

THE DYNAMICS OF SOCIAL RELATIONSHIPS AMONG
FEMALE CHACMA BABOONS (Papio cynocephalus
ursinus) IN ZULULAND

by

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This thesis is dedicated to the memory of

Joanna Copley

ABSTRACT

The focus of this study is the effect of environmental conditions on the social relationships among females in a free-ranging troop of chacma baboons (Papio cynocephalus ursinus), in a southern woodland habitat. The female dominance hierarchy, rank related differential costs and benefits to individuals, and the nature of special relationships between females, were followed. The study was conducted for a total of 18 months during three years, at Mkuzi Game Reserve, Zululand, South-Africa. The study troop occupy a rich woodland habitat with abundant food resources. Visibility under these conditions is poor and the baboons are subjected to leopard predation. Intra-troop competition for food among female primates and its effect on lifetime reproductive success, has been widely stressed to be a major cost for low ranking females. No evidence of competition for food was found among females at Mkuzi. It is suggested that the main cause for mortality may be predation by leopards, and that females compete mainly over a safe spatial position. The following characteristics of female sociality at Mkuzi may support this suggestion:

1. While no indication of rank related feeding behaviour, reproductive success, or 'attractiveness' to others was found, the higher ranking females had more access to central, and thus better protected, spatial

positions in the troop.

2. The importance of social associations among females at Mkuzi seems to lie in mutual grooming and protection from predation by the vicinity to each other, and not in coalitionary support. Female associates were thus not necessarily adjacent ranking and probably not kin.

3. Although female dominance hierarchy was usually stable, the lowest ranking adult female has promoted her rank independently, following the disappearance of her only female associate and during her pregnancy, when she was probably subjected to high risk of predation.

4. Following troop fission, most females chose to improve their own rank position by adopting the AYS strategy (Abandon Your immediate Superior in rank), rather than joining associates. It is suggested that the resident males were responsible for the initiation of troop fission, in order to decrease the high cost of sexual competition to them, by reducing the number of males in each daughter troop. High intensity of competition between males was the result of the high female reproductive success. Risk of predation, and therefore the cost to individual females, increased after fission.

This study may present an additional example to accumulating evidence on the flexibility of social and behavioural adaptations of primates to various environmental conditions.

PREFACE

The experimental work described in this thesis was carried out in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from January 1989 to December 1992, under the supervision of Professor S. Peter Henzi.

These studies represent original work by the author and have not been submitted in any form to another University. Where use was made of the work of others it has been duly acknowledged in the text.

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This list will not be completed without thanking the baboons for letting me into their intimate world and providing me, through those wonderful hours with them, with fascinating insights on their lives, as well as most amusing moments.

I wish to express here my sorrow about the tragedy of Joanna Copley's death, and my sympathies with her family. I also wish to express my sincere hopes that Stephen Whitehead will be able to complete the writing of his thesis, which will, no doubt, be an important contribution in this field.

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CHAPTER 1: GENERAL INTRODUCTION

"We must acknowledge, as it seems to me, that man, with all his noble qualities...still bears in his bodily frame the indelible stamp of his lowly origin." (Darwin, 1874). This very stamp has been the main trigger for many studies of primates since the beginning of this century. The importance of sociality in most primate species has formed a focus of interest in them (as defined by Darwin, 1874: "Animals endowed with the social instincts take pleasure in one another's company, warn one another of danger, defend and aid one another in many ways"). Following the pioneer work of Goodall (1968) and others (e.g., Bolwig, 1959; Washburn and DeVore, 1961), in the late fifties and early sixties, many field studies of primate behaviour and social organization in their natural habitats, were conducted (e.g., see Dunbar, 1988).

Baboons were probably the subject of more different studies than any other non-human primate (Baldwin and Teleki, 1972). Eugene Marais observed chacma baboons, at the beginning of this century, in northern Transvaal (published in 1969), and during the last 3-4 decades, the ecology, behaviour and social organizations of free-ranging baboons have been the focus of many short-term and long-term studies throughout Africa (e.g., Bolwig, 1959; Washburn and DeVore, 1961; Hall, 1962; Rowell, 1966; Kummer, 1968; Altmann and Altmann, 1970; Stoltz and Saayman, 1970; Seyfarth, 1976; Hamilton et al., 1978; Ransom, 1981; Sharman, 1981; Wasser, 1983; Dunbar, 1984; Norton et al., 1987; Strum, 1987; Byrne et al., 1989). More than 20 years ago Baldwin and Teleki (1972) have listed about 40 different field researches of baboons, and others were established since.

Marais (published in 1969) has already noted: "An

outstanding characteristic of the chacma (baboons) is their ability to thrive in the most varied environments...It will be realized how very different their habits and general way of life must be to render existence possible under such radically different sets of natural conditions...None the less, they are the same species." Indeed, the importance of studying many different troops of savannah baboons, and for long periods, lies in the accumulating of comparative data on the remarkable variability in social structure and behaviour that is found in this species, in various types of habitats and under different environmental and demographic conditions (e.g., Rowell, 1966; Altmann and Altmann, 1970; Stoltz and Saayman, 1970; Ransom, 1981; Strum, 1987; Dunbar, 1988). This variability found in baboon populations, as well as in other primate species, is generally attributed to the environmental conditions and selective pressures each population is subjected to (e.g., Eisenberg et al., 1972; Jolly, 1972; S. Altmann, 1974; Popp, 1983; Whiten et al., 1987; Dunbar, 1988; van-Schaik, 1989; Lee, 1991).

Baboons occupy a large variety of different types of habitats, from desert to forest, throughout Africa south of the Sahara, from Senegal to Ethiopia in the North and up to Cape point (Altmann and Altmann, 1970; Baldwin and Teleki, 1972; Ransom, 1981). Studies of baboons, however, do not cover proportionally the different types of habitats occupied by baboons. Due to logistic problems and other considerations that dictate choice of study site and troops (Sharman and Dunbar, 1982), many of the long-term studies took place in open savannah habitats (e.g., Altmann and Altmann, 1970; Strum, 1987; Hamilton and Bulger, 1993). Other studies have focused on baboon populations living in extreme conditions of 'atypical' habitats (e.g., Rowell, 1966; Davidge, 1978; Ransom, 1981; Whiten et al., 1987; Brain, 1990).

While climatic patterns during the emergence of Papio (Brain, 1981) make it unlikely that any single habitat type can accurately be referred to as 'the environment of adaptedness', it nevertheless remains true that, currently, the habitat type most available to the animals will comprise one or other variant of woodland. As such the behavioural ecology of baboons in such habitats should be appropriately represented in a larger data set. The study site chosen for this project may be regarded as a rather representative environment of a southern woodland habitat (Henzi et al., submitted ms.).

As mentioned above, their intensive sociality is one of the most important characteristics of primates (e.g., Dunbar, 1988). The costs and benefits of sociality have been of major interest in many socio-ecological studies of primates (e.g., Marais, 1969; Kummer, 1971; Jolly, 1972; Axelrod and Hamilton, 1981; Goodall, 1986; Dunbar, 1988). Wrangham (1980) has attributed the formation of female-bonded primate societies to competition between groups of females over food patches. Other studies (e.g., Dittus 1987) conform with this concept. Van-Schaik and van-Noordwijk (1985), Anderson (1986) and Dunbar (1988), on the other hand, have concluded that the major benefit of sociality to primates is in protection from predation.

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 and van-Noordwijk, 1985; Anderson, 1986; Dunbar, 1988; Boesch, 1991).

The important role of adult females in the formation, organization and stabilizing of primate groups has been widely recognized (e.g., Seyfarth, 1976; Altmann, 1980; Wrangham, 1980; Smuts, 1985; Dittus, 1987). While male baboons and macaques tend to emigrate from their natal troop, during adolescence or early adulthood, the females

usually remain throughout their lives in the same troop and form its stable core (e.g., Strum, 1987; Dunbar, 1988). The social relationships among adult female baboons and macaques have thus been the focus of many studies (e.g., Seyfarth, 1976; Altmann, 1980; Dunbar, 1980; Walters, 1980; Hausfater et al., 1982; Wasser and Starling, 1986; van-Schaik, 1989; Giacoma and Messeri, 1992; Barton and Whiten, in press). A comparison of the social relationships among female baboons under different ecological and demographic conditions may spread light on the various factors affecting these relationships.

Different troop members may experience different costs and benefits in group-living, according to their gender, age or dominance rank. Janson (1990) for example, has shown that the highest ranking adult individuals in a troop of capuchin monkeys (*Cebus apella*) choose a spatial position with the highest expected foraging success. Juveniles choose the spatial positions that are most protected from predators, and subordinate adult troop members avoid the high ranking individuals and are thus forced to occupy the less favorable positions in the troop in both terms of foraging success and protection from predation.

Competition among adult males is mainly over access to receptive females. While high dominance rank may help males to get more access to receptive females, males may also use other tactics, such as forming coalitions between them or forming long-term alliances with females, for example (e.g., Smuts, 1985; Strum, 1987; Bercovitch, 1988; Bercovitch, 1991). Cowlshaw and Dunbar (1991) have stressed the importance of the operational sex ratio, i.e. the number of oestrous females per male in the troop, at any time, to the intensity of male sexual competition.

Intra-troop competition for food among female primates and its effect on female lifetime reproductive success has been widely stressed to be a major cost for low ranking

females. Food deficiency can affect the female's own development, onset of reproduction and life expectancy, her infants' development and the consequent inter-birth intervals, and infant survival (e.g., Melnick and Pearl, 1987 for Cercopithecines in general; Hausfater, 1975; Altmann, 1983; Strum, 1987; Altmann et al., 1988; Barton, in press; Barton and Whiten, in press, for baboons; Furuichi, 1983; van-Noordwijk and van-Schaik, 1987; Soumah and Yokota, 1991, for macaques).

Competition for food may be evident in direct displacements over food patches (e.g., Barton, in press), or in differential percentages 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 and van-Schaik, 1987).

Competition between females can also be evident in suppression of reproduction by aggressive harassments of the lower ranking females and their infants by the higher ranking individuals (e.g., Dunbar and Dunbar, 1977; Wasser, 1983; Wasser and Starling, 1986; Maestripieri, 1993). Meikle and Vessey (1988) have found correlation between a female's rank and lifetime survivorship of her male offspring in rhesus monkeys.

Intra-troop competition over limited resources is generally assumed to lie in the basis of the development of dominance hierarchies (Jones, 1981). Through a stable dominance hierarchy animals may resolve social conflicts and avoid active aggression (Hand, 1986). This way, the establishing of dominance hierarchies contribute to social tolerance and affiliative bonding among the troop members (de-Waal, 1986).

Female dominance hierarchies in baboons and macaques have been described as linear and stable, not only from year to year but also from generation to generation. A

female's rank is usually maintained through support coalitions between maternal kin, who also tend to occupy adjacent ranks (e.g., Hausfater, 1975; Seyfarth, 1976; Hausfater et al., 1982; Melnick and Pearl, 1987; Strum, 1987; Altmann et al., 1988; de-Waal, 1991b). These stable social positions may be also maintained by the effect of maternal rank on female personality (Welker et al., 1992).

However, some cases of change in females' dominance rank were described for baboons and macaques. A promotion in a female's dominance rank may be achieved usually through coalitionary support from female or male associates (e.g., Gouzoules, 1980; Walters, 1980; Samuels et al., 1987; de-Waal, 1989). Rank reversals may be the result of deterioration in a female's physical condition due to old age or disease (Gouzoules, 1980; Silk et al., 1981; Strum, 1987). Rank changes occur also during formation of new troops in captivity (Silk et al., 1981) or following troop fission (Koyama, 1970). Small (1990) have described an independent rise in rank by a female Barbary macaque (Macaca sylvanus).

Seyfarth (1976) has given a comprehensive account of agonistic and affiliative social behaviour of adult females in a small troop of chacma baboons in a rocky, mountainous terrain. The main conclusions of his study were: "1. All females are most attractive to others when they are lactating, and 2. In all reproductive states, high ranking females are more attractive than low ranking females." These two principles of female relationships were examined in the present study in a larger troop of chacma baboons, occupying a rich woodland habitat.

Seyfarth (1976) has found a distinctive tendency of females to form social associations with other females who occupy adjacent rank positions to theirs. A similar pattern has been described in other baboon and macaque studies and has been attributed to kin selection or advantage to

individuals. The significance of these alliances is assumed to lie mainly in the coalitionary support between female associates in their agonistic encounters with others (e.g., Hausfater et al., 1982; Strum, 1987; Altmann et al., 1988; Dunbar, 1988; de-Waal, 1991b).

Troop fission in these taxa usually occurs when lower ranking females withdraw from the original group, and is therefore "horizontal" in terms of female rank. This kind of splitting pattern results in close relatives, who are also allies and occupy adjacent ranks, staying together after fission. This way social alliances are maintained (e.g., Chepko-Sade and Sade, 1979; Dittus, 1988; Prud'Homme, 1991, Menard and Vallet, 1993, for macaques; Dunbar, 1988; A. Whiten (Department of Psychology, University of St. Andrews, Scotland), pers. comm., for baboons).

Troop fission, as a measure of group size control, is generally thought to be triggered by female competition for food (e.g., S. Altmann, 1974; Dittus, 1988; Dunbar, 1992). The initiation of fission is usually attributed to low ranking females, who withdraw from the original group and are then joined by low ranking or associate males (e.g., Dittus, 1988; Dunbar, 1988).

In the present study the nature of dyadic relationships among females in a free-ranging troop of chacma baboons (Papio cynocephalus ursinus) at Mkuzi Game Reserve, Zululand, South-Africa, is explored. The study troop occupies a rich woodland habitat with abundant food resources, but due to conditions of poor visibility the baboons were subjected to leopard predation. An attempt was made to estimate the effect of these environmental conditions on the social behaviour of the females.

The differential cost to individual females according to their dominance rank, formed the main focus of this study. An attempt was made to estimate the selection pressures

that these females are subjected to in their environment, and their social and behavioural adaptations to these conditions. It was examined 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. The effect of dominance rank on lifetime reproductive success, was also examined, in terms of inter-birth intervals, infant survival or female survival, throughout the study period. The main concept examined here is that the females in this troop were not competing for food but may have been competing for a safe spatial position, and that the main cost for low ranking females was a higher risk of predation by leopards.

Special associations between pairs of individuals were recorded: the identity of the associates and the nature of their relationships; the effect of changes in individuals' reproductive state on their social, agonistic and affiliative interactions; and the effect of an individual's dominance rank on her social interactions. The changes in female relationships following troop fission were also examined.

Stability and changes in female associations and dominance hierarchy were followed throughout the study, before and after troop fission. The factors that affect the choice of a new troop, following fission, by individual females, were explored.

It is suggested that fission in this troop may have been initiated by the resident males, and triggered by the high cost of sexual competition to them, as a result of the scarcity of cycling females in the group.

G. Schaller (1987) has noted in his foreword to 'Almost

Human' by S. Strum: "If a scientist takes too much vocal pride in objectivity, beware. Observing is subjective: the animal described is only an illusion created out of a personal perspective, based on which questions are raised, which facts written down, which information ignored. Another biologist asking different questions will create a different animal. The conspicuous, easily described behaviour is turned into statistics; the difficult but no less real behaviour tends to be ignored or considered irrelevant." As much as I have tried to 'stick to facts'; to collect my data with utmost care; to use the proper statistical tests for data that can thus be tested, but at the same time not to ignore qualitative and anecdotal data; to avoid unbased speculations; and to restrain my natural tendency for antropomorphism, I still realize my observations and interpretations are necessarily subjective and should be regarded as such.

"The baboons are individuals, not mere statistical entities" says Schaller "Each has its own temperament and idiosyncrasies, each has its own desires and goals. Despite their value, scientific papers cannot express the fundamental charm, the fleeting social entanglements, the perishable moments of a baboon's life; they cannot deepen our love and understanding of another species, they cannot establish a heartfelt unity with creatures that were once part of our past." Bearing these limitations in mind, I present this thesis in hope that it will still form some contribution to our accumulating attempts to understand one of the many faces of the complex and variable social life of these enchanting relatives of our species.

This thesis is presented as a series of manuscripts, submitted for publication (chapters 3-6 and appendices I-II). These manuscripts cover the various aspects of the dynamics of the social relationships among the female baboons at Mkuzi, and are tied together with general introduction, methods and discussion (chapters 1, 2, and 8). Each manuscript is a separate chapter, presented as it was submitted for publication, except for the acknowledgements and references, which are summarised to one complete list, each. Each manuscript was edited so that it will conform with the instructions for authors of the journal it was submitted to. However, the typescript, headings and pagination were edited in a uniform way that conforms with the faculty of science's style manual for theses. The journal each manuscript was submitted to is stated in a note. The tables and figures are numbered in a way that indicates the chapter and table or figure number within that chapter.

Chapter 3 is an attempt to approach the question of what is the major selection pressure females are subjected to at Mkuzi, what are the major costs to low ranking females, and how this affects their social behaviour. Chapter 4 gives a general account of the female social - agonistic and affiliative relationships, the relation to female rank and reproductive state, and the nature of special relationships among individuals. The effects of the environmental conditions on female relationships are explored. Chapter 5 presents a study case, of the independent rise in rank of one exceptional female, and the way it conforms with the general concept expressed here. Chapter 6 refers to the strategy adopted by the troop females in their choice of a new troop following fission, as it is related to the more general characteristics of their sociality as described above. A short version of this manuscript was accepted for

publication and is presented in Appendix II. Chapter 7 presents the suggestion that this troop fission was not initiated by the troop females, but rather enforced upon them by the males. Appendix I is an addition to the methods section and describes a method developed to identify individual females under poor visibility conditions.

CHAPTER 2: METHODS

This study was conducted on a troop of chacma baboons (Mtshopi Troop) for a total of 14 months between January 1989 and July 1990 and for additional 4 months on August-November 1991, at Mkuzi Game Reserve, Zululand, South-Africa.

Mtshopi troop grew from about 44 individuals in June 1986 (Henzi et al. in prep.) to 76 in March 1990 (Table 1). Between March and May 1990 the troop entered a phase of social instability that followed a longer phase of increasing tendency for subtrooping, since October 1988 (S. Whitehead, Department of Zoology, University of Natal, Pietermaritzburg, pers. comm.) and concluded with its division into two new daughter troops: Darth's Troop with about 43 individuals and Flash's Troop with about 33 troop members (Table 1).

Mkuzi Game Reserve (27°30'S; 32°05'E) comprises 290km² and is located on the coastal plain, east of the Lebombo Mountains, in north-eastern Natal Province, South-Africa. While the western border is fenced, the reserve is bounded on the north and east by the Mkuzi River, and on the south by Msunduzi River (Henzi et al., submitted ms.).

The Mtshopi troop was one of at least 14 troops in the reserve, with a home-range of about 28.6 km², (S. Whitehead, Pers. comm.) next to the fenced western border of the reserve. Density was estimated as 2.7 animals/km² in 1987 and 2.81 animals/km², in 1990. Three troops overlapped 11.2% of the study troop's range. The mean annual day range for 1989/1990 was 4.87 km (range of monthly means 2.84-8.98 km). The shortest day journeys were undertaken during March, and the longest during November. The troop used seven sleeping sites, five were cliffs on the banks of two streams, and two were tree groves at the

eastern edge of the home range and both together were used on 5.6% of all nights (Henzi et al., submitted ms.).

Climate at Mkuzi is described as a warm to hot, humid sub-tropical climate. Mean annual rainfall at park headquarters is 630mm (median=628mm). Rainfall in this region is highly seasonal, from October through March, with an average of >50mm per month, peaking in February. The period of aridity runs from April through September, with the month of lowest rainfall being June. Mean annual temperature in Mkuzi is 22.4°C. Summers are hot, with a maximum of 45°C, and winters are warm, with a mean daily temperature of 17.8°C in the coldest month (Henzi et al., submitted ms.).

Mkuzi may be divided into nine major vegetation types which overlap along complex environmental gradients. The reserve is representative of three veld types: Coastal Forest and Thornveld, Lowveld, and Zululand Thornveld. Among the common trees are a number of Acacia spp., Combretum apiculatum, Dichrostachys cinerea, Ziziphus mucronata and Sclerocarya caffra. The baboons utilized at least 92 different plant species. These items represent about 10-20% of the species available in the home range. At least eight invertebrate species and a skink (Mabuya sp.) were also eaten. Two incidents of predation by this troop were recorded, one of a quail (Coturnix sp.) and one of an unidentified antelope fawn. Twenty-one large herbivore species occur in the reserve. Of the larger predators, leopard, spotted hyena and black-backed jackal are common and cheetah have been re-introduced (Henzi et al., submitted ms.).

Mtshopi Troop's home range, around the Mtshopi area, comprises a wide range of the available habitat types at Mkuzi. The habitat through most of this area is a mixed Acacia/Combretum woodland with abundant food resources all year round, but with seasonal water shortages. Visibility

conditions in this habitat type are very poor due to the topography, tall grass and relatively dense tree cover (Henzi et al., submitted ms.).

