1997; Belisle & Chapais, 2001; Ventura et al., 2006; Tiddi et al., 2011; Dubuc et al., 2012), we can describe females in FBV as tolerant. This result is consistent with the expectation for female primates experiencing contest competition between groups (Sterck et al., 1997). However, even females of despotic species can show some degree of co-feeding, particularly between closest kin (Belisle & Chapais, 2001). Therefore, we need comparable data in order to link variation in the degree of tolerance to variation in between group contest competition among females. In our search of the literature, we did not find data that allowed a direct comparison with our results, because association indexes are calculated in a different manner and/or data on competition between groups are not reported (e.g., Belisle & Chapais, 2001; Tiddi et al., 2011; Ventura et al., 2012). The study conducted by Tiddi et al. (2011) suggest that *S. nigritus* in Iguaçu National Park are less tolerant (ca. 4–7% of co-feeding) than *S. libidinosus* in FBV, but the authors used a different index to calculate co-feeding, included adult males and females in the analyses, and did not report contest competition between groups. Thus, although we can describe females in FBV as resident nepotistic tolerant, at this time we cannot affirm that the tolerance is linked to contest competition for food between groups.

In summary, several relationships predicted by Sterck et al. (1997) between features of food resources and competitive regimes over food among female primates, and between competitive regimes and the pattern of social relationships among females are supported by our results. This is evidence favouring this model in a population of a New World primate species living in a savannah-like environment.

4.4. *Tool using and sociality in FBV*

Females in FBV spent a small proportion of their feeding time using tools and consuming foods obtained with these tools (on average 4% of feeding time). However, because more than 90% of tool use episodes involved processing palm nuts of *catulé* and *piçava*, species with large and rich endosperm (composed of 60% fats, 30% carbohydrates and 10% proteins; D.M. Fragaszy, W. Mattos and B. Wright, unpublished data), it is possible that foods obtained with tools provide females with a greater energy return per unit intake in comparison with other foods (Fragaszy et al., 2010). Thus, although foods accessed with tools are one of several fallback-foods (Wright et al., 2009; Spagnoletti et al., 2012), they seem to be valuable resources for capuchins in FBV.

In general, tool sites supported fewer individuals at one time and had shorter residence times than other clumped food resources. Given that usurpability and, thus, contest competition are predicted to be proportional to residence time (in clumped sources of intermediate size), unexpectedly tool sites were the second most frequent feeding context in which disputes took place. Females were significantly less tolerant (measured as co-feeding) with each other when they were feeding on tool sites than when they were feeding on the other clumped food sources. Our results indicate that using percussive tools at FBV generates within-group contest competition among females in the same way as a usurpable food source does. Thus, we suggest that the habitual use of percussive tools in feeding contributed to the linearity and stability of females' dominance hierarchies observed in the present study. The low tolerance among females at tool sites in FBV (in comparison to the other types of clumped sources) is perhaps related to the particular features of the sites that make them easily usurpable and less easily shared than palms and trees. Unlike trees and palms, the tool sites are not a food source themselves. Instead, the animals have to collect each nut on the ground and transport it to the tool site (Visalberghi et al., 2008, 2009) and normally few

nuts can be transported at one time (personal obs.). Most tool sites have a surface of 1.89 m² or less and a single hammer stone (Visalberghi et al., 2007). Hammer stones are rare, limiting the opportunity for an individual to bring another stone to a tool site.

To the extent that tolerance supports learning food processing technologies (Coussi-Korbel & Fragaszy, 1995; Fragaszy & Visalberghi, 2004), including feeding tool use in nonhuman primates, it is somewhat surprising that the use of tools provokes less tolerance among females than other feeding contexts. Further studies are necessary to address if tolerance will be evident towards young individuals not yet competing with adults for food resources, but not among adults and older juveniles.

In conclusion, the present study enlarges our knowledge about a New World primate species, for which few longitudinal and naturalistic studies are available, by adding systematic findings on a population living in a semi-arid habitat that uses tools to process foods. It adds to evidence linking the features of food sources with food competition and social relations in female primates.

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