

Mating and feeding competition in white-faced capuchins (*Cebus capucinus*): the importance of short- and long-term strategies

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Summary

I investigate the ecological context of intergroup agonism (IGA) in white-faced capuchins (*Cebus capucinus*) to elucidate the roles of feeding and mating competition, explicitly exploring both long- and short-term competitive strategies. Short-term mating competition is not a major function of IGA in *C. capucinus*. Males were the primary participants in IGA, but did not attempt to prevent extra-group copulations by herding females, and there was no relationship between IGA rate and conception rate. Long-term mating competition, on the other hand, may be important: 41% of interactions were low intensity, as would be expected if males were assessing the composition of neighboring groups in anticipation of a takeover. However, 59% of intergroup interactions escalated to chases or physical contact and females were frequent participants in IGA, directing aggression at adults of both sexes and at juveniles. These findings are not consistent with male mating competition and, in conjunction with overlapping home ranges, high interaction rate, and a positive relationship between IGA rate and both food availability and fruit patch size, they indicate that intergroup feeding competition may be important for capuchins. However, interactions do not preferentially occur at food sources, suggesting that capuchins may gain long-term, rather than short-term, benefits from IGA.

Keywords: intergroup competition, between-group contest competition.

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Introduction

Competition over limited resources shapes the relationships between neighboring groups of animals (Wrangham, 1980; Mills, 1982, 1989; Packer et al., 1990; Heinsohn & Packer, 1995; Gompper, 1996; Koenig, 2002). In primates, it is also hypothesized to promote group living and shape social organization and female–female relationships (Wrangham, 1980; van Schaik, 1989; Isbell, 1991). Although social groups may compete over a variety of resources (e.g., sleeping sites; Anderson, 1984), most studies of intergroup agonism (IGA) have focused on food resources and/or mating opportunities because of their direct effects on individual fitness (Kinnaird, 1992; van Schaik et al., 1992; von Hippel, 1996; Steenbeek, 1999; Fashing, 2001; Wich et al., 2002; Cooper et al., 2004; Kitchen et al., 2004; Bayart & Simmen, 2005; Korstjens et al., 2005). Intergroup competition over food resources is predicted to lead to systematic differences in the energetic status of both males and females across social groups. When groups vary in their power and/or have decided dominance relationships, between-group contest competition (BGC) should lead to an imbalance in energy intake: individuals in dominant groups are expected to consume more calories than individuals in subordinate groups (Wrangham, 1980; Janson & van Schaik, 1988; van Schaik, 1989). This imbalance could potentially affect the reproductive success of both sexes (Wrangham, 1980; van Schaik, 1983; Janson & van Schaik, 1988; Robinson, 1988; Sterck et al., 1997; Koenig, 2002). In contrast, intergroup competition over mating opportunities primarily benefits males. During intergroup encounters, males from one group often attempt to mate with females from the other group (Reichard, 1995; Reichard & Sommer, 1997; Korstjens & Noe, 2004; Sicotte & Macintosh, 2004). Resident males try to prevent these extra-group copulations by either driving off the intruders or by herding females away from the interaction (Cheney, 1981; Kumar & Kurup, 1985; Mehlman & Parkhill, 1988; Kinnaird, 1992; Saito et al., 1998). Intruding males may also pursue long-term reproductive strategies by attempting to aggressively displace resident males and thereby gain regular mating access to the females in a group (Fedigan & Jack, 2004).

A number of studies have taken advantage of the fact that different factors limit male and female reproduction (Trivers, 1972), to distinguish between feeding and mating competition among primate social groups. Female participation in IGA is thought to reflect competition for food resources (e.g.,

Cercopithecus mitis: Rowell et al., 1991; *Semnopithecus entellus*: Borries, 1993), whereas male participation indicates competition for access to mates (e.g., *Presbytis pileata*, Stanford, 1991; *Papio ursinus*, Cowlshaw, 1995; *Macaca fuscata*, Majolo et al., 2005). Often, however, intergroup relationships are too complex to be fully explained using this paradigm. For example, in many species, both sexes participate at least occasionally in IGA (e.g., *Macaca silenus*, Kumar & Kurup, 1985; *Colobus guereza*, von Hippel, 1996; Fashing, 2001; *Colobus polykomos*, Korstjens et al., 2005; *Macaca fuscata*, Majolo et al., 2005). Additionally, competition for food and competition for mates are not mutually exclusive (Fashing, 2001). Males may defend food resources to increase the reproductive rate of the females in their social group (Emlen & Oring, 1977; Fashing, 2001) or as a by-product of their mate defense ('hired guns' *sensu* Rubenstein, 1986). For example, although male *Colobus guereza* are the primary participants in IGA and mate defense is one function of these interactions (Fashing, 2001), recent studies suggest that resource defense is also important (Fashing, 2001; Harris, 2006a). Similarly, in chimpanzees (*Pan troglodytes*) it has been demonstrated that when male IGA leads to a home range expansion and increases the group's resource base, females reproduce more quickly (Williams et al., 2004). Thus, male participation does not rule out feeding competition as a cause of intergroup agonism.