Observations were made at the beginning of the study, in January 1989, from over 50 meters away, and by March-April 1989 from about 20 meters away. This distance was gradually reduced, and by the end of this study, in November 1991, most of my observations were made from a distance of 1-5 meters from individual baboons, and I could move freely among them. Toward the end of the study one male juvenile actually approached and touched me briefly.

I could identify all the adult males individually, by natural markings, by March 1989, and all the adult females and subadult individuals by July 1989. These identifications were confirmed by S. Whitehead on September 1989 (see Appendix I). S. Whitehead also provided data on the troop from June 1986. Due to the poor visibility conditions most of the juveniles were not identified and it was impossible to census them accurately throughout the study. Relatedness among females is unknown. Females were defined as subadults from their first visible perineal swelling and as adults from first parturition (e.g., Eisenberg et al., 1981). Females reproductive status (sexual cycling, pregnancy or lactation), swelling of the perineal skin (as defined by Rowell, 1967), and consorting with males, were recorded daily. The menstrual cycle length is 25-47 days and the females may conceive on the first day of deflation or 1-5 days prior to deflation of the perineal skin, when it is fully swollen (e.g., Wildt et al. 1977). Infant age classes were defined according to Whitehead et al. (1990).

I followed the baboons on foot, from dawn to dusk, for over 800 hours prior to fission and for over 400 additional hours after the fission. Data were collected using scan sampling (recording identity, activity and food items of

all visible troop members, every 30 minutes, throughout the day); focal sampling (recording a focal animal's activity, food items, neighbours, and interactions, every 2 minutes., in samples of 20 minutes.); and ad libitum data (including daily records of all observed individuals, their physical condition, female reproductive state, consortships and special events). Records of all observed agonistic events and their context and outcome, were derived from focal samplings and ad libitum data. Similarly, all observed grooming sessions were also recorded including the identity of the initiator of each session and who terminated it, reciprocity and bout length. Feeding bout lengths of females were recorded while feeding on all the major food items, from the time they commenced to handle a certain food type and until they stopped feeding on that item. (For methods of collecting data see also Altmann, 1974; and Eisenberg et al., 1981). Checksheets used are given in Appendix II.

Dominance rank was established through win-loss matrices of the outcomes of all recorded agonistic encounters (e.g., Hausfater 1975), including threats and submissive gestures, spatial displacements and events of escalated aggression involving a chase or physical contact.

Rates of female aggression, affiliative behaviour, and vicinity to others were derived from focal samplings. Individual time budgets and diet composition were derived from scan samplings.

Behaviour categories referred to in chapter 4 are same as defined by Seyfarth (1976). All the other behaviour categories mentioned, unless stated differently in the text, are same as defined elsewhere (e.g., Altmann, 1980).

The statistical analyses included in this work will be referred to separately, in the text, wherever relevant (for more details see also, Siegel, 1956; Martin and Bateson, 1986).

TABLE 2.1: Mtshopi Troop composition before and after troop fission.

	March 1990	May 1990'	
	Mtshopi troop	Darth's troop	Flash's troop
Adult males	8	4	4
Subadult males	3	2	1
Adult females	17	8	9
Subadult females	6	3	3
Lactating infants	5	4	1
Older infants and juveniles	32-37	21-26	10-15
Total	71-76	42-47	28-33

CHAPTER 3:
DO FEMALE CHACMA BABOONS COMPETE FOR A
SAFE SPATIAL POSITION
IN A WOODLAND HABITAT IN ZULULAND, SOUTH-AFRICA?

*This manuscript was submitted to Behavioural Ecology and Sociobiology, by T. Ron, S. P. Henzi and U. Motro.

3.1. SUMMARY

It seems to be the case that in our study troop of chacma baboons in Mkuzi Game Reserve, Zululand, South-Africa, where we found no evidence that food may be a limiting resource for survival or reproduction, and where we suggest that the main cause for mortality may be predation by leopards, female baboons invest much time, energy and risk in agonistic interactions in order to maintain a high dominance rank. The higher-ranking females can be better protected from predation, through access to more central spatial positions in the troop.

Only 6.4% of all agonistic events were over food patches (Figure 1), and no significant correlation was found between a female's dominance rank and proportion of time spent feeding, feeding bout length or diet composition (Table 1). Mean inter-birth interval at Mkuzi is relatively short (18.53 months) and inter-birth intervals are not correlated with dominance rank (Table 1). Infant mortality rate is extremely low and of 41 recorded pregnancies of 21 females, only one pregnancy terminated with an abortion and one other infant died.

Female mortality, however, was related to dominance rank and all of the five females who disappeared during the study were low-ranking (Table 2). 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 at Mkuzi with almost no occurrences of support coalitions. Most of the female-to-female agonistic encounters at Mkuzi were in a social context, and more than half were over a spatial position next to other adult troop members (Figure 1). It is suggested here that these females were competing for safe spatial positions, protected from leopards. Indeed, a positive correlation was found between a female's dominance rank and the time spent next to other adult troop members.

Both high and low ranking females were involved in significantly more agonistic encounters than middle-ranking females. As expected, most of the aggression took place among similar ranking females. More aggression was, however, recorded between the high and low ranking females than between each of these groups and the middle-ranking females (Table 3 and Figure 2). Obviously, when approaching a group of individuals, it is easier for a high-ranking female to displace the lowest ranking individual in that group. Thus, both the high-ranking and the low-ranking females are more frequently involved in such conflicts than middle-ranking females.

Further evidence supporting the suggestion that females at Mkuzi compete to avoid predation is found in the higher rates of aggression and closer spatial positions between individuals after troop fission (Table 4), and in hours of higher predation risk, in the evening and in the morning.

3.2. 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 rate) 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., Hausfater 1975; Altmann 1980; Altmann 1983; Melnick and Pearl 1987; Strum 1987; van-Noordwijk and van-Schaik 1987; Altmann et al. 1988; Soumah and Yokota 1991; Barton, in press; Barton and Whiten, in press).

Competition for food may be evident in direct displacements over food patches (e.g., Barton, in press), 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 and van-Schaik 1987).

Competition between females can also be evident in the suppression of the reproduction of lower-ranking females by aggressive harassments from the higher-ranking ones (e.g., Wasser and Starling 1986). Meikle and Vessey (1988) have found a correlation between a female's rank and lifetime survivorship of her male offspring in rhesus monkeys.

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 behavior, feeding bout length and diet composition were tested. We have also tested the effect of dominance rank on lifetime reproductive success, as may be evident in inter-birth

intervals, infant survival or female survival, throughout the study period.

We will try to show that the females of this troop were not competing for food but may have been competing for a safe spatial position, and that the main cost for low-ranking females was a higher risk of predation by leopards. It has been shown that predation pressure may be an important selective factor in primate evolution affecting primate social organization and behavior (e.g., van-Schaik and van-Noordwijk 1985; Anderson 1986; Dunbar 1988; Boesch 1991).

3.3. 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. Following a long phase of social instability, since October 1988 (S. Whitehead, pers. comm.) the troop has divided into two new daughter troops by May 1990: DARTH's Troop with about 43 members, including 4 adult males, 8 adult females, 3 subadult females, and FLASH's Troop with about 33 members, including 4 adult males, 9 adult females, 3 subadult females.

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

All adults were individually identified by natural markings (Ron and Whitehead, in press) 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 (Whitehead, in prep.). 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).

The baboons were followed on foot from dawn to dusk for over 800 hours prior to troop fission and over 400 hours after fission. Data were collected using scan sampling, focal sampling and ad libitum data records (as in Altmann 1974).

All observed individuals, female reproductive status and births were recorded daily. The outcome and context of all observed female-to-female agonistic encounters were recorded. Dominance rank was established through win-loss matrices of the outcomes of these agonistic encounters (e.g., Hausfater 1975), including threats and submissive gestures, spatial displacements, chase or physical contact. 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 minutes throughout the study. 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.

3.4 RESULTS

3.4.1. 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 (Figure 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., Dougal et al. 1964; Waterman 1984). There was no significant correlation between a female's dominance 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).

3.4.2. 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 ($r_s=-0.0417$, $n=17$). (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 very old, one very young, and three other females have disappeared during the study. One other very old female had no births recorded).

1. Average inter-birth interval was relatively short. Using cluster sampling techniques (as in Cochran, 1977), it was

18.53 \pm 1.81 months (mean \pm SE), with a minimum of 8 months (median=18 months).

4. Infant mortality rate was extremely low. Of 41 recorded pregnancies of 21 females (including data prior to the study period), 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.

3.4.3. Female mortality

Female mortality was related to dominance rank (Table 2). One female disappeared before troop fission, and four 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 increasingly seen over the last year of the study. Leopard feces containing baboon fur were found close to the sleeping-sites.

3.4.4. Female aggression

We have recorded high rates of female aggression: 1.13 \pm 0.12 female-to-female agonistic events/hour (of which 19.4%

involved a chase or physical contact) prior to fission. Yet, only three female coalitions and four male-female support events were recorded, all in 800 observation hours prior to fission (Ron et al., in press).

Most of the aggression took place among similar ranking females, or was directed by the top ranking toward the lowest ranking females (Table 3 and Figure 2). 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-Kuels test, performed at an experimentwise error of 0.05, shows that the high-ranking females had the highest level of aggression (1.52 events/hour), but not significantly higher than the low-ranking females (1.36 event/hour). Both show a significantly higher level of aggression than the middle-ranking females (0.69 events/hour).

3.4.5. 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.

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 neighbor, 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.

On 52.3% of the agonistic events a female was displaced from a spatial position within five meters from at least two other adult troop members (Figure 1). A significant positive correlation was found between dominance rank and time spent "in company" (Spearman's coefficient of rank correlation: $r_s=0.5686$, $n=17$, $P<0.01$). (Table 4).

3.4.6. Spatial position and aggression in relation to predation risk

The percentage of time spent "in company" during morning hours was significantly higher than the percentage of time spent "in company" during daytime; in the evening higher than during daytime; 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 daytime. In the evening they were involved in more agonistic events than during daytime 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 of the leopard predation occurs during the night or during early morning and late evening hours (e.g., Altmann 1980, S. Wasser, pers. comm.). Close neighbors recorded during early mornings and late evenings usually represent the same spatial position baboons occupy during the night. (e.g., Altmann 1980; D. Forster, pers. comm.)

The females spent more time "in company" after troop fission, but not significantly (t-test for paired observations: $t=0.23$, $df=14$, $P>0.50$) (Table 4). However,

after troop fission, with fewer members in each daughter troop, probability considerations suggest that each female would spend less time close to others. Increased time spent "in company" after fission may be the result of the increased risk of predation to individuals after fission. Indeed, aggression levels also rose, and very significantly after troop fission (Table 4) (t-test for paired observations: $t=9.60$, $df=14$, $P<0.001$).

3.5. 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, Zululand,

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 and Pearl 1987; Altmann et al. 1988; Johnson 1989; Barton and Whiten, in press). At Mkuzi, however, our results suggest that competition for food does not have an 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 a 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 behavior (e.g., Anderson 1986; Dunbar 1988; Boesch 1991; Dunbar 1992). Van-Schaik (1989) has suggested that social relationships among female primates reflect the relative importance of competition for food and safety. Barton et al. (1992), as well as Strum (1987), have mentioned that a major factor in home-range selection by baboons was staying close to safe sleeping-sites.

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 (Figure 1). Moreover, a positive correlation was found between a female's dominance rank and time spent next to other adult troop members (Table 4).

Barton (in press) indicated that competition over spatial positions may be over favorable feeding sites. At Mikumi National Park, Tanzania, where baboons suffer extremely high leopard predation rates, most of the agonistic events were over spatial positions next to other troop members (S. Wasser, pers. comm.). Wasser has suggested that females may be competing over spatial positions next to other troop members not only for protection from predation, but also for social support, which was found to be an important factor in the study troop at Mikumi (Wasser and Starling 1986). At Mkuzi, however, food competition as well as support coalitions were not recorded as an important factor in the females' social life. 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.

Strum (1987) has suggested that dominance stability and aggression levels may be related to the importance of the resource to the individuals competing over it. 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 a female's reproductive success depends on the relative success of her infants and the resources available to them, as is the case when competition is for food (e.g., Seyfarth 1976; Altmann 1983; Barton, in press), there is a positive correlation between dominance rank and levels of aggression. Competition is most intense between adjacent ranking females, and 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 and Figure 2). This distinct situation can have a possible explanation, that is analogous to the selfish herd idea of Hamilton (1971), and is consistent with the high risk of predation at Mkuzi. Obviously, when approaching a group of individuals, it is easier for a high-ranking female to

displace the lowest ranking individual in that group. Thus, the high-ranking and the low-ranking females are both more frequently involved in such conflicts than middle-ranking females. In addition, being the ones most susceptible to predation risk, the low-ranking females have high rates of aggression among themselves, since fighting for their rank and spatial position is crucial for their survival.

Further evidence, supporting the suggestion that females at Mkuzi compete for a safe spatial position to avoid predation, is found in the higher rates of aggression and closer spatial positions between individuals in hours of higher predation risk, as well as after troop fission, when individual risk of predation increased. This trend is in contrast to what would be expected if they were competing for food. Indeed, of the five females who disappeared in the course of our study, four did so during the period following troop fission.

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, the observed inter-individual distances 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 hand. 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. Another important question that rises is why did the troop split at all, if troop fission had such a high cost for females. We have reason to believe that the troop fission was initiated by the males, and forced upon the females (Ron, submitted ms.)

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

TABLE 3.1. Correlation between female dominance rank and parameters of time budget and reproductive success: percentage of total time spent feeding, percentage of total time spent in grooming and social behaviour, percentage of feeding time spent feeding on fruits and seeds, average feeding bout length (minutes), 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. Spearman's coefficient of rank correlation is given for each parameter. All coefficients of rank correlation are not significant.

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
<u>rs</u>		0.1667	0.0460	-0.0343	0.0417	-0.0417	-0.0166

TABLE 3.2. The five females who disappeared during the study: their identity, dominance rank prior to troop fission, their new troop affiliation after fission (D=Darth's Troop; F=Flash's Troop), 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

* 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.

TABLE 3.3. Mean number of agonistic events/hour 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 3.4. Percentage of time females spent "in company" (within a distance of up to five meters from at least two other adults), and aggression levels (number of agonistic events/hour per female), for each female, according to her dominance rank, before and after troop fission.

Name of female	Rank	Time "in company" (% of total time)		Aggression rate (agonistic events/hour)	
		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.

FIGURE 3.1. The percentages of the different contexts of female-to-female agonistic encounters (feeding context: while at least one of the females involved was feeding; social context: while at least one of the females involved was engaged in any social interaction with other troop members; spatial displacements: over a position of up to five meters from at least two other adult troop members).

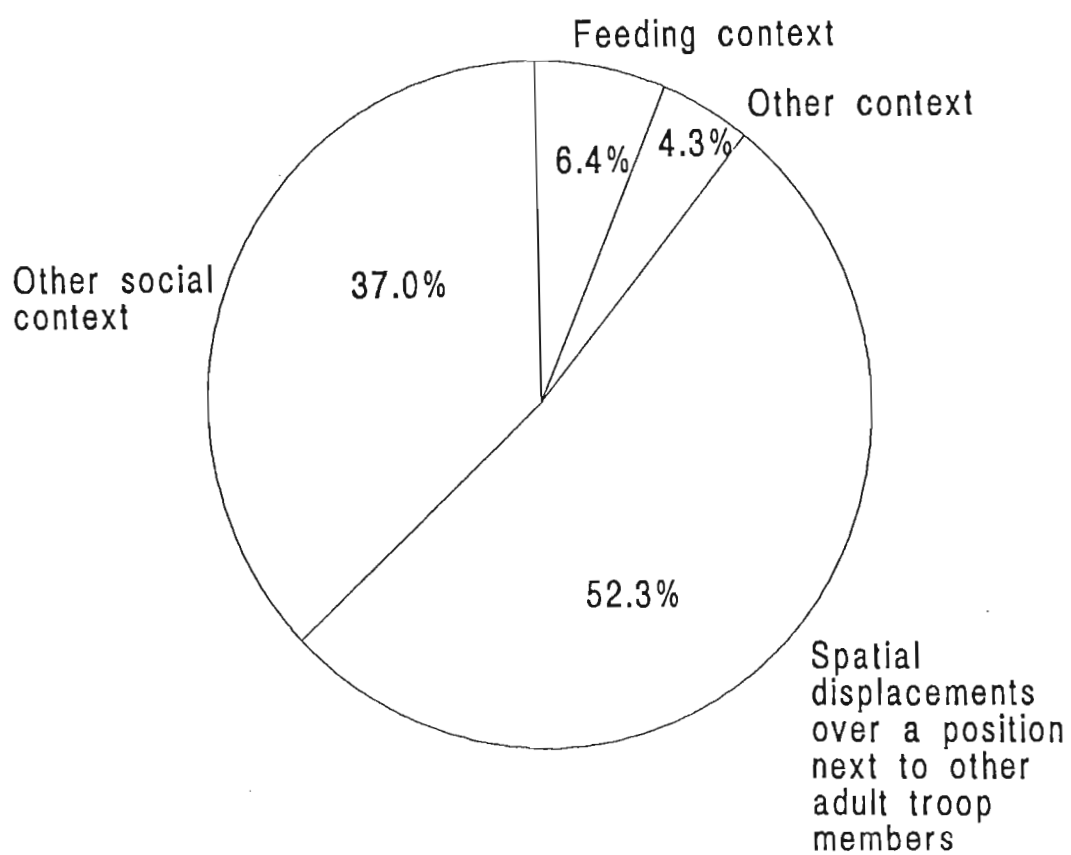
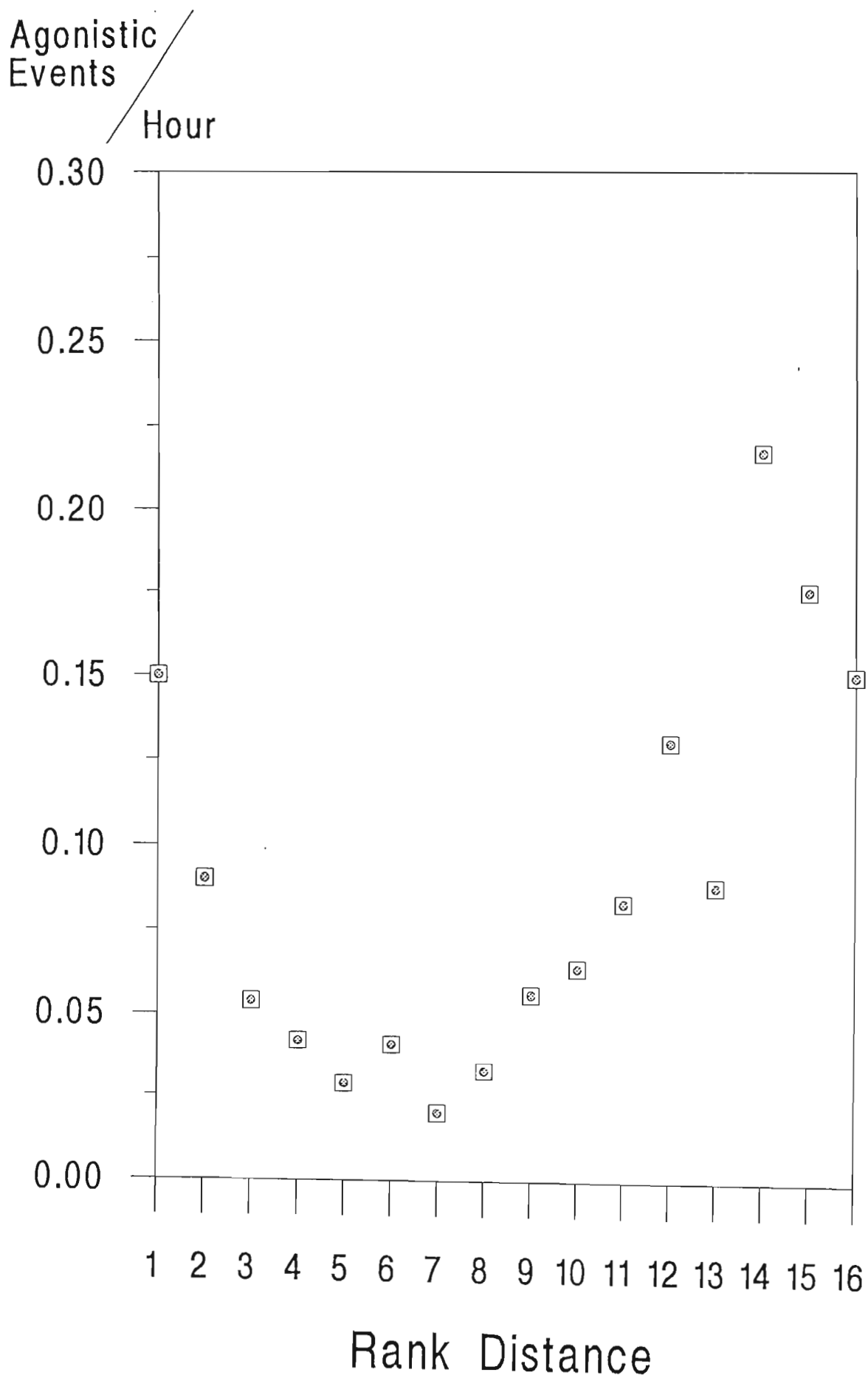


FIGURE 3.2. Correlation between female-to-female aggression rate (number of agonistic events/hour) per each pair of females and rank distance between the two females involved.



