

RESEARCH ARTICLE

Predicting the Frequency of Food-Related Agonism in White-Faced Capuchin Monkeys (*Cebus capucinus*), Using a Novel Focal-Tree Method

E.R. VOGEL^{1,2*} AND C.H. JANSON¹

¹Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York

²Department of Anthropology, University of California–Santa Cruz, Santa Cruz, California

Food abundance and distribution have played a central role in the conceptual theory of primate socioecology [Janson, *Behaviour* 105:53–76, 1988; Isbell, *Behavioral Ecology* 2:143–155, 1991; Sterck et al., *Behavioral Ecology and Sociobiology* 41:291–309, 1997; van Schaik, In: Standen V, Foley RA, editors, *Comparative Socioecology*. Oxford: Blackwell. p 195–218, 1989]. This theory predicts that agonistic (“contest”) competition should occur when food is distributed in discrete, defensible patches; in contrast, when food sources are distributed uniformly or randomly, non-agonistic (“scramble”) competition is expected. Primatologists usually measure resource density and patchiness from a botanical perspective, ignoring the biology of the animal being studied. Such an approach may be irrelevant in terms of how animals view the dispersion of resources. Using a novel focal-tree method that measures resource availability on a scale that is both spatially and temporally relevant to the animal under investigation, we take a cost-benefit approach to predict the frequency of food-related agonism in white-faced capuchin monkeys (*Cebus capucinus*) from 11 ecological and social variables. We retained four variables in the regression model: two representing the opportunity for aggression (i.e., feeding bout length and the number of feeding adult females), and two representing opportunity costs (i.e., fruit abundance and the number of potential feeding sites in the focal tree). The results of this study indicate that the amount of food-related aggression in white-faced capuchins can be predicted by variables representing the costs

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*Correspondence to: E.R. Vogel, Department of Anthropology, University of California–Santa Cruz, 1156 High Street, Santa Cruz, CA 95064. E-mail: evogel@ucsc.edu

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INTRODUCTION

The study of primate socioecology assumes that most social behaviors are influenced by an animal's surrounding environment and ecological conditions. Several variants and extensions of Wrangham's [1980] socioecological model have been proposed to explain how resource characteristics affect feeding competition and ultimately relate to the diversity of female social relationships observed in nonhuman primates [Isbell, 1991; Isbell & Young, 2002; Koenig, 2002; Sterck et al., 1997; van Schaik, 1989]. In support of these models, there is a consensus that aggressive interactions in the context of feeding are more common when resources are limited and patchily distributed [Barton & Whiten, 1993; Borries, 1993; Isbell, 1991; Janson, 1988a,b; Pruett & Isbell, 2000; Shopland, 1987; Sterck & Steenbeek, 1997; van Schaik & van Noordwijk, 1988]. If resources are limiting reproductive success and can be easily defended, within-group contest competition is expected and selection should favor the formation of formal dominance hierarchies [Sterck et al., 1997; Koenig, 2002; Vogel, 2004]. On the other hand, if resources are highly dispersed and/or abundant enough for all group members to be satiated, aggressive defense is not profitable, and indirect or scramble competition over resources should be the prominent competitive regime. In this case, dominance rank will not enhance food acquisition within a social group [van Schaik, 1989].

While most studies have supported the predictions of socioecology theory [Isbell et al., 1998; Janson, 1986, 1988a; Koenig, 2000; Stevenson & Castellanos, 2000], some studies reported that decreased agonism is associated with food resources that are clumped and/or limited [Deusch & Lee, 1991; Gore, 1993; Hall, 1963; Loy, 1970; Stevenson et al., 2000]. These discrepancies may reflect the facts that the authors used different units for analysis (food items vs. food patches) and different methods to assess patchiness, or may indicate that the scale of available resources is not relevant to how the feeding monkeys themselves perceive such resources (see Isbell et al. [1998] for a detailed discussion). Surprisingly, very few studies have actually measured food characteristics on a scale that is relevant to the species or animals under investigation (but see Janson [1987], Koenig et al. [1998], Pruett and Isbell [2000], and Saito [1996]). Although this scale can be difficult to estimate, for social foragers it probably can be reasonably approximated by the spatial spread of the foraging group.

When measuring agonism over food resources, it is important to consider what criteria animals may use to assess the value of potential resources. Such criteria would include 1) the size of the feeding tree in relation to feeding group size; 2) the area an individual can actually defend; 3) the amount, size, and nutritional quality of the fruits available within the feeding tree; 4) the alternative resources that are actually available; and 5) the depletion rate of the patch [Janson, 1990; Isbell et al., 1998; Pruett & Isbell, 2000]. In this study we applied a novel focal-tree method (see Materials and Methods) that allowed us to measure the first four criteria on a scale that is both spatially and temporally relevant to the animals under investigation.

