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DO FEMALE CHACMA BABOONS COMPETE FOR A SAFE SPATIAL POSITION IN A SOUTHERN WOODLAND HABITAT?

by

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Summary

In this study troop of chacma baboons (*Papio cynocephalus ursinus*) at Mkuzi Game Reserve, Zululand, South-Africa, it is suggested that risk of predation and competition over safe spatial position had more importance and effect on female behaviour than did competition for food. Only 6.4% of all agonistic events were over food patches and no significant correlation was found between a female's dominance rank and proportion of time spent feeding, feeding bout length or diet composition. Parameters of reproductive success, such as inter-birth intervals and infant mortality were not correlated with female dominance rank. Female mortality, however, was related to dominance rank and all of the five females who disappeared during the study were low-ranking. Four of the five females disappeared after troop fission. There is circumstantial evidence supporting the suggestion that predation by leopards is the main cause of mortality of females at Mkuzi. High levels of female aggression were recorded, with almost no occurrences of support coalitions. Most of the aggression took place among similar ranking females, or was directed by the top ranking toward the lowest ranking females. Most of the female-to-female agonistic encounters were in a social context, and more than half were over a spatial position next to other adult troop members. Aggression among females increased after troop fission. It is suggested that

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the higher-ranking females may be better protected from predation, through access to more central spatial positions in the troop. Indeed, a positive correlation was found between a female's dominance rank and the time spent next to other adult troop members. It may be that avoiding food competition by keeping larger distances from others, while foraging, was translated in lower ranking females to a cost of higher predation risk.

Keywords: baboons, *Papio cynocephalus ursinus*, dominance hierarchy, predation, female competition, spatial position.

Introduction

The costs and benefits of sociality in general, as well as the differential costs and benefits to individual troop members, are central issues in primate socio-ecology (*e.g.* Altmann, 1974; Wrangham, 1980; Dunbar, 1988; van Schaik, 1989). Intra-troop competition for food among female primates and its effect on female lifetime reproductive success parameters (*i.e.* onset of reproduction, life expectancy, inter-birth intervals and infant survival) have been widely stressed to be a major cost for lower ranking females. Many baboon and macaque studies stressed the importance of food competition among females (*e.g.* Altmann, 1980, 1983; Meikle & Vessey, 1988; Melnick & Pearl, 1987; Strum, 1987; van Noordwijk & van Schaik, 1987; Altmann *et al.*, 1988; Soumah & Yokota, 1991; Barton, 1993; Barton & Whiten, 1993).

Competition for food may be evident in direct displacements over food patches (*e.g.* Barton, 1993), or in differential percentage of time spent feeding (*e.g.* Rasmussen, 1985) as well as other time budget components (*e.g.* Altmann, 1980; Dunbar, 1992), feeding bout length (*e.g.* Post *et al.*, 1980) or diet composition (*e.g.* van Noordwijk & van Schaik, 1987). Thus, where there is contest competition for food, the more dominant individuals are expected to have more access to higher quality food items and to be less disturbed during feeding. They would, therefore, have longer feeding bouts, but on the whole, would spend less time feeding and would be able to spend more time in social interactions.

The present study was conducted on a troop of free-ranging chacma baboons (*Papio cynocephalus ursinus*), occupying a rich woodland habitat, in Zululand, South-Africa. We have tested whether the females in this troop were competing for food. For this end the context of displacements were recorded and the relation between a female's rank and percentage of time

spent feeding, percentage of time spent in social behaviour, feeding bout length and diet composition were tested. We have also tested the effect of dominance rank on reproductive success, as may be evident in inter-birth intervals, infant survival or female survival, throughout the study period.

It has been shown that predation pressure may be an important selective factor in primate evolution affecting primate social organization and behaviour (*e.g.* van Schaik & van Noordwijk, 1985; Anderson, 1986; Dunbar, 1988; Boesch, 1991). Our data suggest that competition over safe spatial position among the females of this study troop was more important than competition for food and that the main cost for low-ranking females was a higher risk of predation by leopards.

Methods

The study was conducted on a troop of chacma baboons (Mtshopi Troop) for a total of 18 months between January 1989 and November 1991 at Mkuzi Game Reserve, Zululand, South-Africa. On March 1990 Mtshopi troop consisted of about 76 individuals, including 8 adult males, 17 adult females, 6 subadult females and about 45 immature members. The troop grew from about 44 individuals in June 1986 (S.I. Whitehead, pers. comm.). By May 1990 the troop divided into two new daughter troops with about 43 and 33 members. All records of births and deaths in this study include records from June 1986 (S.I. Whitehead, pers. comm.) until November 1991.