CHAPTER 4:
SOCIAL RELATIONSHIPS AMONG ADULT FEMALE CHACMA BABOONS
IN ZULULAND, SOUTH-AFRICA

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4.1. ABSTRACT

The following measures of female 'attractiveness' were defined by Seyfarth (1976): the amount of grooming a female received, and number of females that gave her grooming; the amount of friendly gestures she received; the effectiveness of her presents; and the effectiveness of her grooming solicitations. Female chacma baboons (Papio cynocephalus ursinus) at Mkuzi Game Reserve, South-Africa, were found to be most attractive to other females when they were lactating, and especially mothers of young infants. However, measures of female attractiveness were not related to the female dominance hierarchy. Some attractiveness was recorded between dyads of female associates.

Females at Mkuzi had a linear and stable dominance hierarchy. Each female had 1-4 stable associates who were not necessarily adjacent ranking and probably not kin. Female associates did not support each other in coalitions. The importance of these associations is assumed to lie in mutual grooming and protection from risk of predation by the vicinity to each other. Under these circumstances kinship or rank distance of associates is not necessarily relevant. The context and quality of female agonistic behaviour at Mkuzi also indicate the effect of predation risk on female social behaviour in this troop.

4.2. INTRODUCTION

The important role of adult females in the formation, organization, and stabilizing of primate groups has been widely recognized (e.g., Seyfarth, 1976; Altmann, 1980; Wrangham, 1980; Smuts, 1985; Dittus, 1987). The social relationships among adult female baboons and macaques have been the focus of many studies (e.g., Seyfarth, 1976; Altmann, 1980; Dunbar, 1980; Walters, 1980; Hausfater et al., 1982; Wasser & Starling, 1986; van-Schaik, 1989; Giacoma & Messeri, 1992; Barton & Whiten, in press.).

Seyfarth (1976) has given a comprehensive account of agonistic and affiliative social behaviour of adult females in a small troop (with eight adult females) of chacma baboons (Papio cynocephalus ursinus), in a rocky, mountainous terrain with marked seasonal changes. The main conclusions of his study were: "1. All females are most attractive to others when they are lactating, and 2. In all reproductive states, high ranking females are more attractive than low ranking females." These two principles of female relationships were examined in the present study in a larger troop of chacma baboons (with 17 adult females), occupying a rich woodland habitat with abundant food resources all year round, at Mkuzi Game Reserve, Zululand, South-Africa.

A remarkable variability was recorded in the social organization and behaviour of primate populations of the same species. This variability is generally attributed to the different selective pressures each population is subjected to, due to specific environmental and demographic conditions. (e.g., Eisenberg et al., 1972; Whiten et al., 1987; Dunbar, 1988; van-Schaik, 1989; Lee, 1991). A comparison of the social relationships among adult female baboons under different ecological and demographic conditions may spread light on the various factors

affecting these relationships.

In the present study I have made an attempt to answer the same questions presented by Seyfarth (1976); i.e., explore the nature of dyadic relationships in the group; the effect of changes in individuals' reproductive state on their social, agonistic, and affiliative interactions; and the effect of an individual's dominance rank on her social interactions. I have also examined the changes in female relationships following troop fission.

4.3 METHODS

The study was conducted on a troop of chacma baboons (Mtshopi Troop) for a total of 14 months between January 1989 and July 1990 and for an additional 4 months on August - November 1991, at Mkuzi Game Reserve, Zululand, South-Africa. By March 1990 Mtshopi Troop consisted of about 76 individuals, including 8 adult males, 17 adult females, 6 subadult females and about 45 immature members. By May 1990, following a long phase of social instability, the troop has divided into two new daughter troops: DARTH's Troop with about 43 members, including 4 adult males, 8 adult females, 3 subadult females, and FLASH's Troop with about 33 members, including 4 adult males, 9 adult females, 3 subadult females.

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

All adult and subadult troop members were individually identified by natural markings (Ron & Whitehead, 1993). Relatedness among females, however, is unknown. Females were defined as subadults from their first visible perineal swelling and as adults from first parturition (e.g., Strum,

1987). The female reproductive cycle is divided into three reproductive states: sexual cycling, pregnancy and lactation. The sexual cycle is further divided into oestrus and nonoestrus (including the other phases of the menstrual cycle as defined in Rowell, 1967; Seyfarth, 1976). Lactation is divided into two phases: phase 1: lactation of infants up to about 6 weeks old; and phase 2: lactation of infants older than 6 weeks (defined as in Whitehead et al., 1990).

The baboons were followed on foot from dawn to dusk for over 800 hours prior to troop fission and over 400 hours after fission. All the data presented here refer to the adult females in the period prior to fission, unless stated otherwise in the text. Data were collected using scan sampling, focal sampling and ad libitum data records (as in Altmann, 1974).

All observed individuals, female reproductive state and births were recorded daily. The outcome and context of all observed female-to-female agonistic encounters, including approach-retreat interactions and interactions involving aggressive behaviour (with a chase or physical contact), as defined by Seyfarth (1976), were recorded from focal samplings and ad libitum records. Dominance rank was established through win-loss matrices of the outcomes of these agonistic encounters (as in Hausfater, 1975). Rates of female agonistic and affiliative interactions were derived from focal samplings. Components of individual time budgets were derived from scan sampling of the troop every 30 minutes throughout the study.

4.4. RESULTS: AGONISTIC BEHAVIOUR

4.4.1. Dominance Hierarchy

As in most female baboons and macaques studied elsewhere

(e.g., Seyfarth, 1976; Dunbar, 1980; Hausfater et al., 1982; Melnick & Pearl, 1987; Strum, 1987; Dunbar, 1988; Chapais et al., 1991), dominance hierarchy among the adult females at Mkuzi was linear and stable. The direction of agonistic interactions (both approach-retreat interactions and interactions involving active aggression - a chase or physical contact) was highly predictable. One female, Joan, has promoted her rank, during the study, from the lowest position in the troop to rank position 5 of the 17 adult females (Ron, submitted ms.). Excluding Joan's interactions, only three (0.68%) reversals were recorded out of 443 outcomes of agonistic encounters, prior to troop fission. All three were between adjacent ranking females.

4.4.2. Changes in Dominance Hierarchy Following Troop Fission

Choice of a new troop by Mtshopi Troop's females, following fission by May 1990, was according to the AYS strategy (Abandon Your immediate Superior in rank). By choosing the opposite troop to that joined by her immediate superior, each of the 14 (of 17) adult and 4 (of 6) subadult females, who adopted this strategy, enjoyed a rank promotion in her new troop (Ron et al., in press).

Dominance rank of all females before fission, relative to others, remained constant, at least during the first three months after fission. By August 1991 two adult females disappeared (presumably died) and four (three adult and one subadult) females moved from one daughter troop to the other. Two of these females lost 2 and 4 rank positions respectively, one promoted her rank by 4 positions and one kept the same rank position, following the changes in their troop affiliation. (Table 1).

One of these females and one other female also disappeared later on. Three of the subadult females, two in

Flash's Troop and one in DARTH's Troop, became adult by August 1991, and four new subadult females were identified, two in each troop (Table 1). These new subadults were not included in the following analysis.

While in some cases of recorded fission in macaque troops, females keep their relative dominance rank after fission (e.g., Chepko-Sade & Sade, 1979; Prud'Homme, 1991), changes in female dominance hierarchy in newly formed troops or following troop fission were documented in other studies (e.g., Koyama, 1970; Dittus, 1988; Gust & Gordon, 1991). At Mkuzi the dominance rank of two pairs of adult females, relative to each other, was reversed, in DARTH's Troop, by August 1991, following the later troop transfers. Two very young females (one was a subadult during fission) promoted their rank position, in relation to other females in their troop, by five and six positions respectively, both in Flash's Troop (Table 1). Rank promotion of young females who acquire their position in the adult hierarchy, has been recorded in other baboon studies (e.g., Cheney, 1977; Walters, 1980; Hausfater et al., 1982; Samuels et al., 1987; Strum, 1987). Excluding these four changes, all rank positions of females, relative to others in their troop, remained constant until the end of this study, in November 1991.

4.4.3. Rank Related Frequency of Agonistic Behaviour

An average frequency of 1.13 ± 0.12 (mean \pm SE) agonistic encounters/hour per female, with other adult females, was recorded prior to troop fission, about 20% (0.22 ± 0.05 events/hour per female) of which included active aggression. Most of the agonistic interactions were recorded among similar ranking females, or were directed by the top ranking toward the lowest ranking females. The five highest ranking and the five lowest ranking adult females

were involved in significantly higher levels of agonistic interactions than the seven middle-ranking females (Ron et al., submitted ms.). Seyfarth (1976), however, found no indication that frequency of agonistic behaviour in particular pairs of females was related to the individual's relative positions in the hierarchy.

4.4.4. Frequency of Agonistic Behaviour and Female Reproductive State

Adult females at Mkuzi were more aggressive during oestrus than during other phases of the menstrual cycle. They were involved in a higher frequency, although not significantly higher, of approach-retreat interactions and in a significantly higher frequency of encounters of active aggression, during oestrus (t-test for paired observations: $t=1.54$; and $t=4.67$, $p<0.001$, respectively, $df=16$). This is in line with Rowell's (1967) finding of a similar trend. Hall (1962), Dunbar & Dunbar (1977) and Wasser & Starling (1986) also recorded increased aggression levels during oestrus, while Hausfater (1975) found less aggression directed toward fully swollen females and Seyfarth (1976) found no changes in frequency of female-to-female agonistic behaviour within the sexual cycle. Bielert & Howard-Tripp (1983) recorded an increase in self-directed aggression in captive isolated female baboons during oestrus.

Similarly to Seyfarth's (1976) findings, frequency of agonistic behaviour among adult females at Mkuzi did not change significantly from sexual cycling to pregnancy (t-test for paired observations: $t=0.54$, $df=10$). (Considering only the 11 females that had infants during the 14 months of the study, prior to troop fission). There was also no significant change in frequency of agonistic encounters during lactation, in comparison to cycling females ($t=0.84$, $df=10$). Altmann (1980) found that mothers of young infants

received more aggression than other females.

4.4.5. The Social Context of Agonistic Behaviour

Of all agonistic encounters of adult females, recorded prior to troop fission, 89.3% were in a social context (Table 2). Approach-retreat strategy was more commonly used than active aggression in all social contexts, but as also recorded by Seyfarth (1976), active aggression among females at Mkuzi was used in agonistic encounters over an adult male in a higher proportion than in any other social context (Table 2).

In the present study, as also recorded by Seyfarth (1976), there was no indication of differences in competition over males between cycling and pregnant or lactating females (t-test for paired observations: $t=0.36$ and $t=0.43$, respectively, $df=10$). Females during oestrus, however, were involved in significantly more agonistic encounters over males and in less encounters over proximity to females than during other phases of the menstrual cycle (t-test for paired observations: $t=5.33$, $df=16$, $p<0.001$; $t=-5.42$, $df=16$, $p<0.001$).

As also indicated by Seyfarth (1976), lactating females and infants of six weeks or younger, were subjected, at Mkuzi, to a significantly higher rate of agonistic encounters over them than older infants and their mothers (t-test for paired observations: $t=6.08$, $df=10$, $p<0.001$).

Relative frequency of agonistic encounters over access to males or females was not significantly related to the female dominance rank (Spearman's coefficient of rank correlations: $r_s=-0.23$ and $r_s=-0.12$, respectively, $n=17$). Higher ranking females were involved in more agonistic encounters over lactating females and infants, but not significantly so ($r_s=0.34$, $n=17$).

4.4.6. 'Friendly' Approach to Lactating Females and Infant Kidnapping

As also recorded in other studies (Rowell et al., 1968; Rowell, 1969; Seyfarth, 1976), lactating females at Mkuzi received more friendly approaches than females in other reproductive states, and more so when their infants were younger. 79.51% of all friendly approaches were directed toward lactating females. A lactating female received 0.58 ± 0.01 /hour (mean \pm SE) friendly approaches from other females. Females lactating younger infants, six weeks old or less, received significantly more friendly approaches than females lactating older infants (t-test for paired observations: $t=9.99$, $df=10$, $p<0.001$).

Frequency of friendly approaches of a female to lactating mothers or those received by a lactating mother from other females were not related to her dominance rank (Spearman's coefficient of rank correlations: $r_s=-0.13$, $n=17$ and $r_s=-0.21$, $n=11$, respectively).

Lactating mothers avoided $33.00 \pm 2.44\%$ (mean \pm SE) of all friendly approaches by other females (using cluster sampling techniques, as in Cochran, 1977). In the present study, as also recorded elsewhere (Rowell et al., 1968; Seyfarth, 1976), mothers of younger infants (six weeks old or less) avoided friendly approaches in a significantly higher frequency than mothers of older infants (t-test for paired observations: $t=15.17$, $df=10$, $p<0.001$). Frequency of avoiding friendly approaches by other females was also not related to the mother's rank but higher ranking females were less avoided by the mothers they approached (Spearman's coefficient of rank correlations: $r_s=0.14$, $n=11$; and $r_s=-0.42$, $p=0.05$, $n=17$, respectively).

The phenomenon of infant kidnapping, has been described in other studies of baboons and macaques, as an aspect of female reproductive competition, by interrupting the

infant's normal activity, feeding and development, and may even have fatal consequences for the infant (e.g., Altmann, 1980; Silk, 1980; Ransom, 1981; Wasser, 1983; Wasser & Starling, 1986; Maestripieri, 1993). An infant at Mkuzi was subjected to 0.23 ± 0.005 (mean \pm SE) kidnapping events/hour, i.e. any case of handling that caused the infant to break touch or enlarge distance from the mother. Infant kidnapping at Mkuzi was related to the infant's age and to females' dominance rank. In all 92 recorded cases of infant kidnapping, before fission, the kidnapping female was higher ranking than the infant's mother. The frequency of kidnapping of younger infants, six weeks old or less, was significantly higher than frequency of kidnapping of older infants (t-test for paired observations: $t=6.53$, $df=10$, $p<0.001$). Higher ranking females kidnapped infants in a significantly higher rate (Spearman's coefficient of rank correlations: $r_s=0.80$, $t=5.15$, $n=17$, $p<0.001$), while higher ranking mothers suffered kidnapping of their infants in a significantly lower rate than others ($r_s=-0.96$, $t=-10.48$, $n=11$, $p<0.001$).

Frequency of infant kidnapping was not related to the reproductive state of the kidnappers. No significant differences were recorded in frequency of kidnapping between cycling and pregnant females or between lactating and cycling females (t-test for paired observations: $t=0.29$ and $t=0.64$, respectively, $df=10$).

4.4.7. Changes in Agonistic Behaviour Following Troop Fission

Frequency of agonistic behaviour increased significantly following troop fission from 1.13 ± 0.12 (mean \pm SE) to 2.21 ± 0.18 agonistic events/hour per female (t-test for paired observations: $t=9.60$, $df=14$, $p<0.001$; Ron et al., submitted ms.). Moreover, there was a significant increase

in frequency of active aggression from an average of 0.22 ± 0.05 to 0.39 ± 0.04 events/hour per female, after fission ($t=5.49$, $df=14$, $p<0.001$). The proportion of active aggression of the total agonistic interactions, however, decreased after fission from about 20% to about 18%.

Changes in context of female-to-female agonistic encounters were recorded following troop fission. The relative frequency of agonistic interactions over a position next to an adult male or adult female increased while the relative frequency of encounters over a lactating female or an infant decreased. A significant increase was recorded in absolute frequencies of agonistic encounters over adult males and females but no significant change was found in the absolute frequency of encounters over a lactating female or an infant (t -test for paired observations: $t=10.47$, $p<0.001$; $t=7.18$, $p<0.001$; and $t=-0.40$, respectively, $df=14$) (Table 2).

4.4.8. Coalitions

The value of social relationships for primate females is held to lie in the coalitions that they facilitate and the importance of support coalitions among female baboons and macaques has been widely stressed as a major factor in female competition and maintaining of dominance rank (e.g., Cheney, 1977; Dunbar, 1980; Walters, 1980; Wrangham, 1980; Hausfater et al., 1982; Wasser, 1983; Wasser & Starling, 1986; Samuels et al., 1987; Strum, 1987; de-Waal, 1989; Chapais et al., 1991). Although high rates of female aggression were recorded at Mkuzi, almost no support coalitions were observed (Ron et al., in press). Excluding the interactions of the female Joan, only three female coalitions were recorded in 800 hours prior to troop fission and none in 400 observation hours after fission. All three occasions of support coalitions were between two

female associates (who did not occupy adjacent ranks), against a third female who was lower ranking than at least one of her opponents.

4.5. RESULTS: AFFILIATIVE BEHAVIOUR

4.5.1. Choice of Female Associates

In most studied troops of baboons and macaques females tend to associate mainly with adjacent ranking females, who are usually also their kin (e.g., Hausfater, 1975; Seyfarth, 1976; Cheney, 1977; Hausfater et al., 1982; Melnick & Pearl, 1987; Strum, 1987; Dunbar, 1988; de-Waal, 1989; Chapais et al., 1991; de-Waal, 1991b).

Most of the females at Mkuzi associated with each other up to 10% of their social time, but each female had only 1-4 close adult and subadult female associates (with an average of 2.12), with whom she spent more than 15% of her total socializing time with females, defined as time spent in touch with each other and in affiliative interactions. Only three of all 27 such pairwise associations, and one of the 18 between adult females, prior to fission, involved females who occupied adjacent ranks (Figure 1).

If any two individuals are chosen randomly out of a group of 23 females with linear hierarchy, and their rank distance is measured (D), then this number is a random variable, with the probability distribution $\text{Prob}(D=k) = (23-k)/253$ ($k=1,2,\dots,22$), and expected value $E(D)=8$.

Looking at the 27 associations that were found prior to the splitting of the group, the mean difference in rank between female associates was 7.74 places. Moreover, the distribution of these differences is not significantly different from what is expected under the above mentioned, random model. This conclusion is based on a chi-square test for goodness of fit. Since the test involves many expected

frequencies that are quite small, the P value was estimated by computer simulations. Thus, based on 1000 simulated samples, the estimated P value is 0.839.

Relatedness among females at Mkuzi is unknown. However, it is apparent, since female associates were not adjacent ranking, that female relatives either did not necessarily associate with each other or did not occupy adjacent ranks, or both. If kinship was the only or major factor affecting choice of female associates, females would be expected to form distinctive clusters of mutual associates, comprised of females of the same matrilineal lineages. This, however, was not the case at Mkuzi. Of the 27 pairs of female associates, prior to fission, only 9 shared one mutual female associate, and none shared more than one associate. In fact, of 23 females, there were only three triads of mutual associates (two remained after fission - one in each troop, and only one triad remained by August 1991). Looking at the whole network of female associations it seems highly unlikely that all pairs of female associates are kin of first or second degree, unless the whole troop is comprised of one big happy family! (Figure 1).

Some studies of chacma baboons (Anderson, 1981; Byrne et al., 1989; Hamilton & Bulger, 1992) indicate that females who share the same male associate also tend to associate with each other. A female at Mtshopi Troop had 1-3, with an average of 1.6 male associates, with whom she spent at least 25% of her socializing time with males. Of the 27 pairs of female associates, 12 pairs shared one male associate and one pair shared two, while 14 pairs did not share any of their male associates. Females at Mkuzi also did not necessarily choose to associate with other females of the same age group. Dividing the females into four relative age groups - subadults, young, middle-aged and old - 12 pairs of female associates were within the same age group and 15 were between females of different age groups.

The factors that determine choice of associates among females in this short-term study, remain unclear. It may well be determined by a combination of various factors. The whole network of associates, however, where all females are tied together, is noteworthy (Figures 1 & 2).

4.5.2. Changes in Female Associations Following Troop Fission

Following troop fission, female baboons and macaques tend to remain in the same troop with their former female associates (e.g., Koyama, 1970; Chepko-Sade & Sade, 1979; Dittus, 1988; Dunbar, 1988; Prud'Homme, 1991; Menard & Vallet, 1993; and A. Whiten, pers. comm. for Papio anubis).

Only nine of the 23 females of Mtshopi Troop remained in the same troop with all of their former female associates following fission, while five females lost all of their close associates (Figure 1). The 27 pairwise associations in the original Mtshopi Troop were distributed in such a way, that any splitting into two distinct new groups would have resulted in breaking some of these associations. In splits into groups of 11 and 12 females, 24 pairwise associations could be retained. The actual split of Mtshopi Troop disconnected 10 and retained 17 (Figure 1), not significantly more than what one should expect under the assumption of random splitting (Ron et al., in press).

Following fission, five females remained with no female associates in their new troop. By August 1991 two of these females died and one moved to the other troop and joined her former associates. Two other females, of the four that moved by August 1991 from one daughter troop to the other, lost thus all of their former associates, while one female lost one associate and regained another and another only regained a former associate. In total, five pairwise associations were lost due to the later troop transfers,

while two were regained. The five females that lost all of their former associates, following the troop fission or the later demographic changes in troop affiliations, were involved in all seven completely new pairwise associations that were established by the end of this study (Figure 2).

