Social Spacing and Subgrouping in One Community of White-Faced Capuchins (*Cebus capucinus*)

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Abstract

I studied social spacing in one group of eight white-faced capuchin monkeys (*Cebus capucinus*) over seven mornings at La Suerte Biological Field Station, Costa Rica. I recorded 528 instantaneous focal animal samples, consisting of individuals' activity, diet, distance from their nearest neighbor, diameter of the occupied tree crown, and the age composition of individuals sharing the same tree crown. *C. capucinus* spent a majority of their time feeding and foraging, and overwhelmingly consumed fruit during the study period. Individuals were alone in trees during 53.6% of samples, and subgroups averaged 2.1 ($\sigma = 1.8$) individuals. Average subgroup size differed by focal animal activity, from 1.4 ($\sigma = 0.8$) individuals while traveling to 2.8 ($\sigma = 1.1$) while socializing. Focal animals were most often (50.6%) at least ten meters from their nearest neighbor. Excluding socialization, distance from neighbors was greatest while feeding and least while traveling.

Keywords: *New World monkeys,* Cebus*, age, activity, diet, social spacing, subgroup*

1 Introduction

Capuchin monkeys are classified as omnivores, consuming most of their calories from fruit and their protein from invertebrate prey. In order to consume enough insect protein to satiate their 4 kg body size, *Cebus capucinus* must spend a great deal of time foraging, and are thus considered "energy maximizers" (Fragaszy, Visalberghi, & Fedigan, 2004). The species shows a high degree of problem-solving skill and shows marked ability to consume hard-to-access foods, with the thickest tooth enamel of any nonhuman primate relative to tooth size (Jack, 2011). The mean *C. capucinus* group size is 16.36 individuals, with a male-to-female ratio of 0.71 (Fragaszy et al., 2004).

An animal's placement within its group has a profound impact on its feeding success as well as the time it spends in vigilance (as a proxy for risk of predation). In a 26-month study of wedge-capped capuchins (*Cebus olivaceus*) in Venezuela, Robinson (1981) documented individuals' foraging success correlated directly with the distance from their nearest neighbor, but increased distance also led to more time spent in vigilance against predators. In a similar study of intragroup spacing in *C. capucinus*, Hall and Fedigan (1997) recorded dominant adults occupying a front-center position within the group, balancing predation risk with access to food. It has been argued, however, that because *C. capucinus* tend to forage independently while *C. capucinus* forage successively, intragroup feeding competition may not play a major role in the former's spatial behavior (Fragaszy et al., 2004).

The vast majority of mammals are not social, yet 80% of interactions between New World monkeys are affiliative (Sussman & Garber, 2005). Thus, it would be expected that there are some benefits to group cohabitation. Many benefits have been hypothesized or identified, including infant care, reduced predation risk, and better reproductive success (Fragaszy et al., 2004). The most prevalent theory is that of feeding competition, describing primate groups as large enough to allow for predator detection yet small enough to minimize intragroup feeding competition. Sussman and Garber (2011) argue that there is little empirical basis for theories to accurately depict predation risk; they propose that primate social groups are more flexible than normally assumed, explaining why directly agonistic behavior accounts for a minimal amount of primate activity.

Relative to body size, primates have evolved a juvenile period much longer than all other mammals (Harvey & Clutton-Brock, 1985). This juvenile period is associated with significant development of social skills (Joffe, 1997) and foraging behavior (Rapaport & Brown, 2008). Joffe (1997) also found that length of a species' juvenile period correlated positively with group size, suggesting that greater social development allows for larger social structures. It has been theorized that juveniles may learn certain behaviors by staying in close proximity to adult role models (Sherrow & MacKinnon, 2011) Alternatively, Strier (2007) hypothesizes that they learn social skills by preferring proximity to other juveniles to facilitate play. In *C. capucinus*, juveniles have been observed actively begging for food from adults (Perry & Rose, 1994) and show markedly more interest in adult food-processing behavior than do adults (O'Malley & Fedigan, 2005). To facilitate such interactions, it was predicted that juveniles would physically associate with other individuals at a higher rate and in closer proximity than would adults.

