

1 **TITLE:** FOOD COMPETITION IN A SEMIFREE-RANGING *Cebus apella* GROUP

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1 **ABSTRACT**

2 The competitive regime faced by individuals is fundamental to modelling the evolution of
3 social organisation. In this paper, we assess the relative importance of contest and scramble
4 food competition on the social dynamics of a provisioned semifree-ranging *Cebus apella*
5 group (n= 18). Individuals competed directly for provisioned and clumped foods. Effects
6 of indirect competition were apparent with individuals foraging in different areas and with
7 increased group dispersion during periods of low food abundance. We suggest that both
8 forms of competition can act simultaneously and to some extent synergistically in their
9 influence on social dynamics; the combination of social and ecological opportunities for
10 competition and how those opportunities are exploited both influence the nature of the
11 relationships within social groups of primates as well as underlying the evolved social
12 structure.

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2 INTRODUCTION

3 The distinction between contest (or direct) and scramble (or indirect) competition is
4 fundamental to modeling the evolution of social organization (Isbell, 1991; van Hooff &
5 van Schaik, 1992; Sterck *et al.*, 1997; Isbell *et al.*, 1998; Isbell & Young, 2002; Boinski *et*
6 *al.*, 2000). In addition, ecological constraints are important factors shaping social
7 interactions. When food is found in clumped or usurpable patches, the benefits of contest
8 competition outweigh the costs of potential wounds or energy expenditure resulting from
9 aggressive interactions. In these cases, where direct competition prevails, the establishment
10 of linear dominance hierarchies is predicted, and coalitions are expected between group
11 members if foods can be shared among coalitionary partners (Sterck *et al.*, 1997; Boinski
12 *et al.*, 2000; Isbell & Young, 2002). When indirect competition prevails, as in the absence
13 of clumped resources, groups are thought to form more egalitarian or unstable hierarchical
14 relationships, and coalitions are thought to be rare or irrelevant to the dynamics of food
15 competition, although coalitions may form for reasons such as access to reproductive or
16 other socially valuable partners (Sterck *et al.*, 1997; Boinski *et al.*, 2000; Isbell & Young,
17 2002).

18 Analyses relating proximate ecological conditions to the nature of social groups,
19 and to social interactions and behavioral patterns within these groups contribute to
20 developing socio-ecological models. However, while behavior indicative of contest
21 competition is readily observable, e.g. overt aggressive conflicts associated with food and
22 those associated with hierarchical maintenance (Janson & van Schaik, 1988; Sterck *et al.*,
23 1997), the behavioral manifestations of scramble competition are harder to distinguish.
24 Suggestive short term indicators of scramble competition are: a) increases in home-range
25 and/or day-range size (e.g. larger groups needing larger home ranges, or increases in day

1 ranges during periods of food scarcity (Isbell *et al.*, 1998) and b) decreased cohesiveness
2 among individuals in groups facing heightened competition (White & Chapman, 1994) or
3 during periods of food scarcity (Dunbar, 1988). Lower fertility in larger groups (Oates,
4 1987) may be regarded as a longer term consequence of scramble competition, although
5 not a behavioral one.

6 In wild capuchin monkeys (genus *Cebus*), both contest and scramble competition
7 occur. For *Cebus capucinus*, aggression was less frequent when individuals foraged in
8 dispersed patches than when foraging in clumped food resources (Phillips, 1995a, b; see
9 also Vogel & Janson, 2007). In *C. apella*, overt contests over clumped feeding sites
10 resulted in the establishment of a linear hierarchy, such that dominant individuals had a
11 four-fold increase in food intake over that of subordinate members when foraging in
12 preferred fruit trees. As a result, dominants had a significantly greater total energy intake,
13 particularly during the dry season (Janson, 1985).

14 Scramble competition in *Cebus* groups is indicated by a decrease in time devoted to
15 social activities in groups inhabiting poorer habitats relative to those inhabiting richer
16 habitats (Rose, 1994). In periods of low food abundance diets shift to lower quality but
17 more abundant resources; groups minimize the risks of starvation in periods of low food
18 abundance by having a larger home range and using it as a function of the abundance of
19 fruit trees in different periods (Robinson, 1986; Galetti & Pedroni, 1994). In *C. olivaceous*
20 and *C. apella*, individuals in larger groups spend more time foraging, have a longer daily
21 travel distance and a tendency to spend more time in both grooming and aggression (de
22 Ruiter, 1986; Janson, 1988; Izar, 2004).

23 The combined importance of contest and scramble competition in the social
24 dynamics of capuchins is suggested by the relationship between rank and the positioning of
25 the individuals during their daily activities. Non-random positioning typifies capuchin

1 groups (Robinson, 1981; Janson, 1990a, b; Hall & Fedigan, 1997) and influences the
2 foraging success of individuals: the best foraging positions (front-center) are occupied by
3 the alpha male and female, higher predation risk positions (periphery) are occupied by
4 subordinate adults and safer positions (center) by juveniles. It remains unclear whether
5 these positions are the outcome of receiving aggression (Janson, 1990b), of the active
6 avoidance of dominants (Hall & Fedigan, 1997), of the alpha's tolerance of immatures
7 (Robinson, 1981), or of an interaction with opportunities for contest as noted by Vogel &
8 Janson (2007). The relations between food competition and positioning patterns are not yet
9 clear and these vary by species and ecological characteristics of the study area.

