

Karen Pazol · Marina Cords

## Seasonal variation in feeding behavior, competition and female social relationships in a forest dwelling guenon, the blue monkey (*Cercopithecus mitis stuhlmanni*), in the Kakamega Forest, Kenya

Received: 2 November 2004 / Revised: 16 March 2005 / Accepted: 29 March 2005 / Published online: 3 May 2005  
© Springer-Verlag 2005

**Abstract** Socioecological models relate differences in feeding strategies to variation in the nature of female social relationships. Among the African forest guenons, females consume large quantities of fruit and other plant reproductive parts, resources which are thought to promote contest competition, yet these monkeys have been characterized as having agonistically undifferentiated relationships in which rank, if discernible at all, does not correlate with fitness benefits. To determine whether female relationships become more hierarchical under relevant ecological conditions, we monitored the adult females of two blue monkey groups (*Cercopithecus mitis stuhlmanni*) over a complete annual cycle in the Kakamega Forest, Kenya. Females competed aggressively for plant reproductive parts more often than any other resource type, and in both groups we detected linear dominance hierarchies. Nonetheless, agonism rates remained low throughout our study, and did not vary with changes in ecological conditions. Rather, when plant reproductive parts were scarce, subordinate females spent more time feeding and less time resting in an apparent attempt to compensate for a reduced efficiency of food intake. The effects of rank and food abundance were not reflected, however, in the distribution of grooming. The use of alternative feeding strategies appeared to blunt competition – females of all ranks were unlikely to be near others while feeding and spent more time consuming alternative resources when plant reproductive parts were scarce. The diverse diet of this

species may allow females to avoid conflict so that dominance has only subtle effects that are difficult to detect. While socioecological models often simplify the connection between resources and female interactions, our results emphasize that the behavior of animals consuming particular resources, and not the resources themselves, are critical predictors of social patterns.

**Keywords** Dominance rank · Feeding competition · Resource utilization · Socioecology

### Introduction

Socioecological models relate variation in social behavior to differences in the way that animals interact with their environment. Efficient acquisition of food and effective protection from predators or conspecifics are two benefits that animals may derive by living in groups. For group-living animals, the presence of conspecifics then becomes another aspect of the environment that influences the patterning of social exchange. Aggregation may impose upon individuals the foraging costs associated with intragroup competition for limiting resources, and these costs, together with the benefits of sociality, influence the size, structure and organization of social units (Alexander 1974; Clutton-Brock and Harvey 1977; Bertram 1980; Wrangham 1980; Pulliam and Caraco 1984). In mammals, the nutritional constraints of gestation and lactation make access to food critical for female reproductive success, yet in spite of the prospect for competition, females form stable aggregations in many species. Within the diurnal primates, females show a remarkable tendency to live in groups (Sterck et al. 1997; van Schaik and Kappeler 1997) and display a wide range of social organizations (Janson 1992). Numerous investigators studying the ecological underpinnings of social behavior therefore have focused on nonhuman primates (see Isbell and Young 2002; Koenig 2002 for reviews), although the same principles are applicable to many other animal species (Clutton-Brock

Communicated by J. Setchell

K. Pazol (✉)  
Yerkes National Primate Research Center, Emory University,  
954 Gatewood Drive NE,  
Atlanta, GA 30322, USA  
e-mail: kpazol@rmy.emory.edu  
Tel.: +404-727-9376  
Fax: +404-727-8088

M. Cords  
Department of Ecology, Evolution and Environmental Biology,  
Columbia University 10th floor,  
1200 Amsterdam Avenue,  
New York, NY 10027, USA

1988: red deer; Palomares and Delibes 1993: Egyptian mongooses; Cavallini and Nel 1995: yellow and Cape grey mongooses; Holekamp et al. 1996: spotted hyenas; Gilchrist and Otali 2002: banded mongooses; Magliocca et al. 2002: sitatungas; Boydston et al. 2003: spotted hyenas).

Socioecological models suggest that the distribution of limiting resources and the rate at which they are depleted from feeding sites determine the form of competition that predominates in primate societies, which in turn shapes the patterning of social relations among female group members (Wrangham 1980; van Schaik 1989; Isbell 1991; van Hooff and van Schaik 1992; Sterck et al. 1997; Isbell and Young 2002; Koenig 2002). When limiting resources are found in high quality patches that can be monopolized or profitably usurped (Isbell et al. 1998), within-group contest competition is expected to predominate. Agonism should be frequent and females should form nepotistic alliances that maintain stable linear dominance hierarchies determining priority of access to resources. Affiliation also should be frequent with positive interactions directed toward the most effective coalition partners. By contrast, when limiting resources occur in patches that are either low quality, highly dispersed or quickly consumed (and thus are not usurpable), within-group scramble competition should predominate. Agonism should occur infrequently, and even when dominance hierarchies can be detected they should be unstable, weakly reinforced, and have little influence on access to resources. Coalition formation should be absent, and without the need to cultivate alliance partners, females should affiliate infrequently and distribute their interactions randomly among partners. However, while this basic dichotomy of female relationships is predicted, strong between-group contest competition may mitigate the effects of within-group competition. Because high-ranking females risk losing the support of low-ranking individuals when they enforce the advantages of rank too strongly, pronounced between-group contest competition may increase the tolerance of high-ranking individuals, which in turn may produce hierarchies that are shallow and marked by frequent reversals against the prevailing order (van Schaik 1989; van Hooff and van Schaik 1992; Sterck et al. 1997; Isbell and Young 2002; Koenig 2002).

This socioecological model relating feeding ecology to female social relationships has been developed on the basis of numerous observational field studies and experimental manipulations of resource quality (see Isbell and Young 2002 for a review). However, until recently there has been a strong phylogenetic bias in the available data used both to develop and confirm theoretical predictions, with a clear over-representation of a few species of Old World cercopithecine and colobine primates (Strier 1994; Boinski et al. 2002). Within the cercopithecines, research has focused on baboons, macaques and vervets. Since comparatively little is known about female relationships among the forest dwelling guenons, these species have figured little in the development of socioecological theory, even though they represent one of the largest primate radiations (Cords 2000, 2002).

Because the forest dwelling guenons appear to depart from some predictions of theory, a better understanding of female relationships in these species could add to our understanding of the complexity of ecological influences on social relationships. Indeed, fruit and other plant reproductive parts constitute a large component of their diet (Rudran 1978; Struhsaker 1978; Cords 1986; Gautier-Hion 1988; Lawes 1991) and have been thought to occur in monopolizable patches or other usurpable units more often than other types of food (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell and Pruettz 1998), yet several authors have classified the forest guenons as species in which females have unstable dominance hierarchies and undifferentiated social relationships (Isbell 1991; Cheney 1992; Sterck et al. 1997; Isbell and Young 2002). This apparent mismatch between food type and social characteristics certainly could be attributed to the oversimplified use of dietary categories. However, two studies of individually recognized forest guenons (both conducted on *C. mitis*: Cords 2000; Payne et al. 2003) have shown that most aggressive competition between females takes place over fruit, and that females compete for this resource more often than expected by chance. These observations suggest that at least some fruits in the *C. mitis* diet can be monopolized or profitably usurped, and this conclusion is supported by data on the length of fruit-feeding bouts (Cords 2002, p. 301, mean of 10.2 min for 68 bouts which included some that were truncated by the observer), as well as the phenology and spatial distribution of the plant species that produce the fruits, flowers and seeds that females consume (Cords 1987; Struhsaker 1997). Consistent with the importance of contest competition, both Cords (2000) and Payne et al. (2003) detected stable linear hierarchies among *C. mitis* females once they had monitored their study groups for long enough to compensate for low rates of social interaction and thus were able to assess the directionality of interactions among a sufficient proportion of group members. Nonetheless, in neither study was rank associated clearly with diet, feeding patterns, receipt of grooming, or the rate of viable offspring production.