Intergroup agonism in white-faced capuchin monkeys (*Cebus capucinus*) has generally been attributed to mating competition because of the prominent role played by males during intergroup encounters (Fedigan, 1993; Rose, 1994; Rose & Fedigan, 1995; Perry, 1996). In this species, males transfer among social groups throughout their lives, moving from groups with less profitable sex ratios (fewer females per male) into groups with more profitable sex ratios (Fedigan & Jack, 2004; Jack & Fedigan, 2004b). Therefore, in addition to being opportunities for extra-group copulations (short-term mating competition), intergroup encounters may be used to assess the sex ratio of neighboring groups and determine the defensive potential of resident males in anticipation of a takeover (long-term mating competition; Fedigan & Jack, 2004; Jack & Fedigan, 2004a,b).

Several characteristics of white-faced capuchin behavior, social organization and foraging ecology suggest that intergroup competition over food resources might also be important. In all populations where the relevant data are available, adult females participate in some of the agonistic intergroup encounters (Barro Colorado Island, Oppenheimer, 1968; Mitchell,

1989; Santa Rosa, Rose, 1994; Lomas Barbudal, Perry, 1996). In addition, female *C. capucinus* typically remain in their natal group. This trait has been hypothesized to be an adaptation to intense intergroup feeding competition (Wrangham, 1980). Finally, white-faced capuchins eat a diet of high-quality fruits that are found in medium to large trees, and could be defended against exploitation by other groups. BGC is hypothesized to be a successful foraging strategy when resources are defensible (Wrangham, 1980; Janson & van Schaik, 1988; van Schaik, 1989).

The role of BGC has not been thoroughly investigated in *C. capucinus*. Perry notes that at her study site, IGA does not take place at feeding sites and neither group gains access to resources as an immediate consequence of interactions (1996). However, skewed energy intake can occur in two ways: through competitive interactions over specific food sources that result in immediate differences in energy intake among groups (short-term BGC, e.g., Janson, 1985), or through the cumulative effects of dominance relationships that allow certain groups to feed in higher quality areas, have larger home ranges, or be avoided by other groups (long-term BGC, e.g., Srikosamatara, 1987; Robinson, 1988; Harris, 2006a,b). Short- and long-term BGC are not mutually exclusive. The interactions that cause immediate differences in caloric intake among groups can also serve to establish and reinforce relationships. Likewise, interactions that do not have immediate caloric consequences can still have important effects on the long-term energetic balance among groups.

In this paper, I investigate the ecological context of IGA in a population of *C. capucinus* to elucidate the roles of feeding and mating competition in the intergroup relationships of this species. I consider both short- and long-term strategies for mating and resource competition. Home range overlap among neighboring groups is a prerequisite for either short- or long-term BGC (prediction 1), because it forces neighbors to share resources and permits groups to interact regularly (prediction 2). Participation by females (prediction 3) is usually a good indicator of feeding competition, but the possibility that they are acting to prevent infanticide must also be considered. If female involvement in IGA reflects an anti-infanticide strategy, their aggression should be directed towards adult males.

Short-term BGC exists when groups gain foraging advantages by displacing one another at feeding sites. Under this kind of competitive regime, IGA should occur at fruit trees more often than expected given the amount of

time that groups spend foraging and feeding on fruit (prediction 4). Short-term BGC has also been linked to several aspects of resource distribution and abundance, including the availability of large, high-quality patches (Wrangham, 1980; Janson & van Schaik, 1988; van Schaik, 1989) and low food abundance (Isbell, 1991). Therefore, I predict that if immediate caloric gain is an important driver of intergroup competition, rates of IGA should be positively related to average patch size (prediction 5) and negatively related to food availability (prediction 6). In contrast, long-term BGC assures future access to resources. It is, therefore, expected to occur in seasons of resource abundance, when immediate caloric needs can be easily met and potentially expensive investments in future foraging success can best be afforded (prediction 7).

Male participation in IGA (prediction 8) is necessary to propose that mating competition drives intergroup relationships in *C. capucinus*, but it is not sufficient to prove it. If IGA in *C. capucinus* is a short-term reproductive strategy that provides extra-group mating opportunities, as is the case in a number of primate species (e.g., *Hylobates lar*, Reichard & Sommer, 1997; *Presbytis thomasi*, Steenbeek, 1999; *Papio cynocephalus ursinus*, Kitchen et al., 2004), males might herd the females in their group away from the intruders. This behavior has not been previously reported in *C. capucinus*, but an extra-group copulation was observed during this study (Crofoot, pers. observ.). Although it did not occur during an intergroup encounter, this anecdote suggests that short-term reproductive strategies should be considered as possible drivers of IGA. When intergroup relationships are shaped by short-term mating competition, males are expected to direct aggression towards the females in their group during intergroup encounters (prediction 9). Additionally, if males are able to predict when conceptions occur, IGA rate should also be positively related to conception rate (prediction 10). Although platyrrhines do not have exaggerated sexual swellings, male *C. capucinus* are nonetheless able to detect the female periovulatory period (Carnegie et al., 2005), and it has been suggested that they may base the timing of their reproductive strategies on the strong seasonal conception peak (Fedigan & Jack, 2004). A positive relationship between IGA rate and conception rate would also be consistent with long-term reproductive strategies. Individuals attempting to overthrow resident males risk physical injury and, if successful, only benefit if they are able to reproduce before being overthrown themselves. This strategy would be most cost effective when females are able to

conceive and, thus, males may time their take-over attempts to coincide with annual conception peaks.