2 Methods

2.1 Study Site

La Suerte Biological Field Station is located in northeastern Costa Rica (10.442° N, 83.771° W), approximately 50 m above sea level. The site covers 300 ha of tropical forest as well as 300 ha of formerly-logged secondary forest and regenerating pasture (Mallott, Garber, & Malhi, 2017). Bisecting the land is a river, Río La Suerte, which flows to the Caribbean. Annual precipitation in the region averages 3962 mm, peaking in June-July and November-December (Sanford, Paaby, Phillips, & Luvall, 1994). Neighboring the field station are several plantations of coconut and oil palms, of which the coconut plantation was observed to be a feeding site for the capuchins. In addition to white-faced capuchins, the site is also inhabited by mantled howler monkeys (*Alouatta paliatta*) and black-handed spider monkeys (*Ateles geoffroyi*), which were both observed at least once during the study period occupying the same tree crown as *C. capucinus* individuals.

2.2 Study Group

One habituated group of white-faced capuchins was identified. The group was not marked and thus it was not possible to record data on or sex particular individuals. It was nevertheless estimated that the group consisted of eight individuals (5 adults, 3 juveniles) during the study period. No individuals were identified as infants. Juveniles were defined as individuals not dependent on their mother yet still immature, with age determined based on size relative to adults.

2.3 Observational Data Collection

Information on subgrouping and individuals' activity was collected at two-minute intervals from dawn until midday using an instantaneous focal animal sampling technique (Altmann, 1974). 528 samples were collected from January 2 to 8, 2018, totaling 17.6 h of behavioral data (see Appendix A for a template of the data recording format). An effort was made to follow focal animals for 2 h before changing to a second target, but the capuchins' rapid locomotion made losing sight of focal animals a regular occurrence.

Table 1: Activity Budget and Age

	N	Activity (%)					
		Feeding	Foraging	Traveling	Socializing	Resting	Unknown
Adult	318	37.4	24.5	28.9	3.1	5.7	0.3
Juvenile	210	50.0	20.5	27.1	0.0	1.9	0.5
Total	528	42.4	22.9	28.2	1.9	4.2	0.4

Note: N, sample size; %, percent of age class data (rows add to 100%); Total, all activities regardless of age

Table 2: Diet and Age

	N	Food Type (%)				
		Fruit	Leaves	Flowers	Invertebrate	Unknown
Adult	119	83.2	3.4	0.0	10.1	3.4
Juvenile	105	81.9	1.9	1.0	15.2	0.0
Total	224	82.6	2.7	0.4	12.5	1.8

Note: N, sample size; %, percent of age class data (rows add to 100%); Total, all activities regardless of age

2.3.1 Activity budget

Information on focal animals' activity and diet was recorded. Activities were defined as: feeding – manipulation and ingestion of a potential food item; foraging – locomotion within the same tree crown for the immediate purpose of obtaining food; traveling – locomotion within the same tree crown or adjacent tree crowns not for the immediate purpose of obtaining food; social – reciprocal affiliative or agonistic interaction with at least one other individual; resting – a period of inactivity; other – any activity not otherwise listed; unknown – not able to discern. Diet was recorded as fruit, leaves, flowers, or invertebrate prey, as well as unknown. When possible, fruit consumed was identified to species. Plant identification was performed with the assistance of local staff supplemented with botanical reference texts.

Social spacing. The identity of and distance to a focal animal's nearest neighbor was recorded each sampling interval. Nearest neighbor was considered to be the *C. capucinus* individual closest to the focal animal in three-dimensional space without regard to canopy terrain. Distances were estimated visually as "in contact" (0 m), less than 1, 1 to 3, 3 to 5, 5 to 10, and greater than 10 m. Similarly, the diameter of the tree crown in which a focal animal resided was visually estimated to less than 5, 5 to 10, 10 to 15, and greater than 15 m. The number of individuals in the same tree crown was considered to be a subgroup, assuming that a focal animal has some affinity with those it shares a tree with (Bezanson, Garber, Murphy, & Premo, 2008), and the age composition of such subgroups was also recorded.

2.4 Interpretation

Data was converted from human- to machine-readable format in C# and compiled in Microsoft Excel. Bivariate analyses were generated using PivotTables.