Cost-Benefit Approach

One way to test predictions of socioecological theory is to quantify the ecological costs and benefits associated with resource competition. In the case of food-related agonism, one must consider under what conditions aggression is expected to occur among gregariously foraging animals. In a cost-benefit approach, the benefits of obtaining the resource will depend on both the value of the contested resource and the availability of alternative resources (i.e., the opportunity costs of aggression). In conventional game-theory models of aggression [Maynard Smith, 1974], higher mean values for gaining access to a resource lead to a higher chance that any contestant will fight. However, if there are alternative resources available that are similar in value to the contested feeding site, individuals are expected to spread out and avoid agonism, since the alternative resources decrease the benefit of securing the primary resource through fighting. The nearest food to a contested feeding site is likely to be within the same tree crown, if it is large enough or has enough fruit. Once a tree crown contains enough food to satiate more than one monkey, the increased nutritional value is expected to lead to reduced agonism since potential contestants will move to other feeding locations rather than contest access to occupied sites. Thus, depending on the actual amounts of food in the feeding trees visited, the effect of increasing crown energetic value on agonism could be positive, negative, or both (positive for small values, and negative for large values of crown energetic value). This logic concurs with more recent models of social-foraging theory that predict that the amount of aggression should follow a concave-downward parabolic relationship with respect to resource value [Dubois & Giraldeau, 2003; Dubois et al., 2003].

It is difficult to estimate the physical cost of aggression in field studies because fights over food resources rarely result in an individual actually being injured [Dubois & Giraldeau, 2003]. However, one can estimate the “opportunity cost” of aggression (i.e., the benefits an individual could have obtained by avoiding aggression and using alternative feeding sites). One way to measure opportunity costs is to use the costs that result from an individual losing access to a feeding site (e.g., the amount of time a displaced animal spends searching for food after aggression to find an alternate feeding site) [Janson, 1985, 1988a]. An alternative measure of the opportunity cost that does not rely on the behavior of the displaced monkey is based on the number of alternative food trees outside the feeding tree that are actually available to the foraging animal. A more local measure of opportunity cost is the number of feeding sites available in the crown of the feeding tree. As this number increases, agonism is expected to decrease. Finally, the larger the number of competing monkeys in a tree crown, the lower the availability of food in these alternative feeding sites. Thus the amount of agonism is expected to increase with increasing numbers of cofeeding monkeys in a tree crown, all other factors being equal.

In this paper we consider the costs and benefits of contesting a food resource by analyzing variation among feeding trees in the frequency of agonism in white-faced capuchin monkeys (*Cebus capucinus*) as a function of social variables representing the opportunity for aggression, and ecological variables that should index the benefits of accessing the resource and the opportunity costs of obtaining access to a given feeding site.

Hypotheses

We tested a large number of social and ecological variables that are likely to be related to the amount of agonism within a feeding tree [Janson, 1987]. These

variables can be divided into sets of broad explanations for increased amounts of agonism observed within a tree crown.

The first set of hypotheses predicts the effect of variables that represent the opportunity for aggression on the frequency of agonism. Agonism might be explained simply by social variables that have proximate effects on the frequency of agonism. It is possible that high levels of agonism do not directly reflect any ecological costs or benefits, and instead are associated with increases in the number of feeding individuals, which would lead to an increase in the opportunity for aggression [c.f., de Waal & Hoekstra, 1980; McFarland-Symington, 1988; Stevenson et al., 1998]. The simplest null hypothesis is that agonism occurs at a constant rate per unit time per individual.

Thus, our first hypothesis was that the number of agonistic interactions per feeding bout would correlate positively with feeding bout length and the average number of individuals feeding in the tree crown.

Because access to food resources is hypothesized to limit female reproductive success to a greater extent than male reproductive success [van Schaik, 1989], effects of feeding ecology on female behavior should be reflected in intragroup female competition and strategic decisions made by females while foraging. On the other hand, while food may also limit male reproduction, the main limiting factor of male reproductive success is access to fertile females [Trivers, 1972]. Although males may compete for food resources, there will be less aggression, relative to females, in the form of intragroup food competition. Although socioecological models make predictions about the effects of female competition for food and safety on female social relationships, both males and females are expected to compete over food resources. Even if resources are less important for males and nonadults than for adult females, increasing numbers of the former will still likely increase food competition overall, although the effects may be less significant.

Our second hypothesis was that if agonism occurs with increased crowding, then the number of interactions should increase with the number of adult females, adult males, and nonadults in the tree crown, but the numbers of males and juveniles should have weaker effects.

It is also possible that ecological variables indirectly affect the amount of agonism in a tree strictly by controlling how many and what kinds of individuals feed together at a time. The likelihood that agonism will occur between particular individuals probably depends on the social (i.e., rank) and state-level (i.e., hunger) attributes of the contestants [Janson & Vogel, in press]; however, such analyses are beyond the scope of this paper (but see Vogel [2005]).

Our second set of hypotheses were concerned with ecological variables, such as the ecological benefits of resource defense or the opportunity costs of aggression, that may have a direct effect on the amount of agonism observed within a feeding tree. Significant effects of ecological variables, with the variables representing the opportunity of aggression held constant, would provide support for cost-benefit models of agonism.

For our third hypothesis, we predicted that if focal-tree crown energy (see Materials and Methods) is considered an ecological benefit, the frequency of agonism in trees characterized by high crown energetic value should be higher because there is more to be gained from winning (e.g., the benefits of access are greater). However, if all individuals can be satiated in the tree, one would expect scramble competition and a decrease in agonism. If fruit abundance is hypothesized to represent the value of a resource, it should follow the same

parabolic pattern as focal-tree crown energy with respect to the amount of observed agonism.

Finally, the amount of agonism may also depend directly on the ecological opportunity for individuals to avoid confrontations by feeding apart from each other. Monkeys may be able to avoid agonism by using other feeding locations both within and outside the crown of a given feeding tree. The benefits the individuals could have obtained by using these alternative sites are called the opportunity costs of choosing to use and contest a particular feeding site.