Since there were only about half of the females in each daughter troops, after fission, female associates were defined as individuals who spent at least 25% of their socializing time with females together. All pairs of female associates, prior to fission, that remained in the same troop, remained associates until the end of this study, i.e. no female pairwise associations were disconnected, as long as both females remained in the same troop (Figure 2).

4.5.3. Time Allocation Between Female Associates

An adult female spent $25.64 \pm 3.10\%$ (mean \pm SE, using cluster sampling techniques) of her socializing time with females, with her "best female friend", defined as the female with whom she spent more time than with any others. The number of female associates a female had or the proportion of time she spent with her "best female friend" were not related to her dominance rank (Spearman's coefficient of rank correlations: $r_s = -0.16$ and $r_s = 0.22$, respectively, $n=17$).

Number and identity of each female's associates did not change at any reproductive state. Time allocation between female associates, however, was related to reproductive state. Lactating females spent significantly less time with one "best female friend" than during any other reproductive state (t-test for paired observations: $t=9.18$, $df=10$, $p<0.001$) and thus allocated their social time among more females. Mothers of younger infants (six weeks old or less) spent less time with "best friend" than mothers of older infants ($t=-4.14$, $df=10$, $p<0.01$). Pregnant females spent

more time with "best friend" than cycling females ($t=3.21$, $df=10$, $p<0.01$), and females in oestrus more than in other phases of the menstrual cycle ($t=2.99$, $df=16$, $p<0.01$).

4.5.4. Presents

Presenting (orienting the rump toward the face of another), in non-agonistic social contexts, was recorded by Seyfarth (1976), as related to the female dominance hierarchy. The same relation was also found at Mkuzi. An average of 1.07 ± 0.17 (mean \pm SE) presents/week per female was recorded prior to troop fission. High ranking females presented less often and received more presents than others (Spearman's coefficient of rank correlations: $r_s = -0.83$, $p<0.001$; and $r_s = 0.88$, $p<0.001$, respectively, $n=17$).

An average of $39.56 \pm 1.90\%$ (mean \pm SE, using cluster sampling techniques) of the presents were responded to by a friendly gesture to the presenting female. The proportion of her presents that were responded to, was not related to a female's dominance rank ($r_s = 0.14$, $n=17$).

There was no indication that the frequency of presenting varied with changes in reproductive state. Lactating females, for example, did not present or received presents in a significantly different frequency than cycling females (t-test for paired observations: $t=0.82$, and $t=0.64$, respectively, $df=10$). However, a larger proportion of presents by lactating females were responded to than at any other reproductive state ($t=4.31$, $df=10$, $p<0.01$). Presents by mothers of younger infants (six weeks or less) were responded to more frequently than presents by mothers of older infants ($t=3.50$, $df=10$, $p<0.01$). The same trend was found by Seyfarth (1976), who interpreted it as a measure of the female's "attractiveness" to others at the time of presenting.

4.5.5. Grooming Solicitations

A female solicited grooming (as defined by Seyfarth, 1976) 0.34 ± 0.04 times/hour (mean \pm SE) and $28.27 \pm 0.85\%$ (using cluster sampling techniques) of her grooming solicitations were responded to. In the present study, as also recorded by Seyfarth (1976), females showed higher rates of grooming solicitations during lactation than during other reproductive states (t-test for paired observations: $t=3.60$, $df=10$, $p<0.01$). Mothers of younger infants (six weeks or less) solicited grooming more frequently than mothers of older infants ($t=3.03$, $df=10$, $p<0.02$). Seyfarth (1976) found that the rate of response to grooming solicitations was not higher during lactation, while at Mkuzi, grooming solicitations of lactating females did receive a significantly higher rate of response ($t=4.53$, $df=10$, $p<0.01$).

Both the frequency of grooming solicitations and the proportion of the grooming solicitations that were responded to were not significantly related to the female dominance rank (Spearman's coefficient of rank correlations: $r_s=0.27$, and $r_s=-0.21$, respectively, $n=17$). Seyfarth (1976), however, suggested that females were most likely to respond to the solicitations from higher ranking individuals.

Seyfarth (1976) recorded higher rates of grooming solicitations between adjacent ranking females than between other pairs of females. At Mkuzi, significantly higher rates of grooming solicitations were found when comparing, for each adult female, her average number of grooming solicitations/week, per female, from her female associates (as defined above) and from other adult females (t-test for paired observations: $t=9.48$, $df=16$, $p<0.001$). The average number of grooming solicitations/week of each female to her two adjacent ranking females, per female, however, was

smaller than her average number of grooming solicitations/week from other adult females ($t=-1.23$, $df=16$). This may be explained by the fact that most females at Mkuzi did not associate more with females who occupied adjacent rank positions to theirs.

4.5.6. Grooming and Female Reproductive State

The importance of grooming as a major component in affiliative interactions among baboons (and other primates) has been widely stressed (e.g., Hall, 1962; Seyfarth, 1976; Melnick & Pearl, 1987; Dunbar, 1988; de-Waal, 1989; Dunbar, 1991).

Some differences in grooming behaviour following changes in female reproductive state have been recorded for baboons. Seyfarth (1976) found no relation between grooming and changes either within the sexual cycle or from sexual cycling to pregnancy. He also found that during lactation females received the most grooming and were groomed by more different individuals, but were not groomed for longer bouts than others. Altmann (1980) also recorded higher rates of grooming received by lactating females, especially when the infants are young. Hall (1962) found that during oestrus females received less grooming and groomed others relatively more than during other reproductive states. Rowell (1968) found that females in oestrus generally groomed less and received less grooming, while lactating females received more grooming than others.

In the present study a female received grooming for 4.22 ± 0.42 (mean \pm SE) minutes/hour, from 10.23 ± 0.58 other females per week, prior to fission. Grooming bout length was 5.33 ± 0.38 minutes.

Lactating females received more grooming and groomed others more than during other reproductive states (t -test for paired observations: $t=4.95$, $p<0.001$ and $t=3.62$,

$p < 0.01$, respectively, $df = 10$). Mothers of younger infants (six weeks old or less) received grooming and groomed more than mothers of older infants ($t = 3.71$, $p < 0.01$ and $t = 3.58$, $p < 0.01$, respectively, $df = 10$). Frequency of grooming received or given by pregnant and cycling females were not significantly different ($t = 0.46$ and $t = 0.38$, respectively, $df = 10$). However, during oestrus, females received less grooming and groomed others less than during other phases of the menstrual cycle ($t = 3.14$, $p < 0.01$ and $t = 3.71$, $p < 0.01$, respectively, $df = 16$).

Lactating females also received grooming from more individuals than pregnant or sexually cycling females (t -test for paired observations: $t = 5.52$, $df = 10$, $p < 0.001$) and mothers of younger infants from more individuals than mothers of older infants ($t = 3.52$, $df = 10$, $p < 0.01$). Grooming bout lengths were not significantly different during lactation and other reproductive states ($t = 0.61$, $df = 10$).

4.5.7. Grooming and Female Dominance Rank

Seyfarth (1976) found that higher ranking females received more grooming and were groomed by more different individuals than lower ranking females, but grooming bout length was not related to rank. Altmann (1980), however, found no relation between the amount of grooming a female received or groomed others and her dominance rank. In the present study no significant correlation was found between a female's dominance rank and the amount of grooming she received or gave, the number of individuals that groomed her or her average grooming bout length (Spearman's coefficient of rank correlations: $r_s = 0.08$, $r_s = -0.27$, $r_s = 0.13$, and $r_s = 0.20$, respectively, $n = 17$). Also no correlation was found between dominance rank of lactating females alone and the amount of grooming they received or the number of individuals that groomed them ($r_s = -0.32$,

and $r_s = -0.025$, respectively, $n=11$).

4.5.8. Preference of Grooming Partners

Seyfarth (1976) has recorded a pattern of grooming preference among female baboons where each individual grooms females next to herself in the hierarchy more than she grooms others, and grooms the other females increasingly less as their rank become more different to her own. It has been noted in other studies that female baboons and macaques tend to groom more with their female allies who are usually also their relatives and occupy adjacent ranks to theirs (e.g., Melnick & Pearl, 1987; Strum, 1987; Dunbar, 1988; de-Waal, 1989).

The average amount of grooming each female received (grooming minutes/week per grooming female), prior to troop fission, from adult female associates (as defined above), was compared with that received from other females. Amount of grooming each female received from adjacent ranking females was also compared with that received from others. A female received on the average 17.75 ± 2.03 (mean \pm SE) grooming minutes/week from each of the other adult females. From female associates alone she received 33.03 ± 3.64 grooming minutes/week per female. Females received significantly more grooming from female associates than from other females (t-test for paired observations: $t=8.15$, $df=16$, $p<0.001$). They received, however, significantly less grooming from adjacent ranking females than from others ($t=-3.64$, $df=16$, $p<0.01$). This finding is in line with the finding that only one of 18 associations among adult females was between adjacent ranking females.

As suggested by Seyfarth (1976), grooming between female associates was more persistent and more reciprocal than in other dyads. Each pair of female associates was observed grooming at least once in each of the 14 months of the

study, prior to troop fission, while a female was observed grooming with each of the females, other than her associates, only during 6.29 ± 0.43 (mean \pm SE) of the 14 months before fission. Of all recorded grooming sessions among females, $31.59 \pm 1.07\%$ were reciprocal (using cluster sampling techniques). Among female associates $53.21 \pm 2.34\%$ of the grooming sessions were reciprocal. Average proportion of reciprocated grooming, per dyad, of each female with adult female associates was significantly higher than with other adult females (t-test for paired observations: $t=10.91$, $df=16$, $p<0.001$). Muroyama (1991), on the other hand, have recorded higher rates of reciprocity in grooming among unaffiliated pairs of female Japanese macaques (Macaca fuscata) than between affiliated pairs.

4.5.9. Changes in Affiliative Behaviour Following Troop Fission

After troop fission females stayed, generally, closer to others. This was interpreted as a result of the increased risk of predation to individuals in the smaller daughter troops after fission (Ron et al., submitted ms.). The average total amount of grooming (minutes/hour) that a female was engaged in, also increased after troop fission (t-test for paired observations: $t=2.84$, $df=16$, $p<0.02$).

4.6. DISCUSSION

4.6.1. Context of agonistic behaviour

Most of the agonistic encounters among adult females at MKuzi were in a social context, and more than half were over a position next to an adult male or female. After troop fission, aggression levels among females increased generally, and the proportion of encounters over a position

next to other adult troop members increased compared to other contexts of agonistic behaviour. Moreover, a larger proportion of the agonistic encounters over a position next to adult troop members, and especially next to an adult male, in the present study, involved active aggression, than in any other context (Table 2), as was found also by Seyfarth (1976). All these findings are in line with Ron et al.'s (submitted ms.) suggestion that risk of predation, as mediated by competition over protected spatial positions, may be the main cost to lower ranking females and the main source of female-to-female aggression in the present study troop. The increase in proportion of their time the females spent in social behaviour and in vicinity to other adult troop members, after fission, also support this suggestion.

4.6.2. Parameters related to female dominance hierarchy

Dominance hierarchy among females at Mkuzi was linear and usually stable, as recorded also elsewhere (e.g., Seyfarth, 1976; Hausfater et al., 1982; Dunbar, 1988). Most rank positions of females, relative to each other, remained stable throughout the study (Table 1). Choice of a new troop following fission, by most females, was according to a strategy that enabled each female to promote her own rank position in her new troop (Ron et al., in press).

The changes in troop affiliation, as recorded over a year after troop fission (Table 1), are puzzling. Except for Crab, who gained both rank and her former associates, the three other females lost their rank position, their associates, or both, by moving from one daughter troop to the other. It may well be that these females were driven to leave their former troop due to specific environmental conditions at that time.

As expected by the definition of dominance rank, high ranking females at Mkuzi were more aggressive toward others

and received less aggression. They also received more presents and presented less often than others. Context of agonistic encounters among females was generally not related to their dominance rank. However, high ranking females kidnapped other infants more frequently, while their infants were kidnapped less often than others. Infant kidnapping has been recorded elsewhere as an important aspect of female competition (e.g., Altmann, 1980; Silk, 1980; Ransom, 1981; Wasser, 1983; Maestripieri, 1993)

In contrast to Seyfarth (1976) findings, no indication was recorded at Mkuzi from a correlation between a female's dominance rank and the amount of grooming she gave or received; the number of individuals that groomed her; the amount of friendly approaches she gave or received; the proportion of friendly approaches she avoided; the effectiveness of her presents; or the frequency of her grooming solicitations and their effectiveness. Allocation of a female's socializing time among other females was also unrelated to her dominance rank.

4.6.3. Parameters related to female reproductive state

As also indicated by Seyfarth (1976), lactating females at Mkuzi received more friendly approaches; received and gave more grooming; received grooming from more different individuals; solicited more grooming from others; and their presents and grooming solicitations were more effective than of females at any other reproductive state. All these parameters were higher for mothers of younger infants (six weeks old or less). Mothers of younger infants also suffered more kidnapping of their infants; were the subject of more agonistic encounters over their infants; and avoided a larger proportion of the friendly gestures directed to them, than mothers of older infants. Lactating females, and especially mothers of younger infants,

allocated their socializing time among more individuals, and spent a smaller proportion of their socializing time with one "best friend" than during any other reproductive state.

In contrast to Seyfarth's (1976) findings, but in line with other studies (e.g., Hall, 1962; Rowell, 1967; Dunbar & Dunbar, 1977; Wasser & Starling, 1986), females at Mkuzi were involved in more agonistic encounters, with each other, and especially in more encounters involving active aggression, during oestrus than during other phases of the menstrual cycle. A larger proportion of the agonistic encounters that females were involved in during oestrus were over a position next to an adult male, rather than next to a female, compared with encounters at other times. During oestrus females were engaged in less grooming with other females, and allocated a larger proportion of their socializing time with females to one "best friend" than during other reproductive states. All these findings may be related to the changes in time budgets of females during sexual consortships. Oestrous females, thus spend more time with the consorting male and therefore they spend less time in social activities with other females and with less females. A large proportion of their agonistic encounters with females are over a position next to this male, and they are therefore also involved in more events of active aggression. Changes in the activity budgets of female baboons during sexual consortships were recorded elsewhere (e.g., Bercovitz, 1983; Rasmussen, 1985).

4.6.4. Measures of female 'attractiveness'

Seyfarth (1976) has referred to the following as measures of a female's attractiveness to other females, at any given time: the amount of grooming a female received, and number of females that gave her grooming; the amount of friendly

gestures she received; the effectiveness her presents (the proportion of her presents that were responded to); and the effectiveness of her grooming solicitations

Using these measures he concluded that 1. All females are most attractive to others when they are lactating (and mothers of young infants more than mothers of older infants), and 2. In all reproductive states, high ranking females are more attractive than low ranking females.

The results of the present study also suggest that females are most attractive to other females when they are lactating, and mothers of young infants (six weeks old or less) are more attractive to others than mothers of older infants.

However, at Mkuzi, the above defined measures of attractiveness were not related to the female dominance rank. Some attractiveness was found between dyads of female associates, but Seyfarth's (1976) model of associations among adjacent ranking females as a result of the competition over access to higher ranking females, is not supported in the present study.

While the advantage to lactating females, in their attractiveness to others and grooming they receive is not rank related, the cost of their harassment and kidnapping of their infants, is higher to lower ranking females.

4.6.5. Characteristics of female associations

Most studies of baboons and macaques show that females tend to associate with their kin who also occupy adjacent rank positions to theirs (e.g., Hausfater et al., 1982; Melnick & Pearl, 1987; Dunbar, 1988). Some studies have stressed the role of attractiveness among females with a similar rank (e.g., Seyfarth, 1976; de-Waal, 1991b). Females at Mkuzi did not choose to associate with adjacent ranking females, and although the relatedness among females is

unknown, the data suggest that kinship was probably not the only or major factor in choice of female associates (Figures 1 & 2). Females also did not necessarily associate with other females who shared their mutual male associate or with the females of the same age group.

Female associations at Mkuzi were very stable over time, in all reproductive states. Moreover, while maintaining associates was not the major factor in females' choice of a new troop following fission, all pairs of associates that remained together in the same troop, remained associates throughout the study. New associations were formed by females who lost all of their former female associates following fission or later changes in troop composition (Figure 2). These data indicate the importance of having close associates and maintaining those associations that were already established, to all females.

Female associates at Mkuzi (but not adjacent ranking females) groomed each other more than others; solicited more grooming from each other; and grooming between them was more persistent and more reciprocal, than between other dyads of females.

4.7. CONCLUSIONS:

WHAT ARE FRIENDS FOR?

The importance of support coalitions has been stressed, in many studies of female baboons and macaques, as a major factor in their social associations. This coalitionary support among female associates may be crucial for acquiring and maintaining their rank positions (e.g., Cheney, 1977; Dunbar, 1980; Hausfater et al., 1982; Wasser & Starling, 1982; Strum, 1987; de-Waal, 1989; Prud'Homme & Chapais, 1993). Female associates at Mkuzi usually did not support each other in coalitions against others (Ron et al., in press). This may be related to the fact that

females at Mkuzi probably do not associate exclusively with their kin, do not associate with adjacent ranking females, and did not necessarily choose to remain with their associates following fission.

If the risk of predation is indeed the major source of competition among females at Mkuzi, as indicated by Ron et al. (submitted ms.), the importance of having female associates lies in the importance of staying close to other adult troop members, to minimize predation risk. For this end, high ranking females may displace others over a central position next to other adult troop members, but the safest strategy, with minimum cost to all females is to stay close to certain, well established, associates.

In conditions of high risk of predation, it is also crucial to each individual to be well acquainted with all of the other troop members, and have reliable information flow between them. Females also tend to stay close to the troop center, i.e., to as many as possible other troop members. This could explain the network of relationships that was formed where each female is eventually connected to all others (Figures 1 & 2).

Moreover, there is an advantage to individual females to maintain close associates, who groom and reciprocate each other more than others. While it is advantageous, under these conditions, to each female to have stable associations with reliable female 'friends', kinship and rank distance among such friends is not necessarily relevant. Both the mutual protection from predation inherent in being near other troop members, and 'grooming services' that female associates give each other, are unrelated to their relative dominance rank and do not require kinship between them.

TABLE 4.1. Original female dominance hierarchy prior to troop fission, as recorded in March 1990; new troop affiliation (D=Darth's Troop, F=Flash's Troop) and new rank position of each female after fission, as recorded in May 1990; demographic changes recorded by August 1991; new troop affiliation , new rank position and changes in dominance rank, of each female, by August 1991.

Female	March 1990	May 1990	August 1991				
	Original rank	New troop	New rank	Demographic changes	New Troop	New Rank	Changes in rank
Peri	1	D	1	—	D	1	—
Bonni	2	F	1	—	F	1	—
Doris	3	D	2	—	D	2	—
Suzy	4	F	2	Moved to D	D	4	Lost 2 p.
Joan	5	D	3	—	D	3	—
Jes	6	D	4	—	D	5	Lost 1 p.
Katy	7	F	3	Moved to D	D	7	Lost 4 p.
Mel	8	D	5	—	D	6	Lost 1 p.
Alice	9	F	4	—	F	2	Gained 2 p.
Mod*	10	D	6	—	D	8	Lost 2 p.
Flaggy	11	F	5	—	F	3	Gained 2 p.
Doda	12	D	7	Died	—	—	—
Tiki	13	F	6	—	F	6	—
Esti	14	D	8	Died	—	—	—
Lucy	15	F	7	—	F	7	—
Tombi**	16	F	8	—	F	8	—

Extra	17	D	9	Moved to F Died later	F	9	—
Gili	18	F	9	—	F	4	Gained 5 p.
Honey	19	F	10	Died later	F	10	—
Tina**	20	D	10	—	D	9	Gained 1 p.
Grazia**	21	F	11	—	F	5	Gained 6 p.
Crabs*	22	F	12	Moved to D	D	10	Gained 2 p.
Pitzi*	23	D	11	—	D	11	—

*Subadult females; **Subadult females that became adult by August 1991; died: Doda and Esti have disappeared by August 1991; died later: Extra disappeared on September 1991 and Honey on October 1991; p.=rank positions

TABLE 4.2. The social context of agonistic behaviour among adult females at Mkuzi: average frequency (events/hour per female) and proportion of total, of agonistic encounters over a spatial position next to an adult male, adult non-lactating female, and lactating female or infant, and in other contexts, before and after troop fission. Proportion of approach-retreat interactions and interactions involving active aggression, in each context, are given, prior to troop fission.

Context	Before fission			After fission		
	Frequency (events /hour)	% of total events	% of interactions approach/ retreat active aggression	Frequency (events /hour)	% of total events	
Over male	0.19	16.8	66.6	33.4	0.61	27.6
Over female	0.41	36.3	80.4	19.6	0.85	38.5
Over lactating female/ infant	0.38	33.6	85.5	14.5	0.42	19.0
Other social context	0.03	2.6	86.1	13.9	0.10	4.5
Other context	0.12	10.7	86.0	14.0	0.23	10.4

FIGURE 4.1. The network of associations among females at Mkuzi, prior to troop fission. The rank and abbreviated names of all females are given. A solid line indicates an association between two females that spent at least 15% of their socializing time with females together. Solid dots indicate the pairwise associations that were disconnected following troop fission.