The intense between-group competition that *C. mitis* females face in most populations (Cords 2002) could account for the absence of clear dominance effects. Indeed, the flurry of grooming among many individuals that often follows intergroup encounters (Cords 2002; Payne et al. 2003) is consistent with the hypothesis that maintaining cohesion is important for success in between-group contests (Rowell et al. 1991). However, at most times *C. mitis* females concentrate their grooming on a few individuals of similar rank (Cords 2002; Payne et al. 2003), and across primate species no clear link has been found between the extent to which females participate in between-group contests and the degree to which they distribute their grooming widely among group members (Cheney 1992). Thus, outside the immediate context of intergroup encounters it is not clear that female interactions function to maintain group cohesion or that the need for solidarity has blunted the effects of rank.

The lack of any clear rank advantages, along with the uncertainty that cooperation in between-group contests attenuates the effects of rank, suggests a need to better understand how competition is mediated in *C. mitis* females, and the forest dwelling guenons more generally. In particular, there is a need to evaluate whether the effects of rank become more apparent under ecological conditions that are more likely to induce contest competition. Although *C. mitis* females, like the other forest dwelling guenons, consume large quantities of fruit and other plant reproductive parts over the course of a year, the importance of this food type varies widely on a seasonal basis (Rudran 1978; Cords 1986; Gautier-Hion 1988). Prior studies have not accounted for this temporal variation, yet it is possible that female relationships become more hierarchical during periods when females are consuming large quantities of fruit and other plant reproductive parts, or at times when females must compete for these resources from a smaller resource base. Moreover, even if female relationships do become more hierarchical at certain times, alternative strategies, such as spreading out while feeding (van Noordwijk and van Schaik 1987; Isbell 1991; Barton 1993; Saito 1996; Sterck and Steenbeek 1997) or switching to more abundant or dispersed resources (Isbell 1991; Saito 1996; Cords 2000), might reduce the effects of rank.

In this paper we present the results of a year-long study of feeding patterns and competition among the adult females of two blue monkey groups (*Cercopithecus mitis stuhlmanni*) living in a species-typical forested habitat. Using data from a complete annual cycle we evaluate the hypotheses that rank-based differences among individuals emerge during periods of elevated competition or resource scarcity, and that females adopt alternative feeding strategies during these periods.

## Methods

### Study site and subjects

We conducted this research at the Isecheno study site of the Kakamega Forest, western Kenya (0°14'N 34°52'E; elevation 1560 m). Kakamega is a semi-deciduous, drier type of Guineo-Congolian rainforest (~2000 mm rainfall annually) located at the easternmost edge of the forest expanse of central equatorial Africa (White 1983). Cords (1987) has described the study site in detail.

We collected focal data over an entire annual cycle (October 1997 to September 1998). Along with a team of trained researchers under our direct supervision we also recorded all observed agonistic interactions over a more extended period (June 1997 to October 1998, June 1999 to October 1999), but we used this information solely to rank females in a dominance hierarchy. During the study, the density of blue monkeys at the study site was approximately 220 individuals/km<sup>2</sup> (Fashing and Cords 2000). Subjects were all adult females of two habituated social groups. The  $T_w$  group, which was the focus of Cords' earlier study (2000), had been under observation since 1979.

The G group had been monitored since 1992, although female relationships had not been studied in detail prior to this study. The  $T_w$  and G groups contained 15 and 17 adult females, respectively. All of these subjects were individually recognized on the basis of natural characteristics.

### Behavioral data collection

KP conducted focal animal observations by entering data directly into an HP 100LX palmtop computer equipped with a BASIC program to act as an event recorder. In the focal samples, we kept a continuous record of all grooming and agonistic interactions between the focal subject and other adult monkeys. For the agonistic interactions, we noted the type of behavior, the individuals involved, and the context of occurrence. Types of agonism included: (1) submit spontaneously – trill, cower, gecker or flee in the apparent absence of prior agonism; (2) avoid – move away from another individual before an approach to 2 m; (3) supplant – cause another individual to move away after an approach to 2 m; and (4) inflict aggression – threaten, lunge, chase or attack. Potential contexts of agonism were: (1) feeding – eating or actively searching for food between mouthfuls, including brief movements (<2 m) between feeding sites, but excluding chewing of items already in the cheek pouches; (2) drinking from an arboreal water hole; (3) participating in any type of social interaction; and (4) attempting to pass along a narrow arboreal passageway. At 1-min intervals we also noted the activity of the focal subject and the presence of all other monkeys within a 2 m radius. If the subject was feeding we noted whether the food being sought or consumed belonged to one of the following categories: (1) plant reproductive parts (primarily fruit, but also flowers and seeds); (2) young leaves, including buds and shoots; (3) insects; or (4) mature leaves.

We scheduled focal samples to last 30 min, but occasionally a female was lost in dense vegetation. In this situation, we tried to find the subject and complete the 30 min of observation time. However, after 15 min of searching we discarded segments shorter than 5 min, while we kept those that were longer for completion at the next opportunity. Because it is difficult to locate individuals in groups dispersed over several hundred meters of dense vegetation, we could not implement a completely random sampling schedule. Instead, we followed any female who: (1) had not been observed in a given round of observations, and (2) had not interacted with our prior subject during the last 10 min of the preceding sample. To control for diurnal time scale, we tried to distribute observations for each female similarly across each of three periods (0700–1030, 1031–1430, 1431–1830 h). In addition, because diet and activity patterns likely are linked to vegetation type, we tried to conduct a similar number of observations per female in each major vegetation zone: (1) high canopy forest; (2) woodland with a less continuous canopy of smaller trees and a well developed ground layer of grass and *Pavetta* shrubs; and (3) the boundary of a local village where a number of *Bischoffia javanica* trees had been planted ( $T_w$  group only). To ensure

that females were sampled similarly across the year, we restarted the procedures for selecting focal subjects every month. In  $T_w$  and G, respectively, we obtained  $37 \pm 1.2$  and  $40 \pm 2.1$  h of focal data per month ( $N=12$  months). Over the entire study, we obtained  $29 \pm 0.5$  h of focal data per female ( $N=32$  females) for a total of 916 h of data.

### Phenology surveys

Following Dasilva (1994), we conducted monthly surveys to estimate the availability of plant reproductive parts. Our survey included those tree species that produce fruit, flowers or seeds constituting at least 1.5% of the annual blue monkey diet at Kakamega (see Cords 1987). We tagged a subset of individual trees throughout each group's home range, and in the middle of every month we gave the marked trees a productivity score of 0, 1, or 2, depending on whether they had "no," "some," or "many" food items. We then weighted the mean productivity score for each tree species by the total basal area of that species in each group's home range. To estimate total basal area, we established thirteen  $10 \times 70$  m<sup>2</sup> plots that were located throughout our study site but away from the main trails. We then measured all stems >5 cm within these plots and extrapolated the resultant density to the entire home range area. However, for three tree species (*Bischoffia javanica*, *Ficus thonningi*, and *F. natalensis*) we directly measured the total basal area per home range by locating all stems and summing their diameters at breast height. For the *Ficus* species, this was both necessary and possible because these trees are extremely large yet occur at low densities. Hence, although there were several *Ficus* trees in the study area, by chance only one fell within our vegetation plots. In the case of *Bischoffia javanica*, an exotic species, trees had been planted exclusively along two main trails. Thus these trees did not occur in any of our plots, but were relatively abundant and easy to locate.