For our fourth hypothesis, we predicted that as the opportunity costs of aggression increase, the amount of agonism in a feeding tree should decrease.

To assess this possibility, we measured the presence and productivity of other potential feeding sites within and outside of each feeding tree. The variables used here were 1) the potential number of feeding sites within the focal tree, 2) the number of fruiting trees of the same species (conspecific trees) as the focal tree within 40 m of the focal tree (see Materials and Methods for justification of the 40-m criterion), 3) the number of fruiting trees of different species (nonconspecific trees) within 40 m of the focal tree, 4) an “alternative resource score” (see Materials and Methods), and 5) the minutes lost feeding (MLF) by the displaced individual when agonism occurred. In addition, both fruit abundance and total crown energy can be considered as measures of opportunity costs within the feeding tree, since the benefits of searching for alternative feeding sites in a tree characterized by high amounts of these two variables may outweigh the costs of contesting the resource. In this case, higher levels of these variables would be predicted to reduce the amount of agonism rather than increase it, as would be the case if they were measures of resource value or benefit. A summary of the variables and predicted patterns is presented in Table I.

MATERIALS AND METHODS

Study Site

White-faced capuchin monkeys (*Cebus capucinus*) were studied by E.R.V. in Lomas Barbudal Biological Reserve, the surrounding Instituto Para Desarrollo Agricultura (IDA) property, and the adjacent Finca El Pelón de la Bajura. The Lomas Barbudal Biological Reserve (hereafter referred to as Lomas) is a 2,279-ha reserve located in the northwest of Costa Rica, in Guanacaste Province (10°30' N and 85°22' W). The forest of the study area is generally classified as a tropical deciduous forest [Frankie et al., 1988]. Over 200 tree species have been identified in the reserve (Frankie, unpublished results), and 120 of these are used for food by the monkeys [Vogel, 2004].

Study Subjects and Sampling Period

All of the data reported here were collected from three study groups of white-faced capuchins (groups AA, RR, and QQ) that consisted of 34, 35, and 30 individuals respectively. During this study each group was composed of four adult males, eight to 10 adult females, one to four subadults, seven to nine juveniles, and three to six infants [Vogel, 2004]. The home ranges of the study groups during the study period varied from 2.76 to 4.40 km² and overlapped with those of other white-faced capuchin groups by approximately 10% [Vogel, 2004]. *C. capucinus* are primarily arboreal monkeys that live in mixed-sex cohesive groups with a male-to-female ratio close to 1:2.3. The females are philopatric [Fedigan, 1984, 1993; Oppenheimer, 1968; Vogel, 2004]. Males typically emigrate

prior to or at sexual maturity, and may transfer to different groups throughout their lifetimes [Jack, 2002; Jack & Fedigan, 2004a,b].

Data collection for this study started in December 2000 and was concluded in July 2002. E.R.V. studied groups AA and RR from December 2000 to August 2001, and group QQ from December 2001 to August 2002, for a total of 4,134 contact hours. Most of the data collection took place during the dry season, although it did carry over a few months into the rainy season. Individuals within a social group were identified according to differences in size, facial fur patterns, and other distinctive features (i.e., spots, freckles, scars, and broken tails). Data collection began once all observers (a total of six throughout the study period) were tested and agreed on the identification of all group members that were ≥ 3 years old [Vogel, 2005]. All individuals (both males and females) formed a linear dominance ranking system in the three study groups, and adult males were dominant over females, except for the alpha female in some cases [Vogel, 2004, 2005].

Focal-Tree Method

The main sampling technique used for this study was the focal-tree method [Vogel, 2004]. Specifically, one observer moved to the front of the group and stood under a feeding tree that the group was likely to visit (particularly ones used in the recent past). This observer used a PSION hand-held computer and/or a microcassette recorder to note the time and identification of the first arrival and each successive arrival, and the time and identification of each departing monkey from the tree. The time between the first arrival to the tree to the last departure is the group "feeding bout length." If there were gaps in feeding during the feeding bout, the amount of time in which the monkeys did not feed was subtracted from the total feeding bout length.

The second observer systematically recorded the number, identification, activity, and relative position of all monkeys in the tree at 2.5-min intervals. Thus, at the time of an agonistic interaction, the number of all monkeys and the identity of all adult and older juvenile monkeys within the feeding tree were known. Agonistic interactions included all submissive behaviors (e.g., avoids, cowers, and fear-grins) and all active aggression (e.g., threats, chases, bites, and displacements). Data were taken until the last group member left the tree. The average number of adult males, adult females, and nonadults in the focal tree throughout the feeding bout were calculated from these 2.5-min point samples.

At the time of an agonistic interaction, the first observer recorded the individuals involved and the proximity of all visible individuals in the tree to the interacting animals. This observer also recorded data on who won the interaction and whether the aggressor(s) started feeding at the site of the interaction, and continued recording data on all arrivals and departures. The second observer then followed the displaced monkey and noted the distance traveled from the focal tree and the time when it resumed feeding on fruit. If the feeding bout terminated before the displaced individual fed, the time when the last individual left the tree was recorded. The time between departure from the feeding site as a result of agonism and the earlier of 1) the resumption of feeding by the displaced individual, or 2) the end of the feeding bout in the tree from which it was displaced is called the "minutes lost feeding" (MLF). The MLF by the displaced animal is used to estimate the "opportunity cost" of contesting access to a feeding tree [Janson, 1985, 1988a].

