

Erin R. Vogel

Rank differences in energy intake rates in white-faced capuchin monkeys, *Cebus capucinus*: the effects of contest competition

Received: 11 November 2004 / Revised: 11 April 2005 / Accepted: 12 April 2005 / Published online: 4 May 2005
© Springer-Verlag 2005

Abstract The effect of aggressive competition over food resources on energy intake rate is analyzed for individuals of three groups of 25–35 white-faced capuchin monkeys, *Cebus capucinus*, living in and near Lomas Barbudal Biological Reserve, Costa Rica. An individual's energy intake rate on a given food species was affected by its rank and the number of agonistic interactions within the feeding tree. Dominant group members had higher energy intake rates relative to subordinate group members whether or not there was agonism within the feeding tree. Low- and mid-ranked individuals had lower energy intake rates in trees with higher amounts of aggression, while energy intake rate of high-ranked individuals was not affected by the amount of aggression in the feeding tree. Energy intake was not influenced by the sex of the individual when rank was held constant statistically. Energy intake was positively correlated with total crown energy (measured in kilojoules) within the feeding tree for two of three study groups. This difference may be explained by the quality of each group's territory. Finally, high-ranked individuals are responsible for the majority of agonism within feeding trees and target middle- and low-ranked individuals equally. These findings fit the predictions of current socioecological models for within-group contest competition over food resources. The results of this study suggest that within-group competition affects energy intake rate in white-faced capuchin monkeys.

Keywords Agonism · Within-group competition · Capuchins · Contest · Socioecology

Introduction

Two forms of competition have been recognized among mobile animals: contest and scramble (Nicholson 1954). In the case of scramble competition, indirect or exploitative competition for resources occurs such that as a result, some individuals remove limited food resources from an area before other individuals have the opportunity to feed. In this mode of competition, competitors adjust their spatial distribution in relation to habitat quality and there is no exclusion of weaker competitors by stronger ones (Milinski 1979; Power 1984; Wilson and Vogel 1997). In contest competition, animals restrict access to resources by means of subtle or active aggressive interactions, thereby restraining the energy intake of lower ranking individuals. Although both scramble and contest competition may result in variation in relative fitness among group members, this variation is explained by different mechanisms. Specifically, contest competition will result in differences in average intake rates of food resources among high- and low-ranking group members, whereas scramble competition will result in differences in average intake rates of individuals in different sized groups (van Schaik and van Noordwijk 1988). Several studies have documented the effects of contest competition on individual group members by analyzing rank effects on feeding rates. The majority of these studies have found that dominant individuals have higher food intake rates than subordinates (Janson 1985; Benkman 1997; Robichaud et al. 1996; Saito 1996; Hino 2000; Koenig 2000; Harwood et al. 2003; but see Liker and Barta 2002).

There is a consensus in the primate literature that within- and between-group competition over food and mates have shaped the diverse social relationships observed among group members (Wrangham 1980; van Schaik and van Noordwijk 1986; Janson 1986; 1988a, b; Janson and van

Communicated by J. Setchell

E. R. Vogel (✉)
Department of Ecology and Evolution, Stony Brook University,
Stony Brook, NY 11794, USA
e-mail: evogel@ucsc.edu

E. R. Vogel
Zoological Institute and Museum, University of Hamburg,
Martin-Luther-King Platz 3,
20146 Hamburg, Germany

Present address:
E. R. Vogel
Department of Anthropology, University of California,
Santa Cruz 1156 High Street,
Santa Cruz, CA 95064, USA

Schaik 1988; van Schaik 1989; Isbell 1991; van Hooff and van Schaik 1994). Several variants and extensions of Wrangham's (1980) socioecological model have been proposed to explain the diversity of female social relationships in non-human primates (van Schaik 1989; Isbell 1991; Sterck et al. 1997). When the abundance and distribution of resources do not limit exploitation, or if food patches are too large or abundant to be defended by individual animals, then aggression should be infrequent, and within-group scramble (WGS) competition should be common (van Schaik 1989). In this situation, females should not frequently form coalitions, female relationships are predicted to be egalitarian, and females may disperse from their natal groups to reduce indirect feeding competition by joining a group of a different size (van Schaik 1989; but see Watts 1997). In this case, total energy per individual should be independent of social rank but should decrease with increasing group size, although this relationship may not be linear.

Conversely, when resources are concentrated and thus easily monopolized, selection will favor contest competition. Contest competition is thought to favor hierarchical female social relationships, nepotism, and coalitions between females, especially kin (van Schaik 1989; Chapais 1992; Sterck et al. 1997). When within-group-contest (WGC) is the predominant competitive regime, high-ranking females are predicted to have higher total energy gain and reproductive success relative to low-ranking females (Sterck et al. 1997; Koenig 2002). If high ranking individuals can monopolize a high quality food patch and exclude lower ranking individuals from feeding, then high ranking individual most likely obtain an advantage from doing so.

Recent studies have suggested that local food distribution is an important factor in determining the mode of feeding competition, agonistic behavior, and female social relationships (Mitchell et al. 1991; Sterck and Steenbeek 1997; Isbell and Pruettz 1998; Isbell et al. 1999; Koenig 2002). Because most primates live in stable groups with long-term social relations that are decisive for survival and reproductive success (Altmann and Alberts 2003a; Silk et al. 2003), studies on the effects of dominance rank on food intake rates are quite common. However, actual measures of energy gain remain limited (Koenig 2002); data concerning interrelations of agonistic behavior and energy gain are particularly scant (but see Janson 1985, 1988a). This lack of energy data leaves unexplored whether the rate of agonism is indeed related to energy gain and how it is affected by habitat variables. Ultimately, it leaves the mechanism of feeding competition and its relationship to the benefit of rank unknown. In this paper, an individual's nutritional gain rate was examined as a function of several ecological and social variables hypothesized to affect energy intake rates of social group members. This study was conducted with white-faced capuchin monkey, *Cebus capucinus*, because both males and females form linear dominance hierarchies and they exhibit relatively high amounts of agonism in food trees (Vogel 2004). 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. Thus, the impact of WGC across all adult, subadult, and juvenile female and male group members was also examined.

Based on Janson's (1985) results on feeding competition in *Cebus apella*, three major a priori predictions were made concerning the effect of several ecological and social variables on energy intake rate. First, energy intake rate was hypothesized to increase with trees characterized by higher fruit availability and nutritional biomass, which was assessed by estimates of total energetic value of the fruit pulp in the tree crown (referred to as total crown energy). This is because individuals can spend more time feeding on high quality resources and spend less time searching for alternative food sources, thereby increasing their net energy gain. If within-group contest competition for food is important, then food intake should increase with an individual's dominance status or aggressive success (Janson 1985). Furthermore, if dominants can defend a food patch by either forcing subordinates to leave the tree or forcing them to feed in less productive areas, then this should be reflected in the subordinate animal's food intake rates. For *C. apella*, dominant capuchins had higher feeding rates than subordinates in food trees with high rates of aggression, but in trees with very little or no aggression, there were negligible rank differences in feeding rates (Janson 1985). Thus, the second hypothesis was that subordinate monkeys should have lower energy intake rates than dominant monkeys and this difference in intake rate should increase in trees with higher levels of aggression. In conventional game theory models of aggression (Maynard Smith 1974), higher mean values of obtaining a resource leads to a higher chance that a contestant will fight. Thus, when food patches are small enough to defend and/or have high potential nutritional gain, they are of greater value to the monkeys and thus are expected to result in higher rates of aggression. Following this logic, the third hypothesis was that frequency of aggression should increase in trees characterized by high energy intake rates. This is because in trees characterized by high feeding rates, there are greater energetic incentives for dominant individuals to prevent lower ranking group members from feeding in the tree and/or that lower ranking individuals are more likely to challenge dominants (Janson 1985). Finally, the fourth hypothesis was that if high-ranked group members are responsible for the differences in energy intake rates between the higher- and lower-ranked individuals by means of WGC, then higher-ranked group members should initiate the majority of food-related aggressive interactions, and the targets of dyadic interactions should be of lower rank.