### Data analysis

We used the focal point-samples taken at 1-min intervals to determine activity budgets, the amount of time subjects fed on different food items, and the amount of time they spent in proximity to others. We used the continuous record of behavior to determine the length of grooming bouts, and the rate and context of agonistic interactions.

We used grooming as our primary measure of affiliation because it has been considered a central mechanism that promotes social bonding in primates (Dunbar 1988), and it accounts for the vast majority (96%) of social activity in adult female blue monkeys (Cords 2000).

To facilitate comparison with other studies, we calculated agonism rates in three different ways: (1) the number of interactions with all other individuals per focal hour; (2) the number of interactions with other adult females exclusively per focal hour; and (3) the agonism rate calculated from adult female interactions with each other, corrected

for group size by dividing by the number of potential interactants (the number of females in the group minus one).

We used the MatMan computer program (de Vries 1998) to arrange females in a dominance hierarchy and to determine its degree of linearity. Of the linearity measures MatMan calculates, we selected the index  $h'$ , which is similar to Landau's index of linearity but is corrected for unknown relationships (de Vries 1995). Values of  $h'$  range from 0 to 1 with 1 indicating complete linearity. To document the asymmetry of agonism, we calculated the percentage of interactions that occurred in the less frequent direction.

To evaluate seasonal effects on feeding patterns and agonism rates, we used three measures of the potential for competition over plant reproductive parts to occur: (1) the percentage of time females spent eating plant reproductive parts; (2) the availability of plant reproductive parts in each group's home range, as estimated from the monthly phenology surveys; and (3) the percentage of time females spent eating plant reproductive parts relative to their availability. For each of these measures, we separated the data from the annual cycle into three sets – one including the 4 months with the lowest scores, another including the 4 months with the mid-range scores, and a third including the 4 months with the highest scores. For each month we independently categorized the relative percentage of time females spent feeding and the availability of plant reproductive parts for each of the two monkey groups. The months of data we placed in each category thus did not necessarily match across groups or the three measures we evaluated, and the months we assigned to each category were not necessarily sequential.

In our evaluation of rank effects on behavior, we differentiated high-ranking (in the top half of the hierarchy) and low-ranking females (in the bottom half of the hierarchy). Because there was an uneven number of females in each group (15 in  $T_w$ , 17 in G), we excluded the one female from the very middle of the hierarchy from the analysis. To determine whether high-ranking females received more grooming than low-ranking females we used the matrix correlation methods described by Hemelrijk (1990). In this analysis we compared matrices of grooming received to a hypothesis matrix in which females of successively higher dominance standing were assigned successively greater ranks of grooming received.

We used non-parametric tests to account for the non-normal distribution of data. In all cases, we used two-tailed tests and an alpha value of 0.05 for accepting statistical significance. We also report means  $\pm$  standard error.

## Results

### Activity patterns and agonism rates

Social behavior accounted for only  $7.4 \pm 0.5\%$  of the average female's ( $N=32$ ) activity budget. Grooming was the most common social behavior, accounting for  $89 \pm 1.4\%$  of all social time. The most common non-social



behaviors were resting ( $42\pm 1.1\%$  of activity budget), feeding ( $33\pm 0.9\%$ ), and locomoting ( $11\pm 0.3\%$ ). Females spent the largest fraction of their feeding time consuming plant reproductive parts ( $43\pm 1.0\%$  of feeding budget), but they also spent considerable time consuming insects ( $24\pm 1.2\%$  of feeding budget), young leaves ( $22\pm 1.0\%$ ) and mature leaves ( $7.2\pm 0.7\%$ ). Gums, soil and unidentified foods accounted for the remainder of feeding time ( $3.7\pm 0.3\%$ ). Time devoted to the different types of food clearly differed across the four major categories (Friedman ANOVA:  $\chi^2=81.6$ ,  $df=3$ ,  $P<0.001$ ,  $N=32$  females), and post hoc comparisons revealed that females spent more time eating plant reproductive parts than each of the other major food types ( $P<0.001$  for young leaves, insects and mature leaves, respectively).

While females devoted the largest fraction of their feeding budget to plant reproductive parts, they also competed disproportionately for these resources. Most agonistic interactions of known context between adult females and all potential opponents combined ( $85\%$ ,  $N=213$  interactions) occurred during feeding, and feeding-related agonism was not distributed among the major food types according to their representation in the diet (Chi-square goodness of fit:  $\chi^2=39.5$ ,  $df=3$ ,  $P<0.001$ ). Agonism over plant reproductive parts occurred at 1.41 times the expected rate, while agonism over young leaves and insects, respectively, occurred at just 0.90 and 0.17 times the expected rate. Agonism over mature leaves also occurred more frequently than predicted (at 1.37 times the expected rate), but the biological importance of this finding is unclear given that females devoted only 7% of their annual feeding time to this resource, as compared to  $>40\%$  for plant reproductive parts.

Although females spent the largest proportion of their feeding time consuming plant reproductive parts and competed disproportionately for these resources, agonism rates still were relatively low. The average female engaged in agonism with all other group members at a rate of  $0.39\pm 0.02$  interactions/h ( $N=32$  females), and with other adult females at a rate of  $0.23\pm 0.02$  interactions/h. Corrected for group size, female-female agonism occurred at a rate of  $0.015\pm 0.001$  interactions/h/potential interactant.

Despite low agonism rates, it was possible to detect a significantly linear hierarchy in both social groups ( $T_w$ :  $h'=0.89$ ,  $P<0.001$ ; G:  $h'=0.74$ ,  $P<0.001$ ). Agonistic relationships were asymmetrical with few reversals against the prevailing order (1% of all interactions in  $T_w$ , 8% of all interactions in G). Hence, in  $T_w$ , the reversal rate was well below the  $<5\%$  that typically has been reported for species

with strong dominance hierarchies (Isbell and Young 2002). The reversal rate for G exceeded this level, but was still well below the 15% that has been seen in many species considered to have weak and indiscernible dominance hierarchies (Isbell and Young 2002). Coalitions were extremely rare, occurring in just 1% of all focal agonism.

#### Seasonal trends in feeding and agonism rates

The time females spent feeding on plant reproductive parts varied across the months of the year (Friedman ANOVA:  $\chi^2=66.2$ ,  $df=11$ ,  $P<0.001$ ,  $N=32$  females, range =  $8.4\pm 1.0$  to  $22\pm 2.3\%$  of activity budget from the lowest to the highest month). On a month-by-month basis, the time females spent eating plant reproductive parts did not correlate with the availability of this resource in either group (Spearman rank-order correlation:  $T_w$ :  $r_s=-0.45$ ,  $P=0.15$ ,  $N=12$  months; G:  $r_s=0.21$ ,  $P=0.50$ ,  $N=12$  months). However, in both groups there was a significant negative correlation between the availability of plant reproductive parts and the percentage of time females spent feeding in general (Spearman rank-order correlation:  $T_w$ :  $r_s=-0.59$ ,  $P=0.04$ ,  $N=12$  months; G:  $r_s=-0.64$ ,  $P=0.03$ ,  $N=12$  months). Hence when plant reproductive parts were relatively scarce, females may have had to spend more time feeding to compensate for lower rates of food intake and the need to consume foods of lower nutritional value.

Rates of female-female agonism did not vary in conjunction with seasonal changes in feeding patterns or the availability of plant reproductive parts (Table 1). Female-female agonism rates were not elevated during periods when females were spending more time feeding in general, or during periods when females were spending more time feeding on plant reproductive parts in particular. Similarly, agonism rates were not elevated during periods when the availability of plant reproductive parts was low, or during periods when females were consuming more of this resource relative to its availability.