10 Boinski *et al.* (2000) argued against the use of results collected from populations
11 under conditions of “natural experiments” to evaluate socio-ecological models because
12 many atypical factors influence the social dynamics of such groups. Notwithstanding this
13 caveat, for both natural and “behaviorally altered or disturbed” groups (provisioned or
14 semifree-ranging), a major issue is not the atypical influences on behavior but rather a
15 consistent difficulty in defining the social consequences of either type of competitive
16 regime.

17 We aim to explore the influence of provisioning, if any, on the competitive regimes
18 exhibited within a semifree-ranging brown capuchin (*Cebus apella*) group. Specifically,
19 we aim to assess whether provisioning buffers individuals against energy shortfalls, such
20 that manifestations of feeding competition are rare, or whether provisioning enhances
21 opportunities for competition. Thus, we emphasize the importance of all agonistic
22 interactions as mechanisms to both gain access to resources and to structure hierarchies
23 and underlie competitive success.

24 Two predictions are tested:

- 1 1. If individuals contest over food items which may be both monopolizable and
2 preferred, then aggressive behaviours will increase with the use of clumped
3 provisioned resources. As the provisioning is distributed during the midday period,
4 we would expect an increase in aggressive events during this relative to other
5 period of the day.
- 6 2. If scramble competition occurs, then the extent of the area used by individuals and
7 group cohesiveness will vary between periods of high and low natural food
8 abundance (i.e from wet to dry seasons), irrespective of provisioning.

9 Aspects of contest and scramble competition are distinguished using seasonal variation
10 in activities and in overall agonistic interactions, location within the habitat (ranging) and
11 cohesiveness among group members. Variation in daily patterns of interaction (e.g. that
12 associated with provisioning) and between seasons are controlled for in the analyses. In
13 addition, if these aspects of competition are general across group members, we expect to
14 find similarities across the age-sex classes. These behavioral predictions are expected to
15 produce a pattern of non-random spatial structure (e.g. Janson, 1990 a, b), which can act as
16 the basis for variance in social organization with ultimate consequences for the evolution
17 of social systems (Sterck *et al.*, 1997).

18 19 **METHODS**

20 **Study Group and Study Site**

21 The study group consisted of 20 individuals (3 adult males, 4 adult females, 2 subadult
22 males, 6 juvenile males, 3 juvenile females and 2 infants). There was one clear alpha male,
23 an alpha female and an age-size based hierarchy for the rest of the group (Ferreira, 2003;
24 Izar *et al.*, 2006).

1 The study group was semifree-ranging in what was effectively an island of
2 reforested area of 18ha within the Tietê Ecological Park (total area of 1400 ha in eastern
3 São Paulo State, Brazil). Despite the absence of large predators of *Cebus* (eagles, cats or
4 boa constrictors; Izar, 1994) in this area, dispersal was difficult due to extremely low food
5 abundance in the surrounding area. The group was provisioned daily with five maize cobs,
6 36 bananas, 2 papayas, 10 apples and 8 oranges (approx 5300 kcals total; USDA National
7 nutrient database: www.nal.usda.gov/fnic/foodcomp), and provisioned food was
8 distributed at midday on a circular platform of one-meter diameter. Provisioned foods were
9 of high quality, large (half banana, half apple, half maize cob, half orange, 1/6 papaya),
10 readily monopolizable, but estimated to be sufficient to meet only approximately half of
11 average daily energy requirements of the animals (using total mean body mass and
12 equations for calculating ADMR; e.g. Ulijaszek & Strickland, 1993); as a result the
13 monkeys also foraged for natural foods.

14 Two distinct seasons were defined: one wet and warmer (October to March, mean
15 monthly rainfall of 178 mm; average temperature 19-24°C) and one dry and cooler (April
16 to September, mean monthly rainfall of 69 mm, average temperature 15-17°C). Day length
17 ranges from a maximum of 13 hours (5:30 am to 6:30 pm) in the wet-warm season to 11
18 hours (6:30 am to 5:30 pm) in the dry-cool season.