Methods

Study area and populations

White-faced capuchin monkeys were studied in Lomas Barbudal Biological Reserve, the surrounding IDA Property, and Finca El Pelón de la Bajura. Lomas Barbudal is a 2279 ha reserve located in the Guanacaste Province,

north-west Costa Rica (10°30' N and 85°22' W). The forest is classified as a tropical deciduous forest (Frankie et al. 1988). Trees of Lomas form a discontinuous canopy without distinct stratification. Large trees reach an average height of 20–25 m, although some riparian species reach about 30 m.

The Guanacaste region has distinct wet and dry seasons. Frankie et al. (1988) recognized four seasons in the reserve based on relative moisture. There is one short dry season from late June to early/mid August and one long dry season, from early November to late May. Thus, the rainy season can be also broken up into two seasons, the first from late May–early July and the second from late August–November. The majority of the reserve's 1000–2200 mm of annual rain falls between the months of late May and late November. Because the site is a tropical dry forest, most trees lose their leaves during the dry season, allowing for excellent observation conditions. However, even in the early months of the rainy season, observation conditions were sufficient such that all individuals in the focal tree (see below) could be identified. Over 200 tree species have been identified in the reserve, 101 of which were observed to be used for food by the monkeys (Vogel 2004).

Observation period and study groups

All data reported here were collected from three study groups of white-faced capuchins, Group AA, RR, and QQ, containing 34, 35, and 30 individuals respectively. During this study, each group was composed of 4 adult males, 8–10 adult females, 1–4 subadults, 7–9 juveniles, and 3–6 infants (Vogel 2004). 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%.

Data collection for this study started in December 2000 and ended in August 2002. Most of the data were collected during the longer dry season, although some of the data were collected a few months into the rainy season. Two groups (AA and RR) were studied from December 2000–August 2001, and Group QQ from December 2001–July 2002, for a total of 4134 contact hours. During the 2000–2001 observation time was split equally between the two groups, for a total of 2184 contact hours. AA was habituated in 1990 and RR in 1997 (Gros-Louis et al. 2003). Habituation of a third group, QQ, was started in August 2001. The group was habituated to observers by the end of January 2002. Data collection began once all observers were tested and agreed on the identification and behaviors of all group members, and the monkeys showed no signs of fear or avoidance towards the observers (Vogel 2004). For the 2002 field season, a total of 1950 contact hours were spent with Group QQ.

Observation techniques

Individuals within a social group were identified using differences in size, facial fur patterns, and other distinctive

features (e.g. spots, scars, freckles, missing or broken appendages). Because there were two assistants collecting behavioral data each field season, periodic inter-observer reliability checks were conducted to assure agreement in identification of group members, behavioral activity categories, and identification of fruit trees (Vogel 2004). Throughout the study period, one assistant collected all of the ecological data described below.

For baseline social and feeding data, 10 min continuous focal animal samples were recorded (Altmann 1974), in which all social behaviors and identities of all individuals that interacted with the focal animal were recorded into a PSION handheld computer, except in cases when interactions occurred too quickly, in which case a micro-cassette recorder was used. Focal samples were recorded for all adult males and females. A focal session was discarded if the focal animal was out of sight for more than 1 min of the 10-min focal sample. These samples were taken when tree focals (see below) were not being conducted and were dispersed throughout the day to ensure even data collection on individuals throughout the day. A pseudo-random order of focal subjects was used in which focal samples on all adult group members were completed before beginning another round of samples. An individual was eligible as the next focal subject if she/he had not interacted with, or been in close proximity to (1–5 body lengths), the focal animal in the last 2.5 min of the previous focal follow (Perry 1996). However, when a particular individual was missing from the group, the next round was started without sampling that animal.

The main method used for this study was the Focal Tree Method (Vogel 2004). Specifically, one observer, the primary 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). The primary observer recorded the time and identification of first arrival, each successive arrival, and time and identification of each departing monkey from the tree. The time between the first arrival to the tree and the last departure is the group *feeding bout length*. If there were gaps in feeding during the feeding bout such that no animals were feeding, the amount of time in which monkeys were not feeding was subtracted from the total feeding bout length. To collect ingestion rates, the primary observer recorded 1-min feeding samples of as many individuals as possible during the feeding bout (c.f. Janson 1985). Data on the tree species, the number of food items ingested per minute, and the amount of time spent processing and foraging for all food types were recorded (c.f. Janson 1985). For large fruits that took longer than 1 min to eat, the amount of time it took to ingest one fruit was recorded and the average amount of fruit consumed in 1 min was back-calculated. From these data, *the number of fruits ingested per minute* was calculated for a total of 37 fruit tree species.

The secondary observer at the focal tree recorded the number, identification, activity, and relative position of all monkeys in the tree at 2.5-min intervals. At the time of an aggressive interaction, the number and identity of all monkeys within the feeding tree were known. Data were taken until the last group member left the tree. From these

data, *Individual Minutes* (IM) was calculated by multiplying the average number of monkeys feeding in the tree by the feeding bout length in minutes. This measurement is comparable to Janson's (1988a) calculation of IM. A *standardized rate of aggression* was then calculated by dividing the number of aggressive interactions in a feeding tree by IM.

At the time of an aggressive interaction, the primary observer recorded the individuals involved and the proximity of all visible individuals in the tree to the interacting animals. The primary observer also recorded data on who won the interaction, if the aggressor(s) started feeding at the site of the interaction, and continued recording data on all arrivals and departures. All subsequent aggressive interactions in that feeding tree were also recorded, and when possible the displaced individual was followed by the secondary observer, who tracked the animal until it started to feed again. The time between the displaced animal's leaving the feeding spot or tree and when it started to feed was called the *minutes lost feeding* (MLF) (Janson 1988a). 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 (see below) and the amount of fruit in the focal tree was recorded by the primary observer.

Ecological sampling

Fruit abundance in the focal tree was measured using three different methods. Within 2 days of marking the focal tree, we measured diameter at breast height (DBH), which has been demonstrated to reflect the tree's ability to produce fruit (Chapman et al. 1992), crown height and crown diameter. Crown volume was calculated from the latter two measurements using the equation for the volume of an ellipsoid (as in Janson 1988a). Fruit crop of the focal tree was estimated visually using binoculars, according to the following categories: 1=1–9 fruits, 2=10–99, 3=100–999, 4=1000–9999, 5=10000–99999 and 6>999999 (Janson and Chapman 1999). For small-crowned trees, visual fruit counts were also obtained by a direct count of all visible ripe fruits on the tree. For large-crowned trees with a high quantity of small fruits, an additional method of estimation was used. Five 1-m³ areas of the crown were selected *ad libitum*. Samples were spread throughout the tree crown and the number of fruits within this area was counted (Chapman et al. 1992). The mean of these counts was then calculated and multiplied by the crown volume.

