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

2   **AUTHORS:**

RENATA G. FERREIRA	Dept. of Biological Anthropology University of Cambridge (UK)
PHYLLIS C. LEE	Dept. of Psychology University of Stirling (UK)
PATRÍCIA IZAR	Dept. of Experimental Psychology Universidade de São Paulo (USP) – Brazil

3

4   **RUNNING HEAD:** Food competition in *C. apella*

5   **WORD COUNT:** 5460 (plus two figures, two tables)

6   **KEY WORDS:** Brown capuchins, activity budgets, dominance and competition, social

7   proximity, socio-ecological models.

8   **CORRESPONDENCE TO:** RENATA G. FERREIRA

9

10   **PRESENT ADDRESS:**

RENATA G. FERREIRA	Dep. de Botânica, Ecologia e Zoologia and Pós-Graduação Regional em Desenvolvimento e Meio Ambiente - PRODEMA Universidade Federal do Rio Grande do Norte (UFRN) Campus Universitário – Centro de Biociências Natal – RN Brazil 59072-970 Tel: + 55 84 3215-3189

	rgf27br@yahoo.com.br
PHYLLIS C. LEE	Behaviour and Evolution Research Group
	Dept. of Psychology,
	University of Stirling, Stirling FK9 4LA, UK
	Tel: +44 1786 467656
	phyllis.lee@stir.ac.uk
PATRÍCIA IZAR	Dept. of Experimental Psychology
	Universidade de São Paulo (USP) – Brazil
	Av. Prof. Mello Moraes, 1721, CEP 05508-030, Brazil. Tel: +
	55 011 30914448 – 30.
	patrizar@usp.br

1

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.

13

14

15

16

17

18

19

20

21

22

23

24

25

1

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 19-24ºC) and one dry and cooler (April

16   to September, mean monthly rainfall of 69 mm, average temperature 15-17ºC). 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 months 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   $$x' = \frac{\left(x_m \times \dfrac{F_a}{F_m}\right) + \left(x_{mi} \times \dfrac{F_a}{F_{mi}}\right) + x_a}{F_a \times 3}$$

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% ± 2.6, Dry: 58.4% ± 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 (Tp = 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.

1 **REFERENCES**

2 Boinski S, Treves A, Chapman C (2000). A critical evaluation of the influence of predators

3   on primates: Effects on group travel. In *On the move – How and why animals travel*

4   *in groups* (Boinski S, Garber P, eds.), pp: 43-72. Chicago, University of Chicago

5   Press.

6 Chapais B (1992). The role of alliances in social inheritance of rank among female

7   primates. In *Coalitions and alliances in humans and other animals* (Harcourt AH,

8   De Waal FBM, eds.), pp 29-60. Oxford, Oxford Science Publications.

9 Chapais B (1995). Alliances as a means of competition in primates: evolutionary,

10   developmental, and cognitive aspects. *Yearbook of Physical Anthropology* 38: 115-

11   136.

12 de Ruiter JR (1986). The influence of group size on predator scanning and foraging

13   behaviour of wedge capped capuchin monkeys (*Cebus olivaceus*). *Behaviour* 98:

14   240-258.

15 de Waal FBM, Luttrell LM (1986). The similarity principle underlying social bonding

16   among female Rhesus monkeys. *Folia Primatologica* 46: 215-234.

17 de Waal FBM (1982). *Chimpanzees Politics*. Jonathan Cape Press.

18 de Waal FBM, Harcourt AH (1992). Coalitions and alliances: a history of ethological

19   research. In *Coalitions and alliances in humans and other animals* (Harcourt AH,

20   de Waal FBM, eds.), pp 1-19. Oxford, Oxford Science Publications.

21 di Bitetti MS (1997). Evidence for an important role of allogrooming in a platyrrhine

22   primate. *Animal Behavior* 54: 199-211.

23 Dunbar RIM (1976). Some aspects of research design and their implications in the

24   observational study of behaviour. *Behaviour* 8: 78-98.

25 Dunbar RIM (1988). *Primate Social Systems*. London, Croom Helm.

1   Ferreira RG (2003). Coalitions and social dynamics of a semifree-ranging *Cebus apella*

2   group. Ph. D. Thesis, University of Cambridge, UK.