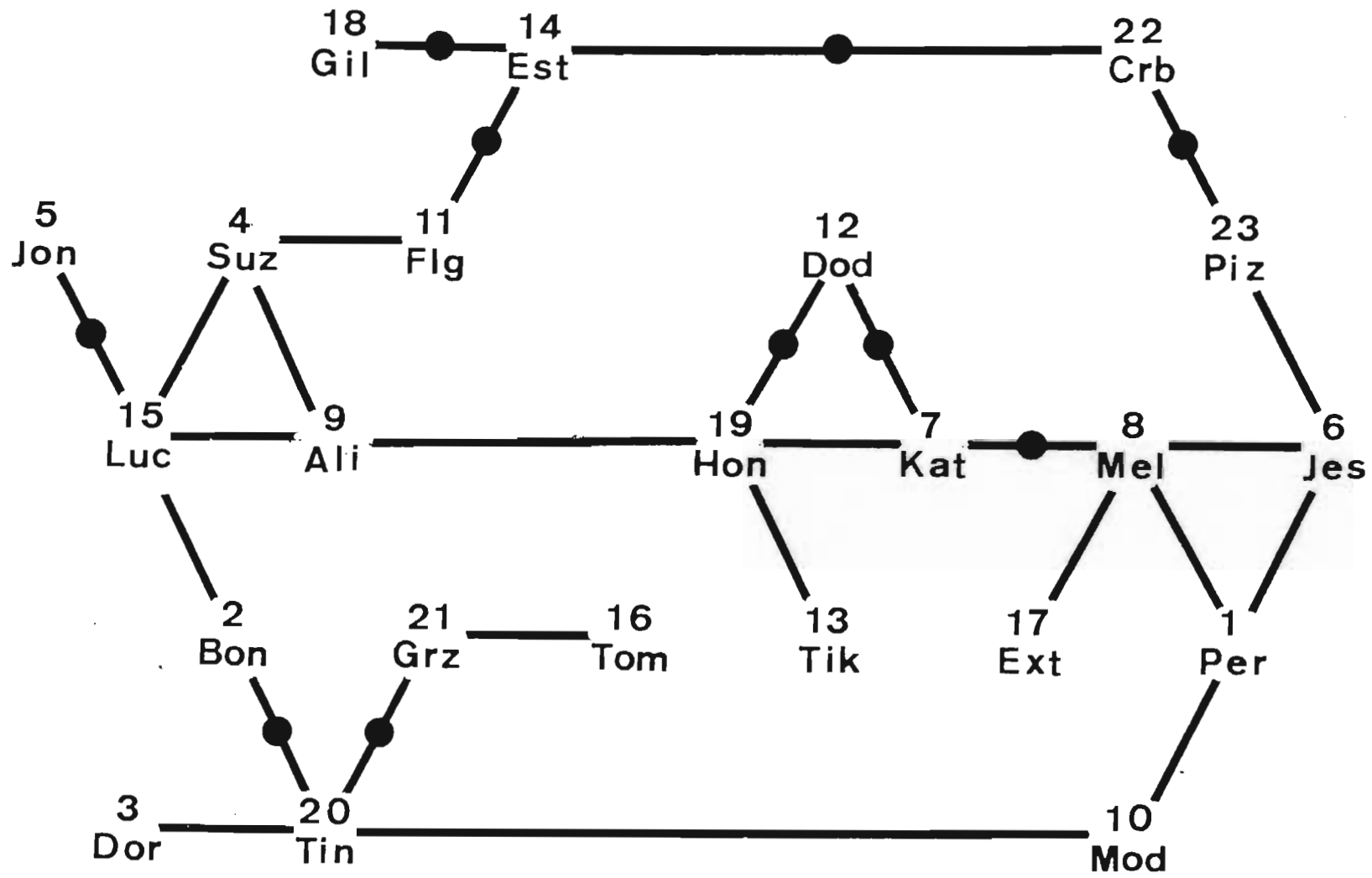
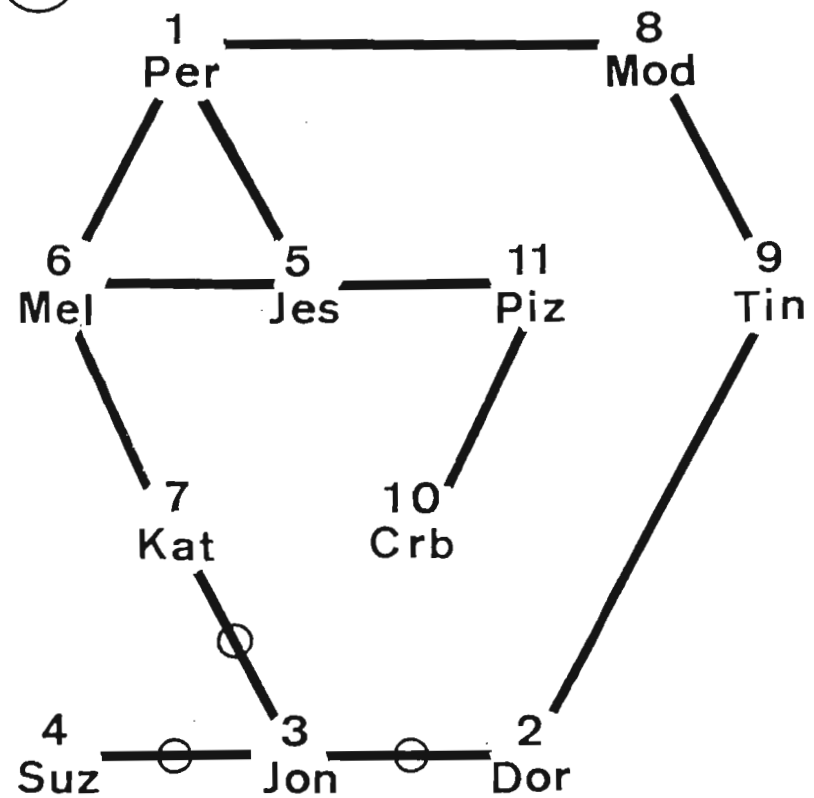
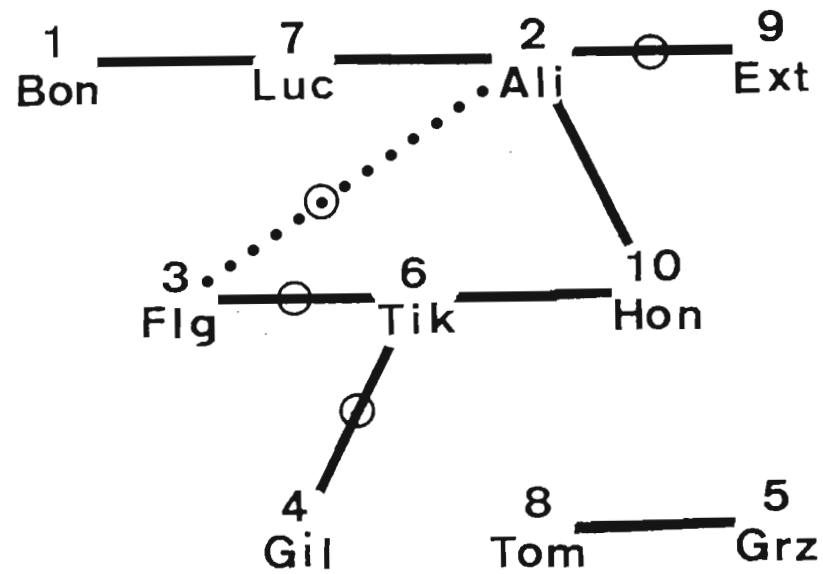


FIGURE 4.2. The network of associations among females at Mkuzi, following troop fission and later demographic changes recorded by August 1991: a. in Darth's Troop; b. in Flash's Troop. The rank and abbreviated names of all females are given. A solid line indicates an association between two females that spent at least 25% of their socializing time with females together. Empty dots indicate newly formed associations following troop fission and the later changes. The dotted line indicates a new association that was formed following the disappearance of Ext and Hon, and recorded on October-November 1991.

a



b



CHAPTER 5:
AN AMBITIOUS BABOON: INDEPENDENT PROMOTION IN
RANK OF A SINGLE FEMALE BABOON

*This manuscript was submitted to Folia Primatologica.

A case study of an independent self promotion in rank of a single female in a free-ranging troop of chacma baboons (Papio cynocephalus ursinus), in Zululand, South-Africa, is presented here. After the disappearance of the only female subordinate to her and her only female associate, Olive, this female, Joan, remained the lowest ranking adult female in her troop (rank 16 of 16 adult females and 4 subadult females). In about 4.5 months she independently rose to rank 5 (of 17 adult and 6 subadult females) without receiving any coalitional support from other troop members.

The dominance rank of a female baboon or macaque may affect her survival and lifetime reproductive success through competition for limited resources, active reproductive suppression or vulnerability to predation (e.g., Dunbar, 1980; Wasser & Starling, 1986; van-Noordwijk & van-Schaik, 1987; Dunbar, 1988; Barton & Whiten, in press). Female baboons and macaques tend to form linear and stable dominance hierarchies where females maintain their dominance rank by support coalitions within and between matrilineal groups against lower-ranking ones (e.g., Dunbar, 1980; Hausfater et al., 1982; Strum, 1987; Chapais et al., 1991). These stable social positions may be also maintained by the effect of maternal rank on female personality (Welker et al., 1992).

However, some cases of change in females' dominance rank were described for baboons and macaques. A promotion in a female's dominance rank may be achieved usually only through coalitional support from female or male associates

(e.g., Gouzoules, 1980; Walters, 1980; Samuels et al., 1987; de-Waal, 1989). Rank reversals may be the result of deterioration in a female's physical condition due to old age or disease (Gouzoules, 1980; Silk et al., 1981; Strum, 1987). Rank changes occur also during formation of new troops in captivity (Silk et al., 1981) or following troop fission (Koyama, 1970; Ron et al., in press). Small (1990) has described an independent rise in rank by a female Barbary macaque (Macaca sylvanus), without coalitionary support. This female macaque initiated her rise in rank by soliciting friendships with high-ranking females and then by directing aggression toward others.

The present study was conducted on a troop of about 76 chacma baboons at Mkuzi Game Reserve, Zululand, South-Africa. Data were collected for over 1200 hours during a total of 18 months, between January 1989 and November 1991, using scan sampling, focal sampling and recording of ad libitum data. All adults were individually identified, but relatedness among females is unknown. Dominance rank was established through win-loss matrices of all recorded agonistic encounters. By May 1990 the troop split into two new daughter troops of about 43 and 33 members.

The dominance hierarchy of females at Mkuzi was usually linear and stable. Excluding Joan, there were only three (0.68%) reversals out of 443 recorded outcomes of agonistic encounters, prior to troop fission. These three reversals were between adjacent ranking females. Females at Mkuzi, however, had a relatively high level of aggression, and a female was involved in 1.13 ± 0.12 (mean \pm SE) agonistic events/hour, of which 19.4% included a chase or physical contact. Yet, except for Joan's interferences, only three female coalitions and four male-female support events were recorded (Ron et al., in press).

Females were defined as associates if they spent over 15% of their socializing time, with females, together,

i.e., grooming or sitting together, in touch. Twenty seven such pairwise associations were recorded for all the 23 adult and subadult females, prior to troop fission, and each female had 1-4 such associates. Since June 1987 (S. Whitehead, pers. comm.) and until September 1989, Joan and Olive were the lowest ranking adult females in the troop, and the only female associates of each other. When last seen in mid-September 1989, Olive was the lowest-ranking adult female and occupied rank 17, while Joan occupied rank 16, of 17 adult females. Only the four subadult females were lower ranking than them. Both females were middle-aged. Olive was cycling when last seen and Joan was in early pregnancy at this time.

After Olive's disappearance Joan started to spend much of her time on trees. Between September 1989 and January 1990 she spent about 37% of her time on trees, 27% before that and 25% after January 1990 and until troop fission. The average time females spent on trees was about 25%. While sitting on trees (but also during other activities, on ground) she scanned the whole troop, and whenever she noticed an agonistic encounter between two other females she rushed over to watch and as the encounter terminated she always chased or threatened the loser (the lower ranking of the two opponents). She was never reciprocated with support coalitions by any female. Of 172 female-to-female agonistic events recorded between September 1989 and January 1990, Joan interfered this way in 42 (24.4%). She interfered in 12 of 31 (38.7%) female-to-female agonistic encounters that included a chase, physical contact and/or screams, and in 30 of 141 (21.3%) encounters that included only a spatial displacement or submissive and aggressive gestures. She then started to displace independently the same females she interfered against, and who were previously higher ranking than herself. The first record of Joan's interference in an agonistic encounter was against

the female ranking just above her, on 19.9.1989.

By 1.10.1989 she occupied rank position 11 and independently displaced all lower-ranking females, and by 1.11.1989 she occupied rank position 8. At 21.1.1990 her infant was born. At that time she occupied rank position 5 of 17 adult and 6 subadult females. She kept that rank until troop fission. After fission and until the end of this study she occupied rank 3 of 11 adult and sub-adult females in her new troop (Ron et al., in press).

As J. Altmann (pers. comm.) has commented Joan's interferences in fights could be defined as coalitionary support. It should be noted, however, that Joan joined fights after they were terminated and always intervened against the looser of the two opponents, she was never reciprocated, and almost no other coalitions were recorded in this troop (Ron et al., in press). A similar pattern of supporting the winners of agonistic encounters by individuals rising in rank were recorded in other primate studies (e.g., de-Waal, 1978).

I believe that Joan's rise in rank may be interpreted as indicating an exceptional intelligence and courage of an individual baboon, but also that this female was "motivated" by special circumstances.

A female's dominance rank at Mkuzi was not related to her reproductive success, and no evidence for food competition was recorded in this troop (Ron et al., submitted ms.). Female mortality, however, was related to dominance rank. The five females (including Olive) who disappeared during the study had significantly lower rank than others. Three of these females were lactating when last seen. Circumstantial evidence suggest that they were preyed on by leopards. It seems that the lower ranking females were forced to the troop periphery and were, therefore, more susceptible to leopard predation (Ron et al., submitted ms.).

After Olive's disappearance Joan has remained as the lowest ranking adult female in the troop, with no female associates, and in about 4-5 months she was going to give birth. She was, therefore, in a high risk of predation. By promoting her rank before giving birth, she probably reduced her risk of predation. It should also be noted that Joan's rise in rank could have been triggered by the death of her female associate. This indicates that although female baboons usually maintain their rank through the support of social associates, such associations may also act as a brake on the ambitions of females who may do better on their own, or that coalitionary support is an adequate alternative to high rank (R. Dunbar, pers. comm.).

Cheney et al. (1986) have suggested that at least some of the aspects of primate intelligence have evolved in a social context. Although the present description of Joan's independent rise in rank is only an anecdotal account of behaviour it may contribute to the accumulating evidence of the high levels of social manipulation and social cognition in non-human primates (e.g., Byrne & Whiten, 1985; Strum, 1987; de-Waal, 1989; Kummer et al., 1990; Small, 1990; de-Waal, 1991b). It may also be an example of individual differences in the ability to use social manipulation for one's own interest. These differences may be the result of some combination of specific circumstances and individual personality and intelligence.

CHAPTER 6:

CHOICE OF NEW GROUP BY FEMALES FOLLOWING FISSION IN A FREE-RANGING TROOP OF BABOONS (Papio cynocephalus ursinus)

*A shorter version of this manuscript was accepted for publication in Animal Behaviour (Appendix II).

6.1. ABSTRACT

Available data on fission of macaque and baboon groups indicate that lower-ranking females tend to withdraw together from the original group. This way close relatives, who occupy adjacent ranks and who are closely socially associated and form support coalitions with each other, stay together after fission. In our study troop of chacma baboons (Papio cynocephalus ursinus) in Zululand, South Africa, females did not rely on support coalitions to establish and maintain their dominance rank, and females who occupied adjacent ranks usually did not associate socially with each other. When the troop underwent fission, most females joined the new daughter group that had not been joined by their immediate superior in rank. By adopting this strategy of AYS (Abandon-Your-Superior), each female improved her own rank. Adoption of the AYS strategy by most females suggests that improvement of relative rank may be the main consideration in choosing a new group by the females of this troop, rather than maintaining social associations.

6.2. INTRODUCTION

A female's rank may affect her survival and lifetime reproductive success through access to limited food and water resources, active reproductive suppression or

vulnerability to predation (Altmann 1983; Dunbar 1984; Wasser & Starling 1986; Altmann et al. 1988; Dunbar 1988; Barton & Whiten 1992). Female baboons and macaques tend to form linear and stable dominance hierarchies, where female close associates, who are also relatives, occupy adjacent ranks (Seyfarth 1976; Cheney 1977; Hausfater et al. 1982; Dunbar 1988; de Waal 1989). These dominance hierarchies are stabilized through support coalitions within and between dominant matrilineal groups against lower ranking ones (Gouzoules 1980; Samuels et al. 1987; Dunbar 1988; Chapais et al. 1991; de Waal 1991).

Troop fission in these taxa usually occurs when lower ranking females withdraw from the original group, and is therefore "horizontal" in terms of female rank (Chepko-Sade & Sade 1979, for Macaca mulatta; Prud'Homme 1991 for Macaca sylvanus; A. Whiten, pers. com. for Papio anubis). This effectively means that groups cleave along the lines of least genetic resistance (Dunbar 1988) where close relatives, who both occupy adjacent ranks and who are closely socially associated, stay together after fission. The significance of this is assumed to be that strong social bonds enable the formation of coherent relationships in the new group and underpin the alliances necessary for successful social functioning (Dunbar 1984, 1988; de Waal 1989, 1991). There are some data to suggest that females may join the same troop as their male allies (Dunbar 1984; Prud'Homme 1991; Hamilton & Bulger 1992).

Here we describe the fission of a troop of chacma baboons in Zululand, South Africa. The females in both the original and daughter troops formed relatively stable and linear hierarchies. These females, however, did not associate with those who occupied adjacent ranks and did not rely on coalitions for establishing and maintaining their rank. Choice of a new troop by the females, during the troop fission, was in accordance to a suggested

evolutionary stable strategy which we have termed AYS (Abandon Your immediate Superior in rank). This splitting strategy indicates that promotion of individual rank, rather than joining associates, was the major consideration in these females' choice of a new group.

6.3. METHODS

This study was conducted on a troop of chacma baboons for a total of 18 months between January 1989 and November 1990 at Mkuzi Game Reserve, Zululand, South Africa. The Mtshopi troop consisted of about 76 individuals (Nadult males=8; Nadult females=17; Nsubadult females=6, as at March 1990). The troop grew from about 44 individuals in June 1986 (Henzi et al., in prep.). The habitat at Mkuzi is a mixed Acacia/ Combretum woodland with abundant food resources. Detailed data on the habitat will be provided elsewhere (Henzi et al, in prep).

All adults were individually identified by natural markings (Ron & Whitehead, submitted ms.) but due to poor visibility conditions most of the juveniles were not identified and it was impossible to census them accurately. Data on the females of this troop were available from June 1987 (Whitehead, in prep.). Relatedness among females is unknown. Females were defined as subadults from their first visible perineal swelling and as adults from first parturition.

Data were collected using scan sampling, focal sampling and ad libitum data (Altmann 1974) for over 800 hours in the 14 months prior to fission and for over 400 additional hours after the fission. Dominance rank was established through win-loss matrices of the outcomes of all recorded agonistic encounters, including threats and submissive gestures, spatial displacements and events of escalated aggression involving a chase or physical contact.

Between March and May 1990 Mtshopi troop entered a phase of social instability that followed a longer phase of increasing tendency of subtrooping, since October 1988 (S. Whitehead, pers. comm.) and concluded with its division into two new daughter troops: DARTH's Troop (N=about 43; Nadult males=4; Nadult females=8; Nsubadult females=3) and Flash's Troop (N=about 33; Nadult males=4; Nadult females=9; Nsubadult females=3).

6.4. RESULTS

Most of the females of Mtshopi troop at Mkuzi did not join the same troop as their immediate superior in rank (Table 1). Indeed, of the 22 females (excluding Peri, who was the top ranking female in the original group), 18 abandoned their superior, and only four joined the same new troop as their superior.

This suggests that most of the females did not adopt the common horizontal splitting strategy, but a different strategy, which we termed AYS (Abandon-Your-immediate Superior in rank). This simple splitting strategy, that has some desirable stability properties, instructs its holders to depart from their immediate superior in the hierarchy, and to join that new group that has not been joined by the superior.

If this strategy is adopted by all, then each individual, except of course, the top ranking one in the original troop, enjoys a rank promotion. Moreover, no "mutant" (i.e., a single individual with a different strategy) can do better, that is, improve her hierarchical position beyond what is achieved by adopting AYS.

As an illustrative example, consider an original troop of six females (denoted by 1,2,3,4,5 and 6). Under the AYS strategy, the split results in forming the new groups {1,3,5} and {2,4,6}.