#### Rank effects on feeding and activity budgets

Rank effects on feeding budgets were subtle and difficult to detect (Table 2). Over the complete annual cycle, females from the top and bottom halves of their hierarchy did not differ in the time they spent feeding in general, or feeding on plant reproductive parts in particular. Similarly, during the

**Table 1** Agonism rates (incidents/h, means  $\pm$  standard error) during periods of differing resource consumption, availability and consumption relative to availability

Measure used to partition data	Period			Test for significant differences across periods <sup>a</sup>
	Low	Mid	High	
Total feeding	$0.27\pm 0.03$	$0.21\pm 0.03$	$0.20\pm 0.03$	$\chi^2=1.2$ , $P=0.54$
Feeding on plant reproductive parts	$0.20\pm 0.03$	$0.24\pm 0.03$	$0.23\pm 0.04$	$\chi^2=4.4$ , $P=0.11$
Availability of plant reproductive parts	$0.20\pm 0.03$	$0.21\pm 0.04$	$0.26\pm 0.04$	$\chi^2=1.2$ , $P=0.55$
Feeding on plant reproductive parts relative to availability	$0.23\pm 0.03$	$0.26\pm 0.04$	$0.19\pm 0.04$	$\chi^2=1.2$ , $P=0.54$

<sup>a</sup> Friedman ANOVA,  $df=2$ ,  $N=32$  females

**Table 2** Rank effects on feeding, expressed as percentage of total activity budget (means  $\pm$  standard error)

	Position in dominance hierarchy		Test for significance <sup>a</sup> by rank
	Top half	Bottom half	
Feeding, complete annual cycle	31.5 $\pm$ 1.5	33.8 $\pm$ 1.1	$U=74, P=0.11$
Feeding on plant reproductive parts, complete annual cycle	14.1 $\pm$ 0.8	14.2 $\pm$ 0.6	$U=102, P=0.65$
Feeding, high agonism periods	30.7 $\pm$ 2.0	33.4 $\pm$ 1.4	$U=105, P=0.76$
Feeding on plant reproductive parts, high agonism periods	13.2 $\pm$ 1.2	14.1 $\pm$ 1.3	$U=101, P=0.63$
Feeding by availability period			
Low availability	34.7 $\pm$ 1.8	40.2 $\pm$ 1.3 <sup>d</sup>	$U=59, P=0.03$
Mid availability	30.0 $\pm$ 2.2	33.9 $\pm$ 1.4 <sup>c</sup>	$U=64, P=0.04$
High availability	29.2 $\pm$ 2.0	27.5 $\pm$ 1.8 <sup>c, d</sup>	$U=103, P=0.68$
Test for significance across availability periods <sup>b</sup>	$\chi^2=4.9, P=0.09$	$\chi^2=19.6, P<0.001$	
Feeding on plant reproductive parts by availability period			
Low availability	12.9 $\pm$ 0.9	16.0 $\pm$ 1.2	$U=66, P=0.05$
Mid availability	15.2 $\pm$ 1.3	16.1 $\pm$ 1.1 <sup>c</sup>	$U=96, P=0.49$
High availability	14.1 $\pm$ 1.8	10.7 $\pm$ 1.2 <sup>c</sup>	$U=78, P=0.15$
Test for significance across availability periods <sup>b</sup>	$\chi^2=2.5, P=0.28$	$\chi^2=8.4, P=0.02$	

<sup>a</sup> Mann-Whitney  $U$ -test,  $N_{\text{high}}=15$  females,  $N_{\text{low}}=15$  females

<sup>b</sup> Friedman ANOVA,  $df=2$ ,  $N=32$  females

<sup>c</sup> Post hoc tests indicate conditions differ at the level of  $P<0.05$

<sup>d</sup> Post hoc tests indicate conditions differ at the level of  $P<0.01$

third of the year with the highest female-female agonism rates, when competition had the potential to have the most pronounced impact on feeding patterns, rank again had no effect on the time females spent feeding in general or feeding on plant reproductive parts in particular. However, during the third of the year in which the lowest availability of plant reproductive parts forced individuals to compete over the smallest supply of this resource, females from the bottom as compared to the top half of their hierarchy spent more time feeding in general and feeding on plant reproductive parts in particular.

The effect of rank on feeding times was related to changes across availability periods in the behavior of females from the bottom half of their hierarchy. High-ranking females showed no significant variation, while low-ranking females increased the time they spent feeding in general and feeding on plant reproductive parts in particular as the availability of this resource declined. As a result of this change, even though dominance had no effect on feeding times during high availability periods, rank differences emerged during periods of low (for feeding in general and feeding on plant reproductive parts in particular), and middle (for overall feeding) availability. These small differences in the feeding patterns of high- and low-ranking females, which emerged only during periods of resource scarcity, are consistent with the hypothesis that low-ranking females foraged less efficiently during these periods, or had to consume lower quality foods, and therefore were forced to spend more time feeding to obtain the resources they needed. When averaged over an annual cycle, these transient rank differences appear to have been diluted so that they were too small to detect.

The increase in the percentage of their activity budget devoted to feeding during low availability periods left subordinate females with less time for resting (Table 3). While resting behavior remained relatively constant in

high-ranking females, low-ranking females reduced their resting time during low as compared to high availability periods. As a result of this change, rank again had a significant effect on resting time only when the availability of plant reproductive parts was low. However, contrary to resting time, social time was unaffected by the availability of resources for either low- or high-ranking females, and during no period was there a significant rank effect (Table 3).

#### Rank effects on grooming patterns

Rank had no clear effect on grooming patterns during any period of analysis (Table 4). Over the complete annual cycle there was no evidence that females systematically preferred to groom higher ranking partners ( $T_w: K_r=44, P=0.57$ ;  $G: K_r=20, P=0.31$ ), and overall females from the top and bottom half of their hierarchy received similar amounts of grooming (Table 4). Within dyads, the amount of grooming the dominant partner received ( $6.8\pm 0.7$  s/observation h,  $N=175$  dyads) nearly matched that which the subordinate partner received ( $5.7\pm 0.5$  s/observation h), and in close to half (54%) of the grooming dyads (94 of 175) the dominant member received more grooming than the subordinate. During the third of the year with the highest agonism rates, when tolerance of high-ranking individuals should have been most valuable, there was again no evidence that females systematically preferred to groom dominant individuals ( $T_w: K_r=110, P=0.92$ ;  $G: K_r=101, P=0.90$ ), and overall females from the bottom half of their hierarchy actually received the most grooming (Table 4). Within dyads, the amount of grooming the dominant partner received ( $10.0\pm 1.3$  s/observation h,  $N=104$  dyads) nearly matched that which the subordinate partners received ( $9.7\pm 0.1$  s/observation h), and in only

**Table 3** Percentage of activity budget spent resting and socializing during periods when the availability of plant reproductive parts was low, intermediate and high (means  $\pm$  standard error)

	Position in dominance hierarchy		Test for significance by rank <sup>a</sup>
	Top half	Bottom half	
Resting by availability period			
Complete annual cycle	44.2 $\pm$ 2.0	40.6 $\pm$ 0.9	$U=75, P=0.12$
Low availability	41.3 $\pm$ 2.6	36.1 $\pm$ 1.3 <sup>c</sup>	$U=63, P=0.04$
Mid availability	45.7 $\pm$ 3.1	41.0 $\pm$ 1.4	$U=94, P=0.44$
High availability	45.9 $\pm$ 2.1	44.8 $\pm$ 1.4 <sup>c</sup>	$U=106, P=0.79$
Test for significance across availability periods <sup>b</sup>	$\chi^2=1.2, P=0.55$	$\chi^2=9.7, P<0.01$	
Socializing by availability period			
Complete annual cycle	7.0 $\pm$ 0.7	7.1 $\pm$ 0.7	$U=107, P=0.82$
Low availability	7.3 $\pm$ 1.0	6.0 $\pm$ 1.2	$U=82, P=0.21$
Mid availability	6.8 $\pm$ 1.0	7.5 $\pm$ 0.9	$U=99, P=0.58$
High availability	7.1 $\pm$ 1.1	7.7 $\pm$ 1.1	$U=92, P=0.40$
Test for significance across availability periods <sup>b</sup>	$\chi^2=1.7, P=0.42$	$\chi^2=4.3, P=0.13$	