The habitat at Mkuzi is a mixed *Acacia/Combretum* woodland with abundant food resources all year round and poor visibility conditions. Detailed data on the habitat is provided elsewhere (Henzi *et al.*, in press).

All adults were individually identified by natural markings (Ron & Whitehead, 1993) but due to poor visibility, resulting from topography, dense vegetation and tall grass, most of the juveniles were not identified. Data on the females of this troop were available from June 1987 (S.I. Whitehead, pers. comm.). Relatedness among females is unknown. Females were defined as subadults from their first visible perineal swelling and as adults from first parturition (*e.g.* Strum, 1987). Despite the poor visibility, it was usually possible to observe all the known troop members on the sleeping cliff during early morning and late afternoon. All adults were observed at least once in 3 consecutive days of observations. A known individual was defined as 'disappeared' if not seen for 10 consecutive days of observations.

The baboons were followed on foot from dawn to dusk for over 800 h prior to troop fission and over 400 h after fission. Data were collected using scan sampling for all visible individuals, every 30 min throughout the whole day, 20 min focal sampling of all the females and *ad libitum* data records (as in Altmann, 1974). Unless stated otherwise, only the data prior to troop fission is presented here.

Ad libitum data included: all observed individuals, female reproductive status and births were recorded daily; the outcome and context of all observed female-to-female agonistic encounters; grooming events and other events. Dominance rank was established through win-loss matrices of the outcomes of all recorded agonistic encounters prior to fission,

including threats and submissive gestures, spatial displacements, chase or physical contact. Excluding one female who changed her rank during the study (Ron, 1994) only three reversals were recorded out of 443 recorded outcomes of agonistic behaviour (using both focal and *ad libitum* records).

Rates of female aggression and a female's vicinity to other troop members were derived from focal samplings. Individual time budgets and diet composition were derived from scan samplings of all the observed troop members every 30 min throughout the study. Feeding was defined as time spent in any type of actual handling of any food item. Social behaviour was defined as grooming or other friendly behaviour, including sexual behaviour and play, in touch with at least one other individual, other than mother-offspring pairs. The other categories of behaviour used for the scan sampling were: agonistic behaviour (as defined above), movement (running or walking), vigilance, resting. Feeding bout lengths were measured separately for all the troop females, while feeding on all the major food items, since they commenced to handle a certain food type until they stopped feeding on that item, even for a very short time or started any other behaviour, including moving away. When cause of termination of any feeding bout could be identified, it was recorded.

Due to poor visibility conditions and the troop division into foraging parties, it was impossible to define the spatial center of the troop. Thus, we have defined a female as being 'in company' if she was within a distance of up to five meters from at least two other adults. We suggest that being 'in company' represents a predation protected spatial position. We have not chosen proximity to only one adult neighbour, since this may be a consorting male or an associate. Such a pair may often be separated from the rest of the troop and therefore be susceptible to a high risk of predation.

Results

Female competition for food

No evidence for food competition was found among the females of Mtshopi Troop:

1. Only 6.4% of the female-to-female agonistic encounters occurred in a feeding context, *i.e.* initiated while one of the females involved was feeding (Fig. 1).
2. No significant correlation was found between female dominance rank and percentage of daytime spent feeding (Spearman's coefficient of rank correlation: $r_s = 0.1667$, $N = 17$) (Table 1).
3. No significant correlation was found between female dominance rank and percentage of daytime spent in social interactions and grooming ($r_s = 0.0460$, $N = 17$) (Table 1).
4. Seeds and fruits are high quality food items (*e.g.* Waterman, 1984). There was no significant correlation between a female's dominance