3   Ferreira RG, Izar P, Lee PC (2006). Exchange, affiliation and protective interventions in

4   semifree-ranging brown capuchin monkeys (*Cebus apella*). *American Journal of*

5   *Primatology* 68: 765-776.

6   Fruth B, Hohmann G (2002). How bonobos handle hunts and harvests: why share foods. In

7   *Behavioural Diversity in Chimpanzees and Bonobos* (Boesch C, Hohmann G,

8   Marchant LF eds.), pp 231-243. Cambridge, Cambridge University Press.

9   Galleti M, Pedroni F (1994). Seasonal diet of the capuchin monkeys (*Cebus apella*) in a

10   semi-deciduous forest in south-east Brazil. *Journal of Tropical Ecology* 10: 27-39.

11   Hall CL, Fedigan LM (1997). Spatial benefits afforded by high rank in white-faced

12   capuchins. *Animal Behavior* 53: 1069-1082.

13   Isbell L (1991). Contest and scramble competition: patterns of female aggression and

14   ranging behavior among primates. *Behavioral Ecology* 2: 143-155

15   Isbell L, Pruetz J, Lewis M, Young T (1998). Rank differences in ecological behavior: A

16   comparative study of patas monkeys (*Erythrocebus patas)* and vervets

17   (*Cercopithecus aethiops*). *International Journal of Primatology* 20: 257-272.

18   Isbell LA, Young TP (2002). Ecological models of female social relationships in primates:

19   similarities, disparities, and some directions for future clarity. *Behaviour* 139: 177-

20   202.

21   Izar P (1994). Análise da estrutura social de um grupo de macacos-prego (*Cebus apella*)

22   em condições de semi-cativeiro. *Master's dissertation*. Universidade de São Paulo.

23   Izar P (2004). Female social relationships of *Cebus apella nigritus* in southeastern Atlantic

24   Forest: an analysis through ecological models of primate social evolution.

25   *Behaviour* 141:71–99.

1   Izar P, Ferreira RG, Sato T (2006). Describing the organization of dominance relationships

2   by dominance directed tree methods. *American Journal of Primatology* 68:189-

3   207.

4   Izawa K (1980). Social behaviour of the wild black-capped capuchin (*Cebus apella*).

5   *Primates* 21: 443-467.

6   Janson CH (1985). Aggressive competition and individual food consumption in wild

7   brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*

8   18: 125-138.

9   Janson CH (1988). Food competition in brown capuchin monkeys (*Cebus apella*):

10   quantitative effects of group size and tree productivity. *Behaviour* 105: 53-76.

11   Janson CH (1990a). Ecological consequences of individual spatial choice in foraging

12   groups of brown capuchin monkeys, *Cebus apella*. *Animal Behavior* 40: 922-934.

13   Janson CH (1990b). Social correlates of individual spatial choice in foraging groups of

14   brown capuchin monkeys, *Cebus apella*. *Animal Behavior* 40: 910-921.

15   Janson CH, van Schaik CP (1988). Recognizing the many faces of primate food

16   competition: methods. *Behaviour* 105 :165-186.

17   Keverne EB, Martensz N, Tuite B (1989). Beta-endorphin concentrations in cerebrospinal

18   fluid of monkeys are influenced by grooming relationships. *Psycho-*

19   *neuroendocrinology* 14: 155–161.

20   O'Brien TG (1991). Female-male social interactions in wedge-capped capuchin monkeys:

21   benefits and costs of group living. *Animal Behavior* 41: 555-567.

22   Oates JF (1987). Food distribution and foraging behavior. In *Primate Societies* (Smuts BB,

23   Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT eds.), pp 197-209.

24   Chicago, University of Chicago Press.

1   Perry S (1997). Male-female social relationships in wild white-faced capuchins (*Cebus*

2   *capucinus*). *Behaviour* 134: 477-510.

3   Phillips KA (1995a). Resource patch size and flexible foraging in white-faced capuchins

4   (*Cebus capucinus*). *International Journal of Primatology* 16: 509-519.

5   Phillips KA (1995b). Foraging-related agonism in capuchin monkeys (*Cebus capucinus*).

6   *Folia Primatologica* 65: 159-162.