<sup>a</sup> Mann–Whitney  $U$ -test,  $N_{\text{high}}=15$  females,  $N_{\text{low}}=15$  females

<sup>b</sup> Friedman ANOVA,  $df=2$ ,  $N=32$  females

<sup>c</sup> Post hoc tests indicate conditions differ at the level of  $P<0.01$

**Table 4** Grooming received (min/observation h) by high- and low-ranking females (means  $\pm$  standard error)

	Position in dominance hierarchy		Test for significance by rank <sup>a</sup>
	Top half	Bottom half	
Grooming received, complete annual cycle	2.2 $\pm$ 0.3	2.2 $\pm$ 0.3	$U=102, P=0.66$
Grooming received, high agonism periods	1.8 $\pm$ 0.4	2.5 $\pm$ 0.3	$U=65, P=0.05$
Grooming received, low availability periods	1.8 $\pm$ 0.3	2.1 $\pm$ 0.4	$U=99, P=0.58$

<sup>a</sup> Mann–Whitney  $U$ -test,  $N_{\text{high}}=15$  females,  $N_{\text{low}}=15$  females

43% of the dyads did the dominant partner receive more grooming than the subordinate ( $N=43$  of 104). Even though rank influenced feeding patterns when plant reproductive parts were scarce, there was still no evidence that females systematically preferred to groom higher ranking partners during periods of low availability ( $T_w: K_r=26, P=0.66$ ;  $G: K_r=53, P=0.24$ ), and overall females from the top and bottom half of the hierarchy still received similar amounts of grooming (Table 4). Within dyads, the amount of grooming the dominant partner received ( $11.2\pm 1.5$  s/observation h,  $N=92$  dyads) again nearly matched that which the subordinate partner received ( $11.1\pm 1.4$  s/observation h), and in only 51% of all dyads did the dominant member receive more grooming than the subordinate.

#### Alternative feeding strategies

While subordinate individuals compensated for the reduced availability of plant reproductive parts by increasing their feeding time, females in general appeared to avoid competition by spreading out while feeding and switching to

alternative resources. Over the complete annual cycle, all females spent a smaller portion of their feeding as compared to their overall activity budget in proximity to other individuals (Wilcoxon signed ranks:  $T^+=528, P<0.001, N=32$  females; portion of feeding time in proximity:  $3.5\pm 0.4\%$ ; portion of total time in proximity:  $14\pm 0.8\%$ ). The tendency for females to space themselves apart from others (Table 5) varied with the availability of plant reproductive parts, and post hoc comparisons revealed that females were less likely to be in proximity to other individuals during low as compared to high availability periods. However, this pattern appeared to result from the general tendency for females to spend more time feeding – an activity most often carried out in the absence of proximity partners – when plant reproductive parts were less available. Considering feeding time exclusively, we found females did not alter their tendency to spread out with the availability of plant reproductive parts.

Like varying food availability, rank had no effect on the tendency for females to maintain proximity to other individuals (Table 6). Rank did not influence the total time or the feeding time that females spent in proximity to others, even

**Table 5** Percentage of activity budget in proximity during periods when the availability of plant reproductive parts was low, intermediate and high (means  $\pm$  standard error)

	Availability of plant reproductive parts			Test for significance across availability periods <sup>a</sup>
	Low	Mid	High	
Percentage of total activity budget in proximity	12 $\pm$ 1.0 <sup>b</sup>	14 $\pm$ 1.0	18 $\pm$ 1.5 <sup>b</sup>	$\chi^2=11.8, P<0.01$
Percentage of feeding budget in proximity	3.2 $\pm$ 0.6	4.2 $\pm$ 0.7	3.2 $\pm$ 0.5	$\chi^2=0.9, P=0.63$

<sup>a</sup> Friedman ANOVA,  $df=2, N=32$  females

<sup>b</sup> Post hoc tests indicate conditions differ at the level of  $P<0.01$

**Table 6** Rank effects on overall time in proximity and time in proximity while feeding over the complete annual cycle and during periods when the availability of plant reproductive parts was low

	Position in dominance hierarchy		Test for significance by rank <sup>a</sup>
	Top half	Bottom half	
Percentage of total activity budget in proximity	14.5±1.9	14.6±1.1	$U=110, P=0.90$
Percentage of feeding budget in proximity	2.9±0.4	3.7±0.6	$U=94, P=0.47$
Percentage of total activity budget in proximity, low availability periods	10.9±1.3	12.7±1.9	$U=98, P=0.55$
Percentage of feeding budget in proximity, low availability periods	2.1±0.4	3.2±0.8	$U=99, P=0.58$

<sup>a</sup> Mann–Whitney  $U$ -test,  $N_{\text{high}}=15$  females,  $N_{\text{low}}=15$  females

**Table 7** Consumption of alternative resources (percentage of activity budget, means ± standard error) during periods of low, intermediate and high availability of plant reproductive parts

	Availability of plant reproductive parts			Test for significance across availability periods <sup>a</sup>
	Low	Mid	High	
Feeding on young leaves	11±0.7 <sup>b</sup>	6.7±0.6 <sup>b,c</sup>	5.0±0.5 <sup>c</sup>	$\chi^2=27.8, P<0.001$
Feeding on mature leaves	3.8±0.4 <sup>c,d</sup>	2.2±0.4 <sup>d</sup>	1.3±0.2 <sup>c</sup>	$\chi^2=24.6, P<0.001$
Feeding on insects	7.1±0.6	6.2±0.6 <sup>c</sup>	8.5±0.6 <sup>c</sup>	$\chi^2=11.4, P=0.003$

<sup>a</sup> Friedman ANOVA,  $df=2, N=32$  females

<sup>b</sup> Post hoc test indicate conditions differ at the level of  $P<0.05$

<sup>c</sup> Post hoc tests indicate conditions differ at the level of  $P<0.01$

<sup>d</sup> Post hoc tests indicate conditions differ at the level of  $P<0.01$

**Table 8** Rank effects on the consumption of alternative resources (percentage of activity budget, means ± standard error) over the complete annual cycle and during periods when the availability of plant reproductive parts was low

	Position in dominance hierarchy		Test for significance by rank <sup>a</sup>
	Top half	Bottom half	
Feeding on young leaves, complete annual cycle	7.2±0.5	8.0±0.6	$U=77, P=0.14$
Feeding on young leaves, low plant reproductive part periods	9.4±1.0	11.9±0.9	$U=74, P=0.11$
Feeding on mature leaves, complete annual cycle	1.7±0.2	2.8±0.3	$U=51, P<0.01$
Feeding on mature leaves, low plant reproductive part periods	2.9±0.3	4.1±0.8	$U=78, P=0.15$

<sup>a</sup> Mann–Whitney  $U$ -test,  $N_{\text{high}}=15$  females,  $N_{\text{low}}=15$  female

when our analysis was limited to the months when plant reproductive parts were least available. The tendency for females to space themselves out while feeding thus appeared strong enough that it was observed under all conditions, even those in which females were not constrained by low rank or the reduced availability of plant reproductive parts.