Plant nutrient content and nutritional intake

All fruit species eaten by the capuchins during the study period were collected from trees in which the monkeys had fed. Only those fruits that were similar in size and maturation stage to fruits selected by the capuchins during the feeding bout were selected. All samples were weighed, di-

vided into components (seed, husk, and pulp), weighed again, and then dried until they maintained a constant weight (Hladik 1977). For all species, at least two samples were collected for a total of 200 samples. The dried samples were then placed in a sealed bag containing 1/8" 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 and Haenisch 1947). The total kilojoules (kJ)/g dry mass for each species was calculated as $(0.1674 \times (\text{sum of \% dry mass as soluble carbohydrates plus protein})) + (0.3766 \times (\% \text{ dry mass in fats}))$ (as in Janson 1985). These values are the standards taken from the human literature, converted to kJ/g from kcal/g, thereby giving an estimate of metabolizable energy (National Research Council 1989). Means and 95% confidence limits were computed for species with multiple samples (Sokal and Rohlf 1995).

To assess the value of a particular resource to a monkey, it is necessary to estimate the monkey's nutritional gain from accessing the focal tree. Technically, nutritional gain is the net increase in nutrients obtained after accounting for the costs of ingesting the food sources. However, it is difficult to estimate energy costs of foraging or manipulating foods either between food types or individuals in a group. If the costs are assumed to be uniform, then nutritional gain will be directly related to nutritional intake. Two related measurements of food intake have been suggested as indices of feeding success: the number of fruits ingested per minute (referred to as feeding rates) and the total Kilojoules of energy ingested per minute (referred to as energy intake rate). Because most optimal foraging models used energy gain rate as the proximate currency of fitness that animals are thought to maximize while foraging, kilojoules of energy ingested/min was used in this study as the main measure of feeding success. Thus, in this study, nutritional gain was estimated by the product of 1) the number of fruits ingested per minute, 2) the weight of each fruit (g dry mass) and 3) kJ/g dry mass, to yield *kJoules of energy ingested per minute*, referred to as *Energy Intake Rate*. This measure was calculated for one to twenty focal animals/group/focal-tree in a total of 37 species of fruit trees. In this study, the focal tree energetic value, referred to as *total crown energy*, was used as the variable representing the value of the focal tree because the analysis described below is designed to predict individual capuchin energy intake rate.

Statistical procedures

Dominance hierarchies were calculated for all three groups based on subtle (i.e. cowers, avoids, fear grins) and active (i.e. chases, bites, lunges) aggressive outcomes and the outcome of dyadic displacements (Janson 1985) during continuous focal follows. Dominance hierarchies were calculated using MatManTM software (Nodus Information

Technology 2003). Hierarchies were calculated using all group members (excluding individuals under 3 years of age) because data from interactions involving all other group members were used in these analyses (Vogel 2004). MatManTM calculates Landau's Linearity Index (h'), which is corrected for ties and unknown relationships, and the *Directional Consistency Index (DCI)*, which is the total number of interactions in the main direction of a dyad minus the number of times the behavior occurred in the less frequent direction divided by the total number of interactions (van Hooff and Wensing 1987; de Vries et al. 1993; de Vries 1995). For this study, individuals with tied relationships that were adjacent in rank were assigned the same rank. Individuals were evenly grouped into 3 rank classes (High, Middle, and Low) to facilitate the interpretation of the multiple regression analysis (Vogel 2004).

The analyses are based on a data from a total of 610 focal trees recorded over a 2 year period. Parametric statistics were used in preference to non-parametric statistics because of their greater flexibility of statistical designs. Linear multiple regression models were used to predict the effect of several ecological and social variables on energy intake rate for individuals of different sex and rank classes. Because some of the independent variables in the linear regression analyses were actually ratios or products of other variables, their variances were often correlated with their means (heteroscedastic). The assumptions of all statistical tests were tested, and data transformed to meet the assumptions before data analysis proceeded; in nearly all cases, taking the logarithm of the original data brought the data into conformity with the assumptions of homoscedasticity and normality of residuals (Sokal and Rohlf 1995). In addition, to accurately interpret the results of the multiple regression model, all variables should be uncorrelated. Thus, all independent variables were checked for independence using pair-wise correlation techniques (Sokal and Rohlf 1995). If any two independent variables were highly correlated, they were not included in the same analysis. When categorical data was included in a model, JMP-SAS 5.0.1a converted the categorical values (levels) into internal columns of numbers and analyzed the data as a linear model. The program uses a *sum-to-zero* coding scheme to create indicator variables and provides information on how different the mean for a specific level was from the mean of the means for each level and also provides directional effects (Sall et al. 2001). One-way analysis of variance was also used to test for rank differences in energy intake rates between the three rank classes and Student's t-Test for Paired Comparisons was used *posthoc* to establish which rank classes were statistically different. Log-likelihood ratio tests for categorical data were evaluated with the Chi-square statistic, with William's correction (Sokal and Rohlf 1995). All statistical procedures were carried out using JMP-SAS 5.0.1a statistical software. All probability levels are two-tailed unless stated otherwise; in all one-tailed tests, the direction of the trend was predicted a priori (Sokal and Rohlf 1995). Significance for all tests was set at $\alpha \leq 0.05$.

Results

Dominance relationships

Dominance hierarchies were calculated for all three groups: RR, AA, and QQ. All three whole group hierarchies (including all males and females and excluding infants) were significantly linear and had a Directional Consistency Index of at least 85% (Table 1; for detailed matrices see Vogel 2004). Dominance hierarchies were also calculated using interactions involving only males and only females. For all three groups, male dominance relationships were linear (Table 1). For females, two groups had linear female relationships while for the third group, RR, female relationships were not significantly linear (Table 1). However, the female dominance order did not change for RR's group when the whole group hierarchy was compared with that calculated for females only (Vogel 2004). The lack of significance is most likely due to the large percentage of unknown relationships (Koenig and Borries, *in press*) and overall lack of aggressive interactions, relative to the other two groups, observed among adult females in this group. For all three groups, the Directional Consistency Index for matrices including all individuals, only females, and only males were above 85%, which may be a more relevant indicator of linearity than Landau's Linearity Index (see Koenig and Borries, *in press*).

Variation in energy intake rate among group members

The amount of between-species variation in both average feeding rates and average energy ingested per minute for several of the fruit tree species in the capuchin's diet during the study period is demonstrated in Table 2. For all statistical tests, the species of the feeding tree accounted for sixty-eight to seventy-five percent of the calculated variation in energy intake rates among focal animal samples, and so it was included in all multiple regression models. This resulted in focal tree species being held constant while all other variables were evaluated.

In this study, fruit availability assessed by visual fruit counts and crown energy were significantly correlated ($n=650$ $r=.83$, $p<0.0001$). When feeding in trees with high fruit availability and/or crown energy, individuals can spend less time searching for food and more time feeding, on high quality fruits (Janson 1985). As predicted, individuals had higher energy intake rates in trees with higher total crown energy (Table 3). This result is not due to variation in total crown energy between tree species, as species was controlled statistically in the analysis.