19

20 **Data Collection**

21 From October 1999 to June 2001, the group was accompanied by an observer (RGF) for
22 867 hours. The data used here derive solely from the period after full habituation of the
23 animals, from Jan 2000 to Jun 2001, but includes a 20-day period of social instability
24 caused by the death of the group's original alpha female. There was a total of 492 hours of
25 contact over two dry and two wet seasons, during which data on events of aggression,

1 coalitions and grooming were collected on an all-occurrences continuous record basis.
2 These data consisted of initiator, recipient, actions and reactions and assumed that there
3 were no systematic biases due to differential visibility. Focal animal data totaling 304
4 hours was collected on individuals observed for a period of 10 minutes, five times each
5 month using a random order of observation of different individuals each day. During each
6 focal scan sample the activity, the identity of their nearest neighbor, and animals spatial
7 position relative to other group members (central, peripheral, front, rear) for all behavioral
8 categories were recorded every minute, while location within the reserve was recorded
9 only once within the observation period (see below).

10 Behaviour recorded on each minute of the focal sample ('scans') was classified into
11 six mutually exclusive activity categories; 1) Foraging: visually searching, procuring,
12 manipulating (including tool use) and ingesting foods. 2) Rest. 3) Locomotion (movement
13 in any direction). 4) Groom (groom other or be groomed). 5) Agonistic interactions which
14 included: a) high intensity aggression (chases, pushes and bites), b) avoidance behaviour
15 (retreats, flees), c) threats and d) signals of submission. 6) Social play. Other activities such
16 as scratching and interacting with other species were excluded from consideration here as
17 they represented only 1.6% and 1.1% of all focal observations respectively. Such activities
18 tended to occur as rapid events within behavioural states. During focal samples,
19 participants, direction and outcome of interactions were also recorded on a continuous
20 basis. Although activities were sampled on a minute by minute basis from individuals,
21 location data at longer intervals were used to determine how the group used the space
22 within the study area.

23 The study site (18 ha) was divided in sub-areas based on special features of the
24 environment (e.g. buildings, large trees, and lakes). The sub-area where the focal animal
25 was observed for *at least* 5 min was assigned as one home range point for that sample.

1 Point samples were taken to represent group location since samples with no other
2 individual within a 10m radius of the focal for more than 5 min were excluded.

3 The number of location samples was compared among three areas of the range
4 which differed in mechanisms of food acquisition:

5 1. Area 1 which included a veterinary clinic, the kitchen or food preparation area, and
6 an area of approximately 30 m to the right and back of the kitchen. This area was
7 poor in plant diversity with only a corridor of *Hibiscus sp* and some orange trees.

8 However, the animals frequently stole food from the kitchen and the trash bins
9 located around the buildings, offering limited opportunities for monopolization and
10 contest competition.

11 2. Area 2 had a variety of plant species including natural food trees, *Siagrus*
12 *romanzoffiana* and some *Nesperina sp*. This area contained one cage with
13 callitrichids (*Callithrix jacchus*) and one with a peccary (*Tayassu albirostris*), and
14 the capuchins constantly stole food from both cages. In addition and most
15 importantly, Area 2 had the platform where the daily food ration was distributed.
16 This area of provisioning and other species' food offered major opportunities for
17 monopolization and contest competition.

18 3. Area 3 was larger, with a greater natural plant density and abundance. Animals had
19 to actively search to obtain food, and opportunities for monopolization of discrete
20 food patches were infrequent.

21 The number of individuals in a radius of 10m of the focal subject, recorded every
22 minute in focal samples, was used as an indicator of cohesiveness. The number of scans
23 (point samples) where only the focal individual was present in a radius of 10m was
24 compared with the number with three or more individuals present within 10m. These
25 individual totals were summed across all focal samples, and no individual contributed

1 disproportionately to the overall totals. While successive records of nearest neighbors can
2 often be autocorrelated within the same focal-scan sample, the use of five bouts of 10
3 minutes scan samples per month diminishes the problem of time dependency on
4 cohesiveness values. Thus although hierarchical dominance and affiliative relationships
5 may influence proximity between individuals, this individually-derived measure of “many”
6 versus “few” neighbors was used to describe cohesiveness. Scans with only mother-infant
7 dyads present were excluded from analyses since these dyads could bias the analysis of
8 group cohesiveness.

9 *Figure 1 about here*

10 **Statistical Analyses**

11 Due to potential effects of energy buffering due to lactation, infants were excluded from all
12 analyses. The two subadult individuals were considered as adults in analyses. Comparisons
13 between ages and sexes were made within each season and limited to two categories: male
14 *versus* female and adult *versus* juvenile.

15 Food was distributed to the monkeys at around midday. Thus interactions and
16 activities would be expected to differ by time of day if there was contest competition over
17 provisioned items. In order to account for differences in the total number of focal samples
18 on each individual and in different periods of the day (two focals from 0600-1059, two
19 from 1100-1459 and one from 1500-1900 on each individual every month), data were
20 normalized according to the following formula:

$$21 \quad x' = \frac{\left(x_m \times \frac{F_a}{F_m}\right) + \left(x_{mi} \times \frac{F_a}{F_{mi}}\right) + x_a}{F_a \times 3}$$

22 where: x' is the proportion of behaviour x for one individual; x_m is the total of scans where
23 that individual performed behaviour x during the morning period; x_{mi} is the total of scans
24 where that individual performed behaviour x during the midday period; x_a is the total of

1 scans where that individual performed behaviour x during the afternoon period; F_m is the
2 total of scans on this individual during the morning period; F_{mi} is the total of scans on this
3 individual during the midday period and F_a is the total of scans on this individual during
4 the afternoon period. The formula was used because individuals had different numbers of
5 good observations within each month.