In five samples (1% of total), the focal animal was recorded as on the forest floor. Because subgroups were defined based on the animal's present tree crown, these data points were not used in the analysis. Values of "other" and "unknown" consisted

3 Results

3.1 Activity and Diet

Members of both age groups spent a plurality of their time engaged in feeding; however, juveniles fed much more (50%) than did adults (37%). This greater time spent feeding came at a cost to time spent in all other

Table 3: Age Composition of Subgroups

		Average representation of age group (%)		
Subgroup size	N	Adults	Juveniles	Adult difference from whole (%)
1	269	–	–	–
2	103	65.2	34.8	4.3
3	69	64.4	35.6	3.1
4	16	70.8	29.2	13.3
5	9	60.0	40.0	-4.0
6	7	66.7	33.3	6.7
8	29	62.5	37.5	–

Note: No recorded subgroups of size 7; Subgroups of size 1 excluded from age distribution; Subgroups of size 8 equivalent to age composition of entire *C. capucinus* group; "adult difference from whole", difference between percentage of adults for subgroup size and percentage of adults in group as a whole; N, sample size; %, percent of individuals making up subgroup on average

behaviors compared to adults (Table 1). *C. capucinus* individuals spent the vast majority of their feeding time consuming fruit (83%). While fruit consumption did not differ greatly by age, juveniles consumed more (15%) invertebrates than did adults (10%) and conversely for leaf consumption (Table 2). Juveniles were never recorded socializing, and adults were only recorded socializing in 3.1% of samples (Table 1). Of these ten recorded social interactions, three were agonistic, five affiliative, and two unknown.

3.2 Subgrouping

Subgroups averaged 2.12 ($\sigma = 1.80$) members in the same tree crown. In a majority of samples (53.6%), *C. capucinus* individuals were observed alone in a tree; thus, the modal subgroup size is 1. Age composition of subgroups differed minimally by age. Excluding subgroups of size 1 and 8, the fraction of adults making up a subgroup averaged a 4.7% difference from the fraction of adults making up the group as a whole. The greatest difference was observed in subgroups of size 4, which on average contained 13.3% more adults than would be expected (Table 3).

Also examined was the difference in subgroup size based on the size of the tree crown in which the subgroup resided. A strong direct correlation was observed, with tree crowns with diameter less than 5 m averaged 1.2 ($\sigma = 0.5$) individuals, while trees greater than 15 m in diameter averaged 3.4 ($\sigma = 2.6$) individuals (Table 4). As with subgroup size in general, there was no correlation between tree crown size and the age composition of subgroups; age composition of subgroups reflected the composition of the *C. capucinus* group as a whole.

Subgroup size was observed to be related to a focal animal's activity. Subgroups ranged from an average of 1.4 ($\sigma = 0.8$) individuals when traveling to 2.8 ($\sigma = 1.1$) individuals when the focal animal was engaged in social interaction. Feeding activity represented the median subgroup size, 2.4 ($\sigma = 2.0$) individuals (Table 5). Again, age composition differed minimally between activities, after taking into account different activity budgets of the age groups.

3.3 Distance to Nearest Neighbor

In addition to the size of subgroups, observations were made on the distance to a focal animal's nearest neighbor. The majority (50.6%) of observations found the focal animal greater than ten meters from its nearest neighbor, and only 5.6% of samples observed animals within one meter of one another, including in contact. The preference for distances greater than 10 m extended to all activities except socialization, which was the only activity not to have the plurality of observations see animals 10 m from each other. Excluding the low-sample-size activities of socialization (N=10) and resting (N=21), the most likely activity to be greater than 10 m apart was feeding (53.7%) and least likely was traveling (46.8%). This correlation extended across both age classes; however, regardless of activity, juvenile focal animals were more likely to be greater than 10 m apart from their nearest neighbor than were adults (Juveniles: 55.1%; Adults: 47.7%). Juveniles were also never observed in physical contact to their nearest neighbor, while adults were observed in contact in 3.9% of samples (Table 6).

Table 4: Subgroup Size and Tree Crown Diameter

Tree diameter (m)	N	Average subgroup size	σ
<5	86	1.2	0.5
5 to 10	149	1.5	1.0
10 to 15	121	1.9	1.0
>15	167	3.4	2.6

Note: N, sample size; σ, one standard deviation of subgroup size

Table 5: Subgroup Size and Activity

Activity	N	Average subgroup size	σ
Feeding	224	2.4	2.0
Foraging	121	2.6	2.3
Traveling	149	1.4	0.8
Socializing	10	2.8	1.1
Resting	22	1.6	1.1

Note: N, sample size; σ, one standard deviation of subgroup size

4 Discussion

4.1 Activity and Diet

Juveniles' time spent feeding and foraging was greater than that of adults, consistent with previous studies of *C. capucinus* at La Suerte Biological Field Station (Bezanson, 2009). Capuchins' primary food source being fruit was also consistent with most previous literature on *Cebus* primates (Jack, 2011).