In addition to the first interaction in the focal tree, all subsequent aggressive interactions in that feeding tree were recorded, and whenever possible the

displaced individual was followed and the MLF and distance traveled were noted. Thus, at the termination of a focal-tree follow, the total number of aggressive interactions within the tree was known. All focal trees were marked with a unique ID for further ecological processing.

Ecological Sampling

For each focal tree we recorded fruit abundance and measured perpendicular crown diameters, from which we calculated the fruiting crown volume by using the equation for the volume of an ellipsoid [Janson, 1988a]. Given the difficulties of accurately assessing fruit availability [Chapman et al., 1992], we measured the ripe-fruit availability of the focal tree using three different methods [Vogel, 2004]. However, we report the “visual fruit count” because it was used consistently across all focal trees and is the most direct estimate of fruit abundance. For small crowned trees, we obtained the visual fruit count by directly counting all visible fruits on the tree. For large trees with many small fruits, an additional method of estimating fruit counts was used. Five 1-m³ areas of the crown were selected on an ad libitum basis [Chapman et al., 1992]. Samples were spread throughout the tree crown, and the number of fruits within each area was counted. The mean of these counts was then calculated and multiplied by the tree crown volume in m³. Slight variations of the visual fruit count method were used depending on whether the unripe and ripe fruit were easily distinguished (for further details, see Janson and Vogel [in press]).

To obtain an estimate of the potential for competition within the focal tree, we calculated the number of potential feeding sites in the focal tree by considering the minimum area an individual would defend while feeding. Because this was not directly measured in the field, an estimate of this variable was derived. One possible alternative to obtaining a direct measurement is to plot the maximum number of feeding animals in the tree against the crown volume and derive an upper limit to the number of animals that “fit” into a crown volume of a given size by drawing a line such that most points lie below the line. The inverse of the slope of the resulting line gives a minimum volume per feeding animal, and this can be used as a crude approximation of the amount of space an animal will defend in a feeding tree. Using this method, we determined the volume that a capuchin monkey would defend to be 200 m³ (a sphere with a radius of 3.63 m). Thus, by dividing the crown volume of the focal tree by 200 m³, we calculated a rough estimate of the number of potential feeding sites within the focal tree.

The MLF is one estimate of the opportunity cost of contesting access to a feeding tree. An additional measure of the opportunity cost that does not rely on the behavior of the displaced monkey is based on the availability of alternative food trees outside a focal feeding tree. For each focal tree, all alternative food resources used by the monkeys during that time of year that were within the average group spread of the focal tree were recorded. Although group spread varied from day to day and hour to hour within a day, a single value for the average group spread was used to calculate the alternative resource availability. In this study the average group diameter was about 80 m [Janson & Vogel, in press]. Thus, all potential feeding trees within a radius of 40 m of the focal tree were recorded, yielding a sample area of almost exactly 0.5 ha.

For each alternative resource, the following variables were measured: perpendicular crown diameters to calculate crown volume, fruit abundance (using the visual fruit count method described above), and the distance of the alternative resource to the focal tree. Because it is too difficult to gather these

data while making behavioral observations, the focal tree was marked on the day of the feeding bout, and within 2 days one observer (the same person throughout the study period) recorded the focal- and alternative-resource tree data.

Nutritional Analyses and Measures of Crown Energy

All fruit species eaten by the capuchins during the study period were collected from trees in which the monkeys had fed, but not necessarily the focal trees. Only those fruits that were similar in size and maturation stage to fruits selected by the capuchins during the feeding bout were selected. The fruits were weighed in its entirety and then divided into components (seed, husk, and pulp). Each component was weighed again and then dried until they maintained a constant weight [Hladik, 1977]. The dried samples were then placed in a sealed bag containing 1/8 inch of silica gel beads, and sent to Prof. Dr. J. Ganzhorn's laboratory in Hamburg, Germany, for nutritional analysis. The composition of the food (% soluble carbohydrates and % fat) was analyzed as in Ganzhorn [1988]. Crude protein was determined using the Kjeldahl procedure for total nitrogen and multiplying by 6.25 [Pierce & Haenisch, 1947]. The total kilojoules (kJ)/g dry mass for each species was calculated as in Vogel [2005].

Focal-tree fruit abundance and crown energy (focal tree fruit biomass \times kJ/fruit) were used as measures of the value of the focal tree. A combined measurement of the nutritional value of all alternative resources within the group spread is also necessary to gain an understanding of the value of a particular resource to an animal. This comparison is needed because the value of a resource is based on the nutritional gain relative to all other potential resources. For this reason, we calculated an alternative resource score (ARS) using the following equation, which was summed across all alternative feeding trees within 40 m of the focal tree:

$$\sum \frac{(\# \text{ fruits/tree})(\text{pulpmass/fruit})(\text{energy/unitmass})}{D + K}$$

where D is the distance of a tree from the focal tree, and K is a scaling constant used to avoid infinite values for the focal trees that had adjacent alternatives and thus a distance of zero ($n = 6$). Each individual focal tree had a respective alternate resource score, which is the sum of energy availability in each alternative tree, discounted by the distance of the alternative resource from the focal tree plus a scaling constant K in meters. For this analysis, a value of K equal to 20 was chosen because previous analyses have shown that trees within 20 m of the focal tree are all more or less equally important to the capuchin monkeys relative to more distant ones [Vogel, 2004]. However, a sensitivity analysis was performed with four different values of K ($K = 1, 10, 20,$ and 40), and the qualitative results of all analyses were consistent.