Male *C. capucinus* continue to change social groups throughout their lifetime, leading Fedigan and Jack (2004) to suggest that intergroup interactions may allow them to assess the profitability of transferring by 'checking out' the sex ratio and the relative strength of the males in neighboring groups. Game theory predicts that when fighting is costly, contestants should assess the competitive abilities of their opponent through ritualized and/or low intensity aggression and withdraw without escalation if they would be unlikely to win an ensuing fight (Parker, 1974; Maynard Smith, 1982). If males are using intergroup encounters to 'check out' other groups, IGA should primarily involve ritualized threat behaviors and should not frequently escalate to involve risky behaviors such as chasing or contact aggression (prediction 11). Additionally, because males that take over social groups often commit infanticide (Fedigan, 2003), groups with newborns are expected to avoid contact with other groups. Although any unweaned infant is a potential target for infanticidal males, most infanticide victims were killed within their first month of life (Fedigan, 2003; but see Manson et al., 2004). If newborns are particularly vulnerable, monthly IGA rate is expected to be negatively related to monthly birth rate (prediction 12).

Methods

Research site

This research was conducted at the Smithsonian Tropical Research Institute on Barro Colorado Island (BCI), Panama (9°10'N, 79°51'W) from November 2004 through August 2005. BCI is a 1500 ha island of semi-deciduous lowland forest that was isolated from the mainland in 1914 when the Chagres River was dammed to form Lake Gatun and the Panama Canal. The average annual rainfall is 2600 mm/year, 90% of which falls between May and December (Dietrich et al., 1996). Patterns of fruit availability relate to this uneven distribution of rainfall: fruit availability is high during the dry season and into the early wet season, and is lowest during the late wet season (Leigh, 1999; Wehncke et al., 2003). Half of BCI is covered by relatively young forest (at least 100 years old) that is still growing back from agricultural clearing. The remainder of the forest is older, and is not thought to

have undergone substantial anthropogenic disturbance in the last 200–400 years. This forest is home to four primate species: mantled howler monkeys (*Alouatta palliate*), black-handed spider monkeys (*Ateles geoffroyi*), Geoffrey's tamarins (*Saguinus geoffroyi*), and white-faced capuchins (*Cebus capucinus*). Approximately 250–300 capuchins, in 15–20 social groups live on BCI (Mitchell, 1989; Crofoot, unpubl. data).

Behavioral observations

Six white-faced capuchin social groups with contiguous home ranges were selected as focal groups for this study (see Figure 1, Table 1). To facilitate finding and following groups, one or two individuals from each group were captured and fitted with radio collars (Advanced Telemetry Systems, Isanti, MN, USA). Behavioral observations were conducted by the author and one field assistant. Each group was observed six times a month (3 times by each observer), except in November and December when they were only observed three times per month (all by M.C.C.). Follows were 3 h long,

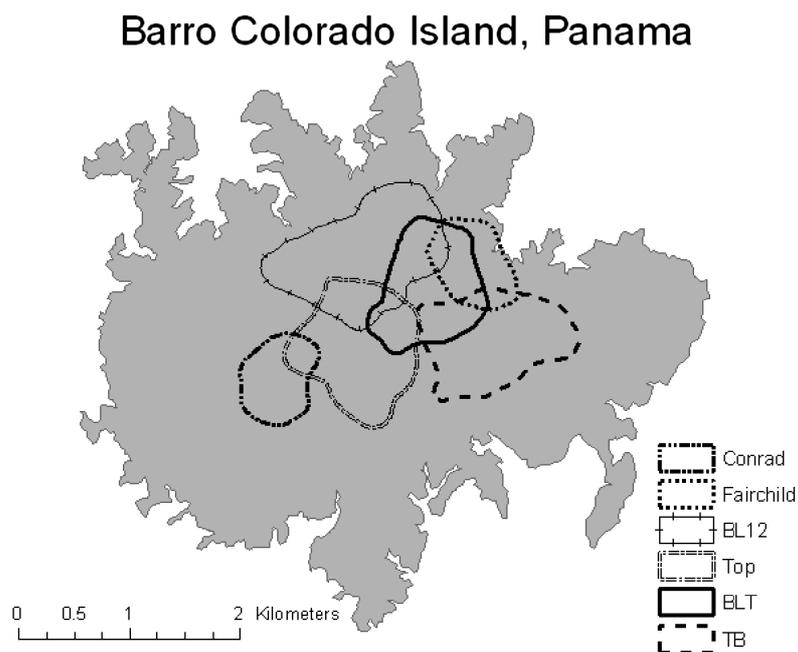


Figure 1. Home ranges (fixed kernel method) of 6 *Cebus capucinus* groups on Barro Colorado Island, Panama.

Table 1. Group size and home range size of the six study groups.