6 Age-sex and seasonal comparisons of activity budgets were made on individuals.

7 Data were tested for normality; when normal, parametric ANOVA (F) and t-student test

8 (T) were used. Otherwise, non-parametric Kruskal-Wallis (U) and Wilcoxon Matched

9 Pairs Signed Ranks (Z) were used for comparisons among states and between conditions.

10 Correlation (Spearman r_s) and Chi-square (χ^2) analyses were performed to explore

11 associations between activities, to compare frequencies of the use of areas, and to test

12 whether cohesiveness was greater during wet than during dry periods, respectively. As

13 with any behavioural study with limited numbers of individuals and observations, the

14 power of statistical tests will be low; however, we report effect sizes which at $p \leq 0.05$, two

15 tailed, are likely to be robust.

16

17 **RESULTS**

18 **Seasonal and diurnal variations in behaviors**

19 Foraging constituted the most frequent activity accounting for 55 to 60% of an individual's

20 time in both seasons (Wet: mean $53.9\% \pm 2.6$, Dry: $58.4\% \pm 2.2$; $N=18$; t-test $T = 1.9$, *NS*),

21 while grooming occupied only a minor fraction (Wet: Median = 0.6, inter-quartile range

22 IQR = 2.9; Dry: 1.1, IQR = 2.9, $N=18$, $Z = 0.7$, *NS*) of an individual's activity budget in

23 both seasons (Figure 2).

24 Average percentage of activity budget for the whole group during Wet and Dry

25 periods is shown in Figure 1. Statistically significant difference was found only in resting

1 behavior with individuals resting more in Wet than in Dry periods ($T_p = 3.9$, $p = 0.001$).
2 While instantaneous samples underestimate rare or brief events such as aggression
3 (Dunbar, 1976), analyses of all occurrences of agonistic behaviors per hour of observation
4 confirm the suggestion that seasonal fluctuations in wild food abundance were unrelated to
5 average agonistic interaction rates (wet: 1.07, dry: 1.08). In addition, the lack of a seasonal
6 trend for changes in time spent foraging suggests that provisioning eliminated many
7 potential seasonal effects on rates of energy acquisition.

8 *Figure 2 about here*

9 In both seasons, individuals started the day foraging with little time spent in social
10 activities (Figure 2). During the period when food was distributed, there was a significant
11 decrease in time spent foraging and significant increases in resting (Table 1). In the Dry
12 season, when natural food availability was lower, grooming and agonistic interactions also
13 significantly increased during the midday period relative to the morning and afternoon
14 periods (Table 1).

15 *Table 1 about here*

16

17 While trade-offs among the time spent in different activities are expected, there was
18 a positive relationship between time spent in foraging and agonistic interactions, and a
19 negative one for foraging and all affiliative (grooming + social play) interactions. This
20 relationship was especially marked during Dry periods (Forage and Agonistic: dry, $r_s =$
21 0.55 , $p < 0.05$; Forage and Affiliative: dry, $r_s = -0.83$, $p < 0.01$; Forage and Affiliative: wet,
22 $r_s = -0.62$, $p < 0.05$, $N = 18$).

23

24 **Age-Sex Differences in Activities**

1 Adult males and females did not differ in the percentage of time spent foraging, in
2 locomotion or resting in either season. Adults, especially males, foraged significantly less
3 but moved and rested significantly more than did juveniles in both seasons (Forage wet:
4 $F_{2,18} = -2.5$, $p < 0.01$, Forage dry: $F_{2,18} = -3.1$, $p < 0.05$; Locomote wet: $F_{2,18} = 3.3$, $p < 0.01$;
5 Locomote dry: $F_{2,18} = 3.1$, $p < 0.01$; Rest wet: $F_{2,18} = 4.1$, $p < 0.01$; Rest dry: $F_{2,18} = 4.3$,
6 $p < 0.01$). Adult females were more involved in grooming interactions than were males and
7 juveniles (significant only for Dry periods; $U = 12.6$, $p < 0.01$) while juveniles played
8 significantly more than adults did in both seasons (Dry: $U = 11.3$, $p < 0.01$; Wet $U = 13.9$, p
9 < 0.01). No age or sex differences were found in the time spent in agonistic interactions.