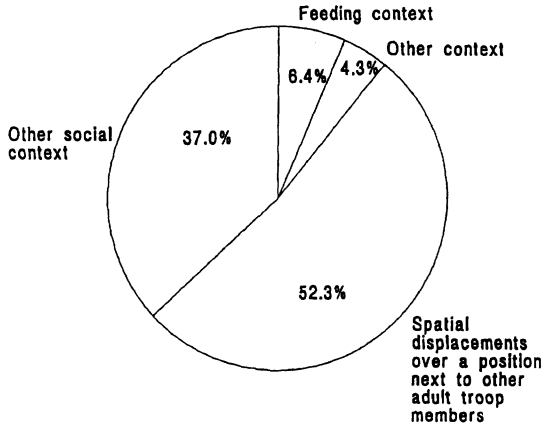

Fig. 1. The percentages of the different contexts of all recorded 443 female-to-female agonistic encounters (feeding context: while at least one of the females involved was feeding; spatial displacements: over a position of up to five meters from at least two other adult troop members; other social context: while at least one of the females involved was engaged in grooming or was in touch with any other troop member, except for each female's own infant).

rank and the proportion of her feeding time which was spent feeding on seeds and fruits ($r_s = -0.0343$, $N = 17$) (Table 1).

5. No significant correlation was found between a female's dominance rank and her average feeding bout length ($r_s = -0.0417$, $N = 17$) (Table 1).

Female reproductive success

There was no evidence for rank related differential reproductive success among females at Mkuzi:

1. No significant correlation was found between a female's dominance rank and the number of infants she had during the study, from June 1987 ($r_s = -0.0417$, $N = 17$) (Table 1).
2. Of the females who had more than one infant during the study, no significant correlation was found between dominance rank and a female's inter-birth intervals ($r_s = -0.0166$, $N = 11$) (Table 1). For five of the 17 females, only one birth was recorded (one female was

TABLE 1. *Percentage of total time spent feeding, percentage of total time spent in grooming and social behaviour (in touch with any other troop member, except for her own infant), percentage of feeding time spent feeding on fruits and seeds, average feeding bout length (min), number of infants each female had throughout the study and average inter-birth intervals (months), for each female at Mtshopi Troop, according to her rank*

Name of female	Rank	% Feeding (of total activity)	% Social (of total activity)	Fruits & seeds (% of total feeding time)	Feeding bout length	Number of infants	Inter-birth interval
Peri	1	45.6	20.6	52.4	3.23	2	18.0
Bonni	2	45.9	22.1	48.9	0.50	2	27.0
Doris	3	30.1	19.4	47.6	2.20	2	17.0
Suzy	4	25.7	20.8	53.1	4.45	1	–
Joan	5	36.0	23.1	46.8	2.12	3	19.5
Jes	6	31.0	18.0	49.3	3.10	0	–
Katy	7	32.0	19.2	51.9	1.14	2	34.0
Mel	8	46.9	21.2	52.6	5.17	4	14.0
Alice	9	38.8	24.8	47.3	3.27	4	13.7
Flaggy	10	42.5	21.2	49.4	0.56	2	14.0
Doda	11	39.4	16.8	50.5	1.26	1	–
Tiki	12	39.6	22.1	52.3	1.40	2	33.0
Esti	13	38.7	14.9	48.4	2.31	1	–
Lucy	14	46.6	20.4	51.4	0.48	3	21.0
Extra	15	33.4	18.4	53.0	2.49	1	–
Gili	16	38.5	24.9	46.7	3.32	1	–
Honey	17	43.3	22.3	49.9	3.25	4	15.0
r_s		0.1667	0.0460	−0.0343	−0.0417	−0.0417	−0.0166

Spearman's coefficient of rank correlation is given for each parameter. All coefficients of rank correlation are not significant.

very old, one very young, and three other females have disappeared during the study. One other very old female had no births recorded).

3. Average inter-birth interval was relatively short. Using clustered sampling techniques (as in Cochran, 1977), it was 18.53 ± 1.81 months (mean $\pm$ SE), with a minimum observed inter-birth interval of 8 months (median = 18 months).

4. Infant mortality rate was extremely low. Of 41 recorded pregnancies of 21 females (from June 1987), only one pregnancy terminated in abortion (to the third ranking female) and one infant died at the age of about 4 months (to the 14th ranking female). Three additional suckling infants disappeared with their mothers.

Female mortality

Female mortality was related to dominance rank (Table 2). One female disappeared before the commence of the process of troop fission, while four disappeared a few months and over a year after fission. All of these females were low-ranking, middle-aged and seemed to be in good physical condition when last seen. The females who disappeared had significantly lower rank than the others (Wilcoxon's rank-sum two-sample test: $t = 2.2646$; $p < 0.01$).