If all adopt the AYS strategy, the best a female can do is to join and adopt AYS. If, for example, female 4 had followed 3, the split would have resulted in {1,3,4,6} and {2,5}, and 4 would have ended up being the third in her new group's hierarchy (instead of being the second had she adopted AYS). As another example, suppose 3 had not abandoned her immediate superior, and joined the same group as 2. The split would have resulted in {1,4,6} and {2,3,5}, and 3 had not improved her position.

A horizontal split results in {1,2,3} and {4,5,6}. Indeed, such a split is more advantageous to certain females (e.g., 5 and 6), but is unstable: there is an advantage to 2 and 3 to move to the other group, and as a consequence, to 4 and 5 not to remain in that group, and so on.

The AYS strategy displays a feature very similar to evolutionary stability (Maynard Smith & Price 1973). However, AYS is not exactly an evolutionary stable strategy (ESS). Indeed, while no mutant strategy can do better, there are mutant strategies that can do just as well (in any mixture). These are the strategies that instruct their holders to definitely depart from their immediate superior if their rank in the original group was an even number (i.e., if they were in rank position 2,4, etc.) whereas, if their rank was an odd number (position 3,5, etc.), they are free to join either group. (In other words, AYS does not fulfill the second requirement in the ESS definition.) Thus, AYS is only collectively stable (Axelrod 1984), that is, a strategy which is in Nash equilibrium with itself.

Nevertheless, AYS features both simplicity and robustness, since it prescribes a fixed, unique pattern of behaviour, which is not sensitive to occasional mistakes in distinguishing between even and odd hierarchical positions (which even a clever baboon is liable to do). Therefore, AYS is likely to be fixed in the population.

As a result of adopting AYS strategy, a splitting group disintegrates into two new groups containing the same number of females, if the number of females in the original group was even or almost the same, if the original number was odd. This was true for the Mtshopi troop which divided into two daughter troops with almost equal number of females (12 and 11).

It is interesting to note that the AYS strategy is somewhat analogous to Fretwell & Lucas' (1970) concept of an ideal free distribution, with hierarchical ranking as the spatially distributed "resource".

If rank improvement was the only or most important factor affecting females' choice of a new troop, (assuming that they were forced to split, for any reason) then this fission pattern, as observed here, is essentially the one that would be expected.

We have statistically tested if the actual fission pattern of Mtshopi troop females fits the model of AYS splitting strategy. Under the assumption of random splitting, for example, the number of "abandonments" should follow a binomial distribution, with parameters $n=22$ and $p=1/2$, and the probability of obtaining at least 18 such "abandonments" (given that a split actually occurred) is only 2.17×10^{-3} . In the "common" (and horizontal in terms of female rank) fission pattern, by definition, all of the females, except for the top ranking ones in each of the new groups, do join their immediate superior in rank.

Only two of the four females who did join their immediate superior, Jes and Crabs, could improve their new rank by choosing the other troop. Tombi's choice of the same troop as her superior improved her own rank by "correcting" the deviation created by Jes. Honey who occupied an odd rank position did just as well by joining Flash's troop as she would have by abandoning her superior. Jes was a very old female and had all of her female and

male associates in Darth's troop, which she chose to join in spite of the consequent loss of one rank position. Crabs' choice of Flash's troop was only temporal and she later on moved to Darth's troop, where she improved her rank and joined her associates. At the time of the troop fission Crabs was a subadult female, still struggling to acquire her social position among the adults.

It is interesting to note that four females who joined Darth's troop, following Jes (Mel, Mod, Doda and Esti) actually lost one rank position by joining a new troop in accordance with the AYS strategy, in comparison with the rank they could acquire by joining the other troop, due to the deviation which was caused by Jes joining her superior, and corrected by Tombi who joined her superior at Flash's troop.

Most of the females at Mkuzi associated with each other up to 10% of their social time, but each female had only from one to four close associates with whom she spent more than 15% of her social time with females. Only three of all 27 such pairwise associations, prior to fission, involved females who occupied adjacent ranks.

Only nine of the 23 females remained with all of their former female associates after fission, while five females lost all of their close associates. The 27 pairwise associations in the original group at Mkuzi were distributed in such a way, that any splitting of the original group into two distinct new groups would have resulted in breaking some of these associations. If we imagine the various females as nodes of a graph, with arcs connecting any two associated females, then, using the terminology of graph theory, the original group represents a connected graph. The actual split of the group disconnected 10 of the pairwise associations (or "arcs"), and retained 17 associations. However, under the assumption of random splitting, the probability of retaining at least

17 associations is estimated to be 0.1216. (This estimate was obtained by randomly drawing 10000 splits, out of the total of $2^{22}-1=4194303$ possible splits, and calculating the proportion of splits that retained at least 17 "arcs"). The apparently large number of associations that were retained in our data is, therefore, not significantly larger than what one should expect under the assumption of random splitting. It should also be noted that if we consider only splits into groups of 11 and 12 females, there are possible splits of the original troop that would have retained 24 pairwise associations.

Of the five females without female associates in the new troop, four found themselves with a male associate. Eighteen of the females went to a troop where they had at least one male associate. If joining male associates was the major factor affecting the females' choice of a new group, then all 23 females could choose to join a troop with at least one male associate. Only a single female however, Doda, ended up in a troop where she had no close allies of any sort.

Females at Mkuzi did not necessarily choose to associate with adjacent ranking females (Ron, submitted ms.). The value of social relationships for baboon females is held to lie in the coalitions that they enable. Compared with other studies on female baboons (Dunbar 1984; Wasser & Starling 1986), we have recorded extremely high rates of female aggression: 1.1 agonistic events/hour with other females (72 events in a sample of 65.5 female hours), of which 19.4% involved a chase or physical contact, in the 14 months prior to fission. Yet, only three female coalitions were observed in the 800 hours prior to fission, and none in the 400 hours after fission. We also recorded only four agonistic encounters, all four prior to fission, during which males came to the support of the females. Consequently the role of support coalitions at Mkuzi seems

negligible in comparison to that recorded elsewhere, in affecting a female's rank (Seyfarth 1976; Wasser & Starling 1986; Samuels et al. 1987; de Waal 1989).

6.5. DISCUSSION

The stability of the AYS (Abandon Your immediate Superior in rank) splitting strategy is a consequence of the assumption that improvement in rank is what matters the most in a female's choice of a new troop. The high coincidence of the observed re-distribution of Mtshopi females with the AYS strategy therefore indicates the importance of a female's individual dominance rank promotion as a main factor in her choice of a new troop, rather than maintaining social associations, as is the case in a horizontal fission. This may be explained by the importance of intrinsic competitive ability, rather than coalitional support in the outcomes of agonistic encounters and in rank maintenance for Mtshopi troop females.

After fission females did not necessarily choose to stay in the same troop with their close associates, although the fission pattern still allowed female relationships, at least partially, to persist. In the commonly recorded situation, where females who occupy adjacent rank positions are close associates, and fission is horizontal, all (or most) pairs of female associates remain together after fission (Dunbar 1988; A. Whiten, pers. comm., for baboons; Chepko-Sade & Sade 1979; Prud'Homme 1991, for macaques).

In a growing population, with high birth rates and low infant mortality rates, as at Mkuzi (Ron & Henzi, in prep.), large families are formed, and two females with a large difference in rank can still be relatives (e.g., Samuels et al. 1987). However, if rank difference and social association are randomly correlated, as suggested by our data, it implies that females do not necessarily choose

to associate with close relatives, or that close relatives do not always occupy adjacent ranks.

This conclusion may be explained by the lack of support coalitions at Mkuzi. In those baboon troops where females support close kin and help them to acquire adjacent rank to theirs, it is assumed to be due to kin selection or considerations of future reciprocation (e.g., Cheney 1977; Hausfater et al. 1982; Dunbar 1988). If female friendships, however, are not translated into spending energy, time and risk in supporting each other in agonistic events, as at Mkuzi, then there is no reason for friends to be necessarily kin. This, in turn, may lead to an individual rank improvement, rather than maintaining associations, as a major consideration in females' choice of a new troop. Another implication of this may be that where alliances are operational, such coalitions can act as a brake on the ambitions of even those females who depend on them for maintaining high rank.

If a female's rank is determined only by her intrinsic competitive ability however, then the daughter troops that are formed by an AYS splitting strategy would not only contain a similar number of females but would also have within them a wider range of competitive abilities than troops that are formed by horizontal splitting. This, in turn, should result in the two troops being more closely matched competitively and lead to a more even redistribution of the resources within the original home range than might have occurred otherwise. If the new troops were more unequal in size and competitive abilities, this would facilitate the displacement of one group by the other from previously common resources (Wrangham 1980).

Data from another observed fission in chacma baboons have also been used to argue that females did not split according to rank or lineage but, rather, reflected individual strategic decisions by choosing to follow a

specific male associate who is a probable father of their infants and may improve the infants' chances of survival (Hamilton & Bulger 1992). In different environmental and social conditions, different factors may affect a female's choice of a new troop during troop fission. A main consideration in the female's choice may be joining female kin and allies, as is the case in horizontal fission (e.g., Dunbar 1988; Prud'Homme 1991), joining male associates, who are also potential fathers of their infants as indicated by Hamilton & Bulger (1992); or individual rank promotion, as suggested at Mkuzi.

Together these data suggest that savannah baboon populations may show a wide range of behavioural flexibility and vary significantly from one another, in ways that are not simply ascribable to specific differences.

Decisions made by individuals in any baboon troop may be affected by the different selective pressures they are subjected to. There is some evidence that leopard predation is the major selective pressure at Mkuzi, with higher predation risk to low-ranking females (Ron & Henzi, in prep.). In other baboon studies competition for food is considered to be the main factor affecting a female's lifetime reproductive success and the main cost for lower ranking females (e.g. Wrangham 1980; Altmann et al. 1988; Barton & Whiten 1992). Predation affects a female's own survival, rather than only the number of surviving offspring during her lifetime, and that could result in the choice of more individualistic strategies by Mkuzi's females, that enable them to improve their own rank, and thereby be less susceptible to risk of predation. This individualistic approach is reflected in that Mkuzi's females do not form support coalitions as well as by their choice of a splitting strategy that improves a female's own rank, rather than joining associates.

TABLE 6.1. The splitting pattern of the Mtshopi Troop females. The original rank order of female in March 1990 is given; new troop affiliation (F=Flash's troop; D=Darth's troop) and new rank of each female, after fission, in May 1990; female associates with whom each female spent over 15% of her socializing time with females, prior to fission, and their new troop affiliation; and male associates with whom she spent over 25% of her socializing time with males, prior to fission, and their new troop affiliation.

Female	Original rank	New troop	New rank	Female associates	New troop	Male associates	New troop
Peri	1	D	1	Mel Jes Mod	D D D	Flash	F
Bonni	2	F	1	Lucy Tina	F D	John	F
Doris	3	D	2	Tina	D	Darth Flash	D F
Suzy	4	F	2	Alice Flaggy Lucy	F F F	Flash	F
Joan	5	D	3	Lucy	F	Ringo Flash	D F
Jes	6	D	4	Mel Peri Pitzi	D D	Ter	D
Katy	7	F	3	Mel Honey Doda	D F D	Ter Darth	D D
Mel	8	D	5	Peri Jes Kat Extra	D D F D	Ter Darth	D D
Alice	9	F	4	Honey Suzy Lucy	F F F	Flash	F

Mod*	10	D	6	Peri Tina	D D	SAM Darth	D D
Flaggy	11	F	5	Suzy Esti	F D	Flash John	F F
Doda	12	D	7	Katy Honey	F F	Flash	F
Tiki	13	F	6	Honey	F	Flash Ringo	F D
Esti	14	D	8	Flaggy Crabs Gili	F F F	Darth John	D F
Lucy	15	F	7	Bonni Alice Suzy Joan	F F F D	John	F
Tombi*	16	F	8	Grazia	F	Darth	D
Extra	17	D	9	Mel	D	Goose	F
Gili	18	F	9	Esti	D	John	F
Honey	19	F	10	Alice Katy Doda Tiki	F F D F	Flash	F
Tina*	20	D	10	Doris Bonni Grazia Mod	D F F D	SAM Darth	D D
Grazia*	21	F	11	Tombi Tina	F D	SAM SAM Ringo	D F D
Crabs*	22	F	12	Esti Pitzi	D D	Darth SAM SAM	D F D
Pitzi*	23	D	11	Jes Crabs	D F	SAM Arc	D D

* subadult females
SAM- subadult males

CHAPTER 7:
WHO IS RESPONSIBLE FOR FISSION IN
A FREE-RANGING TROOP OF BABOONS?

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7.1. SUMMARY

Troop fission is generally attributed to the withdrawal of low-ranking females from the main group, as a result of the cost of food competition and its effect on their reproductive success. In the present study of a troop of chacma baboons (Papio cynocephalus ursinus) at Mkuzi Game Reserve, Zululand, South-Africa, it is suggested that fission may have been initiated by the resident males, and triggered by the high cost of sexual competition, as a result of the scarcity of cycling females in the group. The study troop comprised of about 76 members in March 1990, and split by May 1990 into two new daughter troops, with about 43 and 33 baboons.

No evidence for food competition among females at Mkuzi was found in terms of rank-related time spent feeding or other time-budget components, feeding bout length, diet composition or context of female aggression. Moreover, no evidence for rank related differential reproductive success was found in terms of inter-birth intervals or infant survival. Female mortality, however, was related to dominance rank, with circumstantial evidence suggesting that cause of mortality was predation by leopards. Rate of female disappearances increased from 0.33 per year, prior to troop fission, to 2.67 after fission (Table 1). Aggression levels among females (Table 1) and time spent in proximity to other adult troop members increased after fission.

Relatively short inter-birth intervals and extremely low infant mortality rate at Mkuzi resulted in an operational sex ratio of only 0.175 oestrous females per male in the group, before fission, which increased after fission to 0.225 and 0.325 (Table 1). Reduced cost of male sexual competition after fission was evident in the reduced levels of male aggression and woundings (Table 1). Following fission each male increased his dominance rank (Table 2) by adopting the AYS (Abandon Your immediate Superior) splitting strategy.

The troop fission was preceded by a long process of increasing tendency for sub-trooping. It was initiated by the four resident males who kept large distances from each other, herded female associates during their oestrus away from others and were followed by other females, who generally tended to stay close to associates, males and females. These parties were followed by the peripheral and immigrant males who had no female associates. Females tended to move between the units thus formed but were herded by the males, and eventually two distinct daughter troops were formed.

7.2. INTRODUCTION

Troop fission, as a means of group size control, is generally thought to be triggered by female competition for food (e.g., S. Altmann 1974; Dittus 1988; Dunbar 1992). The initiation of fission is usually attributed to low-ranking females, who withdraw from the original group and are then joined by low-ranking or associate males (e.g., Dittus 1988; Dunbar 1988).

The withdrawal of low-ranking females from the original troop is generally thought to be caused by the cost of food competition to these females and its effect on their reproductive success. Competition for food may be evident

in direct displacements over food patches or in differential percentage of time spent feeding and other time budget components, feeding bout length or diet composition, while the effect of food competition on female reproductive success may be evident in differential inter-birth intervals or infant survival (e.g., Melnick and Pearl 1987; van-Noordwijk and van-schaik 1987; Strum 1987; Dunbar 1988; Dunbar 1992; Barton, in press).

In the present study of a troop of chacma baboons (Papio cynocephalus ursinus), at Mkuzi Game Reserve, Zululand, South-Africa, it is suggested that fission may have been initiated by the resident males, and triggered by the high cost of sexual competition to them, as a result of the scarcity of cycling females in the group. Cowlshaw and Dunbar (1991) have stressed the importance of the operational sex ratio, i.e. the number of oestrous females per male in the troop, to male sexual competition. Hamilton and Bulger (1993) have described a process of fission in chacma baboons, initiated by the withdrawal of one male, joined by his female associates, from the main group as a strategy of male sexual competition.

7.3. 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. Data on birth and survival were available from June 1987 (S. Whitehead, pers. comm.).

The troop grew from about 44 baboons in June 1986 (unpublished data) to about 76, including 8 adult males, 3 subadult males, 17 adult females, 6 subadult females and about 42 juveniles and infants in March 1990 (due to poor visibility it was impossible to census the juveniles accurately). Following a long phase of social instability,

since October 1988 (S. Whitehead, pers. comm.), the troop split into two new daughter troops by May 1990: DARTH's Troop with about 43 members, including 4 adult males, 2 subadult males, 8 adult females, 3 subadult females and 26 juveniles and infants, and FLASH's Troop with about 33 members, including 4 adult males, 1 subadult male, 9 adult females, 3 subadult females and about 16 juveniles and infants.

The habitat at Mkuzi is a mixed Acacia/ Combretum woodland, with abundant food resources all year round and very poor visibility conditions (unpublished data).

The baboons were followed on foot, from dawn to dusk, for over 800 hours prior to troop fission and over 400 hours after fission. Data were collected using focal samplings of females and scan sampling and ad libitum data records of all troop members, every 30 minutes (as in J. Altmann 1974). All adults were individually identified by natural markings but relatedness among females is unknown. Dominance rank was established through win-loss matrices of all recorded agonistic encounters, including threats and submissive gestures, spatial displacements, chase or physical contact.

7.4. RESULTS

7.4.1. Female competition for food

No evidence for contest food competition was found among the females at Mkuzi, prior to troop fission, in terms of rank-related time spent feeding (Spearman's coefficient of rank correlation: $r_s=0.1103$, $n=17$); time spent in socializing and grooming ($r_s=0.049$, $n=17$); a female's average feeding bout length ($r_s=-0.0417$, $n=17$); or proportion of feeding time devoted to various food items (e.g., time spent feeding seeds and fruits, $r_s=0.0343$,

$n=17$); and only 6.4% of female-to-female agonistic encounters occurred in a feeding context. Moreover, no evidence for rank related differential reproductive success was found among females, prior to troop fission, in terms of number of infants a female had during the study, from June 1987 ($r_s=0.0417$, $n=17$); average inter-birth intervals for those females who had at least two infants throughout the study ($r_s=0.1614$, $n=11$); or infant mortality (only one infant died and one other pregnancy terminated with abortion throughout the study). (Ron et al., submitted ms.)

7.4.2. Female mortality and female aggression

Female mortality was related to dominance rank, with circumstantial evidence suggesting that cause of mortality was predation by leopards. The five females who disappeared throughout the study had significantly lower rank than others (Wilcoxon's rank-sum two-sample test: $t=2.2646$; $p<0.01$). (Ron et al., submitted ms.).

Four females disappeared during 18 months after troop fission (2.67 per year), compared with only one in three years prior to fission (0.33 per year) (Table 1). Presumably as a result of increased competition for safe spatial positions, aggression levels among females rose significantly, from 1.13 ± 0.12 (mean \pm SE) agonistic events/hour for a female (based on focal samplings) prior to fission, to 2.28 ± 0.16 after fission (Table 1) (t -test for paired observations: $t=9.60$, $df=14$, $p<0.001$). The time these females spent in proximity to other adult troop members also increased after fission (Ron et al., submitted ms.).

7.4.3. Male sexual competition

Inter-birth intervals at Mkuzi were relatively short (18.53 ± 1.81 months; mean \pm SE), and rate of infant mortality was extremely low. The outcome of this was that only a small number (maximum 4, mean 1.4) of receptive females who could conceive were present in the troop at any one time. Excluding the subadult and four very old females, who had extremely long inter-birth intervals and, therefore, lower probability of conceiving, there were only about 0.7 receptive females at a time. The operational sex ratio, calculated as number of oestrous females per male in the group, at any one time (Cowlshaw and Dunbar 1991) increased from 0.175 before fission to 0.225 and 0.325, in the daughter troops, after fission (Table 1). While this increase was not necessarily caused by fission (but rather by the change in age structure of the females, i.e., the increase in number of subadult females), following troop fission the number of male competitors in a group decreased.

High levels of male sexual competition at Mkuzi resulted in high costs to the males, which have decreased after fission. This was indicated by the reduced levels of aggression among them, following the reduction in number of male competitors in each group. Male-to-male aggression rates, based on data available from scan samplings every 30 minutes, decreased after troop fission. Although agonistic encounters are usually short events and under-represented in the scan samplings (e.g. J. Altmann 1974), a general comparison of records before and after troop fission, can still be conducted. The males spent, on the whole, 2.36% of their time in aggressive activities (including all recorded agonistic events, in which males were involved) prior to fission, and only 1.54% after fission (The females, for comparison, spent 0.46% of their time in aggressive encounters prior to fission, and 0.92% after fission) (Table 1). Five of the males were severely

wounded in three years prior to fission (1.67 per year), and one young male was permanently crippled. No severe wounds were observed in males after the troop fission (Table 1).

