Nearest Neighbor Distance in Relation to Behavior in White-Faced Capuchin Monkeys, *Cebus capucinus*

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Abstract

Individuals in a group of white-faced capuchin monkeys, *Cebus capucinus*, were studied in a tropical rainforest of Costa Rica. Spatial preferences to the nearest white-faced capuchin neighbor in relation to different behavioral activities were the main focus of this study. Feeding, foraging, locomotion, and resting were the behaviors that were tested. The purpose of this study was to analyze the correlation between competitive behaviors as opposed to non-competitive behaviors and their effects on individual preferences in distance to a nearest neighbor. Also, we assessed patterns in terms of sex, age, and class differences. We concluded that there was a relationship between competitive behaviors and greater spatial distances as well as non-competitive behaviors and smaller spatial distances.

Background

Behavior is usually the result of decisions relating to survival, child rearing, mating, and the acquisition of food. If an organism's behavior is advantageous for its environment and will help the organism to increase its offspring, natural selection will select for this behavior and filter out less advantageous ones. Similarly, closeness to the nearest neighbor is determined by exposure to predators, access to food, and the potential for interaction with other group members. Many studies on neighbor preferences in wild and captive primates have shown there is strong neighbor preference. Spatial distance preferences are important for understanding which behaviors the proximity of neighbors have been evolutionarily beneficial. Studies in spatial relations also help to show how behaviors influenced by ecological pressures result in different spatial preferences.

A number of studies have exposed different motivations pertaining to proximity. Hamilton discussed the proximity of individuals in context of the group as a whole and how the position of each group member may affect its exposure to predators.³ A study done on wild mountain gorillas (Gorilla gorilla beringei) revealed closer proximity between female gorillas with unweaned infants and silverbacks for greater protection against infanticide.⁴ Another study of brown-faced capuchin monkeys (Cebus apella) found that females forage closer to the edge of the group than do males.⁵ Females may reduce confrontation by deliberately avoiding the center of a group while foraging for resources that are in limited supply.⁵ An additional study done on white-faced capuchins found that dominant individuals in the group preferred a center position. In conclusion, multiple factors such as predator surveillance, offspring protection, competition, social status, and opportunity for interaction determine the preference for nearest neighbor distances in primates.

Certain characteristics documented for white-faced capuchins have provided different possibilities for understanding why particular spatial preferences are preferred over others during various activities. First, white-faced capuchin groups contain both multiple males and multiple females, and are comprised of six to thirty individuals.⁷ Within such groups, the hierarchy includes an alpha male.⁸ In addition, they are considered female-bonded with females forming long term bonds with one another. Also, both sexes form coalitions.⁹ Female-female aggression, however, has been documented.⁹ Another doumented characteristic of capuchins is that those who spend more time grooming will more frequently form coalitions than those who do not.⁸

Capuchins are omnivores that eat mostly fruit and insects. Females tend to exploit smaller embedded invertebrates while males are more likely to capture more mobile prey. Fruit trees, spaced out with food in clumps, are monopolized by more dominant group members. Both sexes do quarrel over food. However, both sexes tend to avoid aggressive encounters. 8

From factors including group size, associative patterns, and diet, it can be reasoned that there will be a correlation between certain behavioral activities and nearest neighbor distance preferences. The alternative hypothesis is that there is no relationship between behavioral activities and spatial preferences. Based on the hypothesis, several questions regarding spatial distance preference were asked. First, during activities where competition is greatest, such as foraging and feeding, will spatial distances be greatest in order to avoid competition and aggression and, therefore, decrease unnecessary energetic expenditures? Secondly, when competition for resources is not a direct component of the activity, will the spatial distance preference be closest so that the subject will have a higher potential for social and grooming interactions and, therefore, increase the possibility of forming coalitions?

Materials and Methods

Study Site: The study region was a tropical rainforest at La Suerte Biological Field Station. The field station is on a 750 acre ranch located in northeastern Costa Rica. As a result of logging, the tropical rainforest contains both secondary and primary forest. The subjects, *Cebus capucinus*, were mostly observed and followed by a set of trails. There are two species of primate that live in this area other than *Cebus capucinus* including *Alouatta palliate* (mantled howler monkey) and *Ateles geoffroyi* (spider monkey).