7   Robinson JG (1981). Spatial structure in foraging groups of wedge-capped capuchin

8   monkeys *Cebus nigrivitatus*. *Animal Behavior* 29: 1036-1056.

9   Robinson JG (1986). *Seasonal variation in use of time and space by the wedge-capped*

10   *capuchin monkeys, Cebus olivaceus: Implications for foraging theory.* Smithsonian

11   Contributions to Zoology, 431. Washington DC, Smithsonian Institution Press.

12 Ron T, Henzi P. & Motro U. (1996). Do female chacma baboons compete for a safe spatial

13   position in a southern woodland habitat? *Behaviour, 133*: 475-490.

14 Rose LM (1994). Sex differences in diet and forging behavior in white-faced capuchins

15   (*Cebus capucinus*). *International Journal of Primatology* 15: 95-114.

16 Sterck E, Watts D, van Schaik C (1997). The evolution of female social relationships in

17   nonhuman primates. *Behavioral Ecology and Sociobiology* 41: 291-309.

18 Ulijaszek SJ, Strickland SS (1993). *Nutritional anthropology: prospects and perspectives*.

19   London, Smith-Gordon & Co.

20 van Hooff J, van Schaik C (1992). Cooperation in competition: the ecology of primate

21   bonds. In *Coalitions and alliances in humans and other animals* (Harcourt AH, de

22   Waal FBM eds.). pp 357-390. Oxford, Oxford Science Publications.

23 Vogel ER (2005). Rank differences in energy intake rates in white-faced capuchin

24   monkeys, *Cebus capucinus*: the effects of contest competition. *Behavioral Ecology*

25   *and Sociobiolog*y 58: 333-344

1   Vogel ER, Janson C (2007). Predicting the frequency of food-related agonism in white

2   faced capuchin monkeys (*Cebus capucinus*) using a novel focal-tree method.

3   *American Journal of Primatology* 69: 533-550.

4   Vogel ER, Munch SB, Janson CH (2007). Understanding escalated aggression over food

5   resources in white-faced capuchin monkeys. *Animal Behaviour* 74: 71-80.

6   White F, Chapman C (1994). Contrasting chimpanzees and bonobos: nearest neighbour

7   distances choices. *Folia Primatologica* 63: 181-191.

8

1 **ACKNOWLEDGMENTS**

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

1   **Figure legends:**

2

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

4

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
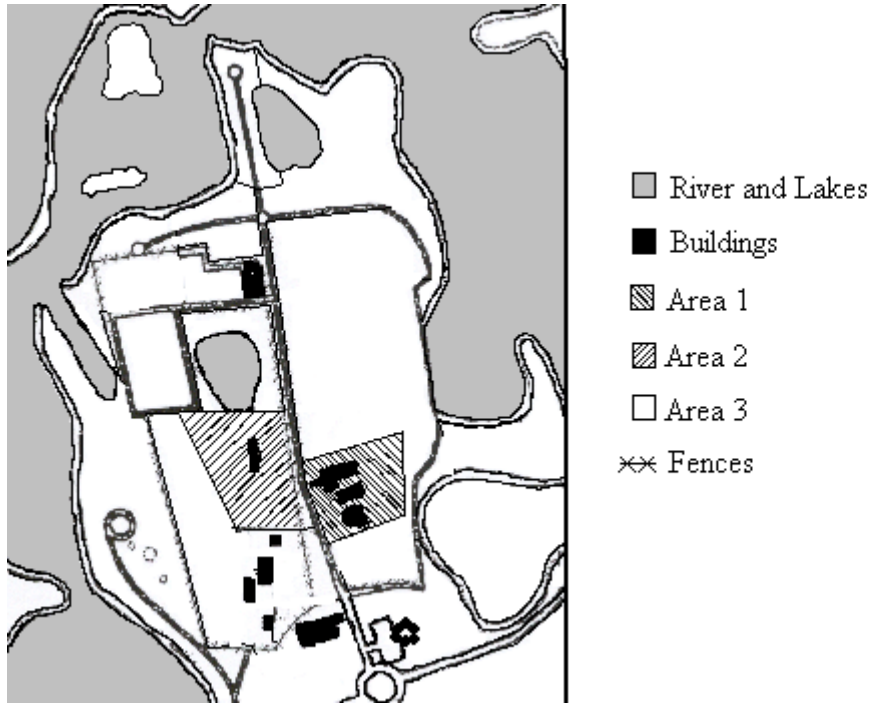
7   in table 1.