7.4.4. The process of troop fission

The troop fission in May 1990 was preceded by a long process of increasing tendency for sub-trooping that started around October 1988 (S. Whitehead, pers. comm.). This process was initiated by four males resident in the troop (for two years or more), who had at least three close female associates each, and had priority in access to those females when oestrous. These resident males kept large distances from each other (an average of about 50 meters apart), and herded their female associates away from other males, when they were in oestrus. These consorting pairs were followed by other cycling, lactating and pregnant females, who generally tended to stay close to associates, males and females (on the average a female spent 37.0% of her time within a distance of up to five meters from at least two other adult troop members, prior to troop fission). These parties were followed by the two immigrant males (both joined the troop around October 1989) and the two peripheral males (one very old and one crippled). Small parties were thus formed and foraged separately, at first only during daytime, and later (since July 1989) they gradually started to split at night and use two separate sleeping sites.

Until May 1990 only seven of the 23 adult and subadult females followed only one specific male each, while most females moved between two or three different male associates and their units. After fission and until August 1991 four females still moved from one daughter troop to the other. In inter-troop encounters of the two daughter

troops, females trying to join the other troop were herded away and chased back by their troop's males (cf. Cheney and Seyfarth 1977).

7.4.5. Choice of a new troop by Mtshopi troop members

Choice of a new troop by females at Mkuzi was according to a strategy we termed AYS (Abandon Your immediate Superior in rank). By choosing the opposite troop to that joined by her immediate superior each female improved her own rank (Ron et al., in press.). The same splitting pattern was adopted by the males at Mkuzi (Table 2). The males' hierarchy was unstable and each male occupied a range of 2-3 ranks throughout the study. Adjacent ranking males joined the opposite troops to each other, and this pattern strengthens the suggestion that the males tried to avoid competition, by staying away from similar ranking males, considering that no male coalitions were recorded.

7.5. DISCUSSION

The increased risk of mortality and increased rates of aggression for females after fission (Table 1) indicate that troop fission may have had a high cost to the females at Mkuzi. There was also no evidence for female contest competition for food or for competition effects on female reproductive success. If predation, rather than competition for food, is the main selective pressure that the females at Mkuzi are subjected to, as suggested (Ron et al., submitted ms.), it is expected that troop fission would be disadvantageous to them (e.g., S. Altmann 1974; Anderson 1986). Females are thus unlikely to have initiated fission. This is corroborated by the observations which suggest that males were responsible for troop fission.

Males could benefit from troop fission, in terms of

increased reproductive success and reduced cost of sexual competition over receptive females (e.g., Prud'Homme 1991), by reducing the number of competing males in a troop. This is in line with Cowlshaw and Dunbar's (1991) finding that high ranking males' ability to control access to females for mating declines as the number of males increases, with what seems to be a catastrophic threshold of four males in the group. Following the increase in the operational sex ratio (number of oestrous females per male in the group) at Mkuzi after fission, the intensity of male sexual competition and levels of aggression declined (Table 1). Following fission each male also increased his dominance rank (Table 2) by adopting the AYS splitting strategy (Ron et al., in press).

Additional clear contribution to increasing male reproductive success following troop fission is in reducing the uncertainty of paternity of the infants in each troop, by reducing the number of other potential fathers (e.g., Hamilton and Bulger 1993). The probability of paternity of immature troop members, whom the males protect from external danger, is obviously an important factor in their reproductive success (e.g., Busse 1985; Cowlshaw and Dunbar 1991). Troop fragmentation, however, may increase the risk of predation to their offspring.

Young male baboons frequently transfer from one group to another in order to maximize access to reproductive females, but they are generally not followed by their natal troop females (e.g. Cheney and Seyfarth 1977).

A similar tendency for subtrooping in chacma baboons, to that described here, was recorded by Anderson (1981). Byrne et al. (1989) have described the formation of stable one-male units in a troop of chacma baboons. This kind of social organization resembles the one-male units of Hamadryas baboons (e.g., Kummer 1968). Another similarity to hamadryas baboons, the herding of females by the

dominant adult males in their troop, has also been described for chacma baboons elsewhere (Cheney and Seyfarth 1977). Cheney and Seyfarth have suggested that the herding of females enables the males to maintain access to females in oestrus and to promote intragroup cohesion by maintaining spatial separation between groups. They have also stated that males were most likely to herd females with whom they had the closest long-term social bonds.

Hamilton and Bulger (1993) have described a process of troop fission initiated with the formation of a separate unit by one male who withdrew from the main group, and was followed by his female associates, and thus increased his reproductive success. Prud'Homme (1991) has described the withdrawal of low-ranking matriline in a process of troop fission in Macaca sylvanus, but has suggested that these females joined their male associates who initiated the splitting as a strategy of sexual competition.

Thus, it may be that the formation of two troops at Mkuzi was the result of some balance between conflicting interests of the males, to form smaller units, and of the females, to stay in a large group. The males tend to stay apart from each other (mainly from similar ranking males) in order to reduce the cost of sexual competition, but at the same time try to stay close to receptive females. The females, on the other hand, in order to reduce predation risk, try to keep their proximity to other adult troop members, males and females. Males herded females in oestrus away from others and were joined by other females. These parties, comprised of resident males and their associating females were followed by peripheral and immigrant males who had no female associates. Females still tended to move between these parties, and the two distinct troops were eventually formed through the herding of each daughter troop's females away from the other troop, by the males in their troop.

TABLE 7.1. Comparison of parameters related to competition and reproductive success of males and females at Mkuzi: rate of female disappearances per year; average number of female-to-female agonistic events/hour per female; operational sex ratio (average number of oestrus females per male in the troop at any time); percentage of their total time the males spent in agonistic encounters; percentage of their total time females spent in agonistic encounters; and rate of male severe wounding per year.

<u>Parameter</u>	<u>Prior to troop fission</u>	<u>After troop fission</u>
Rate of female disappearances per year	0.33	2.67
Average agonistic events/hour per female	1.13	2.28
Operational sex ratio	0.175	0.225 & 0.325
Percentage of the total time the males spent in agonistic encounters	2.36	1.54
Percentage of the total time the females spent in agonistic encounters	0.46	0.92
Rate of male severe wounding per year	1.67	0

TABLE 7.2. The splitting pattern of the males at Mkuzi: the range of dominance rank positions (1-3 positions) each male at Mkuzi occupied, prior to troop fission; each male's new troop affiliation (F=Flash's troop; D=Darth's troop); and the range (1-2 positions) of the new rank positions each male occupied after fission.

Male	Original rank	New troop	New rank
John	1-3	F	1-2
Darth	1-3	D	1
Flash	1-3	F	1-2
Ter	4-6	D	2-3
Eric	4-6	F	3
Arc	4-6	D	2-3
Ringo	7-8	D	4
Goose	7-8	F	4

CHAPTER 8: GENERAL DISCUSSION

Primate populations are known to present a wide variety of behavioural adaptations to different habitats and ecological conditions (e.g., Lee, 1991). This study on the social behaviour of female chacma baboons, in a southern woodland habitat, compared with other baboon studies, presents an example of the social and behavioural flexibility of baboons, that enables them to adapt to a wide range of environmental conditions.

Dunbar (1988) has suggested that increase in group size of baboons and the formation of multimale groups, was a direct result of increased susceptibility to predators following the invasion of open habitats. The transition of baboons from arboreal to more terrestrial life, was the result of the reduction in forest cover, during the Pliocene. Larger groups were thus formed as related females remained together when matrilineal groups increased in size. This increased group size have resulted in higher costs to the troop members in terms of time, energy and social stress. The social costs can be offset by the formation of coalitions, which may be achieved by intensification of the relationships between closely related females, and troop membership is thus stabilized. The important role of predation in the evolution of primate social behaviour was also indicated elsewhere (e.g., Anderson, 1986; Boesch, 1991; Barton et al., 1992).

Wrangham (1980), on the other hand, has developed a model of formation of female-bonded primate troops as a result of competition between female groups over high quality food patches. Cooperation between females enables them to get control over limited food resources. The effect of competition for food on social structure of primate groups was stressed mainly in habitats with limited food

resources (e.g., Byrne et al., 1993).

Van-Schaik (1989) has suggested that social relationships among female primates reflect the relative importance of competition for food and safety.

Group living may have different costs and benefits to the various troop members, due to difference in age, gender, dominance rank or other specific conditions (e.g., Janson, 1990).

Competition for limited food resources is generally considered to be of major importance in female relationships within a group. Various aspects of competition for food, and its effect on lifetime reproductive success were widely stressed as the main cost for the lower ranking females in baboon troops (e.g., Altmann, 1983; Rasmussen, 1985; Melnick and Pearl, 1987; Altmann et al., 1988; Johnson, 1989; Barton and Whiten, in press).

At Mkuzi, however, no evidence of competition for food was found among females. This troop occupies a rich habitat with abundant food resources. Most of the female-to-female agonistic encounters were in a social context, and only a small proportion in a feeding context. Moreover, a larger proportion of the agonistic encounters over a position next to adult troop members, and especially next to an adult male, involved active aggression, than in any other context.

No significant correlation was found between a female's dominance rank and time spent feeding, feeding bout length or diet composition. There was also no evidence in this troop of rank related differences in reproductive success among females. Inter-birth intervals were relatively short, and not related to rank, and infant mortality rate was extremely low.

Female mortality, however, was rank related. The five females who disappeared during this study had significantly

lower rank than others. Three of these females were lactating when last seen and there is circumstantial evidence indicating that they were probably preyed on by leopards. It is suggested here that the females at Mkuzi were competing over a safe spatial position, next to other adult troop members, in order to avoid predation. Indeed, the percentage of time a female spent next to more than one other adult troop member, was significantly correlated with rank. Increased proximity and increased aggression levels among females, in hours of higher risk of predation and after troop fission, further support the suggestion that the females were competing over safe spatial positions, to avoid predation. Moreover, the proportion of encounters over a position next to other adult troop members increased after fission, in comparison to other contexts of agonistic behaviour.

Whatever the source of conflict between troop members is, a well established dominance hierarchy may serve to resolve the social conflict and avoid active aggression (Jones, 1981; Hand, 1986). The formation of large groups with stable membership of females, that remain in their natal troops, enable the formation of linear and relatively stable dominance hierarchies among female baboons (e.g., Seyfarth, 1976; Hausfater et al., 1982; Melnick and Pearl, 1987; Strum, 1987; Dunbar, 1988). Female baboons and macaques usually form matrilineal hierarchies where closely related females occupy adjacent rank positions. A female's dominance rank in these societies is usually maintained through support coalitions within and between adjacent ranking matrilineal lines (e.g., Hausfater, 1975; Gouzoules, 1980; Hausfater et al., 1982; Melnick and Pearl, 1987; Strum, 1987; Altmann et al., 1988; de-Waal, 1989; Chapais et al., 1991; Prud'Homme and Chapais, 1993).

Cases of rank stability over generations in animal groups have led to the concept of 'inheritance of

dominance' as expressed by Dewsbury (1990) and Moore (1990). Barrette (1993) has suggested, however, that only the tendency to achieve high rank may possibly be inherited. The maintenance of stable social hierarchies over time, through the effect of maternal rank on female personality was also indicated by Welker et al. (1992).

Some cases of changes in female dominance hierarchy were, however, described for baboons and macaques. A promotion in a female's dominance rank may be achieved through coalitionary support from female or male associates (e.g., Gouzoules, 1980; Walters, 1980; Samuels et al., 1987; de-Waal, 1989). Rank reversals may also be the result of deterioration in a female's physical condition due to old age or disease (Gouzoules, 1980; Silk et al., 1981; Strum, 1987). Rank changes may occur during the formation of new troops in captivity (Silk et al., 1981), or following troop fission (Koyama, 1970). Small (1990) has described an independent rise in rank by a female Barbary macaque (Macaca sylvanus), by soliciting friendships with high ranking females and then by directing aggression toward others.

Dominance hierarchy among females at Mkuzi was linear and usually stable. The direction of agonistic interactions was highly predictable. Rank positions of most females, in relation to each other, remained constant throughout the study, in spite of troop fission and other demographic changes. The rank positions of three females, relative to others, changed following their transferring from one daughter troop to the other after fission, and two very young females promoted their rank position, in relation to others, after fission.

One female at Mkuzi adopted an individual strategy of independent rank promotion. This female, Joan, has promoted her own rank by 11 places in about 4.5 months, without any coalitionary support from others. During this period she

actively threatened or chased the loser of any two opponents in nearly one quarter of all female-to-female agonistic encounters, and later started to displace these females independently. Joan's rise in rank is presumed to have been triggered by the death of her only female associate, Olive. Following Olive's disappearance, Joan remained the lowest ranking female in the troop, with no associates, and was pregnant. She was thus subjected to high risk of predation. By promoting her rank position this risk was probably much reduced.

Cheney et al. (1986) have suggested that at least some of the aspects of primate social intelligence have evolved in a social context. Although Joan's independent rise in rank forms only an anecdotal account of behaviour it may contribute to the accumulating evidence of the high levels of social cognition and social manipulations in non-human primates (e.g., Byrne and Whiten, 1985; Goodall, 1986; Strum, 1987; de-Waal, 1989; Kummer et al., 1990; Small, 1990; de-Waal, 1991a; Aureli, 1992). Primate social cognition may be expressed in different ways as a result of some combination of individual differences and specific circumstances.

As predicted by the definition of dominance rank, high ranking females at Mkuzi were obviously more aggressive toward others and received less aggression. They also received more presents and presented less often than others. Context of agonistic encounters among females were generally not related to their dominance rank.

The highest levels of aggression, as expected, due to considerations of rank maintenance (e.g., Johnson, 1989), were among similar ranking females. Higher aggression levels, however, were directed by the high ranking toward the low ranking females, than between each of these two groups and the middle ranking females. Judge and de-Waal (1993) have similarly recorded higher levels of submissive

gestures from the lowest to the highest ranking animals among rhesus monkeys (Macaca mulatta), which they attributed to conflict avoidance among them, in crowded situations, in captivity. This pattern may also be a result of the nature of female competition.

In those troops where females are competing over food resources (e.g., Seyfarth, 1977; Altmann, 1983; Barton, in press), the competition is over the relative success of their offspring and a positive correlation, is therefore expected, between dominance rank and levels of aggression. If, however, females are competing over an absolute resource, and in fact over a spatial position, which may be crucial to individuals' own survival, it is expected that they will focus their aggression on those individuals who present the lowest risk to them. This situation is somewhat analogous to the selfish herd idea of Hamilton (1971).

Competition among female baboons may also be evident in suppression of the reproduction of lower ranking females by active aggressive harassments from higher ranking animals (e.g., Rowell, 1970; Dunbar, 1980; Wasser and Starling, 1986). The phenomenon of infant kidnapping may be regarded as an important aspect of female reproductive competition. Frequent kidnapping of an infant from the mother, as described in some studies of baboons and macaques, may interrupt the infant's normal feeding, activity and development, and may even have fatal consequences for the infant (e.g., Altmann, 1980; Silk, 1980; Ransom, 1981; Wasser, 1983; Wasser and Starling, 1986; Maestripieri, 1993). High ranking females at Mkuzi kidnapped infants of other females more frequently, while their own infants were kidnapped less often, than others.

The following measures of female 'attractiveness' to others were defined by Seyfarth (1976): the amount of grooming a female received; number of different females that groomed her; the amount of friendly gestures she

received; the effectiveness of her presents (the proportion of her presents that were responded); and the effectiveness of her grooming solicitations. Using these measures, and in line with Seyfarth's (1976) findings, females at Mkuzi were found to be most 'attractive' to others when they were lactating, and especially mothers of younger infants (six weeks old or less). At Mkuzi, however, female attractiveness to others, was not related to her dominance rank. Yet, it should be noted that while benefits of their attractiveness to others, for lactating females (in terms of grooming and protection through vicinity to others) are not rank related, the cost they bear (in terms of harrassments and infant kidnapping) is higher for low ranking females.

Seyfarth (1976) has developed a model of associations among adjacent ranking females as a result of the competition over access to higher ranking females. De-Waal (1991b) has also stressed the role of attractiveness among females with a similar rank. In most studied troops of female baboons and macaques females tend to associate mainly with those females who occupy adjacent rank positions to theirs. Since dominance hierarchies in these systems are usually matrilineal, such adjacent ranking female associates are normally close kin. The value of such associations is assumed to lie in the coalitionary alliances they enable between female associates who support each other in their agonistic encounters with others (e.g., Hausfater, 1975; Cheney, 1977; Dunbar, 1980; Walters, 1980; Hausfater et al., 1982; Melnick and Pearl, 1987; Samuels et al., 1987; Strum, 1987; Dunbar, 1988; de-Waal, 1989; Chapais et al., 1991; Prud'Homme and Chapais, 1993).

Although high rates of female aggression were recorded at Mkuzi, almost no support coalitions were observed. Females at Mkuzi did not necessarily choose to associate with adjacent ranking females. The meaning of this is that

close relatives either did not occupy adjacent ranks or did not associate with each other, or both. Although relatedness among females is unknown, the data suggest that kinship was probably not the only or even major factor in choice of female associates.

Associations among females, were however, very stable and all pairs of female associates that remained together in the same troop remained associates throughout the study. All of the females that lost all of their former associates following troop fission and other demographic changes, have established new associations with other females in their new daughter troop.

If risk of predation is indeed the major source of competition among females at Mkuzi, as indicated here, the value of female associates lies in the protection they offer each other from risk of predation, given merely by their vicinity to each other. Strategies of maintaining central, and thus safer, spatial positions within the troop may be twofold: higher ranking females may displace others over spatial positions next to other adult troop members. Yet, the safest strategy, with minimal cost to all females is to have reliable and well established associations with certain females who tend to stay close together. Moreover, female associates groom and reciprocate grooming with each other more than with others.

While under these environmental conditions it is important to each female to maintain reliable and stable associations with certain other females, kinship and rank distance, are not necessarily relevant considerations in choice of female associates.

Dunbar (1988) has indicated that coalition formation is the response to size-dependent stresses in a troop, that further demands a more permanent form of social life, whereas predation risk only requires that individuals remain together on a temporary basis. This general rule is

applicable in other taxa of animals. Brown and Brown (1993), for example, have found that increased predation risk served to reduce the magnitude of the kin-biased territorial defence in trout (Oncorhynchus mykiss).

While social alliances may be used to maintain or even acquire a desired social position, they may also restrict the possibilities of independent rank promotion by individual females. This concept may be indicated here by Joan's independent rise in rank, as well as by the strategy adopted by most females at Mkuzi, in their choice of a new daughter troop, following fission.

Troop fission, as a means of group size control, is generally thought to be triggered by female competition for food (e.g., S. Altmann, 1974; Dittus, 1988; Dunbar, 1992). The initiation of fission in most studied troops of baboons and macaques, is usually attributed to the withdrawal of lower ranking matriline from the original group as a result of the high ecological costs they will experience by staying in the large group, and the potential effects on their lifetime reproductive success. These females are then joined by low ranking males or by their male associates (e.g., Dittus, 1988; Dunbar, 1988)

Pattern of fission is thus usually 'horizontal' in terms of female rank (e.g., Chepko-Sade and Sade, 1979; Prud'Homme, 1991; Dittus, 1988; Menard and Vallet, 1993, for macaques; A. Whiten, pers. comm., for baboons). This means that groups cleave along the lines of least genetic resistance (Dunbar, 1988) where close relatives, who are also close allies and occupy adjacent rank positions, stay together after fission. The significance of this is assumed to be that strong social bonds enable the formation of coherent relationships in the new group and underpin the alliances necessary for successful social functioning (Dunbar, 1984; Dunbar, 1988; de-Waal, 1989; de-Waal, 1991b). There are some data to suggest that females may

join the same troop as their male allies (Dunbar, 1984; Prud'Homme, 1991, Hamilton and Bulger, 1992).

Most of the females at Mkuzi adopted a strategy that was termed here the AYS strategy (Abandon Your immediate Superior in rank) in their choice of a new troop following fission. This splitting strategy instructs its holders to join whichever new group that has not been joined by their immediate superior in the hierarchy. If this strategy is adopted by all females, then each one, except of course for the top ranking individual in the original troop, enjoys a rank promotion. Moreover, no individual adopting a different strategy can do better, in terms of rank improvement. It is interesting to note that the AYS strategy is somewhat analogous to Fretwell and Lucas' (1970) concept of an ideal free distribution, with dominance hierarchy being the spatially distributed 'resource'.

Females at Mkuzi preferred to adopt the AYS strategy to keeping their female or male associates. Thus, improving individual rank seemed to be the major consideration for the Mtshopi Troop females in choosing a new group. This, in turn, may be explained by the fact that almost no support coalitions were observed among females at Mkuzi. The loss of social associates, who merely provide protection by the vicinity to each other, may be compensated for, as indeed happened, by the formation of new associations. Rank promotion under these conditions, may however, be crucial to individual survival. The importance, to females at Mkuzi, of promoting individual rank position, may be indicated both by Joan's active rise in rank and by adopting the AYS splitting strategy by most females.

Some data suggest that, in fact, troop fission may have had a high cost to females at Mkuzi, in terms of increased predation risk, and the following increase in aggression

levels among females. Indeed, four females disappeared in about 18 months following troop fission, compared with only one in more than three years prior to the fission. This fact combined with the increased levels of aggression and proximity among them, indicate this cost of troop fission to the females at Mkuzi. Why then, did they split at all?