In addition to spreading out while feeding, females spent more time consuming alternative resources (young and mature leaves) when the availability of plant reproductive parts was low (Table 7). The amount of time females spent feeding on insects also varied with the availability of plant reproductive parts, but not in a way that was consistent with the hypothesis that insects serve as an alternative resource – females actually spent more time feeding on insects when the availability of plant reproductive parts was high as compared to intermediate, while they showed no difference between the most extreme periods of low and high availability. It could be that insects are a desirable rather than an alternative food and were consumed more during periods when the availability of plant reproductive parts was high simply because peak availability of these two resource types coincided.

Dominance rank had no clear impact on the use of alternative resources (Table 8). Although young leaf consumption increased during periods when the availability of plant reproductive parts was low, females from the top and bottom halves of their hierarchy did not differ in their consumption of this resource, either over the complete annual cycle or during periods when the availability of plant reproductive parts was low. By contrast, on an annual basis, females from the bottom as compared to the top half of their hierarchy spent more time eating mature leaves. However, when the availability of plant reproductive parts was low, the effect of rank on the amount of time females spent eating mature leaves was not significant. Moreover, the biological importance of this finding is unclear given that mature leaves accounted for only 7% of the annual feeding budget.

## Discussion

The forest dwelling guenons challenge theoretical predictions that relate particular diets and patterns of resource distribution to distinct modes of female interaction. Although



fruit and other plant reproductive parts are a large part of their diet (Rudran 1978; Struhsaker 1978; Cords 1986; Gautier-Hion 1988; Chapman et al. 2002), these monkeys have been characterized as having relatively egalitarian and undifferentiated relationships (Isbell 1991; Cheney 1992; Sterck and Steenbeek 1997; Isbell and Young 2002). Because a large portion of the foods that *C. mitis* females consume occur in high quality patches that can be profitably usurped, this pattern does not appear to accord well with prevailing socioecological theory. However, in this and two other recent studies of individually recognized *C. mitis* females (Cords 2000; Payne et al. 2003) it has been possible to detect linear dominance hierarchies and differentiated social relationships with the accumulation of sufficient observation hours to compensate for low female interaction rates. Our study, spanning a complete annual cycle, goes one step further in demonstrating that subtle rank differences in feeding patterns may emerge at times of year when the availability of plant reproductive parts is low. The use of alternative feeding strategies appears to account for the subtlety of these effects. Low-ranking females increased the time they spent feeding in general and feeding on plant reproductive parts in particular when the availability of this resource was low, and females of all ranks increased their consumption of leaves during these periods. Moreover, at all times females spaced themselves apart from other individuals while they were feeding.

The finding that the effects of rank varied with the availability of plant reproductive parts can be used to evaluate prevailing hypotheses about the ways in which resource use influences female social behavior. Studies showing that competitive behavior varies with the consumption of high quality monopolizable resources (Sugiyama and Ohsawa 1982; Whitten 1983; Altmann and Muruthi 1988; Boccia et al. 1988; Barton 1993; Barton and Whiten 1993; Gore 1993; Barton et al. 1996; Saito 1996; Koenig et al. 1998; Pruettz and Isbell 2000; Mathy and Isbell 2001), along with studies demonstrating that differences in social behavior correspond to differences in resource utilization among closely related species (Mitchell et al. 1991; Isbell and Pruettz 1998; Isbell et al. 1998, 1999; Pruettz and Isbell 2000; Boinski et al. 2002; Korstjens et al. 2002), provide some of the best evidence supporting socioecological theory (Boinski et al. 2002; Koenig 2002; Korstjens et al. 2002). In this study, there were seasonal changes in the effects of rank on feeding behavior, but the rate of overt contest competition did not vary with the consumption, availability, or consumption relative to availability of the most contested resource – plant reproductive parts. Moreover, this rate was similar to that which Cords (2000) previously found (one interaction every 2.2 vs. 2.6 h in this study) using similar methods to monitor female relationships among a subset of the same subjects in this study over a more limited period when the availability of plant reproductive parts was low. Although differences in observation techniques make comparisons across studies difficult, this rate is low, at only 5–50% of the rate found among some of the more commonly studied species of wild cercopithecines (Cords 2000). In our study, rank effects emerged even though rates

of contest competition did not increase, suggesting that differences in access to resources were imposed through avoidance from below rather than aggression from above. Thus, contrary to the most simplistic reading of socioecological theory, the use of high quality resources that can be profitably usurped does not necessarily lead to overt contest competition and the predicted interrelated set of female social interaction patterns (see also Koenig 2002).

The lack of a clear preference for grooming higher ranking females and the extreme rarity of coalition formation documented in this and previous studies of individually recognized *C. mitis* females (Cords 2000; Payne et al. 2003) accords well with the suggestion that rank differences are maintained by avoidance from below rather than aggression from above. If rank differences were imposed through aggression, preferential grooming of dominant individuals might be expected as a mechanism for promoting tolerance at feeding sites, even in the absence of coalition formation (Barrett et al. 1999; Henzi and Barrett 1999). However, if low-ranking group members will not even approach high-ranking individuals in situations that might trigger contest competition, there is no value in using grooming as a tool for promoting tolerance, let alone as a means for gaining support in agonistic interactions.

Although detectable, dominance rank had a very small effect on feeding behavior that became apparent only during periods when plant reproductive parts were relatively scarce. These rank differences emerged as an increase in the time low-ranking females spent feeding in general and feeding on plant reproductive parts in particular. This increase may have been due to the tendency for subordinate females to switch to foods of lower nutritional quality (Whitten 1983; Nakagawa 1989; Saito 1996) or to have lower rates of food intake (Post et al. 1980; van Noordwijk and van Schaik 1987; Barton and Whiten 1993). Our data indicate that both high- and low-ranking females increased their consumption of young and mature leaves when plant reproductive parts were relatively scarce, but an analysis of the particular items consumed and their nutritional value could reveal that subordinate females must switch to even lower quality foods and therefore have to feed longer to obtain the resources they need. Similarly, although we did not measure rates of food intake, when Cords (2000) looked at ingestion times for four important fruit species she found an absence of rank differences among a subset of the same subjects in this study. Assuming that intake rates fail to differ for other foods as well, we find it difficult to explain the increased feeding time by low-ranking females from a functional perspective.

Given the subtlety of the rank-effects we found, it also is unclear that they are of any real biological importance. Resting has been regarded as an uncommitted reserve of time that can be allocated to other activities (Dunbar and Sharman 1984; Dunbar 1992), and previous *C. mitis* studies have shown that females spend a substantial proportion of their daylight hours resting (30%: Cords 2000; 32%: Payne et al. 2003). Even when plant reproductive parts were relatively scarce, we found that low-ranking females still devoted over 36% of their activity budget to resting,

and they showed no reduction in the time they spent socializing. It is likely therefore that these females were able to easily accommodate within their activity budgets the additional 4–6% of time (relative to high-ranking females) that they had to spend feeding during periods when the availability of plant reproductive parts was low to intermediate. Hence it remains to be shown whether a slight decrease in feeding efficiency can impose upon females any real costs in ultimate terms. Indeed, looking at reproductive output among *C. mitis* females with a known reproductive history of at least 6 years, Cords (2002) was unable to detect any rank effects on reproductive rates.

Even the high-ranking females in our study may have followed the alternative strategies of spreading out while foraging and switching to alternative resources because the diversity of foods in the *C. mitis* diet allowed them to do so at little cost. The forest guenons are known for their exceptional degree of dietary flexibility – displaying more variation in the consumption of plant foods within a single group across time than they do between groups, forests and species (Chapman et al. 2002) – and the ability to consume many different types of food can mitigate the effects of competition by allowing individuals to switch to alternative resources (Lambert 2002). However, dietary flexibility and the ability to switch between resources has been noted as a generalized characteristic of cercopithecine primates (Lambert 1998, 2002). Hence, although blue monkeys are known for their highly variable diet, detailed studies using comparable methods are needed to evaluate the relative degree of dietary diversity across primate lineages (Chapman et al. 2002), and to determine whether the extreme subtlety of dominance effects we observed can be attributed to an unusual degree of dietary flexibility.