10

11 **Rank Differences in Activities**

12 During the dry period, a significant negative correlation was found between individual
13 dominance rank and time spent foraging ($r_{s18} = -0.54$, $N = 18$, $p < 0.05$, partial correlation
14 controlling for the effects of age) and between rank and locomotion ($r_{s18} = 0.74$, $N = 18$,
15 $p < 0.01$, partial correlation controlling for the effects of age) with dominant individuals
16 spending more time foraging and less time in locomotion than did subordinates (note that
17 hierarchy is numbered with higher ranking individuals having smaller numbers. Therefore,
18 negative correlations means higher ranking doing more, and positive correlations mean
19 higher ranking doing less). Other correlations between rank and behavior during the dry
20 period and all correlations during the wet period were not significant.

21

22 **Use of Space**

23 The group made intensive use of the area with the most natural vegetation: $\chi^2_{dry} = 97.013$,
24 $df = 2$, $p < 0.001$, $\chi^2_{wet} = 20.64$, $df = 2$, $p < 0.01$ (expected values based on approximate
25 proportional size of each area: 1 = 1/18; 2 = 2/18 and 3 = 15/18 – table 2). During dry

1 periods of low natural food abundance, group members tended to spend more time in Area
2 1 (where food could be stolen), while in wet periods of higher abundance they used Area 3
3 most ($\chi^2 = 6.2$, $df=2$ $p = 0.045$). Group cohesion also varied seasonally. Proximity between
4 group members decreased during drier periods and thus the group became less cohesive (χ^2
5 = 11.5, $df=1$, $p<0.01$, Figure 3).

6

7 *Table 2 and Figure 3 about here*

8

9 **DISCUSSION**

10 **General Activity Budgets**

11 In spite of provisioning, the unconfined use of an 18ha area resulted in an activity budget
12 very similar to that of wild groups of *Cebus* (Robinson, 1981; Rose, 1994) with a mean of
13 c. 50% forage, 15% locomotion, 15% rest, and less than 2% for grooming, social play and
14 agonistic interactions. Individuals started the day foraging for natural foods and finished
15 the day foraging and playing. During the midday period of food distribution, agonistic and
16 grooming interactions peaked, but only during the dry season.

17 This midday increase in agonistic interactions and grooming could have two
18 explanations. Izawa (1980) described grooming among a wild provisioned group of *C.*
19 *apella* as an activity occurring predominantly during resting periods. Thus it is possible
20 that after eating, relaxed and satiated individuals engage in grooming before resting. A
21 second possibility is that grooming was used to reduce tension among group members.
22 Janson (1985; 1988) and di Bitetti (1997) observed that most grooming interactions in wild
23 *C. apella* groups occurred during visits to larger fig fruit trees, and suggest that grooming
24 serves as a mechanism to reduce aggression (e.g. Keverne *et al.*, 1989) while feeding in

1 close proximity on a valued and clumped resource (Fruth & Hohmann, 2002).
2 Furthermore, Phillips (1995b) describes increases in rates of aggression and of affiliative
3 behavior between *C. capucinus* individuals during the use of clumped resources. Grooming
4 during such times is suggested as being used to reduce tension and to facilitate coalitionary
5 behavior between dyads in order to defend a feeding patch.

6

7 **Effects of Provisioning**

8 While Boinski *et al.*'s (2000) caveat about exploring functions of behavior in non-natural
9 groups needs consideration, the development and refinement of socio-ecological models
10 have been achieved in part as a result of studies conducted under such conditions (e.g. de
11 Waal & Luttrell, 1986; Chapais, 1992, 1995). Moreover, many influential contributions to
12 the understanding of the dynamics of coalitionary and grooming behaviors come from
13 studies conducted on captive or semi-captive groups (e.g. de Waal, 1982; de Waal &
14 Harcourt, 1992).

15 For the study group, provisioning probably accounted for the lack of seasonal
16 differences in activity budgets of adults and relatively constant rates of agonistic
17 interaction, although Ferreira *et al.* (2006) found that coalitions were more frequent during
18 feeding contexts than during other activities. Provisioning was insufficient to meet the
19 metabolic needs of all individuals in the group, but could be monopolised. As a result,
20 there was an association between dominance rank and time spent foraging and in
21 locomotion specifically during the dry season High ranking individuals were able to meet
22 their daily metabolic requirements more easily, spending less time foraging and with a
23 reduced need to travel through the area. Seasonality also affected the use of space and
24 group cohesion. Daily opportunities for direct contest competition for preferred foods

1 were induced via the clumped nature of the provisioning while scramble competition could
2 be inferred from changes in cohesiveness and use of different foraging areas during periods
3 of lower natural food abundance, rather than through consistent differences in the
4 allocation of time to different activities.

5

6 **Characteristics of competition**

7 Analyses show that both of our predictions were confirmed, and three characteristics of
8 competition for resources (regarding direct competition, use of space and cohesiveness)
9 can be proposed. Firstly, the individuals in this group actively competed for clumped
10 (provisioned) resources. During food distribution, rates of aggressive behavior peaked (e.g.
11 Figure 2), and this was especially marked during the dry season when natural foods were
12 limited in availability. Increased rates of aggression during the use of preferred food
13 sources have consistently been found for other *Cebus* groups (Janson, 1985; O'Brien,
14 1991; Izar, 1994, 2004; Rose, 1994; Perry, 1997). The mean rate of 0.9 agonistic events/hr
15 observed here was higher than in other studies of *C. apella* (Izar, 1994; Janson, 1985), and
16 of *C. capucinus* groups where rates of aggression vary between 0.86 - 0.72 events/hr
17 (Phillips, 1995b).