Group	Group size	Adult males	Adult females	Home range (ha)	IGIs observed	Animal ID	Sex	ARTS data	No. of locations
TB	10	2	7	102	4	51	F	11-4/04-05	10638
						87	F	03-05/04-05	4147
BLT	9	2	3	91	7	52	M	11-4/04-05	8515
						53	F	11-4/04-05	9665
Top	16	3	7	109	6	54	F	11-4/04-05	8000
						55	M	11-4/04-05	10653
BL12	25	4	9	161	6	57	F	11-4/04-05	7871
						58	M	03-05/04-05	7437
FC	17	3	4	48 ^a	7	83	F	03-05/04-05	1667
						84	F	03-05/04-05	1662
Conrad	17	3	7	45 ^a	4	85	F	03-05/04-05	2242
						86	F	03-05/04-05	2073

^a The home ranges for these groups are minimum estimates, as they were based on only two months of location data. The home ranges of the other four groups were based on six months of data.

and were distributed evenly throughout the daylight hours (2 follows per month starting between 6–7 am, 2 starting between 10–11 am and 2 starting between 2–3 pm). This yielded a total of over 750 observation hours.

A standard scan sampling methodology was used to record the behavior of all visible females in the group every 10 min. These data were used to determine the percentage of time spent feeding and foraging in fruit trees. During follows, all intergroup encounters were noted and ad libitum data were taken on the interactions. Encounters occurred when two social groups came into visual contact. Following Perry (1996) an individual was considered a participant if she/he remained in visual contact with members of the opposing group after the initial contact, and made vocal, facial, or physical threats. These included alarm calls and vocal threats (Perry, 1996), threat faces, grimaces and overlords (Oppenheimer, 1968; Perry, 1996), and branch breaking, chases and physical contact. Interactions comprised solely of vocal exchanges were not included, nor were interactions between social groups and extra-group males. Encounters were uniformly agonistic, but varied in intensity. An encounter was categorized as low intensity if it only involved avoidance or vocal, facial or physical threats, and as high intensity if it escalated to chasing and/or physical contact. For each IGA, I recorded the sexes of the participants and towards whom their aggression was directed. It was also noted if either group had been feeding at the start of the interaction. In some instances, this could be determined because the groups were the subject of simultaneous behavioral observations. For the remaining interactions, as soon as the observer became aware of the presence of a second group, an attempt was made to determine if that group was feeding. The presence of large fruiting trees was also noted, and in these analyses, to be conservative, this was considered evidence of feeding for non-focal groups.

A total of 23 IGIs were observed in the course of the study. Due to the relatively small sample size, data for all groups were combined to yield a monthly IGI rate (IGIs observed per observation hour) for all correlation analyses. For logistic regressions, monthly data for each group were considered separately.

The dates when newborns were first observed were recorded during group follows. Dates of birth were then used to calculate dates of conception, assuming a gestation period of 165 days (Hartwig, 1996). Two of the 21 infants born in the course of this study were conceived before systematic data collection started and, therefore, I excluded them from the analyses.

The white-faced capuchins in this study demonstrated strong reproductive seasonality. Births occurred between March and July with over half (12/21) taking place in a two-month period (June–July). The conception peak for this population occurred in December and January.

Phenology

To assess food abundance and distribution, I walked phenology trails (1 km in each group's home range) twice a month. I collected data on the species, number of fruits (1, 2-10, 11-100, 101-1000, 1001-10001), state (ripe, unripe, aborted) and location of all fallen fruit within 0.5 m of either side of the trail. I assessed ripeness based on color and firmness. A fruit patch was defined as 'capuchin food' if it was a species and state which the capuchins had been observed to consume on BCI (Oppenheimer, 1968; Mitchell, 1989; Crofoot, unpubl. data). Using only data on 'capuchin foods', I calculated the number of fruits per trail by multiplying the number of patches recorded in each size category by the median value for that category (i.e., 55.5 for the 11-100 size category). To produce a monthly measure of island-wide food availability, I took the average of the number of fruits recorded on all 6 km of the phenology trail each month. Monthly patch size values were calculated by dividing the number of capuchin fruits by the number of patches recorded for the trail. Additionally, I calculated a group-specific measure of monthly food availability based on the portion of the phenology trail in each group's home range (1 km per group). A month was classified as having high food availability if the average number of fruits was greater than the median value for that home range across the study.

Space use

The location data used to calculate home ranges for each group were collected using an Automated Radio Telemetry System (ARTS, additional information available online at <http://www.princeton.edu/~wikelski/research/>; for a technical description, see Cochran & Lord, 1963; Larkin et al., 1996). ARTS is a multi-user infrastructure which continuously and simultaneously monitors the location of multiple radio-collared animals. For this study, two individuals in each social group were radio-collared and their locations were recorded every 10 min for a period of 2–6 months (4 groups were monitored for 6 months, 2 groups were monitored for 2 months, see Table 1 for sample

sizes). Calculations of home range overlap were based on data from the four groups that had the most complete location data sets. Home ranges and home range overlaps were calculated using a fixed kernel estimator implemented in the BIOTAS software package (Ecological Software Solutions, Hegymagas, Hungary).

Hypotheses were tested with non-parametric statistics ($\alpha = 0.05$) implemented in SPSS version 14.0 (SPSS, Chicago, IL, USA). To further explore hypothesis 7, I used a logistic regression with Generalized Estimating Equations (GEE, Diggle et al., 2002) which control for repeated observations of the same groups (SAS Institute, Cary, NC, USA).