Statistical Procedures

Because the study groups did not differ in the use of aggression over food sources (Wald statistic = 1.02, $df = 604$, $P = 0.16$), the focal tree data were pooled for all three groups. The analyses are based on data from a total of 604 feeding bout visits to over 350 different focal trees of 37 species recorded over a 2-year period. The dependent variable in all analyses was the number of agonistic interactions (referred to as the frequency of agonism) throughout a single feeding bout. Because some of the independent variables were actually ratios or products of other variables, their variances were often correlated with their means

(heteroscedastic). Thus, for the frequency of agonism analysis, all variables were log-transformed and the normality of residuals was analyzed [Sokal & Rohlf, 1995]. Plots of the residuals of the dependent variable against the predictor variables showed that the residuals were uncorrelated with the value of the predictor variables.

Poisson regression models were used to predict the relationship between several ecological and social variables and the frequency of agonism per feeding bout. We used 11 variables (Table I) to explain variation in the frequency of agonism for each visit to a given focal tree. To test for the predicted concave-downward parabolic relationship between both fruit abundance and crown energetic value and the frequency of agonism, we included both the quadratic and linear term for these variables in the full Poisson regression model. Because none of the pairwise correlations between any of the independent variables was greater than 0.68, we did not consider collinearity to be a major problem in interpreting the results given below.

The complete analysis limited the sample size of focal tree feeding bouts to 374, and included only trees in which at least one agonistic interaction was observed, because the MLF is defined only when agonism was observed. Thus, the

TABLE I. List of Potential Explanatory Variables Used in the Multiple Regression Model Predicting the Frequency of Agonism and the Predicted Linear Direction of the Regression*

Variable	Hypothesis ^a	Expected sign of effect
Feeding bout length in minutes	Opportunity for agonism; Null Model (1)	+
Average number of feeding adult females in focal tree	Opportunity for agonism; (2)	+
Average number of feeding adult males in focal tree	Opportunity for agonism; (2)	+
Average number of feeding non-adults in focal tree	Opportunity for agonism; (2)	+
Focal tree crown fruit abundance	Resource value (3)	+ (Small values)
	Opportunity costs (4)	- (Large values)
Focal tree crown energy	Resource value (3)	+ (Small values)
	Opportunity costs (4)	- (Large values)
Number of potential feeding sites in focal tree	Opportunity costs (4)	-
No. alternate fruiting trees of same species as focal tree within 40 m of focal tree	Opportunity costs (4)	-
No. alternate fruiting trees of different species from focal tree within 40 m of focal tree	Opportunity costs (4)	-
Minutes lost feeding = time until displaced individual feeds again	Opportunity costs (4)	+
Alternate resource score, visual fruit count, K = 20	Opportunity costs (4)	-

*The predicted relationship between both crown fruit abundance and crown energetic value and the frequency of agonism is parabolic; however, their non-linear relationships arise from different causal mechanisms as indicated by the below hypotheses.

^aCorresponding hypothesis number is given in parentheses.

inclusion of this variable in the analysis severely restricted sample size and may have biased the results, as trees with no agonism were necessarily excluded. Therefore, we also recalculated all analyses with this variable removed. This increased the sample to 604 focal tree feeding bouts, including those in which no agonism occurred. We used the Akaike information criterion (AIC) to reduce the regression model to a smaller number of explanatory variables [Quinn & Keough, 2002]. All statistical procedures were carried out using Statistica 5.5[®] and JMP-SAS 5.0.1a[®] statistical software. All probability levels are two-tailed, and significance for all tests was set at $\alpha \leq 0.05$.

RESULTS

Social Variables and the Frequency of Agonism

The overall regression model including all 11 variables in Table I was highly significant ($\chi^2 = 18.36$, $df = 361$, $P < 0.0001$). In support of the first set of hypotheses, with all other variables held constant (Table I)¹, the greater the average number of monkeys in the feeding tree, the greater the number of aggressive interactions (estimated model coefficient for average number of monkeys in the feeding tree = 1.41, Wald statistic = 10.02, $df = 1$, $P = 0.001$). Inclusion of the MLF in the analysis did not improve the overall fit of the model (likelihood ratio = 156.79, $df = 231$, $P = 0.99$) and because it limited the sample size and excluded trees without aggression, the MLF was excluded from the remainder of the analyses described below.

The best subset regression model, determined using AIC, retained five important variables (Table II). Although the model-selection algorithm used by AIC is objective, it does not guarantee conventional significance of each chosen predictor variable. Because the AIC values for the first few candidate models were so close, we selected the second model in Table II because of 1) the biological relevance of the included variables, and 2) the conventional statistical significance level of each chosen predictor variable. The only predictor variable that did not reach conventional significance ($P < 0.05$) in the chosen model (Table III) was crown fruit abundance (Wald statistic = 2.71, $df = 1$, $P = 0.10$). Although the best-fit model selected using AIC included the number of nonadults in the feeding tree, we did not include this variable in our final model to explain variation in the frequency of agonism because the inclusion of this variable in the analysis did not improve the overall fit of the model (likelihood ratio = 2.07, $df = 1$, $P = 0.15$).