While the ability to switch to alternative resources can minimize overt competition, the absence of significant predation risks also has the potential to reduce aggression levels by allowing females to space themselves out while feeding (Janson 1988; van Schaik 1989; but see Isbell and Enstam 2002). Blue monkey groups at Kakamega are quite dispersed at times, with individuals separated by hundreds of meters so that they are out of sight of one another and unlikely to hear quieter intragroup calls. However, despite the difficulty of obtaining accurate data on predation rates (Janson 2000), there is no inherent reason to suspect that blue monkeys or any of the forest guenons are free from significant predation risks. Indeed, observed predator attacks, specialized male alarm calls, and the tendency for all group members to dive into the lower strata of the forest when aerial predators or harmless look-alikes are sighted all suggest that predation has been a significant evolutionary force for these monkeys (Cords 1987; Gautier-Hion and Tutin 1988; Cordeiro 1992; Zuberbuhler 2002).

In other gregarious primates, low-ranking females incur the costs of feeding in peripheral locations where they face greater predation risks, must maintain high vigilance rates, and have reduced foraging efficiencies (Robinson 1981; van Noordwijk and van Schaik 1987; van Schaik and van Noordwijk 1988; van Schaik 1989; Janson 1990; Ron et al. 1996; Hall and Fedigan 1997). To date there

are insufficient data from Kakamega or any other guenon study site to determine whether lower-ranking females experience more predation (Cords 2000, 2002). Future studies will need to monitor the location of females within their groups to determine whether low-ranking individuals are forced into more dangerous, peripheral positions when preferred food is scarce. Nonetheless, our informal observations over many years of study suggest no obvious rank effect on spatial position within the group.

The results of this study highlight the need to move beyond dietary categories when evaluating ecological influences on social behavior (Koenig 2002). Over the past two decades it has been recognized increasingly that dietary categories cannot adequately predict whether a particular resource can be profitably monopolized or usurped, and that it is important to consider the quality, distribution and depletion time of the foods that animals consume (Whitten 1983; Mitchell et al. 1991; Saito 1996; Isbell et al. 1998; Koenig et al. 1998; Koenig 2000). While these factors are important, we have shown in this study that it is also necessary to consider the behavioral strategies that animals use while feeding. Even when females consume high quality foods that can be monopolized or profitably usurped, the use of alternative strategies, such as switching to more abundant resources or spreading out while feeding, may minimize the value and hence the occurrence of overt competition. When females are able to follow alternative foraging strategies, the effects of competition may be blunted so that they are subtle and difficult to detect.

**Acknowledgements** We thank the Government of Kenya for permission to conduct research in the Kakamega Forest and the Institute for Primate Research (National Museums of Kenya) for local sponsorship. We are most grateful to Praxides Akelo and Benjamin Okalo for assistance observing monkeys in the field, to Benjamin Okalo and Wilberforce Okeka for help with identifying the local trees, and to the research teams of 1997 and 1998 for their observations of rare events. Dorothy Cheney, Julie Gros-Louis, Robert Harding and four anonymous reviewers provided helpful suggestions on earlier versions of this manuscript. This research was funded by the Anthropology Department of the University of Pennsylvania, the Wenner Gren Foundation, the L. S. B. Leakey Foundation, and two National Science Foundation grants to M.C. (SBR 95-23623, BCS 98-08273). The investigations described herein comply with the laws of the United States and Kenya

---

## References

- Alexander RD (1974) The evolution of social behavior in groups. *Annu Rev Ecol Syst* 5:325–383
- Altmann J, Muruthi P (1988) Differences in daily life between semiprovisioned and wild-feeding baboons. *Am J Primatol* 15:213–221
- Barrett L, Henzie SP, Weingrill T, Lycett JE, Hill RA (1999) Market forces predict grooming reciprocity in female baboons. *Proc Roy Soc Biol Sci Ser B* 266:665–670
- Barton RA (1993) Sociospatial mechanisms of feeding competition among female olive baboons, *Papio anubis*. *Anim Behav* 46:791–802
- Barton RA, Byrne RW, Whiten A (1996) Ecology, feeding competition and social structure in baboons. *Behav Ecol Sociobiol* 38:321–329