Trees with higher energy intake rates were associated with higher standardized rates of aggression (Table 3). However, there was no effect of whether the occurrence of aggression occurred before or after the feeding rate sample was recorded (Table 3). Energy intake rates differed significantly among the dominance rank classes in the direction predicted a priori: higher ranked

Table 1 The results of the analyses of linearity of the dominance hierarchies for all three social groups using MatMan™ software. Analyses are reported for the entire social group (excluding any individuals less than 3 years of age), which includes male and females,

only females, and only males in the matrices. DCI = Directional Consistency Index. Significance levels are: NS = Not Significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, **** = $p < 0.0001$

Group	Landau's Corrected Index of Linearity (h')			DCI			p-value			# of interactions (number of individuals)			% unknown dyadic interactions		
	RR	AA	QQ	RR	AA	QQ	RR	AA	QQ	RR	AA	QQ	RR	AA	QQ
Whole Group	0.35	0.48	0.55	0.92	0.89	0.850	***	****	***	217 (21)	306 (22)	532 (23)	41	32	27
Females	0.31	0.7	0.65	0.92	0.97	0.87	NS	***	***	26 (9)	77 (11)	163 (12)	59	29	21
Males	50.6	0.5	0.59	0.94	0.92	0.90	*	*	**	66 (12)	76 (11)	110 (11)	38	37	25

Table 2 Average feeding rates and energy intake rates for 37 species of fruit trees used by white-faced capuchins. Feeding rates and energy gain rate were determined as in Methods

Tree species	Energy (KJ/g)	Average feeding rate (items/min)	Average energy gain rate (KJ/min)
<i>Anacardium excelsum</i>	15.20	3.50	37.70
<i>Anacardium occidentale</i>	12.26	0.76	111.80
<i>Ardisia revoluta</i>	14.75	15.60	6.00
<i>Brosimum alicastrum</i>	6.02	3.23	3.95
<i>Bursera simaruba</i>	5.77	11.03	7.41
<i>Byrsonima crassifolia</i>	13.52	3.69	17.13
<i>Casearia arguta</i>	14.22	6.62	6.82
<i>Casearia slyvestris</i>	13.27	11.23	0.17
<i>Coccoloba sp.</i>	6.79	7.75	3.59
<i>Cochlospermum vitifolium</i>	4.64	0.64	4.07
<i>Curatella americana</i>	2.54	14.83	0.48
<i>Diospyros nicaraguensis</i>	7.61	2.61	9.82
<i>Dolioscarpus dentatus</i>	13.56	10.90	1.53
<i>Erthroxylum havanense</i>	9.47	23.64	14.77
<i>Eugenia monicula</i>	12.76	11.50	2.96
<i>Ficus sp.</i>	8.00	11.65	16.40
<i>Genipa americana</i>	12.22	0.68	46.77
<i>Garcinia edulis</i>	8.47	4.98	19.46
<i>Guettarda macrosperma</i>	8.46	0.21	1.02
<i>Guazuma ulmifolia</i>	8.20	2.55	27.89
<i>Inga vera</i>	5.01	1.43	1.26
<i>Luehea speciosa</i>	7.73	1.41	0.19
<i>Mangifera indica</i>	14.33	0.47	105.63
<i>Manilkara chicle</i>	11.66	15.96	119.92
<i>Miconia argentea</i>	8.37	28.93	3.01
<i>Muntingia calabura</i>	10.41	6.21	19.46
<i>Prockia crucis</i>	5.40	17.87	1.34
<i>Psychotria pubescens</i>	9.88	12.13	5.69
<i>Quercus oleoides</i>	4.98	2.27	4.75
<i>Sciadodendron excelsum</i>	4.05	12.25	1.68
<i>Simarouba glauca</i>	7.38	3.67	1.58
<i>Sloanea terniflora</i>	24.92	2.64	2.46
<i>Spondias purpurea</i>	12.49	4.09	45.97
<i>Stemmadenia obovata</i>	23.27	0.41	7.94
<i>Sterculia apetala</i>	6.89	0.74	7.01
<i>Tabebuia ochracea</i>	6.62	4.00	17.63
<i>Ximenia americana</i>	6.95	4.20	13.38

individuals had higher intake rates than lower ranked individuals ($F_{2,1047}=5.70$, $p=0.003$, Fig. 1). A *post hoc* multiple comparison of all pairs revealed that the high rank class had significantly higher energy intake rates than both middle and low classes, but there was no difference between

the latter two rank classes (Student's t test, Alpha < 0.05 ; Fig. 1). To test if these rank differences may have been a byproduct of sex, the sex of the feeding individual was also included in the analysis. When sex was held constant, the results of the model did not change: dominance rank

Table 3 The effect of ecological and demographic variables on energy intake rate in white-faced capuchin monkeys. Aggression/No aggression refers to whether the feeding rate calculation was measured in a tree with aggression or without aggression. Before Ag-

gression/After Aggression refers to whether the feeding rate was recorded before or after there had been aggression in the tree at all. Whole Model test $F=211.73_{43,1091}$, $p<0.0001$, $r^2=0.90$, $n=1092$. Dependent variable: kilojoules of energy ingested/min

Source of variation	Predicted effect	Resulting effect	SS	DF	F	p
Tree species			285.77	36	213.63	<0.0001
Crown energy	+	+	0.505	1	13.58	0.0002
Standardized rate of aggression	+	+	0.414	1	11.13	0.0009
Aggression/no aggression	+	+	0.017	1	0.45	0.503
Before aggression/after aggression	-	-	0.091	1	2.46	0.1170
Sex of individual			0.016	1	0.44	0.508
Broad rank class (high, mid, low)	-	-	0.401	2	5.40	0.0046

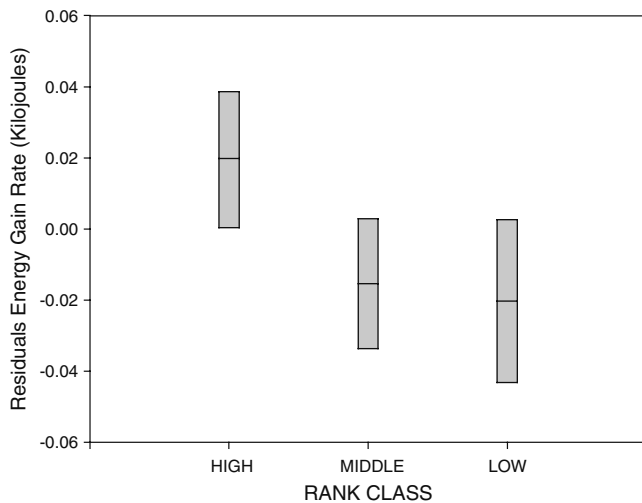


Fig. 1 Differences in average energy gain rate between high, middle, and low ranked individuals throughout the feeding bout. High ranked individuals had significantly higher energy gain rates than middle and low ranking individuals, while there was no difference between low and middle ranked individuals. The residuals resulted from the analysis in Table 3 but excluding the variable “Broad Rank Class”

classes still differed significantly in energy intake rates. Likewise, when rank was held constant, there were no sex differences in energy intake rates (Table 3). High-ranked individuals also had higher intake rates in trees in which no aggression was observed ($F_{2,271}=4.62$, $p=0.01$). Low- and mid-ranked individuals had lower energy intake rates in trees with higher amounts of aggression ($t=-1.79$, $df=2$, $p=0.035$, one-tailed), while energy intake rate of high-ranked individuals was not affected by the amount of aggression in the feeding tree ($t=1.02$, $df=2$, $p=0.301$, one-tailed).