Based on van Schaik's [1989] socioecological model, we predicted a priori that the average number of adult females in a feeding tree would be a strong predictor of agonism, but the numbers of males and juveniles would have weaker effects, since food sources are typically more important for adult females. In support of van Schaik's [1989] model, there was a positive relationship between the number of adult females in the feeding tree and the frequency of agonism (Table III). The relationship between the number of adult males and nonadults and the frequency of agonism in the feeding tree was nonsignificant.

A possible "trivial" explanation for the stronger relationship between female numbers (compared to adult male numbers) and the frequency of agonism is that there were more adult females in the study groups, and thus there was a greater

¹Instead of using the numbers of adult females, adult males, and nonadults in the analysis, we included the variable "average number of monkeys in the feeding tree."

TABLE II. Results of the Best-Subset Poisson Regression to Explain the Variation in Number of Agonistic Interactions Per Visit to a Feeding Tree by White-Faced Capuchin Monkeys*

Variables included in the model	Degrees of freedom	AIC
(1), (2), (4), (5), (6)	5	775.69
(1), (2), (5), (6)	4	776.01
(1), (2), (5)	3	776.17
(1), (2), (4), (5), (6), (8)	6	776.28
(1), (2), (3), (4), (5), (6), (8)	7	777.50
(1), (2), (3), (4), (5), (6), (8), (9)	8	779.13
(1), (5)	2	780.53
(1), (2), (3), (4), (5), (6), (7), (9), (10)	9	780.74
(1)	1	781.92
(1), (2), (3), (4), (5), (6), (7), (8), (9), (10)	10	782.49

*The candidate model with the subset of variables with the lowest AIC is the best fit model. The test is based on 604 focal tree visits. The chosen best-subset model (in bold) was highly significant $\chi^2 = 37.92$, $df = 5$, $P < 0.0001$. The variables included in the model selection were as follows: (1) Feeding bout length in minutes, (2) Average no. of feeding adult females, (3) Average no. of feeding adult males in focal tree, (4) Average no. of feeding non-adults in focal tree, (5) Number of potential feeding sites in focal tree, (6) Crown Fruit Abundance, (7) Crown energy, (8) No. alternate fruiting trees of same species as focal tree, (9) No. alternate fruiting trees of different species from focal tree, (10) Alternate resource score.

TABLE III. Results of the Parameter Estimates from the Selected Best-Subset Poisson Multiple Regression Model as Determined by the AIC

Variable	Expected sign	Slope (beta)	Standard		
			Error (beta)	Lower 95% CL	Upper 95% CL
Intercept		-2.478	0.308	-3.083	-1.874
Feeding bout length in minutes	+	0.977	0.221	0.544	1.411
Average number of feeding adult females in focal tree	+	1.394	0.546	0.325	2.464
Number of potential feeding sites in focal tree	-	-0.663	0.330	-1.309	-0.016
Crown fruit abundance	+, -	-0.075	0.058	-0.189	0.039

potential range in the number of females across focal trees. Greater variation in the independent variable is often associated with greater regression slopes because of measurement error in the independent variable [e.g., Pagel & Harvey, 1988]. However, this possibility was not supported. Even though the mean number of females in a focal tree was twice that of males, the average number of adult males across focal trees had a standard deviation (SD) that was about equal to that of adult females (Fig. 1). The effect of increasing the number of adult females in the feeding tree was strong: Under the current model, the value of the slope suggests that if the number of adult females within the feeding tree were to increase by one individual, the expected rate of agonism would increase multiplicatively by $e^{1.394} = 4.03$ (confidence interval (CI) = 1.38–11.75) [McCullagh & Nelder, 1989].

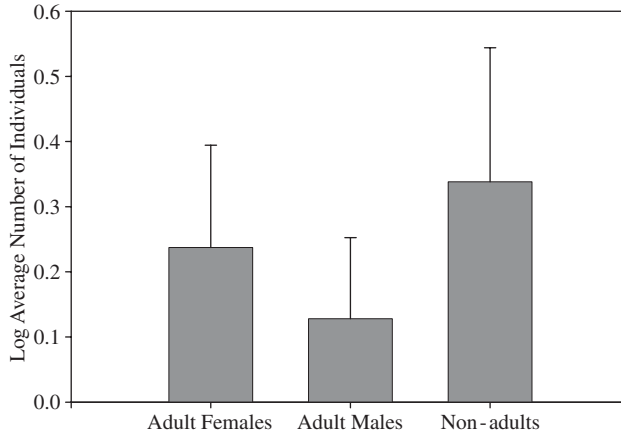


Fig. 1. The log average number of feeding adult females (0.23 ± 0.15), males (0.12 ± 0.13), and nonadults (0.33 ± 0.21) in focal trees throughout the feeding bout. Means \pm SDs are reported ($n = 609$).

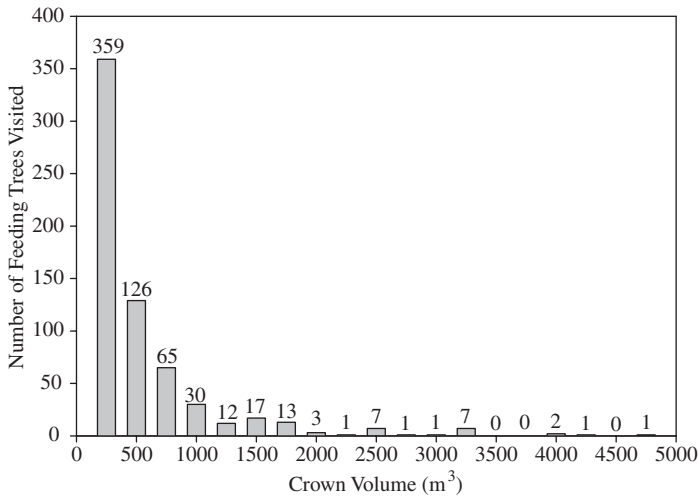


Fig. 2. The distribution of crown sizes of feeding trees used by *C. capucinus* throughout the study period. Mean = 428.56, SE = 23.63, $n = 649$. The number of trees in each crown volume class size is given above the bar.