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Study Subjects: At the study sight there were two main groups of white-faced capuchins, *Cebus capucinus*. Eighteen members including infants were estimated in each group. Both groups had been extensively observed by humans in the past and were habituated to human observers.

Sampling Techniques: The study took place for eight days from June 9 - June 16 2005. All data were taken during the rainy season. Eleven hours of data were collected during the study. Instantaneous focal sampling was used in continuous one minute intervals. In the focal animal sampling technique a subject was selected and focused on for a maximum of ten minutes before the focal animal was replaced. Spatial distance preference was measured by determining the distance of the focal animal to its nearest neighbor. The nearest neighbor was determined by scanning the entire area and concluding the nearest white-faced capuchin to that focal animal.

During each one-minute interval, age, sex, behavior, and nearest neighbor distance were recorded. The behaviors included were social, feeding, foraging, locomotion, and resting. However, due to the fact that most social behaviors require having a nearest neighbor distance of touching or close (grooming, biting, food sharing, etc.) it was decided that social behaviors would not be included in the final data analysis. Foraging and locomotion behaviors were differentiated by determining whether an animal was searching for food (i.e. slowly moving while scanning or manipulating substrate) as opposed to moving from one place to another as in locomotion.

The distances were categorized into five categories: 1. touching 2. close (0.1-2 meters) 3. far (2.1-10 meters) 4. very far (10.1-20 meters) 5. out of sight.

Focal animals were chosen at random with equal females and males included in this study. Infants that had not been weaned were not included in the analysis. Juveniles were not distinguished by sex. We strived to pick focal animals that did not change their behavior when a human observer was around. Also, we attempted to collect equal morning and afternoon samples.

Methods for analysis: Data were analyzed by taking the total amount of one-minute interval samples for each sex and age group and totaling the different nearest neighbor distances for each behavior. Patterns were assessed by analyzing a time budget table. The time budget table shows the percentage of time that each sex or age group spent in a given distance to its nearest neighbor during a certain behavior.

Data were also entered into an SPSS (14.0 for Windows) spreadsheet. The Pearson chi-square analysis was then applied to the data to check for a statistical relationship between distance and type of behavior (competitive or non-competitive).

Results

General results: All females, males, and juveniles had similar activity budgets. The most recorded behaviors for males, females, and juveniles were locomotion, foraging, and resting, respectively. Of the eleven hours of data, males and females were not visible 17% of the time and juveniles 22% of the time. All social behaviors were the least recorded behaviors for all the groups.

The chi-square analysis showed that the p-value for com-

petitive opposed to non-competitive behaviors was equal to 0.381 with four degrees of freedom. This data proves that the relationship between distance and behavior is not significant using a 5% significance level and the null hypothesis (no relationship) cannot be rejected (Table 1).

Table 1. The observed and expected count assigned to all competitive (foraging and feeding) and non-competitive (resting and locomotion) behaviors for each group of distances to their nearest neighbor.

			Behavior		Total
			Competitive	Non- competitive	
	Touch- ing	Count	0	2	2
		Expected Count	0.7	1.3	2.0
Distance	Close	Count	32	80	112
		Expected Count	38.1	73.9	112.0
	Far	Count	70	117	187
Distance		Expected Count	63.6	123.4	187.0
	Very Far	Count	40	69	109
		Expected Count	37.1	71.9	109.0
	Out of Sight	Count	25	56	81
		Expected Count	27.5	53.5	81.0
T-4-	.1	Count	167	324	491
Total		Expected Count	167.0	324.0	491.0

However, when locomotion and feeding behaviors were removed and only foraging and resting behaviors were compared with nearest neighbor distances, the chi-square test showed a statistically significant relationship (Figure 2). The p-value for this analysis was 0.005 with four degrees of freedom.

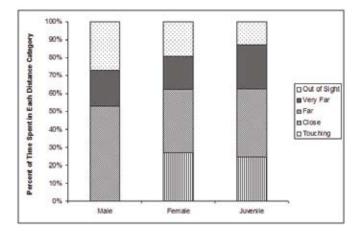
Table 2. The actual and expected count for the behaviors resting (non-competitive) and foraging (competitive) for each group of distances to their nearest neighbor.