While cause of disappearance is not known, there is circumstantial evidence suggesting that they were preyed on by leopards. Leopards are known to be predators of baboons and other primates (*e.g.* Dunbar, 1988). When a healthy looking female baboon disappears overnight, and there is no other evident cause of mortality, predation is commonly assumed to be the cause (*e.g.* Altmann, 1980). There were leopards resident around the core-area and the three main sleeping-sites of the troop and they were

TABLE 2. *The five females which disappeared during the study, their dominance rank prior to troop fission, their new troop affiliation after fission, reproductive status when last seen, relative age and the month when they were last seen*

Female	Rank	New troop	Reproductive status	Relative age	When disappeared
Olive	low*	–	cycling	middle	9/89
Doda	11	D	lactating	middle	9/90
Esti	13	D	lactating	middle	9/90
Extra	15	F**	cycling	middle	9/91
Honey	17	F	lactating	middle	10/91

D = Darth's Troop; F = Flash's Troop.

* Was the lowest ranking female when disappeared, before the whole female dominance hierarchy was established.

** Moved from Darth's Troop to Flash's, just before she disappeared.

increasingly seen over the last year of the study. Leopard feces containing baboon fur were found close to the sleeping-sites. None of the females who disappeared was observed later in adjacent troops.

Female aggression

We have recorded high rates of female aggression (Table 4): 1.13 ± 0.12 female-to-female agonistic events/h (of which 19.4% involved a chase or physical contact). Yet, only three female coalitions and four male-female support events were recorded, all in 800 observation hours prior to fission (Ron *et al.*, 1994).

Most of the aggression took place among similar ranking females, or was directed by the top ranking toward the lowest ranking females (Table 3). The females of Mtshopi Troop can be divided into three more or less equal groups consisting of five high-ranking, five low-ranking and seven middle-ranking females. One-way ANOVA shows a significant difference between average number of agonistic events per hour of the females in the three groups ($F_{2,14} = 11.32$, $p < 0.005$). A Student-Newman-Keuls test, performed at an experimentwise error of 0.05, shows that the high-ranking females had the highest level of aggression (1.52 events/h), but not significantly higher than the low-ranking females (1.36 events/h). Both show a significantly higher level of aggression than the middle-ranking females (0.69 events/h).

Female aggression and spatial position

Most of the agonistic events among females at Mkuzi (89.3%) were in a social context, *i.e.* while at least one of the females involved was in any social interaction with at least one other troop member.

TABLE 3. *Mean number of agonistic events/h per pair (adjusted for the actual number of encountering pairs) within and between the three dominance groups*

	High-ranking	Middle-ranking	Low-ranking
High-ranking	0.175	0.027	0.130
Middle-ranking	–	0.064	0.031
Low-ranking	–	–	0.150

TABLE 4. *Percentage of time spent 'in company' (within a distance of up to five m from at least two other adults), and aggression rate (number of agonistic events/h per female), for each female, according to her dominance rank, before and after troop fission*

		Time 'in company' (% of total time)		Aggression rate (agonistic events/h)	
Female	Rank	Before fission	After fission	Before fission	After fission
Peri	1	59.1	38.4	1.4	3.1
Bonni	2	48.3	32.5	1.3	2.7
Doris	3	41.5	60.2	2.1	2.9
Suzy	4	26.0	37.7	0.9	1.9
Joan	5	48.1	62.4	1.9	2.6
Jes	6	29.9	36.4	0.7	0.9
Katy	7	41.2	56.4	0.6	1.8
Mel	8	52.7	29.1	1.0	1.7
Alice	9	47.7	34.5	0.4	0.8
Flaggy	10	46.2	25.4	0.5	1.9
Doda*	11	25.6	–	0.9	–
Tiki	12	18.8	49.9	0.7	2.2
Esti*	13	20.8	–	1.1	–
Lucy	14	25.7	51.2	1.3	2.4
Extra	15	14.5	22.9	1.4	2.8
Gili	16	43.1	19.7	1.2	2.6
Honey	17	40.2	42.8	1.8	2.9

* Disappeared shortly after troop fission.

On 52.3% of the agonistic events a female was displaced from a spatial position within 5 m from at least two other adult troop members (Fig. 1). 16.8% of these events were over proximity to males (or a male and females together) and the rest over proximity to females only. A significant positive correlation was found between dominance rank and time spent 'in company', as defined in the methods section (Spearman's coefficient of rank correlation: $r_s = 0.5686$, $N = 17$, $p < 0.01$) (Table 4).