Overall, high-ranked individuals had higher energy intake rates than mid- and low-ranked individuals across tree species. This pattern did not extend to all of the resources. Despite up to a 4-fold increase in energy intake of dominants in some species (e.g. *Anacardium occidentale*, *Sciadodendron excelsum*, *Spondias purpurea*), for other species there were no differences in energy intake rates between individuals of different rank classes. In general, little difference in energy intake between rank classes occurred in species with fruits that had long processing

times (e.g. *Luehea speciosa*, *Sloanea terniflora*), trees that have many small fruits with little or no pulp (e.g. *Guazuma ulmifolia*, *Bursera simaruba*), and trees that were generally found in patches in which individuals could spread out over a large area and avoid aggression (*Mangifera indica*). However, in 78% of the species included in the analysis, dominants had higher mean energy intake rates than low ranking individuals.

Interactions between group, energy intake rate, and all of the independent variables included in the analysis were evaluated because data were combined for all three groups. None of the variables except for total crown energy showed in an interaction with study group when predicting energy intake rate ($F_{2,1091}=3.56$, $p=0.02$). Total crown energy had no effect on energy intake rate for Group QQ, while for Groups RR and AA group the relationship was positive. It is possible that this interaction may have resulted because Group QQ fed on trees of higher energetic quality than the other two groups. In this case, total crown energy would not affect energy intake rates because feeding rates are limited by food processing rather than search time. Indeed, holding tree species constant, Group QQ fed on trees with higher total crown energy than the other two groups ($F_{2,625}=2.90$, $p=0.013$). Thus, while Group RR's and AA's energy intake rate increased with focal tree crown energy, this was not the case for Group QQ. Although Group QQ fed on trees of higher energetic quality, its standardized rate of aggression did not differ from the other groups ($F_{2,625}=0.7456$, $p=0.48$).

Given this difference in food tree quality among groups, the relationship of energy intake rate to dominance rank classes was examined to determine whether it could be related to differences in the use of aggression among the three groups. Specifically, the slope of energy intake rate against rank class was calculated for each focal tree species for each study group and then regressed against the mean standardized rate of aggression for each focal tree species. If WGC competition is important, then as aggression rates increase, the difference in intake rates between dominants and subordinates should increase. The only group with this relationship was Group AA (Fig. 2). There was no rank effect (slope of energy intake against rank class close to zero) when aggression rates were very low, but as the rate of aggression increased, the rank effect on energy intake

Fig. 2 The degree of bias between individuals of different rank plotted against the standardized rate of aggression (# interactions/IM) for AA's group, across tree species ($n=12$ tree species)

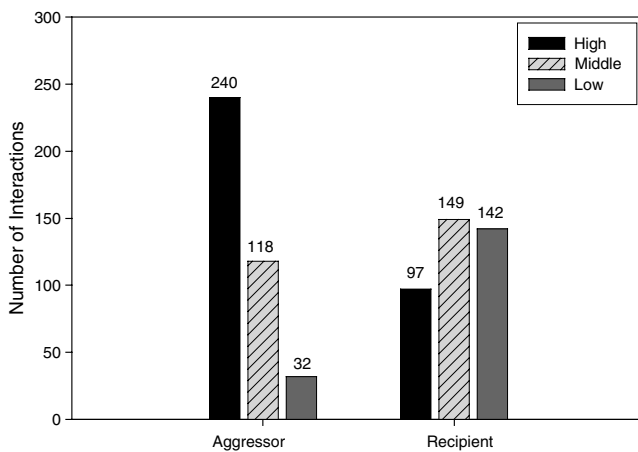
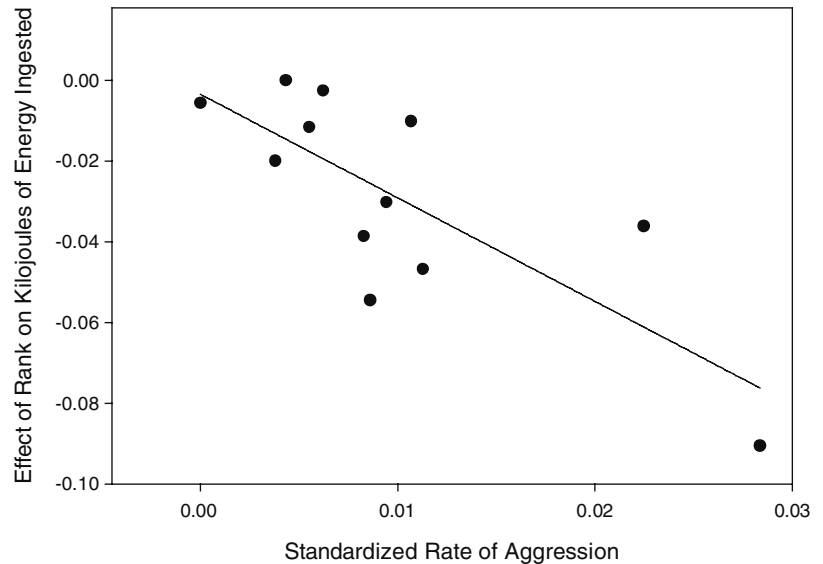


Fig. 3 The number of dyadic interactions that individuals of different rank classes initiated (aggressor) or received (recipient). High ranked individuals initiated aggression significantly more than middle and low ranked individuals. Low and mid-ranked individuals received aggression more than expected by random chance

rate increased significantly for this group ($n=12$, $r^2=0.60$, $p=0.003$).

Characteristics of the givers and recipients of aggression

In support of the fourth hypothesis, high-ranked individuals were the initiators of aggression in feeding trees more than expected based on the number of high-, middle- and low-ranked individuals present in the group ($n=390$, $df=2$, $\chi^2_{adj} = 123.49$, $p<0.0001$; Fig. 3). Likewise, when comparing only mid- versus low-ranked individuals, aggressors are more likely to be mid-ranked individuals and less likely to low-ranked than expected based on the number available in each rank class ($n=150$, $df=1$, $\chi^2_{adj} = 36.6$, $p<0.0001$).

Therefore, it is not surprising that low- and middle-ranked individuals were more likely to be the targets of aggression ($n=388$, $df=2$, $\chi^2_{adj} = 31.99$, $p<0.0001$; Fig. 3). However, mid-ranked individuals were no more likely to be the targets than low-ranked individuals ($n=291$, $df=1$, $\chi^2_{adj} = 1.69$, $p=0.1938$).

Discussion

Understanding the relationship between ecology and feeding behavior

The finding that dominants had higher mean energy intakes than subordinates for 78% of tree species studied agrees with results with results of several studies that have found that rank differences in feeding rates depended on the type of food being contested and that this relationship was not consistent across all food types (Janson 1985; van Schaik and van Noordwijk 1988; Barton and Whiten 1993). There is a possibility that the observed differences in energy intake rate were a consequence of individual differences in body mass. Body mass differences were not directly measured in this study, but given that adult males are about 20% larger than adult females in *Cebus capucinus*, the fact that no sex differences in intake rates were observed probably rules out any effect of body mass on energy intake rates. In support of this conclusion, Janson (1985) found that in *Cebus apella*, a species with even greater variation in body size between adults males and females, body mass did not account for any significant variation in feeding rates observed among group members once dominance rank was factored out. Although there was no difference in energy intake rate between males and females *C. capucinus*, there may have been differences in the diet choice of males and females that were not reflected in the fruit component of their diet. Rose (1994) concluded that males may compensate for the higher energy costs associated with a larger body size by

feeding on higher quality vertebrate and invertebrate prey than females.