			Behavior		Total
			Foraging	Resting	
	Touch- ing	Count	0	2	2
Distance		Expected Count	0.9	1.1	2.0
	Close	Count	15	39	54
		Expected Count	24.4	29.6	54.0
	Far	Count	39	44	83
		Expected Count	37.5	45.5	83.0
	Very Far	Count	24	19	43
		Expected Count	19.4	23.6	43.0
	Out of Sight	Count	12	5	17
		Expected Count	7.7	9.3	17.0
Total		Count	90	109	199
		Expected Count	90.0	109.0	199.0

We chose to examine a relationship between foraging and resting while excluding locomotion and feeding for several reasons. Foraging compared to feeding should have a higher rate of competition because once the food source is attained by an individual, competition for it should decrease. We also chose to leave out locomotion and focus solely on resting while computing the second statistical relationship because some types of locomotion capuchins use may require greater distances solely for the range of motion and not for the competitive aspect of the behavior (i.e. leaping). Further dialogue of characteristics and the competitive aspects of these behaviors are discussed in greater detail later in this article.

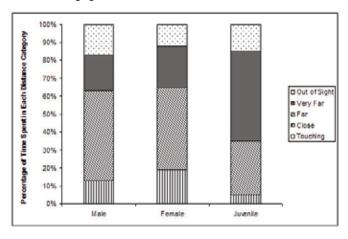
Feeding: Most of the feeding behaviors were recorded for all groups as "far" from the nearest neighbor. Females and juveniles had a significant amount of data where feeding occurred "close" to the nearest neighbor (35% for females and 38% for juveniles), while no data for males was recorded as anything closer than "far" to their nearest neighbor (Figure 1).

Figure 1. The percentage of time that adult male, adult female, and juvenile white faced capuchin monkeys spent in distances categorized as touching, close, far, very far, and out of sight to their nearest neighbor while in the behavior of feeding.



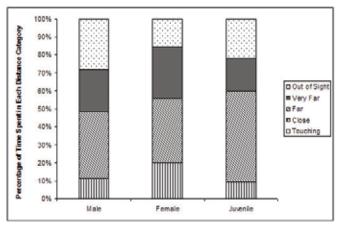
Foraging: Males and females had the same basic pattern of spatial distances to their nearest neighbor with "far" being the most common distance. Juveniles spent the most time being "very far" from their nearest neighbor (50% while foraging), doubling the amount of data points that the adult males and females were recorded in that category (Figure 2).

Figure 2. The percentage of time that adult male, adult female, and juvenile white faced capuchin monkeys spent in distances categorized as touching, close, far, very far, and out of sight to their nearest neighbor while in the behavior of foraging.



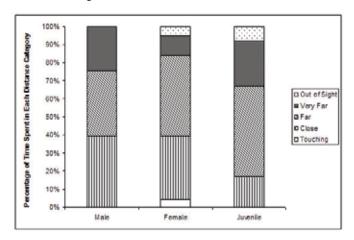
Locomotion: When in locomotion, all three groups tended to lean towards being "far" through "out of sight". The adult females were the only group that had more time spent being "close" to their nearest neighbor when in locomotion (versus being "out of sight" to the nearest capuchin) (Figure 3).

Figure 3. The percentage of time that adult male, adult female, and juvenile white faced capuchin monkeys spent in distances categorized as touching, close, far, very far, and out of sight to their nearest neighbor while in the behavior of locomotion.



Resting: Most of the data points for resting were at a distance of "far" or "close". Juveniles were the exception to the adults and spent greater amounts of time being "very far" (25%) versus being "close" (17%) to their nearest neighbor (Figure 6). The least amount of time was spent "touching" and being "out of sight" to their nearest neighbor for all the groups.

Figure 4. The percentage of time that adult male, adult female, and juvenile white faced capuchin monkeys spent in distances categorized as touching, close, far, very far, and out of sight to their nearest neighbor while in the behavior of resting.