8

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
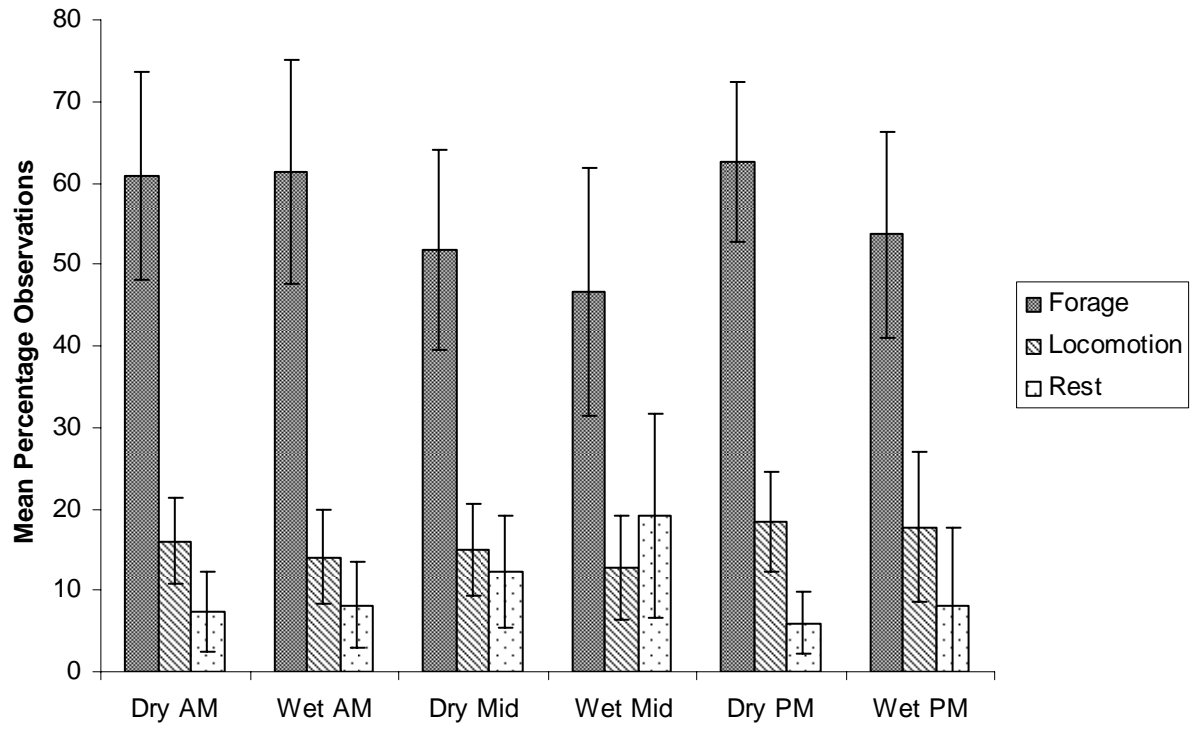
11 (N = 18) by wet and dry season.