Results

Prediction 1: The home ranges of adjacent social groups overlap

The average home range size in this population was 116 ha (95% fixed kernel, $N = 4$, range 91–161 ha, see Figure 1). Neighboring social groups had an average dyadic home range overlap of 20% (range 3.0–52.2%). Total overlap was only known for BLT, the most centrally located group. This group shared 89% of its home range with at least one other social group.

Prediction 2: Neighboring social groups interact regularly

Agonistic intergroup encounters occurred at an average rate of 0.027 IGA/observation h (range 0–0.078 IGA/observation h), which translates into an average of 0.33 interactions per 12-h day (range 0–0.94).

Prediction 3: Females participate in IGA

Adult females were involved in 25% (5/20) of the agonistic intergroup encounters where the sex of all participants could be determined. In two of these cases, they remained at the site of interaction and vocalized. It was not clear whether this behavior was directed at the males or the females from the opposing group. In the remaining three interactions, the females (including, in one instance, a female with a young infant) chased members of the opposing group, in addition to performing vocal and physical threats. In one case, female aggression was directed at juveniles, in another at adult males, and in the final, at adults of both sexes.

Prediction 4: IGA occurs at fruit trees more often than expected by chance

IGA interactions started at feeding trees in 5 of 23 instances (22%), which is no more than would be expected by chance, given that this population spent on average 25.3% of their time feeding or foraging in fruit trees (binomial test: $p = 0.46$).

Prediction 5, 6, and 7: IGA rate should be positively correlated with patch size and negatively correlated with food availability if short-term BGC is important, and positively correlated with food availability if long-term BGC is important

Monthly IGA rate was positively correlated with the average size of food patches (one-tailed Spearman's rank, $r_s = 0.76$, $p < 0.01$, $N = 10$ months, see Figure 2). Consistent with the predictions for long-term, but not short-term BGC, food availability was positively related to IGA rate (one-tailed Spearman's rank, $r_s = 0.71$, $p = 0.01$, $n = 10$ months, see Figure 3). Food availability and average patch size were significantly related to one

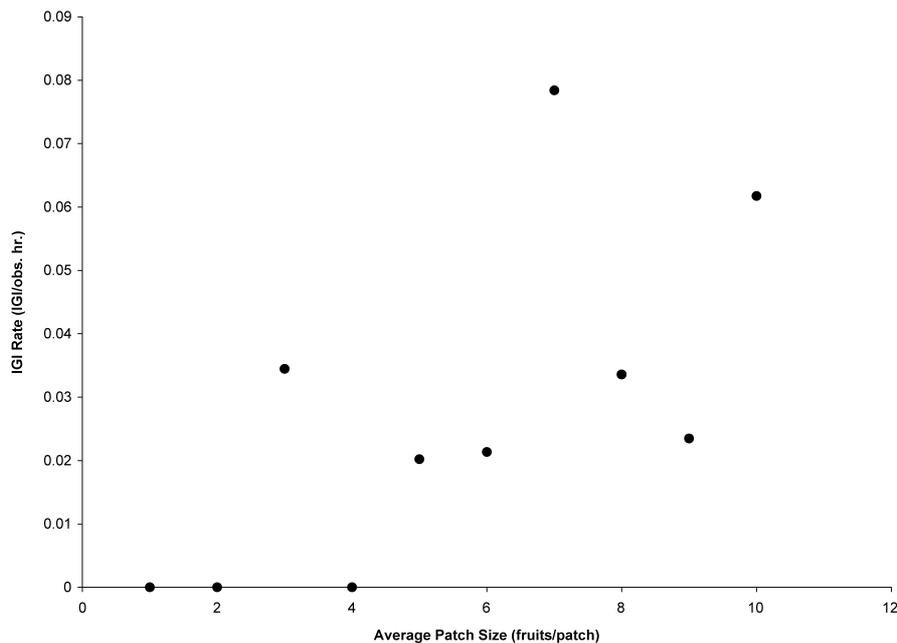


Figure 2. The relationship between monthly intergroup interaction rate and average monthly patch size (Spearman's rank test: one-tailed, $r_s = 0.76$, $p < 0.01$).