Predicting the Frequency of Agonism From Ecological Variables

Given that increases in the number of feeding monkeys in the tree were related to higher amounts of agonism, we were particularly interested in whether ecological variables would be informative in predicting agonism. Food trees used by capuchins in this dry forest were characterized by primarily small to medium crown volumes (Fig. 2). The potential number of feeding sites within the average feeding tree during the study period was 2.19 feeding sites (SE = 0.12).

There was a positive relationship between feeding bout length and the frequency of agonism. A linear correlation could result if the *rate* of agonism (number of interactions/unit time) was constant throughout the feeding bout. On a log-log scale, as used here, strict proportionality would be represented by a slope of 1.0. Because the CI for feeding bout length included a value of 1.0 (Table III), we do not rule out the hypothesis that there is a constant rate of agonism.

As predicted if fruit abundance represents a measure of the opportunity cost of aggression, trees with lower fruit abundance had higher amounts of agonism than trees with high fruit abundance (Table III). However, although crown fruit abundance was included in the AIC regression model, it did not reach conventional statistical significance (Wald statistic = 2.71, $df = 1$, $P = 0.10$). Trees with fewer potential feeding sites within the crown were also characterized by higher amounts of agonism (Table III). The inclusion of these two ecological variables (crown fruit abundance and the number of potential feeding sites within the crown) significantly improved the overall fit of the regression model (likelihood ratio = 15.58, $df = 5$; $P = 0.008$). The relationship between crown energy and the frequency of agonism was nonsignificant. When the quadratic term for fruit abundance and crown energy were included in the model, the model did not explain any additional variation in the frequency of agonism (likelihood ratio = 0.01, $df = 1$, $P = 0.92$), and the variables included in the best subset Poisson model did not change.

A foraging individual should not make a decision to contest a resource based only on the potential benefits and alternative feeding opportunities inside a feeding tree. Instead, it should evaluate the *net* benefits of staying in the feeding tree (i.e., the benefits inside the feeding tree minus the costs of agonism) vs. leaving the tree and searching for alternative resources. In this study the frequency of agonism was not significantly related to any of our measures of opportunity costs outside of the feeding tree (e.g., the number of conspecific and nonconspecific alternative trees, the MLF due to agonism, and the alternative resource score).

DISCUSSION

Indirect Effects of Ecology on the Frequency of Agonism

The results of this study suggest that both social and ecological variables are important in explaining the amount of food-related agonism observed for *Cebus capucinus*. As the number of individuals in a feeding tree increases, so does the likelihood of agonism, because subordinate individuals will approach dominants too closely [Vogel, 2005]. In fact, Janson [1996] reported that dominant individuals on food platforms reduce the feeding success of subordinates only within a 10-m radius of the dominant animal. In general, the food trees used by capuchins in this study were characterized primarily by small to medium crown volumes, which means that group members had two options when foraging for fruit: 1) crowd into fruiting trees until dominant individuals no longer tolerate subordinates and force them to leave by means of active agonism, or 2) search for alternative resources and avoid any costs associated with agonism. Contest competition is an important tactic used by dominant capuchin monkeys during feeding bouts [Vogel, 2005]. Because increases in the average number of adult females and decreases in the number of potential feeding sites within the focal tree were both associated with increases in the frequency of agonism, it appears that individuals chose the first of the two options.

The best-fit model selected with AIC included the number of juveniles. However, we did not include this variable in our final model, for three reasons: First, it was not close to conventional significance, and thus the relationship between the number of juveniles and the frequency of agonism was weak. Second, the inclusion of this variable in the model did not explain any additional variation in the frequency of agonism. Third, adult females are very tolerant of subordinate juveniles in the feeding tree, and direct the majority of their aggression toward

other adults [Vogel, 2004] (Vogel, personal observation). It is not surprising that the number of adult males was not a predictor of the frequency of agonism. Because males are dominant to most other group members, if alternative feeding sites are available, males are able to spread out and utilize trees because the likelihood of being displaced is low [Vogel, 2004]. Thus, adult males may avoid confrontations by spreading out. Future studies will examine sex differences in the initiator and targets of agonism within feeding trees.

Ecological Costs and Benefits of Agonism: Why Fight?

In this study we do not emphasize the importance of any one variable within a set belonging to one of the broader hypotheses; rather, we use the results for any of the variables merely to indicate the importance of the biological hypothesis it represents (Table I). The results of this study suggest that white-faced capuchins may contest a food resource based on the ecological costs and benefits associated with a particular resource. The four retained variables in the final model represented the opportunity for aggression (i.e., the feeding bout length and the number of adult females), and opportunity costs (i.e., the number of potential feeding sites and the crown fruit abundance). Because the rate of agonistic events may be constant throughout the feeding bout, individuals have more opportunity to fight if they spend longer periods of time in close proximity within the feeding tree.