If group members use contest competition in food trees as a strategy to increase energy gain rates, then high-ranking individuals are predicted to initiate aggression and as a result, have higher intake rates in feeding trees (Janson 1985). The data presented here support these predictions for members of wild groups of white-faced capuchin monkeys. There was a strong positive relationship between energy intake rate and rank, and subordinate individuals suffered lower energy intake in food trees with high rates of aggression, whereas energy intake of dominant individuals was not affected. This pattern held true for both males and females in food trees, even when the alpha male was excluded from the analysis (Vogel 2004).

Because dominant individuals were the initiators of the majority of food-related agonism, they were the ones controlling access to the food tree and were aggressive particularly when the net benefits exceed the costs of excluding others from the feeding tree. Although dominant individuals still had higher intake rates than subordinate individuals in trees in which no aggression was observed, it is possible that subtle avoids of subordinates directed at dominants were missed by the observer such that very low levels of contest competition went undetected. Janson (1985) found that for Peruvian *Cebus apella*, dominants did not consume more than subordinates when group members did not contest resources. However, subordinate *C. apella* did have relatively lower feeding rates in food trees characterized by high levels of aggression, while dominants were unaffected. Thus, it appears that contest competition is important for both *C. capucinus* and *C. apella* and occurs more when the benefits of feeding in a tree increase.

The fact that no relationship was found between energy intake rate and total energy within the tree crown in Group QQ, although such a relationship occurred in the other two study groups, warrants discussion. Energy intake rate is expected to increase with the amount of energy in the tree until it reaches a saturation point where any additional increases in crown energy no longer produce an increase in energy intake rate because feeding rates are limited by food processing rather than searching (Fig. 4). Thus, modest variations in crown energy will have little or no effect on feeding rates at high quantities above the saturation point, but will influence feeding rates at low quantities. When crown energy is lower than the saturation point, a dominance effect will be present and a positive relationship between total crown energy and energy intake rate is expected. However, as the amount of energy in the feeding tree's fruit increases so that the costs to dominants of restricting access to the resource exceed the benefit obtained (because the alternative feeding spots will still be at high enough nutritional value for maximal energy intake rates), scramble competition should be the mode of competition and the effect of total crown energy on feeding rates should weaken. Further analysis revealed that Group QQ was feeding on resources with higher nutritional quality. It is possible that the higher average quality of food trees for Group QQ reduced the rank effects on energy intake rates. Furthermore, Group

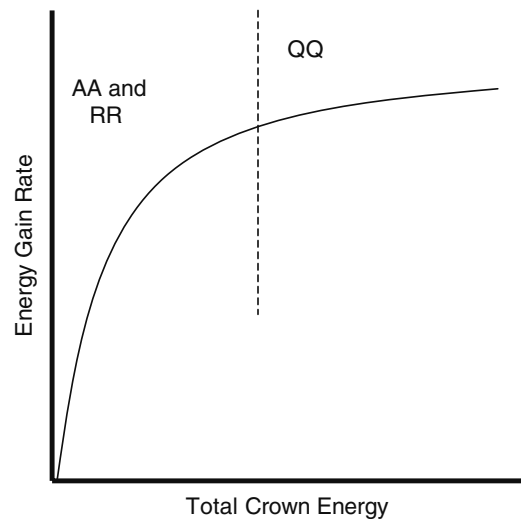


Fig. 4 Diagram of the effect of total crown energy on energy gain rate in the three study groups. Total crown energy and energy gain rate increase asymptotically up to the point where increases in total crown energy no longer have an effect on energy gain rate (where group QQ lies on the curve)

QQ always won inter-group encounters with Group AA ($n=16$, unpublished data). In fact, in an overlapping area of Groups AA and QQ, there was a large patch of *Anacardium occidentale* and *Mangifera indica* that had at least 20 fruiting trees during the dry season. Thus, QQ was able to feed in this area consistently more than AA's group, because they fed in the patch almost every other day during the month of April while the fruits were ripe. It may be that rank differences affect Group AA's and RR's energy intake rates more than in Group QQ because the former are feeding on trees of overall lower nutritional quality and thus they are somewhere on the increasing part of the curve, while Group QQ is feeding on trees of higher overall nutritional quality and thus lies on the more saturated part of the curve (Fig. 4).

Quality of resources may also affect the relationship of dominance to energy intake rate within groups. The expected correlation was found in Group AA, but not in the other two study groups. Group AA was subordinate to both of the other two study groups during the study period in that they always retreated when an inter-group encounter occurred with either group (Vogel, unpublished data). Although the data to relate this to overall quality of the territory are not available, Group QQ fed on higher quality trees than the other two groups. It may be that the intensity of WGC was greater for Group AA because it occupied a poorer territory. However, more specific data on between-group competition is needed to demonstrate this relationship.

Comparisons with other primate species

Different modes of competition are expected to be observed depending on the distribution and abundance of alternative food resources. For species that feed on dispersed

resources or are able to alleviate competition by separating into smaller feeding parties (i.e. fission-fusion societies), rank differences in food intake rates are not expected (van Schaik 1989). In support of this argument, when group members fed on dispersed resources, a rank effect on food intake was not observed among yellow baboons (*Papio cynocephalus*: Altmann 1980; Post et al. 1980), vervets (Whitten 1983), or brown capuchins (*Cebus apella*: Janson 1985). For long-tailed macaques (*Macaca fascicularis*), subordinate individuals' fruit intake rate was almost equal to more dominant animals' rates when they fed outside of the main feeding party (van Noordwijk and van Schaik 1987). Thus, subordinates were able to compensate for a feeding disadvantage while feeding in the main party by temporarily leaving the main group to find alternative resources. Although dominants did not have higher overall intake rates, they had reduced energy expenditure and thus higher net energy gain than subordinates (van Schaik and van Noordwijk 1988).

Several researchers have demonstrated that when food is distributed in defendable clumps, subordinate individuals often have reduced food intake rate relative to more dominant group members (Robinson 1981; Whitten 1983; Janson 1985; Barton 1993; Gore 1993; Koenig 2000; but see Cords 2002). Robinson (1981) found that rank correlated with intake rate within age-sex classes in wedge-capped capuchins (*Cebus olivaceus*). Likewise, Whitten (1983) found that when vervet monkeys fed on clumped resources, high-ranking individuals consumed food significantly faster than low ranking individuals. In provisioned groups of olive baboons, the high-ranking individuals fed from three to six times faster than low rankers (Barton 1993). Even for a folivorous species, the Hanuman langur (*Semnopithecus entellus*), it appears that when resources are clumped, high-ranking females have higher net energy intake rate than subordinates (Koenig 2000). Deutsch and Lee (1991) found that although there were no differences in total intake between high-ranking and low-ranking captive female rhesus monkeys, high-ranking females had priority of access to feeding sites and also produced more surviving offspring than subordinates.