18 A second characteristic of competition was the differential use of space from wet to
19 dry periods. Fluctuations in the use of space suggest that seasonal variation in natural food
20 availability influenced the competitive regime within the group, forcing individuals to
21 adjust their foraging areas and thus altering their access to natural resources. We propose
22 that these changes in the ways in which individuals forage through space reflect the
23 outcome of scramble competition since no clumped wild foods that could be monopolized
24 were detected (Ferreira, 2003).

1 A third aspect of food competition relates to the decrease in cohesiveness seen
2 during periods of low food abundance, which we suggest acted to minimize both direct and
3 scramble competition while foraging for insects or other embedded resources. This
4 decrease in inter-individual proximity is again indicative of general spatial and behavioral
5 mechanisms to reduce competition among group members, irrespective of its predominant
6 mode.

7 Coalitionary behavior among female capuchins has been related to contest
8 competition (see Perry, 1997; Vogel *et al.*, 2007). Unrelated females in this group did not
9 form coalitions with each other or in support of offspring, and most of the coalitions
10 observed were adult males supporting immatures (Ferreira *et al.*, 2006). However, most
11 coalitions did occur during contests over food, with the alpha male as the intervener in rare
12 disputes among adult females (Ferreira *et al.*, 2006). The lack of coalitions among females
13 and of obvious nepotism is unlikely to be an artifact of the “experimental” conditions of
14 the study site, since direct contests for food did occur, and provisioning did indeed provide
15 opportunities for contests over resources as well as close proximity (e.g. Vogel & Janson,
16 2007). In addition, being low ranking in the group implied significant disadvantages to
17 individuals in terms of time spent foraging or locomotion during the dry period, but not for
18 other social behaviors, or for use of central and peripheral positions (Ferreira, 2003). While
19 we have not directly assessed caloric intake rates by rank (e.g. Vogel, 2005), a lack of
20 preponderant rank effects on activities again suggests that contest competition alone did
21 not underlie the organization of the group.

22 In conclusion, we suggest that provisioning enables the assessment of the relative
23 importance of modes of contest for social dynamics, and that the relative importance of
24 each form of competition will vary as a function of changing internal group dynamics and
25 variability in the nature and distribution of foods, whether natural or provisioned. Teasing

1 apart the combination of social and ecological opportunities for and constraints on modes
2 of competition contributes to an understanding of how competition influences relationships
3 within social groups of primates, and may contribute to refinement of socio-ecological
4 models.

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- 8

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1 **Figure legends:**

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3 **Figure 1.** General view of the study area

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5 **Figure 2:** Mean and SD activity budgets by time ad season. N= 18 individuals in each
6 seasonal (Dry or Wet) and Time period (am, midday, pm.) Significant comparisons shown
7 in table 1.

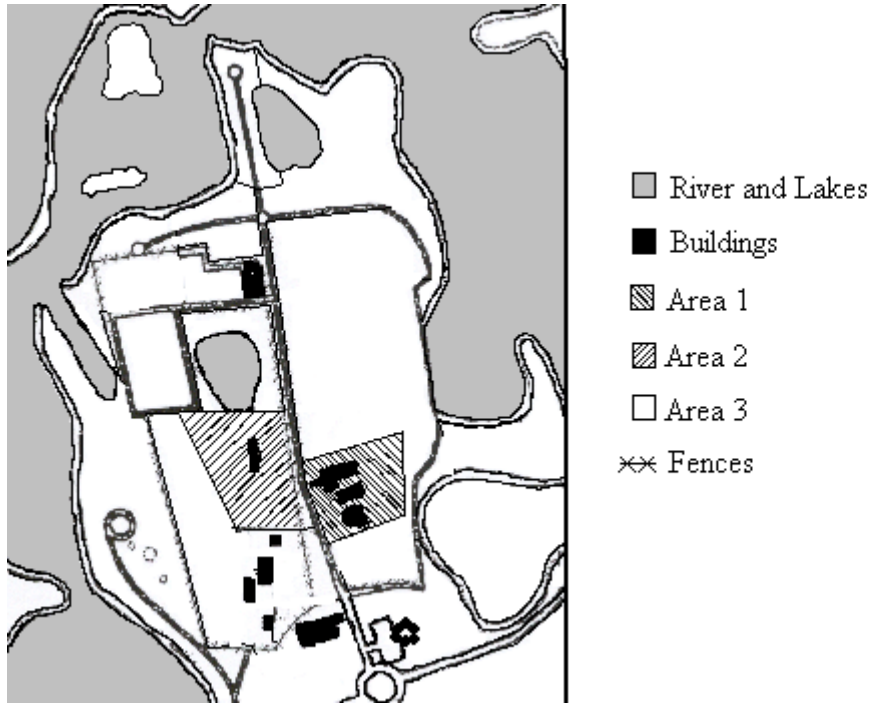
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9 **Figure 3:** Cohesiveness of the group measured as the mean percentage of samples with
10 either no neighbours or three or more neighbours within a 10m radius of the focal animals
11 (N = 18) by wet and dry season.