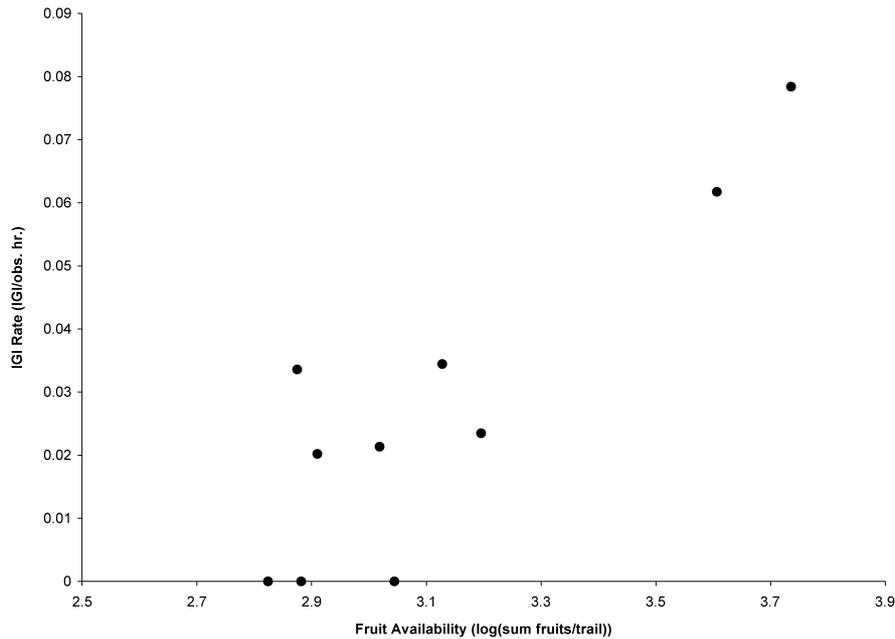


Figure 3. The relationship between monthly intergroup interaction rate and food availability (Spearman's rank test: one-tailed, $r_s = 0.71$, $p = 0.01$).

another (two-tailed Spearman's rank, $r_s = 0.83$, $p < 0.01$), but due to the small sample size and non-normal distribution of the data, I was not able to determine the independent effect of either variable on IGA rate.

IGA rate and range-specific food availability varied among groups. Therefore, I used a logistic regression with repeated measures to test the hypothesis that groups were more likely to participate in at least one IGA in months when the food availability in their home range was high (greater than the median availability for their home range across the course of the study). The odds of an IGA occurring were 241% greater during high fruit months than during low food months (odds ratio: 3.41, $\chi_1^2 = 4.92$, $p = 0.026$).

Prediction 8 and 9: Males are the primary participants in IGA, and they direct aggression at the females in their group

Males participated in all instances of IGA (23/23), and were the sole participants in 15 of the 20 encounters where the sex of all individuals could be determined. However, males were never seen attacking or chasing the females in their group.

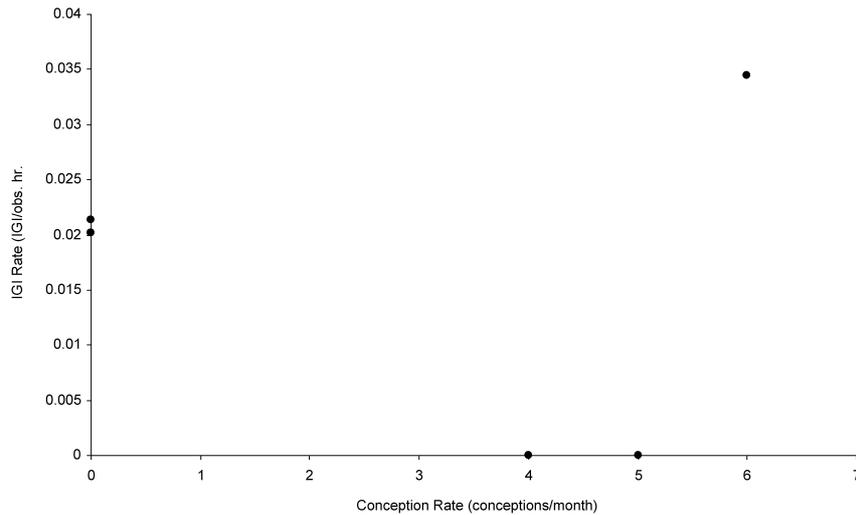


Figure 4. The relationship between monthly intergroup interaction rate and conception rate (Spearman's rank test: one-tailed, $r_s = 0.00$, $p = 0.50$).

Prediction 10: IGA rate is positively correlated with conception rate

The conception peak in this population occurred in December and January, which corresponds to the end of the wet season and the beginning of the dry season. IGA rate was not correlated with conception rate (one-tailed, $r_s = 0.00$, $p = 0.50$, $N = 6$ months, see Figure 4).

Prediction 11: Intergroup encounters do not involve risky behaviors such as chasing and physical aggression

All intergroup interactions were agonistic, but the intensity of that agonism varied considerably. They ranged from avoidance to vocal and visual threats and branch crashing to chases with or without physical contact. Low intensity interactions, where agonism did not escalate beyond avoidance or threats and displays, comprised 41% of IGA (avoidance 9%, threats/displays 32%). The remaining IGA were high intensity, meaning that at least two individuals were involved in chases (46%) or chases with physical contact (13%). Wounding attributable to IGA was observed in only one case: following an intense and fast moving interaction, an adult male in one of the study groups was bleeding from puncture wounds on the right side of his face which were consistent with bite wounds. Although I did not see this injury occur, the