The results of this study agree with those from investigations on other species: dominant group members had higher intake rates relative to more subordinate group members. Socio-ecological models have proven successful in understanding the effect of ecology on the diverse array of social organizations observed both between and within non-human primate species. Specifically, these models have demonstrated the ability of species to adapt to their local ecology, even within a single population. Most empirical tests of socioecological models have supported their predictions, demonstrating that they are useful for predicting the links between ecology, energy gain, and aggression and serve to help understand the evolution of social relationships in non-human primates. Given this growing body of evidence that the distribution and abundance of food resources influences rank differences in energy intake rate among group members, the next logical question is to ask how these differences translate into fitness gains.

Dominance rank has also been demonstrated to influence a number of variables including energy expenditure (chickadees: Pravosudov et al. 1999), reproduction (vervet monkeys: Whitten 1983; Hanuman langurs: Borries et al. 1991; long tailed macaques: van Noordwijk and van Schaik 1999; Eurasian badgers: Revilla and Palomares 2001; ponerine ants: Gobin et al. 2003; see Clutton-Brock 1988 for review), offspring survival (chacma baboons: Busse 1982; Bulger and Hamilton 1987; savannah baboons: Altmann and Alberts 2003b; meerkats: Russell et al. 2003), spatial positioning in the group (wedge-capped capuchin monkeys and Robinson 1981; long-tailed macaques: van Noordwijk and van Schaik 1987; brown capuchin monkeys: Janson 1990; olive baboons: Barton 1993) and the acquisition of mates (jungle fowl: Johnsen et al. 2001; savannah baboons: Alberts et al. 2003; bonobos: Illius et al. 2003). Another benefit of dominance may be to counteract the effects of "aggressive neglect" (Hutchinson and MacArthur 1959). In other words, once a dominance hierarchy is established, dominant individuals do not have to invest as much time in aggression and can spend more time in other activities such as feeding and reproduction (Jones 1980). Recent analyses on long term data from baboons has shown that there is a clear relationship between dominance rank, feeding rates, and reproductive success (Altmann and Alberts 2003a, b; Silk et al. 2003). Dominant females have access to the best quality food patches and higher feeding rates than subordinate females and also have high reproductive success. Although several studies on a variety of species have shown a clear relationship between rank and reproductive success (see above references), I do not have the data to test whether feeding advantages in dominant individuals translate into high reproductive success in my study populations. Thus, future investigations on rank differences in reproductive fitness for *Cebus capucinus* populations that have been studied for longer periods are warranted. Only by gaining an understanding of the ultimate mechanisms that have shaped hierarchal relationships, can we begin to understand the variation observed in within-group social relationships.

Acknowledgements This work could not have been done without the expert field assistance of Alexander Fuentes Jiménez, Juan Carlos Ordonez, Yoella Teplitsky, Thomas Pendergast, and Anastasia Cronin. I am grateful to the Costa Rican Servicio de Parques Nacionales and the ACT for granting me permission to work in Lomas Barbudal Biological Reserve; Finca El Pelón de la Bajura for granting me permission to work on their private lands; Professor Dr. Joerg Ganzhorn, of the University of Hamburg, who generously analyzed the nutritional composition of the fruit eaten by white-face capuchins; my dissertation committee for all of their insights on previous versions of this manuscript; Charles Janson, Andreas Koenig, John Fleagle, Carel van Schaik, Ivan Chase; Waleed al Gharaibeh for statistical advise; Mitch Irwin, Oliver Schuelke, Julia Ostner, and three anonymous reviewers for comments and constructive criticism of a previous draft; and Julie Gros-Louis, Susan Perry, and Joseph Manson, who provided logistical assistance in the field. This research was funded by grants to E.R.V. from NSF (DIG 23720-1021441-1), the Leakey Foundation (431-1770A), the Organization for Tropical Studies, a Graduate Aid in Areas of National Need (GAANN) Fellowship, and the Department of Ecology and Evolution at Stony Brook Slobodkin Research Award

and Sokal Travel Award. This study complied with and was approved by the Institutional Animal Care and Use Committee (IACUC).