In general, individuals kept distances of about 2-5 m from a nearest neighbour while moving or feeding and about 0.5-2 m while resting (unless grooming or in touch). Usually, a group of up to 10 individuals could sit together without interruptions of landscape elements such as rocks, trees, *etc.* In any such group most of the females were, naturally, sorrounded by others, while some were in the periphery. When a high ranking female joined such a group she displaced those females who were in the periphery, and sat between them and others, thus pushing them further away,

and sometimes behind landscape elements. While feeding lower ranking females kept larger distances from others and in many cases fed hidden from others by landscape elements. This may mean that avoiding food competition resulted in competition for safe spatial position.

Female aggression and time of the day

We divided the day into three time units, according to season. Evening and morning were equal in time, while mid-day was always longer than both. Yet, the percentage of time spent 'in company' during morning hours was significantly higher than during mid-day; in the evening higher than during mid-day; and in the morning higher than in the evening (t-test for paired comparisons: $t = 9.80$, $t = 8.01$ and $t = 4.47$, respectively, each with $df = 16$; all t values are highly significant in an experimentwise error level of 0.01). In the morning the females were also involved in significantly more agonistic events than during mid-day. In the evening also more than during mid-day and in the morning more than in the evening, but in both latter cases the difference is not significant (t-test for paired observations: $t = 2.91$, $t = 1.55$ and $t = 1.65$, respectively, each with $df = 16$). Generally most (but not all) of the leopard predation occurs during the dark hours (*e.g.* Altmann, 1980; S. Wasser, pers. comm.). Close neighbours recorded during early mornings and late evenings, on the sleeping sites, usually represent the same spatial positions the baboons occupy during the night (*e.g.* Altmann, 1980; D. Forster, pers. comm.). During most nights the baboons slept in creeks and shelves on cleefs, where sleeping space next to others is obviously limited.

Female aggression following troop fission

After troop fission, with much fewer members in each daughter troop, it would be expected that females would spend less time close to others, if they were competing mainly for food, or even if staying in vicinity to others was merely random. Aggression levels, in that case would be expected to decrease after fission. Risk of predation for each female, however, is higher after fission and the opposite trend is therefore expected if avoiding predation is more important to these females. Females at Mkuzi indeed spent more time 'in company' after fission (Table 4), though not significantly so. On the average they spent $37.05 \pm 3.21\%$ of their time 'in company'

prior to fission, and $37.94 \pm 3.33\%$ after fission. Aggression levels also rose (Table 4), and significantly, from an average of 1.13 ± 0.12 agonistic events/h for a female prior to fission, to 2.28 ± 0.16 after fission (t-test for paired observations: $t = 9.60$, df $= 14$, $p < 0.001$).

Discussion

We suggest that risk of predation, as mediated by competition over protected spatial positions, rather than competition over food resources, may be the main cost to lower-ranking females in our study troop of chacma baboons at Mkuzi. This idea is based on the assumption that vicinity to others indeed gives better protection to individuals, mainly through better chances of detecting a predator, active protection and mobbing of predators, and even through the dilution effect.

Various aspects of competition for food, and its effect on lifetime reproductive success were widely stressed as a major cost for low-ranking females, in many baboon studies (*e.g.* Altmann, 1983; Rasmussen, 1985; Melnick & Pearl, 1987; Altmann *et al.*, 1988; Johnson, 1989; Barton & Whiten, 1993). At Mkuzi, however, our results suggest that competition for food may have a relatively less important effect on low-ranking females and their reproductive success (Table 1). Inter-birth interval in most savannah baboon studies is 18 to 24 months, with 10-30% infant mortality rates in the first year of life (Altmann, 1980). Females at Mkuzi had relatively short inter-birth intervals with very rare occurrence of infant mortality, both parameters indicating a favorable habitat, with abundant food resources. Moreover, poor visibility conditions of this habitat prevent individuals from scanning and controlling food patches occupied by lower-ranking troop members.

Strum (1987) also did not find relation between dominance rank and inter-birth intervals or infant survival among females in Gilgil, Kenya, but has suggested that low-ranking females may have shorter life expectancy.