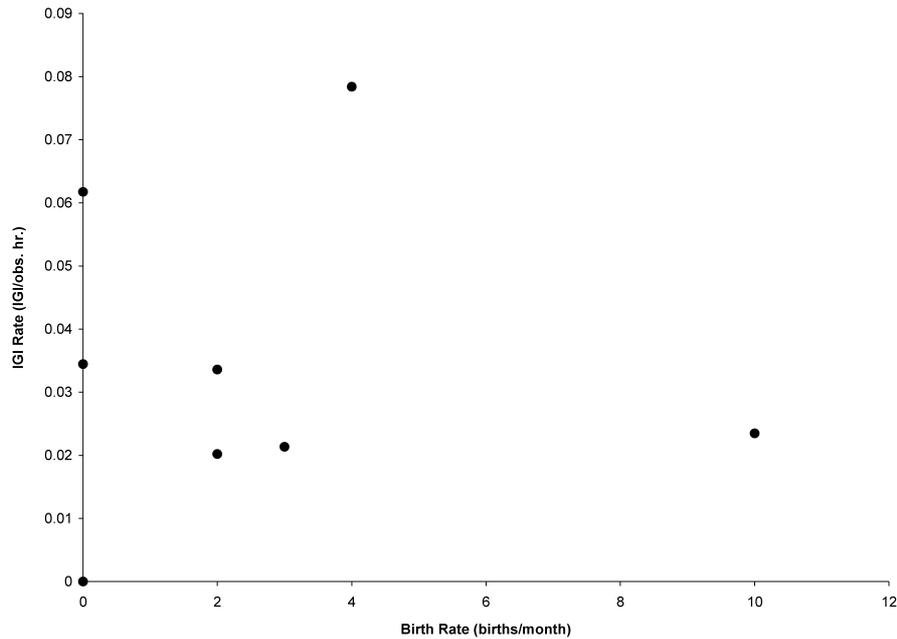


Figure 5. The relationship between monthly intergroup interaction rate and birth rate (Spearman's rank test: one-tailed, $r_s = 0.37$, $p = 0.29$).

male had not been bleeding before the interaction and I first noticed the injury as he returned to his group after chasing off the males from the opposing group.

Prediction 12: IGA rate is negatively correlated with birth rate

Births were distinctly seasonal with over half (12/21) occurring in June and July, 2005. IGA rate was not correlated with birth rate (one-tailed, $r_s = 0.37$, $p = 0.29$, $N = 10$ months, see Figure 5).

Discussion

Primate intergroup relationships have been understudied, and remain poorly understood. A number of recent studies have moved beyond the paradigm of attributing intergroup agonism to either mating or feeding competition based on the sex of the participants, and begun to explore the complexities of intergroup relationships (Saito et al., 1998; Koenig, 2000; Fashing, 2001;

Table 2. IGA dates and participating groups. ‘Focal’ was the group under observation at the time of the interaction. Winners (if known) are denoted with an asterisk.

IGI	Date	Focal	Opponent
1	1/10/2005	BL12*	UNID
2	1/16/2005	Top*	UNID
3	1/22/2005	Top	BL12*
4	3/3/2005	FC	BLT*
5	3/12/2005	Top*	UNID
6	4/6/2005	FC	BLT
7	4/27/2005	BL12	UNID*
8	5/9/2005	BLT*	FC
9	5/12/2005	BLT	FC*
10	5/13/2005	TB*	FC
11	5/14/2005	Conrad	UNID*
12	5/15/2005	Top*	Conrad
13	5/21/2005	Conrad*	UNID
14	6/5/2005	Top*	BL12
15	6/7/2005	BLT	BL12
16	6/8/2005	BL12	BLT
17	7/7/2005	FC	UNID*
18	7/8/2005	TB	UNID
19	8/3/2005	TB	UNID*
20	8/7/2005	Top*	UNID
21	8/12/2005	TB*	BLT
22	8/13/2005	Conrad	UNID
23	8/17/2005	FC	UNID*

Cooper et al., 2004; Sicotte & Macintosh, 2004; Bayart & Simmen, 2005; Korstjens et al., 2005; Harris, 2006a). Several of these studies suggest that male resource defense may be more common than previously recognized (Fashing, 2001; Harris, 2006a). They demonstrate the importance of considering the role of feeding competition in shaping intergroup relationships, even in species where males are the primary participants in IGA. This study tests predictions about the context of IGA in *C. capucinus* to elucidate the role of mating competition and feeding competition. Previous studies indicate that male mating competition drives intergroup interactions in white-faced capuchins (Fedigan, 1993; Rose, 1994; Rose & Fedigan, 1995; Perry, 1996), but the role of BGC has not been investigated.

Consistent with previous studies of intergroup interactions in *C. capucinus*, this study found sex-biased participation in IGA, suggesting that mat-

ing competition may be important in this population. As has been found at other study sites, short-term reproductive strategies do not seem to drive IGA. Males do not direct aggression towards the females in their group during IGA, indicating that extra-group copulations are not a major concern. In addition, there was not a relationship between IGA rate and conception rate. Long-term reproductive strategies, on the other hand, may help to explain patterns of IGA among BCI *C. capucinus*. High rates of male participation and a large percentage of interactions involving ritualized aggression in this study are consistent with the hypothesis that males use IGA to assess the strength and sex ratio of neighboring groups (Fedigan & Jack, 2004). However, I predicted that if males were pursuing this strategy, they should not risk injury during IGA. Although low intensity interactions involving ritualized threats and displays occurred in 32% of intergroup encounters, 59% of interactions involved chasing and/or physical contact. Therefore, while some of the interactions may have involved males 'checking out' neighboring groups, this probably does not explain more than half of all the intergroup encounters observed. Some of these high-intensity interactions may have been attempts to overthrow the resident males and take over the group. Given their frequency, however, and the fact that in some interactions, females from both groups participated, overthrow attempts probably do not account for all high-intensity interactions. The results of this study are consistent with previous investigations of intergroup competition in *C. capucinus*, and provide tentative support for the hypothesis that long-term male reproductive strategies shape patterns of IGA. However, some of interactions cannot be explained by mating competition, and may instead be related to feeding competition.