References

- Alberts SC, Watts H, Altmann J (2003) Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim Behav* 65:821–840
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–265
- Altmann J (1980) Baboon mothers and infants. Harvard University, Cambridge, M.A.
- Altmann J, Alberts SC (2003a) Variability in reproductive success viewed from a life-history perspective in baboons. *Am J Human Biol* 15:401–409
- Altmann J, Alberts SC (2003b) Intraspecific variability in fertility and offspring survival in a non-human primate: behavioral control of ecological and social sources. In: Wachter K (ed) *Offspring: human fertility behavior in a biodemographic perspective*. National Academy Press, Washington, D.C., pp 140–169
- Barton RA (1993) Sociospatial mechanisms of feeding competition in female olive baboons, *Papio anubis*. *Anim Behav* 46:791–802
- Barton RA, Whiten A (1993) Feeding competition among female olive baboons, *Papio anubis*. *Anim Behav* 46:777–789
- Benkman CW (1997) Feeding behavior, flock-size dynamics, and variation in sexual selection in crossbills. *Auk* 114:163–178
- Borries C, Sommer V, Srivastava A (1991) Dominance, age, and reproductive success in free-ranging female Hanuman langurs. *Int J Primatol* 12:230–257
- Bulger J, Hamilton WJ (1987) Rank and density correlates of inclusive fitness measures in a natural chacma baboon (*Papio ursinus*) troop. *Int J Primatol* 8:635–650
- Busse CD (1982) Social dominance and offspring mortality among female chacma baboons. *Int J Primatol* 3:267
- Chapais B (1992) The role of alliances in social inheritance of rank among female primates. In: Harcourt AH, de Waal FBM (eds) *Coalitions and alliances in humans and other animals*. Oxford University Press, Oxford, pp 29–59
- Chapman CA, Chapman LJ, Wrangham R, Hunt K, Gebo D, Gardner L (1992) Estimators of fruit abundance of tropical trees. *Biotropica* 24:527–531
- Clutton-Brock TH (1988) *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press, Chicago
- Cords M (2002) Friendship among adult female blue monkeys (*Cercopithecus mitis*). *Behaviour* 139:291–314
- de Vries H (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Anim Behav* 50:1375–1389
- de Vries H, Netto WJ, Hanegraaf PLH (1993) Matman - a program for the analysis of sociometric matrices and behavioral transition matrices. *Behaviour* 125:157–175
- Deutsch JC, Lee PC (1991) Dominance and feeding competition in captive rhesus monkeys. *Int J Primatol* 12:615–628
- Frankie GW, Vinson SB, Newstrom LE, Barthell JF (1988) Nest site and habitat preferences of *Centris* bees in the Costa Rican dry forest. *Biotropica* 20:301–310
- Ganzhorn JU (1988) Food partitioning among Malagasy primates. *Oecologia* 75:436–450
- Gobin B, Heinze H, Stratz M, Rocas F (2003) The energetic cost of reproductive conflicts in the ant *Pachycondyla obscuricornis*. *J Insect Physiol* 49:747–752
- Gore MA (1993) Effects of food distribution on foraging competition in rhesus monkeys, *Macaca mulatta*, and hamadryas baboons, *Papio hamadryas*. *Anim Behav* 45:773–786
- Gros-Louis J, Perry S, Manson JH (2003) Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). *Primates* 44:341–346
- Harwood AJ, Griffiths SW, Metcalfe NB, Armstrong JD (2003) The relative influence of prior residency and dominance on the early feeding behaviour of juvenile Atlantic salmon. *Anim Behav* 65:1141–1149
- Hino T (2000) Intraspecific differences in benefits from feeding in mixed-species flocks. *J Avian Biol* 31:441–446
- Hladik C (1977) Field methods for processing food samples. In: Clutton-Brock TH (ed) *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. Academic Press, New York, pp 595–601
- Hutchinson S, MacArthur R (1959) Appendix: On the theoretical significance of aggressive neglect in interspecific competition. *Am Nat* 93
- Illius A, Hohmann G, Fruth B (2003) Intra- and inter-sexual aggression by bonobos in the context of mating. *Behaviour* 140:1389–1413
- Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav Ecol* 2:143–155
- Isbell LA, Pruett JD (1998) Differences between vervet (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) in agonistic interactions between adult females. *Int J Primatol* 19:837–855
- Isbell LA, Pruett JD, Lewis M, Young TP (1999) Rank differences in ecological behavior: A comparative study of patas monkeys (*Erythrocebus patas*) and vervets (*Cercopithecus aethiops*). *Int J Primatol* 20:257–272
- Janson CH (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behav Ecol Sociobiol* 18:125–138
- Janson CH (1986) The mating system as a determinant of social evolution in capuchin monkeys (*Cebus*). In: Else J, Lee PC (eds) *Proceedings of the xth international congress of primatology*. Cambridge University Press, Cambridge, pp 169–179
- Janson CH (1988a) Food competition in brown capuchin monkeys (*Cebus apella*): quantitative effects of group size and tree productivity. *Behaviour* 105:53–76
- Janson CH (1988b) Intra-specific food competition and primate social structure: a synthesis. *Behaviour* 105:1–17
- Janson CH (1990) Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Anim Behav* 40:910–921
- Janson CH, Chapman CA (1999) Resources and primate community structure. In: Fleagle JG, Janson C, Reed KE (eds) *Primate communities*. Cambridge University Press, Cambridge, pp 237–268
- Janson CH, van Schaik CP (1988) Recognizing the many faces of primate food competition: methods. *Behaviour* 105:165–186
- Johnsen T, Zuk M, Fessler E (2001) Social dominance, male behaviour and mating in mixed-sex flocks of red jungle fowl. *Behaviour* 138:1–18
- Jones CB (1980) The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: Intra-specific competition for group membership in a folivorous Neotropical primate. *Primates* 21:389–405
- Koenig A (2000) Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). *Behav Ecol Sociobiol* 48:93–109
- Koenig A (2002) Competition for resources and its behavioral consequences among female primates. *Int J Primatol* 23:759–783
- Koenig A, Borries C (in press) The predictive power of socio-ecological models: a reconsideration of resource characteristics, agonism, and dominance hierarchies. In: Hohmann G, Robbins M, Boesch C (eds) *Feeding ecology in apes and other primates*. Cambridge University Press, Cambridge
- Liker A, Barta Z (2002) The effects of dominance on social foraging tactic use in house sparrows. *Behaviour* 139:1061–1076
- Maynard Smith J (1974) The theory of games and the evolution of animal conflict. *J Theor Biol* 47:209–221
- Milinski M (1979) An evolutionary stable feeding strategy in sticklebacks. *Z Tierpsychol* 51:36–40

- Mitchell CL, Boinski S, van Schaik CP (1991) Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedii* and *S. sciureus*). *Behav Ecol Sociobiol* 28:55–60
- National Research Council (1989) United States - Canadian tables of feed composition. In: National Academy Press, Washington, D.C.
- Nicholson AJ (1954) An outline of the dynamics of animal populations. *Aust J Zool* 2:9–65
- Perry S (1996) Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *Am J Primatol* 40:167–182
- Pierce WC, Haenisch EL (1947) Quantitative analysis. Wiley, London
- Post DG, Hausfater G, McCuskey SA (1980) Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. *Folia Primatol* 34:170–195
- Power ME (1984) Habitat quality and distribution of algae-grazing catfish in a Panamanian stream. *J Anim Ecol* 53:357–74
- Pravosudov V, Grubb T, Doherty P, Bronson C, Pravosudova E, Dolby A (1999) Social dominance and energy reserves in wintering woodland birds. *Condor* 101:880–884
- Revilla E, Palomares F (2001) Differences in key habitat use between dominant and subordinate animals: intraterritorial dominance payoffs in Eurasian badgers? *Can J Zool* 79:165–170
- Robb SE, Grant JWA (1998) Interactions between the spatial and temporal clumping of food affect the intensity of aggression in Japanese medaka. *Anim Behav* 56:29–34
- Robichaud D, Lefebvre L, Robidoux L (1996) Dominance affects resource partitioning in pigeons, but pair bonds do not. *Can J Zool-Revue Canadienne De Zoologie* 74:833–840
- Robinson JG (1981) Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. *Anim Behav* 29:1036–1056
- Rose LM (1994) Sex-differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). *Int J Primatol* 15:95–114
- Russell AF, Brotherton PNM, McIlrath GM, Sharpe LL, Clutton-Brock TH (2003) Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behav Ecol* 14:486–492
- Saito C (1996) Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: effects of food patch size and inter-patch distance. *Anim Behav* 51:967–980
- Sall J, Lehman A, Creighton L (2001). *JMP start statistics: a guide to statistics and data analysis*. Duxbury, Thomas Learning, California
- Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. *Science* 302:1231–1234
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*, 2nd edn. W. H. Freeman and Company, New York
- Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41:291–309
- Sterck EHM, Steenbeek R (1997) Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour* 134:749–774
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) *Sexual selection and the descent of man*. Aldine, Chicago, pp 136–179
- van Hooff JARAM, van Schaik CP (1994) Male bonds - affiliative relationships among nonhuman primate males. *Behaviour* 130:309–337
- van Hooff JARAM, Wensing JAB (1987) Dominance and its behavioral measures in a captive wolf pack. In: Frank H (ed) *Man and wolf*. Dr W Junk Publishers, Dordrecht
- van Noordwijk MA, van Schaik CP (1987) Competition among female long-tailed macaques, *Macaca fascicularis*. *Anim Behav* 35:577–589
- van Noordwijk MA, van Schaik CP (1999) The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates* 40:105–130
- van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) *Comparative socioecology*. Blackwell, Oxford, pp 195–218
- van Schaik CP, van Noordwijk MA (1986) The hidden costs of sociality: intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). *Behaviour* 99:296–315
- van Schaik CP, van Noordwijk MA (1988) Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour* 105:77–98
- Vogel ER (2004) *The Ecological Basis of Aggression in White-faced Capuchin Monkeys, Cebus capucinus, in a Costa Rican Dry Forest*. Ph.D. Thesis in Ecology and Evolution. Stony Brook University, Stony Brook, NY
- Watts DP (1997) Agonistic interventions in wild mountain gorilla groups. *Behaviour* 134:23–57
- Whitten PL (1983) Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *Am J Primatol* 5:139–159
- Wilson WH, Vogel ER (1997) The foraging behavior of Semipalmated Sandpipers in the Upper Bay of Fundy: Stereotyped or prey sensitive? *Condor* 99:206–210
- Wrangham RW (1980) An ecological model of female-bonded primate groups. *Behaviour* 75:262–299