12

1 Figure 1

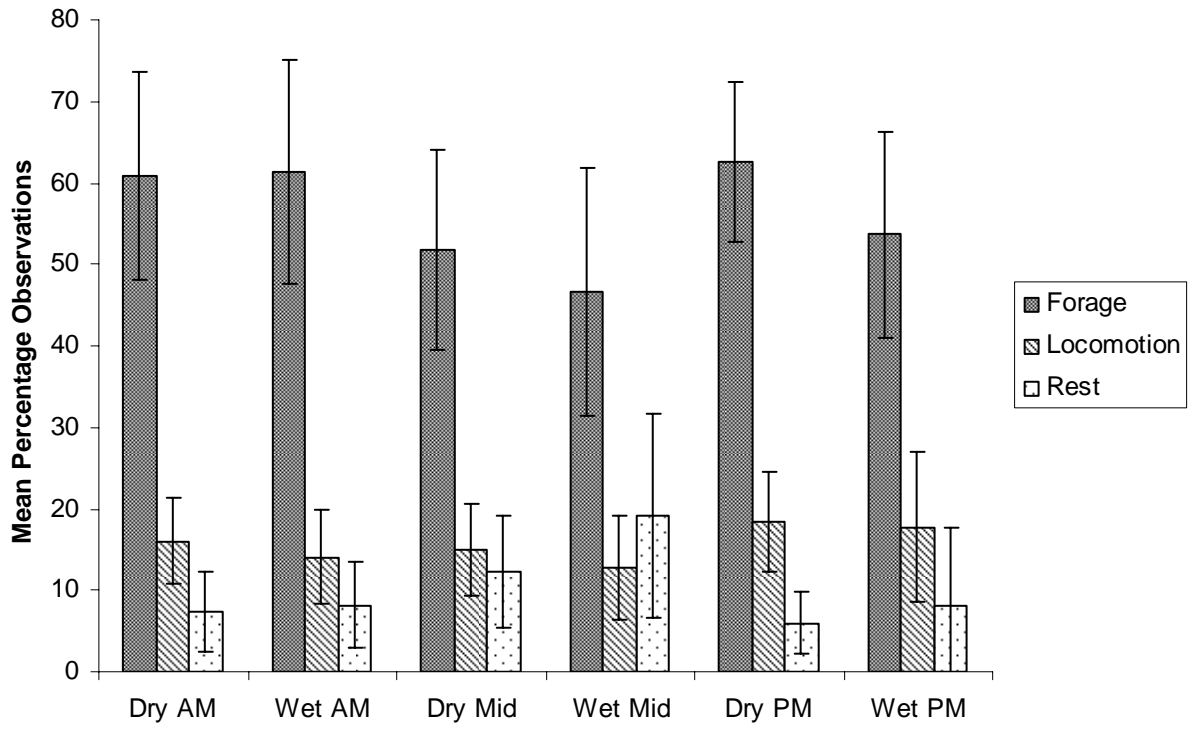
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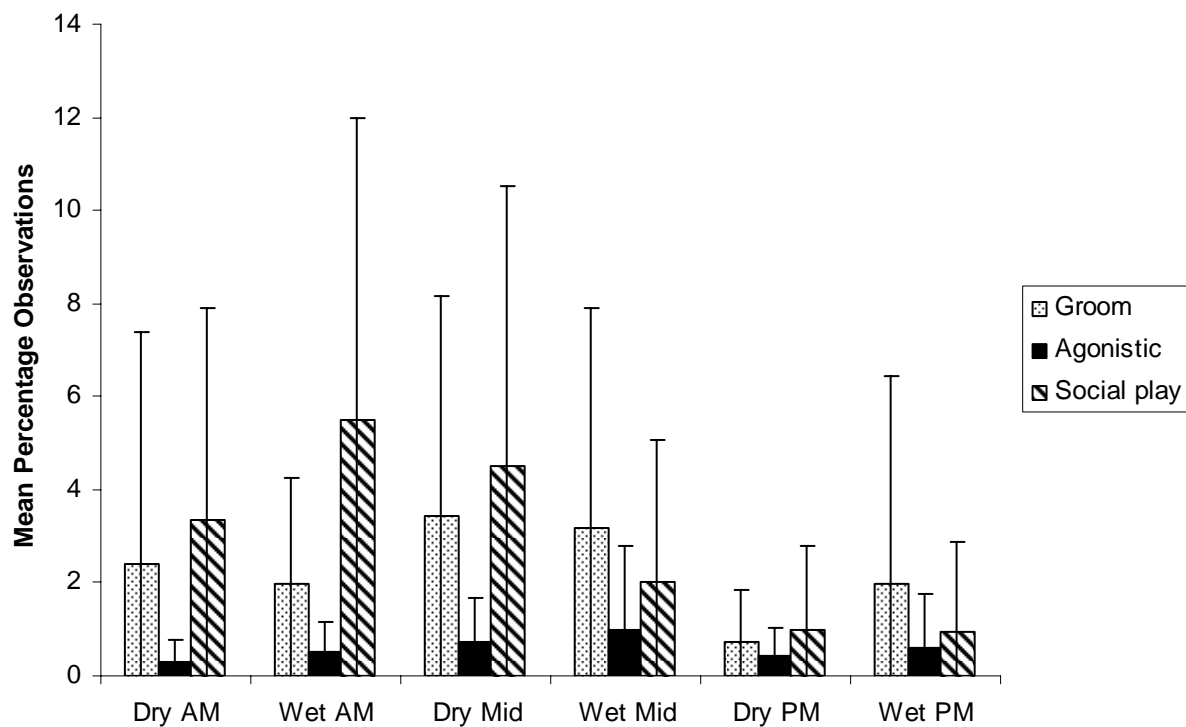
1 Figure 2a:

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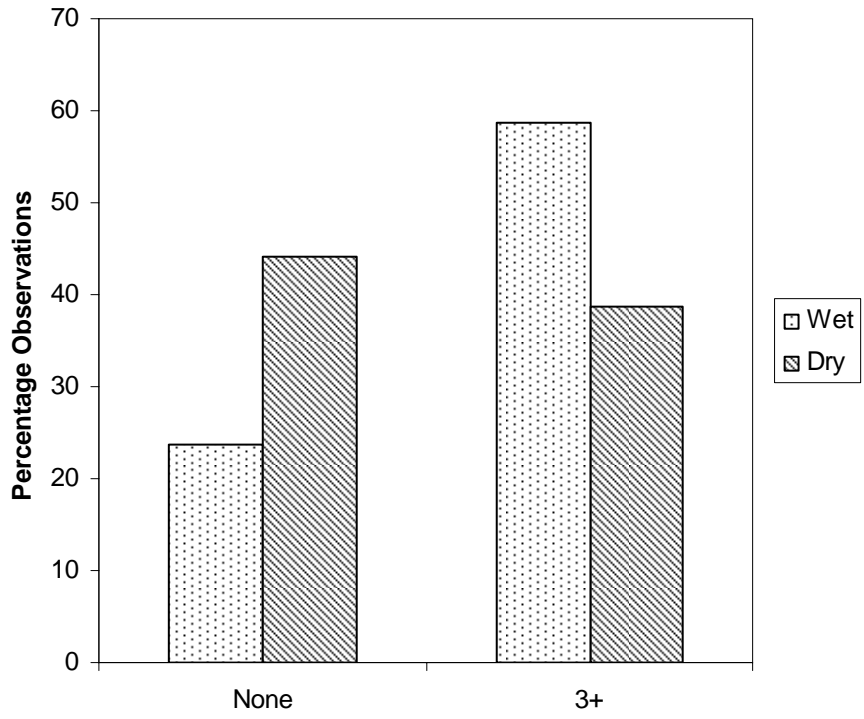
1 **Figure 2b**



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1 **Figure 3**

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1 **Table 1. Statistical comparison of time spent in different activities among the three time periods (Morning, Midday, Afternoon; all N**
 2 **= 52). Only significant comparisons are shown.**

	<i>Forage</i>	<i>Locomotion</i>	<i>Rest</i>	<i>Groom</i>	<i>Aggression</i>	<i>Social Play</i>
Wet	F=5.073 p < 0.01 (post-hoc: m ≠ mid)	F=2.199 p = 0.121	F=6.074 p < 0.001 (post-hoc: m ≠ mid; mid≠a)	χ=3.176 p = 0.204	χ=4.36 p = 0.113	χ=8.667 p = 0.13
Dry	F=4.461 p < 0.01 (post-hoc: mid≠a)	F=1.844 p = 0.169	F=7.111 p < 0.01 (post-hoc: m ≠ mid; mid≠a)	χ=10.073 p < 0.01 (post-hoc: mid≠a)	χ=1.19 p = 0.55 (post-hoc: m ≠ mid; mid≠a)	χ=2.036 p = 0.36

3 M = morning period (06:00 to 10:59am); mid = 11:00 to 14:59; a = 15:00 to 19:00

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1 **Table 2: Frequency of use of the three areas in the two seasons**

	Area 1 (1.2 ha)	Area 2 (1.5 ha)	Area 3 (15.3 ha)
Wet	14.5%	10.2%	75.3%
Dry	25.9%	15.7%	58.3%

2