At Mkuzi, female mortality was related to dominance rank (Table 2). Predation by leopards is suggested to be the main cause of mortality of low-ranking females. Predation has been indicated as an important selective pressure, affecting primate social organization and behaviour (*e.g.* Anderson, 1986; van Schaik, 1989; Boesch, 1991; Barton *et al.*, 1992; Dunbar,

1992). Although most of the leopard predation usually takes place at night, it does happen infrequently also during the day, and it may be that the relative rarity of such events partially reflect the diurnal anti-predator strategies of the baboons, such as adopting safe spatial positions (Cowlishaw, 1994).

Female competition for safe spatial positions at Mkuzi may be evident in that most of the female-to-female agonistic encounters were in a social context, and more than half over a spatial position next to other adult troop members (Fig. 1). Moreover, a positive correlation was found between a female's dominance rank and time spent next to other adult troop members (Table 4). Other studies have also indicated that high ranking female baboons are most often found in clusters (Collins, 1984) or with close neighbours (Busse, 1984).

Janson (1990) has shown that choice of spatial positions in primate foraging groups may be either due to considerations of improving individual foraging success or minimizing predation risk, while low-ranking individuals are forced to the least favorable positions.

As indicated by Strum (1987), dominance stability and aggression levels are obviously related to the importance of the disputed resource. If females at Mkuzi are indeed fighting for their lives, this may be the reason for their high aggression levels. Ransom (1981) has also recorded high aggression levels in a baboon troop subjected to chimpanzee predation in Gombe, Tanzania.

Johnson (1989) has suggested that agonistic events among adjacent ranking individuals are for establishing rank, while aggression of dominant individuals directed towards the lowest ranking ones is related to displacements over desirable resources. When competition is over the relative access to a resource, as is the case in food competition (*e.g.* Seyfarth, 1976; Altmann, 1983), intensity of aggression is expected to be negatively correlated to the rank difference between the two opponents.

At Mkuzi, both high and low ranking females were involved in significantly more agonistic encounters than middle-ranking females. More aggression was recorded between the high and low ranking females than between each of these groups and the middle-ranking females (Table 3). This distinct situation may be explained by the selfish herd idea of Hamilton (1971), and this explanation is consistent with the high risk of predation at Mkuzi. When a high-ranking female approaches a group of individuals,

she displaces one of the lowest ranking females in that group, who is already in its periphery and easier to displace. In addition, higher aggression rates among higher ranking females may be a consequence of establishing their rank, while higher rates of aggression among low ranking females may be due to the fact that they are the ones most susceptible to predation risk and fighting for their rank and spatial position is crucial for their survival. Thus, the high-ranking and the low-ranking females are both more frequently involved in such conflicts than middle-ranking females.

The absence of coalitions among females at Mkuzi may also be a result of competition over a resource that can not be shared, such as safety, in contrast to food.

The increase in female aggression and in the time females spent together following troop fission (Table 4), may also indicate the importance of predation risk rather than food competition to these females. Predation risk obviously increased after fission and of the five females who disappeared in the course of our study, four disappeared well after troop fission. During morning and evening hours higher rates of aggression were recorded among females, as well as higher rates of time spent 'in company' and in social activities, than during mid-day, when females spent more time foraging further away from each other.

It may be expected that if predation risk is the main selective pressure this troop is subjected to, they will all tend to stay very close together. However, very cohesive ranging should not be expected, as may be indicated by the very great interadult spacings in a chacma baboon population under food stress but low predator pressure (Byrne *et al.*, 1990). The observed interadult distances at Mkuzi probably represent some sort of a balance between opposing tendencies, proximity to avoid predation, on one hand, and keeping a personal space to avoid competition for food and disease infection, on the other. According to Altmann (1980), for example, such a personal space has a radius of about two meters. Another factor that may interfere with females' proximity is their attempt to stay close to the males, who generally keep larger distances between themselves, due to their sexual competition (Ron, in press). Sleeping space together in crevices and shelves on the sleeping cleefs, during night, is obviously limited, and aggression among females during the evening may reflect their competition over these safer 'sleeping arrangements'.

It is also possible that feeding competition was translated into competition over safety, among these females. It may be that low ranking females are able to avoid feeding competition only by foraging away from others, thus putting themselves at higher risk of predation while foraging (van Noordwijk & van Schaik, 1987).

Primate populations are known to present a wide variety of behavioural adaptations to different environments and ecological conditions (*e.g.* Lee, 1991). The behavioural characters described for females at Mkuzi may represent their adaptations for living in a rich habitat with abundant food resources, poor visibility and high risk of predation.

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