Foraging and Feeding compared to Resting and Locomotion: When the capuchins were foraging or feeding they spent 43% of their time in large distances ("very far" or "out of sight" categories) while 15% of their activity budget while foraging and feeding was spent at close distances ("close" and "touching" categories). When the capuchins were in locomotion or resting, 34% of their time was spent at large distances ("very far" or "out of sight" categories) and 22% of their time was spent at close distances ("close" and "touching" categories).

Discussion

Most of the data concurred with the hypothesis that there is a relationship between different behavioral activities and certain preferences in nearest neighbor distances. It should be noted, however, that because there were only 11 hours of data collected, some of the results may be skewed to one conclusion over another. More observational time would need to be gathered to verify that the data were not skewed or biased due to, by chance, several outlying points.

Behaviors that involved competition (foraging and feeding) tended to occur at larger distances from conspecifics. This idea supports the concept that maintaining greater distances from other individuals to avoid conflict and competition may outweigh the advantages of being close for predator surveillance, learning, and social interaction during these behaviors. In accordance with this hypothesis, the female and juvenile capuchins when feeding spent more time being "close" to their nearest neighbor than during foraging. Foraging may require more competition because one individual is trying to find the food source before others. Once the food is acquired, the competition in finding it tapers and it is not as necessary to have as great of a distance between the nearest sources of competition. In the behavior of foraging, juveniles had more occurrences in the "very far" (10.1-20 meters) category than any of the other distances (50%). Similarly, while feeding, juveniles spent the most time in "very far" distances than either males or females. This may be a result of juveniles not being able to monopolize certain food sources like the more dominant, older group members and are forced to strike out on their own to obtain food.

Behaviors, including resting and locomotion, do not have a clear competitive component. It is surprising then, that both resting and locomotion occurred at larger (mostly at "far") rather than shorter distances ("touching"). It is not surprising, however, that although the distances occurred further apart than expected, most time was spent at "far" and some at "close" with less time spent at distances "very far" and even less at "out of sight". In these instances, it may be more advantageous to create availability for social interaction and utilize others for predator surveillance by having a closer proximity to other group members rather than creating greater space between group members to avoid competition and confrontation. This is achieved by being "far" and "close" (as it was during resting), but not "very far" or "out of sight". Perhaps, because the research site was a fragmented patch of rainforest, there was a lack of predators living in the area and the benefit of predator surveillance was less necessary. The lack of "close" distances recorded during locomotion is most likely the result of the type of locomotion white-faced capuchins use. White-faced capuchins, when on the move, use mainly three types of locomotion: quadrupedal walking, leaping, and climbing. 11 Although the type of locomotion was not used during this study, other researchers have demonstrated that capuchin monkeys employ mostly leaping (24.7%) and quadrupedal walking (52.2%). 11 Because locomotion like this requires a great deal of space, particularly when leaping, animals tend to space out during movement explaining the "far" neighbor distance recorded.

Conclusion

Using the chi-square analysis, there was not a significant relationship of competitive behaviors versus non-competitive behaviors and distance to the nearest conspecific. However, by looking at the time-budget tables and the chi-square analysis for only resting and foraging, the results of this study show some support for the hypothesis that there is a correlation between different behaviors and individual preferences for distances to the nearest neighbor. More specifically, activities that had a competitive component (feeding, foraging) tended to occur at larger distances. In contrast, non-competitive behaviors (resting, locomotion) tended to occur at somewhat smaller distances. White-faced capuchins, while in a group, must always be weighing the costs and benefits of proximity to a neighbor. This study shows that when competition drives a behavior, an individual in the group will tend to choose to some extent greater distances than normally expected to its neighbor, lessening the competition and potential for confrontation. Wherever competition is not a direct force, animals tend to prefer somewhat of a closer proximity. Nonetheless, this study also shows that the relationship of distance and type of behavior is not as dichotomistic as one would assume.

Acknowledgements

The author thanks her mentors at the field station, Dr. Deborah J. Curtis and Michael Teague O'Mara, for all of their guidance. Also, Gretchen thanks Dr. Mitani for his patience and advice in revisions and the analysis of the data.

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