Increased numbers of adult females and decreased number of potential feeding sites were associated with increased agonism, which suggests that it is easier for individuals to avoid agonism when they feed in large crowned trees. Agonism increased with increased opportunity for aggression, as reflected by a positive relationship with the number of individuals. In this study, the presence of a higher absolute number of individuals in the feeding tree increased agonism via the null hypothesis (i.e., that agonism occurs at a constant rate per unit time per individual) and possibly by reduced opportunity costs, because there would be fewer empty feeding sites and less to eat in them with more feeding individuals in the tree.

The negative relationship between the amount of agonism and focal-tree fruit abundance suggests that fruit abundance is a better measurement of the opportunity cost of aggression than of resource value. This may be explained by the fact that trees with very high fruit counts generally had large crowns and small fruits (i.e., *Sloanea terniflora* and *Ficus* sp. [Vogel, 2004]), a situation that could lead to low levels of agonism because there are many feeding sites per tree that are of similar value. In contrast, in trees with small crowns and larger fruits, fruit abundance and ripeness are likely to vary more between feeding sites.

How individuals view the opportunity costs of aggression will determine whether the quality and/or quantity of alternative resources are important factors when they decide whether to risk aggression by staying in a tree or to leave and search for alternatives. Several researchers have demonstrated that individuals have cognitive spatial maps of food trees within their territories [Garber, 1989; Janson, 1996], but probably make most foraging decisions based on the availability of alternate resources within close proximity to the feeding tree [Janson, 1988a; Janson & Di Bitetti, 1997]. Thus, it is logical to assume that individuals know the potential benefits outside of a specific food tree ("opportunity costs") and consider them when making foraging decisions. The results of this study do not support that assumption. However, this does not necessarily mean that alternative resources are not important factors in making

foraging decisions, since they may be important for making decisions regarding the type of aggression observed and the number of monkeys that feed within the feeding tree [Vogel, 2004].

One other potentially explanatory variable in estimating opportunity costs, the MLF, did not predict the frequency of agonism. There are at least two explanations for this lack of significance. First, because the total time from displacement until resumption of feeding was measured, there may have been periods during which the animals were not searching for food. Second, the displaced animal may have been close to satiation at the time of the displacement, and thus was not necessarily concerned with immediately finding another fruit source. In a previous study of *Cebus apella*, the percentage of time lost feeding was not correlated with the amount of agonism received [Janson, 1985]. Thus, it may be that as long as there are alternative feeding sites close to the contested site, the amount of time it takes to reach them is not as important to these populations of capuchins.

In this study the frequency of agonism was highest when the abundance of fruit in the tree was low and there were few alternative feeding spots within the feeding tree. Thus, as the benefit of obtaining this limited resource increases, because there are few alternative feeding sites of equal value within the feeding tree, the frequency of agonism will also increase. On the other hand, individuals will avoid aggression and spread out when there are increased opportunities to feed elsewhere (i.e., when the opportunity costs of agonism are high). There is a clear cost of remaining in focal trees that are characterized by high rates of aggression: low-ranking individuals have reduced feeding rates relative to high-ranking individuals in trees with a high frequency of agonism [Vogel, 2005]. Thus, it is costly for subordinates to remain in highly contested trees, and they should switch rather than fight if higher energy gain rates can be obtained elsewhere. These results are consistent with the predictions of foraging theory [Giraldeau & Caraco, 2000; Stephens & Krebs, 1986; Parker & Sutherland, 1986].

The results of this study indicate that both social and ecological variables are important for understanding food competition in white faced capuchins (*C. capucinus*). In contrast to the low levels of contest competition reported by Phillips [1995a,b], contest competition over food in the Lomas capuchins was quite high [Vogel, 2005], with an average of 1.5 interactions per focal tree ($n = 657$, $SE = 0.08$). Unfortunately, because the two studies measured resource abundance differently, and alternative resource availability was not reported by Phillips [1995a,b], it is not possible at this time to make direct comparisons of ecological traits that may affect these social differences; however, this will be analyzed in the future. Given that the groups studied by Phillips did not display a rigid dominance structure, while the three groups from this study did [Vogel, 2005], it appears that food resources in the Lomas Barbudal region of Costa Rica may be more limited and/or patchy than those found on Barro Colorado Island. One possible explanation for the difference in the amount of food-related aggression between these two populations is that the Lomas capuchins in the current study lived in groups that were twice as large as those in Barro Colorado. There may be less competition for food among group members living in smaller social groups, as they can spread out more while feeding.

The results from this study agree with Janson's [1985, 1986, 1987, 1988a] work on Peruvian brown capuchins (*Cebus apella*). Although the ecological data obtained in those studies and the present one were collected using different methods, in all of these studies resource availability was measured on a spatial scale that was relevant to the species under investigation. Given their social

similarities, it is not surprising (but is nevertheless gratifying) to find that aggression in both species is associated with the same ecological characteristics—i.e., the number of available potential feeding sites and the amount of fruit within the feeding tree.

For the focal-tree method described here, resource availability should be measured as soon as possible after the behavioral observations are taken. However, it may be difficult to apply the focal-tree method to all types of forests and study species. The method may have to be modified based on the plant and primate species under investigation. For example, depending on the species under investigation, the observer may also want to use the maximum group spread, although this may be labor-intensive and not very practical. We encourage field biologists to modify the focal-tree method as necessary to fit their study species, but urge them to always measure resource availability from the study animal's point of view.

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