Social groups in this population have highly overlapping home ranges and regularly interact with one another. Although males are the primary participants in IGA, females participate in 25% of IGA, including some high intensity interactions where the risk of injury is non-trivial. The frequency of female participation cannot be directly compared to other studies because the definition of intergroup interactions used in this study did not include encounters between groups and extra-group males. However, female *C. capucinus* participate, at least occasionally, in IGA at all sites where they have been observed (Barro Colorado Island, Oppenheimer, 1968; Mitchell, 1989; Santa Rosa, Rose, 1994; Lomas Barbudal, Perry, 1996). In this study, females direct their aggression not only at adult males, as is predicted if they are attempting to prevent infanticide, but also at adult females and juveniles.

In one instance, an adult female with a clinging infant was observed participating in a high-intensity interaction, chasing and threatening adults of both sexes from the opposing group. This behavior is not consistent with an anti-infanticide strategy and, although the sample size in this study is small, these observations suggest that in some interactions, females are pursuing other interests. Their willingness to invest energy and risk injury suggests that the outcome of intergroup competition is important to their fitness. Females are expected to participate in IGA when doing so will increase their foraging success. However, in this study, IGA was not strongly tied to specific food sources: interactions did not occur at fruit trees more often than expected by chance. This pattern differs from many species where feeding competition is important and groups regularly displace one another from feeding trees (e.g., *Semnopithecus entellus*, Borries, 1993; *Lemur catta*, Jolly et al., 1993; *Cercopithecus mitis*, Cords, 2002). Capuchins use mental maps of their habitat (Janson, 1998) and, therefore, it is possible that groups tend to encounter one another and compete before they actually reach food sources. However, this hypothesis cannot be tested with the data currently available.

Despite the fact that white-faced capuchins do not gain immediate energetic benefits from most IGA, interaction frequency is related to the distribution and abundance of their food resources. In accordance with theoretical predictions (Wrangham, 1980; van Schaik, 1989), IGA rate is positively correlated with patch size. Interestingly, there is also a positive relationship between IGA rate and food availability. The odds of a group participating in IGA were 241% greater months with high food availability than in months with low food availability. This relationship does not support the prediction that groups compete when food resources are scarce (Isbell, 1991), but does match data from several other primate species (*Macaca silenus*, Kumar & Kurup, 1985; *Macaca mulatta*, Ciani, 1986; *Cercocebus galeritus galeritus*, Kinnaird, 1992; *Macaca fuscata*, Saito et al., 1998). One possible explanation for these findings is that long-term BGC is more important than short-term BGC in this population. Only a small percentage of interactions (5/23) occurred at fruit trees, indicating that while capuchins may, in some instances, gain immediate energetic benefits from IGA, in most cases (18/23) they do not. However, capuchin monkeys, like most other primate species, live in social groups where membership is relatively stable through time and home range location is more or less constant. This creates a social landscape consisting of a mosaic of home ranges in which every group has

a fixed set of neighbors. The consistency of these relationships should allow neighboring social groups to form stable relationships with one another, as is seen in a number of primate species (e.g., *Cebus olivaceus*, Robinson, 1988; *Macaca fuscata*, Saito et al., 1998; Sugiura et al., 2000; *Colobus guereza*, Harris, 2006b). If social dominance and/or 'ownership' of space are important contributors to a group's foraging success (Srikosamatara, 1987; Harris, 2006b) and lead to long-term imbalances in energy intake and reproductive rate among groups (Srikosamatara, 1987; Robinson, 1988), groups should invest in these relationships. Investment in intergroup dominance is expected during periods of high resource availability when individuals are in good physical condition and can most easily afford the energetic expenditure. The results of this study suggest that mating competition is not sufficient to fully explain patterns of IGA in *C. capucinus*, and are consistent with the hypothesis that long-term BGC may be important. However, they do not provide a rigorous test of this hypothesis. In this population, large social groups tend to beat small social groups (Crofoot et al., unpubl. results), but to fully test the importance of long-term BGC, systematic differences in caloric intake among large and small groups must be demonstrated.

Agonistic intergroup interactions in *C. capucinus* are highly variable in terms of which individuals participate, where interactions occur, how often they occur, and the intensity of the aggression. It is probable that IGA serves several functions, including both long-term feeding and long-term mating competition. Without data on demographic patterns, it is hard to make and test predictions about the male assessment hypothesis ('checking out' hypothesis *sensu* Fedigan & Jack, 2004). The results of this study provide support for the importance of male mating competition, but suggest that the role of male resource defense must be reconsidered. They also emphasize the importance of differentiating between long-term and short-term competitive strategies, and investigating both components of intergroup feeding and intergroup mating competition.

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