4.2 Sociality

Capuchins preferred overwhelmingly to feed and forage alone or in small subgroups, consistent with Phillips (1995)'s finding in *C. capucinus* on Barro Colorado Island, Panama. Individuals were most likely to be over ten meters away from their nearest neighbor when engaged in feeding, and were very rarely observed feeding within three meters of another. Even in trees of large diameter, subgroup size did not increase a commensurate amount. This suggests minimal intragroup feeding competition, consistent with Sussman and Garber (2011)'s hypothesis that feeding competition contributes little to primate social structure.

The time spent in direct social interaction was minimal, significantly less than that recorded in past studies of *C. capucinus* (Sussman & Garber, 2005). This is possibly due to the study being limited to morning hours, and did not observe capuchins during the hottest period of the day, when the study group reportedly engages in more rest (P. A. Garber, personal communication, Jan. 12, 2018). More

4.3 Ontogeny

Ontogeny appears to have played little role in the observed social structure of the study group. Adults and juveniles were just as likely to occupy subgroups of all sizes, trees of all sizes, and spent similar amounts of time in each activity. This is similar to earlier findings of *C. capucinus* positional behavior at La Suerte, in that juveniles resemble adults at six months of age regardless of their sexual immaturity (Bezanson, 2009). In fact, juveniles were significantly more likely than adults to be over 10 m from their closest neighbor. This observation contrasts with the prediction that they would prefer nearby neighbors for either social development (Strier, 2007) or mimicry of adult behavior (Sherrow & MacKinnon, 2011).

Table 6: Nearest Neighbor Distance and Activity

Activity	N	Nearest neighbor distance (%)					
		0 m (in contact)	<1 m	1 m to 3 m	3 m to 5 m	5 m to 10 m	>10 m
Adult	**310**	**3.9**	**2.9**	**6.1**	**16.1**	**23.2**	**47.7**
Feeding	119	1.7	1.7	10.9	17.6	16.8	51.3
Foraging	76	0.0	3.9	3.9	18.4	30.3	43.4
Traveling	88	1.1	2.3	3.4	15.9	33.0	44.3
Socializing	10	90.0	10.0	0.0	0.0	0.0	0.0
Resting	17	0.0	5.9	0.0	5.9	0.0	88.2
Juvenile	**198**	**0.0**	**3.5**	**2.5**	**20.2**	**18.7**	**55.1**
Feeding	99	0.0	1.0	1.0	22.2	19.2	56.6
Foraging	42	0.0	2.4	4.8	16.7	16.7	59.5
Traveling	53	0.0	9.4	1.9	20.8	17.0	50.9
Socializing	0	0.0	0.0	0.0	0.0	0.0	0.0
Resting	4	0.0	0.0	25.0	0.0	50.0	25.0
Total	**508**	**2.4**	**3.2**	**4.8**	**17.7**	**21.5**	**50.6**
Feeding	218	0.9	1.4	6.4	19.7	17.9	53.7
Foraging	118	0.0	3.4	4.2	17.8	25.4	49.2
Traveling	141	0.7	5.0	2.8	17.7	27.0	46.8
Socializing	10	90.0	10.0	0.0	0.0	0.0	0.0
Resting	21	0.0	4.8	4.8	4.8	9.52	76.19

Note: N, sample size; %, percent of samples (rows add to 100%); Total, all activities regardless of age

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Appendix A

Table 1: Sample Data

Time	Focal Animal	Location[1]	Activity	Diet	Social Interaction	Nearest Neighbor Distance[2]	Subgroup Size[3]	Subgroup Composition[4]	Crown Diameter
8:02	Juvenile	O40	Social		Affiliative	In contact	4	AAJJ	<5 m
8:04	Juvenile	O40	Foraging	Fruit		1 m to 3 m	5	Unknown	5 m to 10 m
8:06	Juvenile	O40	Feeding	Invertebrates		3 m to 5 m	5	AAAJJ	10 m to 15 m
8:08	Juvenile	O40	Resting			5 m to 10 m	1	J	>15 m
8:10	Adult	O41	Traveling			>10 m	2	AJ	Unknown
8:12	Adult	O42	Unknown			Unknown	Unknown	Unknown	Unknown
8:14	Adult	Unknown	Other			In contact	On ground	On ground	On ground

[1] The nearest or most recently seen trail marker
[2] Distances estimated based on sight
[3] Number of individuals in the focal animal's tree crown, including the focal animal
[4] Age composition of individuals in the focal animal's subgroup