- Barton RA, Whiten A (1993) Feeding competition among female olive baboons, *Papio anubis*. *Anim Behav* 46:777–789
- Bertram BCR (1980) Vigilance and group size in ostriches. *Anim Behav* 28:278–86
- Boccia ML, Laudenslager M, Reite M (1988) Food distribution, dominance, and aggressive behaviors in bonnet macaques. *Am J Primatol* 16:123–130
- Boinski S, Sughrue K, Selvaggi L, Quatrone R, Henry M, Cropp S (2002) An expanded test of the ecological model of primate social evolution: Competitive regimes and female bonding in three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis* and *S. sciureus*). *Behaviour* 139:227–261
- Boydston EE, Kapheim KM, Szykman M, Holekamp KE (2003) Individual variation in space use by female spotted hyenas. *J Mammal* 84:1006–1018
- Cavallini P, Nel JAJ (1995) Comparative behaviour and ecology of two sympatric mongoose species (*Cynictis penicillata* and *Galerella pulverulenta*). *S Afr J Zool* 30:46–49
- Chapman CA, Chapman LJ, Cords M, Gathua JM, Gautier-Hion A, Lambert JE, Rode K, Tutin CEG, White LJT (2002) Variation in the diets of *Cercopithecus* species: Differences within forests, among forests, and across species. In: Glenn ME, Cords M (eds) *The guenons: Diversity and adaptation in African monkeys*. Kluwer Academic Publishers, New York, pp 325–350
- Cheney DL (1992) Intragroup cohesion and intergroup hostility: The relations between grooming distributions and intergroup competition among female primates. *Behav Ecol* 3:334–345
- Clutton-Brock TH (1988) Reproductive success in male and female red deer. In: Clutton-Brock TH (ed) *Reproductive success: Studies of individual variation in contrasting breeding systems*. University of Chicago Press, Chicago, pp 325–343
- Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organisation. *J Zool, London* 183:1–39
- Cordeiro NJ (1992) Behaviour of blue monkeys (*Cercopithecus mitis*) in the presence of crowned eagles (*Stephanoaetus coronatus*). *Folia Primatol* 59:203–207
- Cords M (1986) Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus ascanius* and *C. mitis*. *J Anim Ecol* 55:811–827
- Cords M (1987) Mixed-species association of *Cercopithecus* monkeys in the Kakamega Forest, Kenya. University of California, Publications in Zoology 117:1–109
- Cords M (2000) Agonistic and affiliative relationships in a blue monkey group. In: Whitehead P, Jolly C (eds) *Old world monkeys*. Cambridge University Press, Cambridge, pp 453–479
- Cords M (2002) Friendship among adult female blue monkeys (*Cercopithecus mitis*). *Behaviour* 139:291–314
- Dasilva GL (1994) Diet of *Colobus polykomos* in Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. *Int J Primatol* 5:655–665
- 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 (1998) Finding a dominance order most consistent with a linear hierarchy: A new procedure and review. *Anim Behav* 55:827–843
- Dunbar R, Sharman M (1984) Is social grooming altruistic?. *Z Tierpsychol* 64:163–173
- Dunbar RIM (1988) Primate social systems. Croom Helm, London
- Dunbar RIM (1992) Time: A hidden constraint on the behavioural ecology of baboons. *Behav Ecol Sociobiol* 31:35–49
- Fashing PJ, Cords M (2000) Diurnal primate densities and biomass in the Kakamega Forest: An evaluation of census methods and a comparison with other forests. *Am J Primatol* 50:139–152
- Gautier-Hion A (1988) The diet and dietary habits of forest guenons. In: Gautier-Hion A, Bourliere F, Gautier J, Kingdon J (eds) *A primate radiation: Evolutionary biology of the African guenons*. Cambridge University Press, New York, pp 257–283
- Gautier-Hion A, Tutin CEG (1988) Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Folia Primatol* 51:149–151
- Gilchrist JS, Otali E (2002) The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose. *Can J Zool* 80:1795–1802
- 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
- Hall CL, Fedigan LM (1997) Spatial benefits afforded by high rank in white-faced capuchins. *Anim Behav* 53:1069–1082
- Hemelrijk CK (1990) Models of and tests for reciprocity unidirectionality and other social interaction patterns at a group level. *Anim Behav* 39:1013–1029
- Henzi SP, Barrett L (1999) The value of grooming to female primates. *Primates* 40:47–59
- Holekamp KE, Smale L, Szykman M (1996) Rank and reproduction in the female spotted hyaena. *J Reprod Fertil* 108:229–37
- Isbell LA (1991) Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behav Ecol* 2:143–155
- Isbell LA, Enstam KL (2002) Predator (in)sensitive foraging in sympatric female vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*): A test of ecological models of group dispersion. In: Miller LE (ed) *Eat or be eaten: Predator sensitive foraging among primates*. Cambridge University Press, Cambridge, pp 154–168
- Isbell LA, Pruettz JD (1998) Differences between vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) in agonistic interactions between adult females. *Int J Primatol* 19:837–855
- Isbell LA, Pruettz JD, Lewis M, Young T (1999) Rank differences in ecological behavior: A comparative study of patas monkeys (*Erythrocebus patas*) and vervets (*Cercopithecus aethiops*). *Int J Primatol* 20:257–272
- Isbell LA, Pruettz JD, Young TP (1998) Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. *Behav Ecol Sociobiol* 42:123–133
- Isbell LA, Young TP (2002) Ecological models of female social relationships in primates: Similarities, disparities, and some directions for future clarity. *Behaviour* 139:177–202
- Janson CH (1988) Intra-specific food competition and primate social structure: A synthesis. *Behaviour* 105:1–17
- Janson CH (1990) Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Anim Behav* 40:922–934
- Janson CH (1992) Evolutionary ecology of primate social structure. In: Smith EA, Winterhalder B (eds) *Evolutionary ecology and human behavior*. de Gruyter, New York, pp 95–130
- Janson CH (2000) Primate socio-ecology: The end of a golden age. *Evol Anthropol* 9:73–86 DOI: 10.1002/(SICI)1520-6505(2000)9:2<73:AID-EVAN2>3.0.CO;2-X
- 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, Beise J, Chalise MK, Ganzhorn JU (1998) When females should contest for food-testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behav Ecol Sociobiol* 42:225–237
- Korstjens AH, Sterck EHM, Noë R (2002) How adaptive or phylogenetically inert is primate social behaviour? A test with two sympatric colobines. *Behaviour* 139:203–225
- Lambert JE (1998) Primate digestion: Interactions among anatomy, physiology, and feeding ecology. *Evol Anthropol* 7:8–20 DOI: 10.1002/(SICI)1520-6505(1998)7:1<8:AID-EVAN3>3.0.CO;2-C
- Lambert JE (2002) Resource switching and species coexistence in guenons: A community analysis of dietary flexibility. In: Glenn ME, Cords M (eds) *The guenons: Diversity and adaptation in African monkeys*. Kluwer Academic Publishers, New York, pp 309–323



- Lawes MJ (1991) Diet of samango monkeys (*Cercopithecus mitis erythrarchus*) in the Cape Vidal Dune Forest South Africa. *J Zool* 224:149–173
- Magliocca F, Querouil S, Gautier-Hion A (2002) Grouping patterns, reproduction, and dispersal in a population of sitatungas (*Tragelaphus spekei gratus*). *Can J Zool* 80:245–250
- Mathy JW, Isbell LA (2001) The relative importance of size of food and interfood distance in eliciting aggression in captive rhesus macaques (*Macaca mulatta*). *Folia Primatol* 72:268–277 DOI:10.1159/000049948
- 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
- Nakagawa N (1989) Feeding strategies of Japanese monkeys against deterioration of habitat quality. *Primates* 30:1–16
- Palomares F, Delibes M (1993) Social organization in the Egyptian mongoose: Group size, spatial behaviour and inter-individual contacts in adults. *Anim Behav* 45:917–925
- Payne HFP, Lawes MJ, Henzi SP (2003) Competition and the exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). *Behaviour* 140:453–472
- Post DG, Hausfater G, McCuskey SA (1980) Feeding behavior of yellow baboons (*Papio cynocephalus*): Relationship to age, gender and dominance rank. *Folia Primatol* 3:179–195
- Pruetz JD, Isbell LA (2000) Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behav Ecol Sociobiol* 49:38–47
- Pulliam HR, Caraco T (1984) Living in groups is there an optimal group size?. In: Krebs JR, Davies NB (eds) *Behavioural ecology: An evolutionary approach*, 2nd edn. Sunderland, MA, pp 122–147
- Robinson JG (1981) Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. *Anim Behav* 29:1036–1056
- Ron T, Henzi SP, Motro U (1996) Do female chacma baboons compete for a safe spatial position in a southern woodland habitat?. *Behaviour* 133:475–490
- Rowell TE, Wilson C, Cords M (1991) Reciprocity and partner preference in grooming of female blue monkeys. *Int J Primatol* 12:319–336
- Rudran R (1978) Socioecology of the blue monkeys (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest, Uganda. *Smithsonian Contrib Zool* 249:1–88
- 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
- Sterck EHM, Steenbeek R (1997) Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour* 134:749–774
- Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41:291–309
- Strier KB (1994) Myth of the typical primate. *Yearbook Phys Anthropol* 37:233–277
- Struhsaker TT (1978) Food habits of five monkey species in the Kibale Forest, Uganda. In: Chivers DJ, Herbert J (eds) *Recent advances in primatology*, vol 1. Academic Press, London, pp 225–248
- Struhsaker TT (1997) *Ecology of an African rain forest*. University Press of Florida, Gainesville
- Sugiyama Y, Ohsawa H (1982) Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. *Folia Primatol* 39:238–263
- van Hooff JARAM, van Schaik CP (1992) Cooperation in competition: The ecology of primate bonds. In: Harcourt AH, de Waal FBM (eds) *Coalitions and alliances in humans and other animals*. Oxford University Press, Oxford, pp 357–389
- van Noordwijk MA, van Schaik CP (1987) Competition among female long-tailed macaques, *Macaca fascicularis*. *Anim Behav* 35:577–589
- van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) *Comparative socioecology: The behavioural ecology of humans and other mammals*. Blackwell Scientific Publications, Oxford, pp 195–218
- van Schaik CP, Kappeler PM (1997) Infanticide risk and the evolution of male–female association in primates. *Proc Roy Soc London, B* 264:1687–1694
- van Schaik CP, van Noordwijk MA (1988) Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour* 105:77–98
- White F (1983) *The vegetation of Africa*. UNESCO, Paris
- Whitten PL (1983) Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *Am J Primatol* 5:139–159
- Wrangham RW (1980) An ecological model of female-bonded primate groups. *Behaviour* 75:262–300
- Zuberbuhler K (2002) Effects of natural and sexual selection on the evolution of guenon loud calls. In: Glenn ME, Cords M (eds) *The guenons: Diversity and adaptation in African monkeys*. Kluwer Academic Publishers, New York, pp 289–308