12

1   Figure 1

2

River and Lakes
Buildings
Area 1
Area 2
Area 3
Fences

3
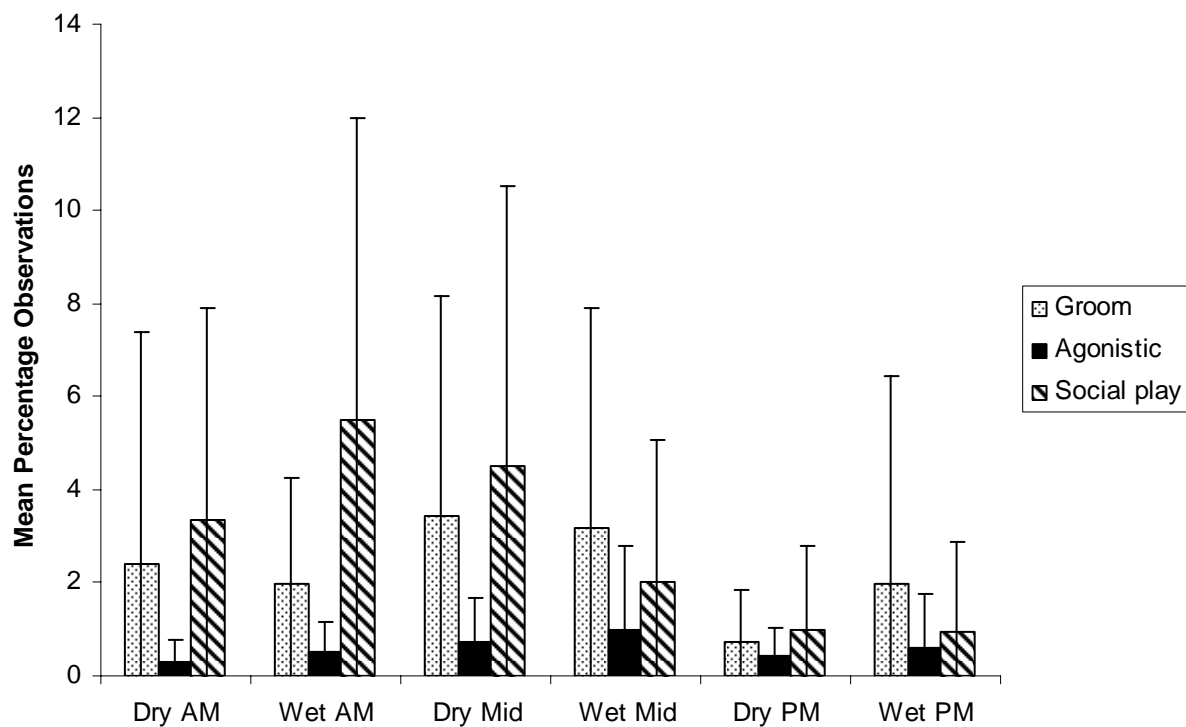4

1   Figure 2a:
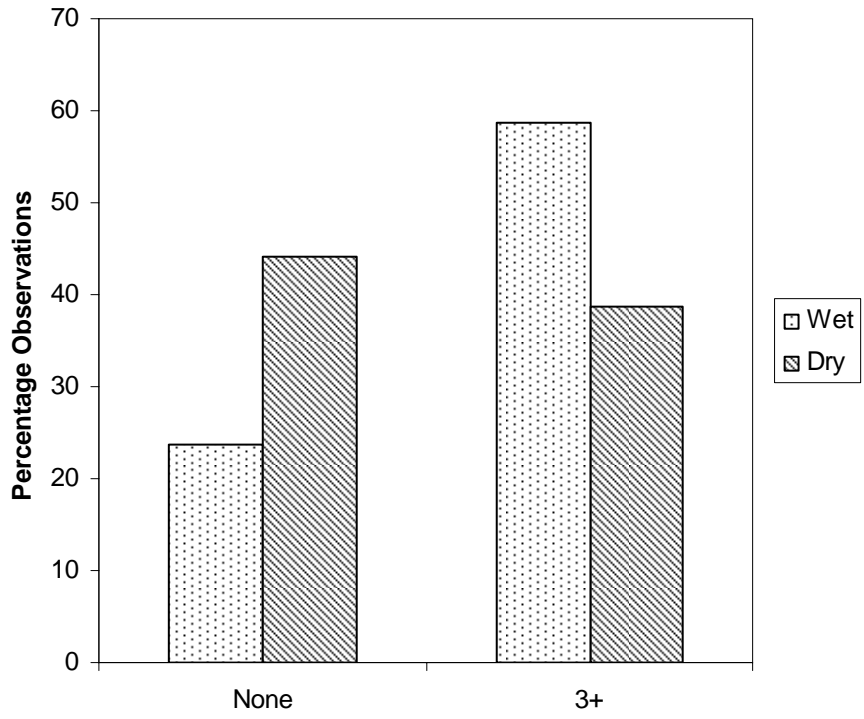
2

3

1   **Figure 2b**

2

1   **Figure 3**

2

3

4

5

6

7

8

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.**

	Forage	*Locomotion*	*Rest*	*Groom*	*Aggression*	*Social Play*
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

4
5

6

7

8

9

10

11

12

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