There is evidence supporting the suggestion that the fission of Mtshopi Troop was not initiated by the troop females, but rather by the resident males, in order to decrease their cost of sexual competition. Indeed, after fission aggression levels among males were reduced and no severe wounds were observed. Five of the eight males were severely wounded prior to fission. The cause for this intensive male competition was probably the presence of a small number of receptive females, who also have a high reproductive value, at any one time, as a result of the favorable habitat. Competition among males, and thus aggression levels among them, decreased following troop fission, simply by the reduction in number of competitors in a group.

The resident males tend to keep large distances from each other. They were joined by female associates and followed by immigrant and peripheral males. The process of troop fission into two new distinct daughter troops seems to be the result of some balance between the females' tendency to stay close to each other and to males, and the males' tendency to stay close to females, but at the same time to keep large distances among themselves.

If troop fission was enforced upon the females, and female mortality is rank related, each female could still minimize her own cost (i.e., risk of predation) by adopting the AYS strategy to maximize her rank position, in her choice of a new troop.

Competition for individual survival, rather than for a relative lifetime reproductive success, as is the case when

females are competing over food resources, may be the reason of their choice of more 'individualistic' strategies. This may be evident in the high aggression levels among the females at Mkuzi; the lack of support coalitions between associates; the females' fission pattern; and the case of an individual rank promotion.

To conclude, it is suggested in this study that the main cost to low ranking females in a southern woodland habitat at Mkuzi Game Reserve, was risk of predation by leopards, rather than competition for food. Females, thus competed mainly over safe spatial positions, next to other adult troop members.

This kind of selective pressure may have resulted in the specific characteristics of the social relationships that were observed among females at Mkuzi and their choice of more 'individualistic' social strategies: a high level of female-to-female aggression; high ranking females displacing others, and mainly the lowest ranking females, over 'safer' positions next to other adult troop members; staying in vicinity to reliable female associates in order to minimize risk of predation, but no coalitionary support among associates their agonistic interactions with others; female associates were therefore not necessarily adjacent ranking and not necessarily kin; choice of a splitting strategy that improves individual rank position, rather than joining associates; and an independent rank promotion by a single female when her risk of predation increased, following the disappearance of her only female associate.

Conflicting interests between females and males, due to the high female reproductive success, resulted in intensive male competition. The resident males have therefore initiated troop fission which reduced their cost of sexual competition, but increased the cost to females.

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APPENDIX I

Brief Reports

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A Key for Identifying Individual Female Baboons under Poor Visibility Conditions

Key Words

Individual identification
Field study
Chacma baboon
Papio cynocephalus ursinus
Natural markings
Recognition of individuals

Introduction

Eugene Marais, who studied baboons at the beginning of this century, noted: 'When we had come to know the members of our troop, we noticed that there was a surprising difference of character between individuals' [1]. The importance of individual recognition in behavioural studies of primates has since been widely recognized [2, 3]. Wherever possible, the identification of primates through natural rather than artificial markings is desirable [2] for practical reasons as well as on grounds of animal welfare. In some other species, natural individual differences are prominent and readily visible to the human eye [4]. However, in contrast to apes and certain macaque species, for example, baboons do not have very distinctive faces or other natural

markings. As in most cercopithecines, female baboons tend to stay in their natal troop. Hence, the females in one troop are usually related to one another [5] and therefore tend to show a high degree of resemblance. Nevertheless, in some studies of baboons good observation conditions facilitate the identification of individuals [5]. Here, we present a method for identifying individual female baboons, despite close resemblance, under difficult observation conditions using an identification key.

Subjects and Study Site

This study was conducted on a troop of chacma baboons (*Papio cynocephalus ursinus*) at Mkuzi Game Reserve, Zululand, South Africa. The baboons' home range is located on hilly terrain in a habitat of dense

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and patchy mixed woodland [Henzi et al., in prep.]. Visibility under these conditions is very poor, and it was never possible to see the whole troop at any one time. In many cases only 1–6 animals were visible simultaneously. The troop had been exposed to gunfire before the beginning of the study (in 1986) and was therefore wary of people. Initially, observations were conducted from a distance of more than 50 m, but by the end of the study (in November 1991) the baboons were fully habituated and we were able to approach as close as 1–5 m. By July 1989, all adult baboons in the troop were individually recognized by both authors. The observation distance at that time was 15–20 m.

In July 1989, there were 63–68 baboons in the study troop (Mtshopi troop), including 6 males, 3 subadult males, 16 adult females, 5 subadult females and 33–38 juveniles and infants. The males were easy to identify from their distinctive markings, some of which resulted from their frequent fights. The females, by contrast, resembled one another closely. Identification was further complicated because only a few females were seen together at any one time so that identification based on instantaneous comparison of individuals was impossible. In addition, females were usually partially covered by vegetation with the result that only part of the body was visible at a time.

A Key for Identifying Female Baboons

In order to identify all adult and subadult females in Mtshopi troop on the basis of natural markings alone, we used a complex of morphological traits. Any traits chosen for this purpose must be: (1) variable between individuals; (2) constant over time; (3) visible and recognizable to the observers [2]. The following traits were used for comparing individual females: (1) relative age as indicated by pelage (smooth in young females and scruffy in old ones) and nipples (pink and button-like in young females; pink-grey and moderately long in middle-aged females; dark grey and long in old females); age categories were: (a) subadults, (b) young adults, (c) middle-aged adults and (d) old adults. (2) tail length: (a)

short, (b) medium, (c) long. (3) tail width: (a) thin, (b) medium, (c) thick. (4) body build: (a) tall with long limbs, (b) medium, (c) stocky. (5) relative size: (a) small, (b) medium, (c) large. (6) muzzle length: (a) long, (b) medium, (c) short. (7) pelage colour: (a) dark grey, (b) light grey, (c) dark brown, (d) light brown or yellowish, (e) mixed. (8) white facial markings: (a) prominent, (b) not prominent, (c) none. (9) shape of the tip of the tail (fig. 1). (10) special morphological traits.

These traits were incorporated into an identification key (Appendix), which permitted an individual identification of all females by a process of elimination.

A Test of the Identification Key

Mtshopi troop females were individually identified by S.W. by October 1988 and by T.R. by July 1989. The identity of all females was verified by both authors, in the field, on September 1989. The identification key was also tested by two volunteers unfamiliar with those females. On May 8, 1990, V. Hayes identified 5 of the troop females, and on September 2–5, 1991, M. Motro identified 6 females, using the key alone (both were tested by TR).

Conclusions

Under conditions of poor visibility, identification of a large number of closely similar individual primates, using natural markings alone, proved to be possible using the identification key presented here. Such a key can be used to pass on individual identifications between consecutive observers of the same troop. Nevertheless, because this method is based on comparison of traits between indi-

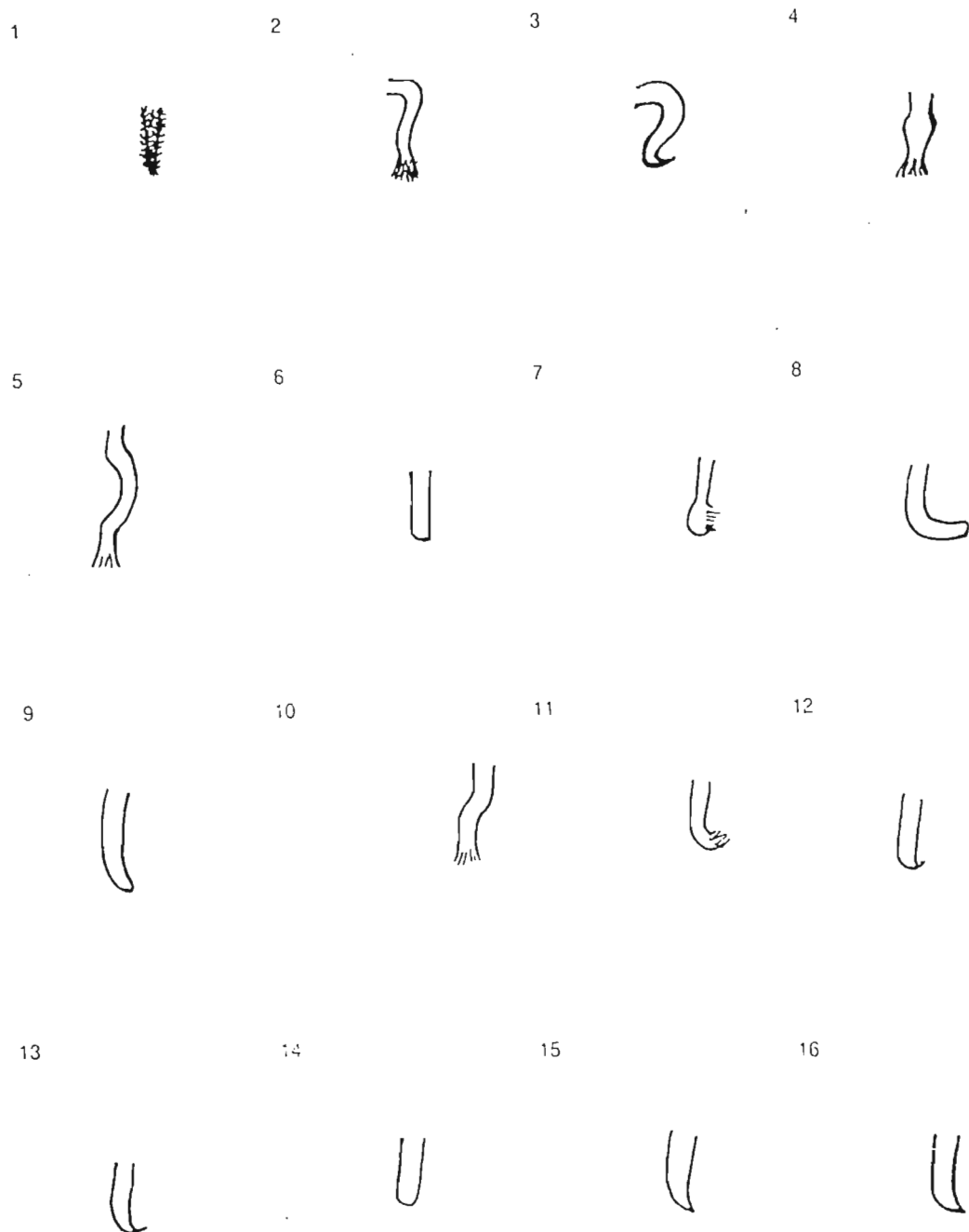


Fig. 1. The shape of the tip of the tail of each female, in the sequence of appearance in the identification key (Appendix).

Appendix: A Key for the Identification of the Adult Females of Mtshopi Troop

(I) (a) Old female, scruffy pelage, long and dark grey nipples, white face markings	II
(b) Other than that	IX
(II) (a) Tail very thin	III
(b) Tail width: thick or medium	IV
(III) (a) Short and very thin tail, very scruffy dark grey pelage, long limbs, long and thin muzzle, protruding cauliflower-shaped ears, hunched back, tip of tail thinning and scruffy	(1) Jessica VI
(b) Other than that	
(IV) (a) Very short tail	V
(b) Long or medium tail length	VI
(V) (a) Stocky female, light grey scruffy pelage, short muzzle, white face markings, tail very short and thick, tip of the tail scruffy and looks torn	(2) Esti
(b) Stocky female, dark grey and long pelage, very prominent white face markings around the eyes and on the muzzle, tail looks like new moon with its tip curved outward	(3) Joan
(VI) (a) Stocky female, very large body, very thick and scruffy tail with medium length, short and wide muzzle, dark brown pelage	(4) Doda VII
(b) Other than that	
(VII) (a) Stocky female, short and wide muzzle, prominent double kink in the middle of the tail	(5) Tiki VIII
(b) Other than that	
(VIII) (a) Very old female with very scruffy light grey pelage, long limbs, long muzzle, very long and dark nipples, small and narrowed eyes, tail long, thickish and straight, white face markings, small scar on muzzle ridge	(6) Doris
(b) Short muzzle, thin, long limbs, medium-sized tail, light grey pelage, white face markings, bottom lip hanging, small white scars on the chin, wide eyes, ball shape at the tip of the tail	(7) Suzy
(IX) (a) Small body size, very smooth pelage, pink and button-like nipples	Subadult females
(b) Other than that	X
(X) (a) Young female, smooth pelage, relatively short and pink nipples	XI
(b) Middle-aged female, pelage neither smooth nor scruffy, middle-sized pink-grey nipples	XII
(XI) (a) Long and thick tail, dark brown and long pelage, long and thin muzzle, thin body, white face markings, very dark tail with a flag-like tip	(8) Flaggy
(b) Light yellowish pelage, thin with long limbs, thin and long muzzle, long, thin and straight tail, white face markings, bags under eyes and 'worried look'	(9) Lucy
(XII) (a) Short or medium-length tail	XIII
(b) Tail long and straight	XV
(XIII) (a) Dark brown pelage, stocky, faint white face markings, one prominent kink in the last third of the tail	(10) Katy XIV
(b) Other than that	
(XIV) (a) Light yellow-brown pelage, short muzzle, large body, short and thick tail pointing outward	(11) Peri
(b) Dark grey pelage, medium size with medium long limbs, medium length and width of tail with a thin point, white face markings, 'wise and good' look	(12) Alice
(XV) (a) Dark grey pelage	XVI
(b) Light yellow pelage	XVII
(XVI) (a) Medium-sized tail, long limbs, thin, short muzzle, thin point at the tip of the tail	(13) Mellisa
(b) Large body, long and straight tail, long limbs, long muzzle, white face markings	(14) Extra
(XVII) (a) Long limbs, small body, wide muzzle, long tail, honey-like colour, protruding and pointed ears, tip of the tail pointed	(15) Honey
(b) Large body, long limbs, long tail, long muzzle, very light pelage with dark tail, tip of the tail pointed	(16) Bonni

viduals, each observer must be acquainted both with the complete set of individuals and with variation in the traits concerned before using the key for definite identification.

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APPENDIX II
CHECKSHEETS USED FOR DATA COLLECTION

1. Daily checksheet (p.137): Daily ad libitum records of troop sleeping site; all observed individuals, their physical condition, female reproductive status and consortships; grooming sessions (identities, initiation, termination and reciprocity); agonistic events (identities, outcome, context); and other events. Qualitative detailed descriptions of observed events were recorded separately.

2. Daily scan sampling (p.138): Identity, activity, location (on ground or off the ground), food species and food part of the visible troop members; distances between individuals; habitat type the troop occupied; and wind condition, every 30 minutes, throughout the day.

3. Focal sampling (p.139): Activity; location; food species and food part; identity of nearest neighbour and distance from nearest neighbour; identity of all neighbours in touch and within 5 meters; number of individuals in a food patch; feeding bout length; mother-infant distance; and activity and food item of the infant, every two minutes, in 20 minute samples of individual females (two checksheets were used consecutively). During the 20 minutes sample all agonistic events and other events (presenting, friendly approach, etc.) the sampled female was involved in were recorded in detail, including identity, result and context. All grooming sessions were also recorded in detail, including identity of groomer and individual being groomed, identity of initiator of grooming session and who terminated it, reciprocity and bout length.

Date

Sleeping site:

Observer:

Working distance: ²⁰⁺ min. Ave.
group:

Diet

Part i.d. age-sex Rep.stat.

♀
Rep.stat. consorts ♂
seen

Grooming

Displacements

Other

[illegible]

COMMENTS

	LEAVES	RETURNS	GROOMING & FLOW CHARTS	about length	AGONISTIC EVENTS
HER:					

APPENDIX III

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A new model of fission in primate troops

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Consider a group of animals, with a fixed linear hierarchy, which is forced to split, owing to ecological or other factors. If rank promotion is the main consideration of individuals in choosing which of the two daughter groups to join, they should adopt the simple splitting strategy we describe here. This strategy, which we term Abandon Your immediate Superior (AYS), instructs its holders to join whichever new group has not been joined by their immediate superior in the hierarchy. We show here that this strategy was indeed adopted by the females of a troop of chacma baboons, *Papio cynocephalus ursinus*.

The AYS strategy has some desirable properties which tend to make it stable. If it is adopted by all individuals, then each one, except of course the top ranking member of the original troop, enjoys a rank promotion. Moreover, no individual adopting a different strategy can do better, in terms of rank improvement.

As an illustrative example, consider an original troop of six females (denoted, according to their ranks, by 1, 2, 3, 4, 5 and 6). Under the AYS strategy, a split results in the new groups {1, 3, 5} and {2, 4, 6}. If, on the other hand, these females split horizontally in terms of dominance rank, resulting in {1, 2, 3} and {4, 5, 6}, such a split, although it is more advantageous to certain females (e.g. 4 and 5), would be unstable: there is an advantage to 2 and 3 to move to the other group, and as a consequence, to 4 and 5 not to remain in that group, and so on.

Although the AYS strategy is similar to an evolutionarily stable strategy (Maynard Smith & Price 1973), it is not identical because it does not fulfil the second requirement of its definition. While no mutant strategy can do better, there are strategies

that can do just as well. These are the strategies that instruct their holders to depart from their immediate superior if their rank in the original group was an even number (i.e. rank position 2, 4, etc.), whereas if their rank was an odd number (position 3, 5, etc.), they are free to join either group. Thus, AYS is only collectively stable (Axelrod 1984): it is a strategy that is in Nash equilibrium with itself. Nevertheless, AYS is both simpler and more robust than any equally valid alternative, since it does not require an individual to know its numerical place in the hierarchy. It is interesting to note that the AYS strategy is somewhat analogous to Fretwell & Lucas' (1970) concept of an ideal free distribution, with dominance hierarchy as the spatially distributed 'resource'.

We saw an apparent case of AYS in a troop of chacma baboons (Mtshopi Troop) at Mkuzi Game Reserve, Zululand, South Africa, which we observed for over 1200 h during 18 months between January 1989 and November 1991. The troop grew from about 44 individuals in June 1986 to about 76 in March 1990, including eight adult males, 17 adult females, six subadult females and about 45 immature individuals. All adults were individually identified, but relatedness between females was unknown. Dominance rank was established through win-loss matrices of the outcomes of all recorded agonistic encounters. By May 1990, following a long phase of social instability, the troop divided into two: about 43 members in Darth's Troop and 33 in Flash's Troop.

Most of the females of Mtshopi Troop adopted the AYS strategy (Table 1). Of the 22 females (excluding Peri, the top-ranking female), 18 abandoned their immediate superior in rank, and only four joined the same new troop as their superior. Under the assumption of random splitting for example, the number of abandonments should follow a binomial distribution, with parameters

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Table 1. The splitting pattern of the Mtshopi Troop females

Female	Original rank	New troop	New rank	Female associates	New troop	Male associates	New troop
Peri	1	D	1	Mel Jes Mod	D D D	Flash	F
Bonni	2	F	1	Lucy Tina	F D	John	F
Doris	3	D	2	Tina	D	Darth Flash	D F
Suzy	4	F	2	Alice Flaggy Lucy	F F F	Flash	F
Joan	5	D	3	Lucy	F	Ringo Flash	D F
Jes	6	D	4	Mel Peri Pitzi	D D D	Ter	D
Katy	7	F	3	Mel Honey Doda	D F D	Ter Darth	D D
Mel	8	D	5	Peri Jes Katy Extra	D D F D	Ter Darth	D D
Alice	9	F	4	Honey Suzy Lucy	F F F	Flash	F
Mod*	10	D	6	Peri Tina	D D	SAM Darth	D D
Flaggy	11	F	5	Suzy Esti	F D	Flash John	F F
Doda	12	D	7	Katy Honey	F F	Flash	F
Tiki	13	F	6	Honey	F	Flash Ringo	F D
Esti	14	D	8	Flaggy Crabs Gili	F F F	Darth John	D F
Lucy	15	F	7	Bonni Alice Suzy Joan	F F F D	John	F
Tombi*	16	F	8	Grazia	F	Darth	D
Extra	17	D	9	Mel	D	Goose	F
Gili	18	F	9	Esti	D	John	F
Honey	19	F	10	Alice Katy Doda Tiki	F F D F	Flash	F

Table I. Continued

Female	Original rank	New troop	New rank	Female associates	New troop	Male associates	New troop
Tina*	20	D	10	Doris Bonni Grazia Mod	D F F D	SAM Darth	D D
Grazia*	21	F	11	Tombi Tina	F D	SAM SAM Ringo	D F D
Crabs*	22	F	12	Esti Pitzi	D D	Darth SAM SAM	D F D
Pitzi*	23	D	11	Jes Crabs	D F	SAM Arc	D D

*Subadult females; SAM = Subadult males. The original rank order of females in March 1990 is given; a new troop affiliation (D = Darth's Troop; F = Flash's Troop) and new rank of each female, after fission, in May 1990; female associates with whom each female spent over 15% of her socializing time with females, prior to fission, and their new troop affiliation; and male associates with whom she spent over 25% of her socializing time with males, prior to fission, and their new troop affiliation.

$N = 22$ and $P = 0.5$, and the probability of obtaining at least 18 such abandonments (given that a split actually occurred) is only 2.17×10^{-3} . As predicted by the AYS strategy, the Mtshopi Troop divided into two daughter troops with an almost equal number of females (11 and 12).

Only two of the four females who did join their immediate superior, Jes and Crabs, could improve their new rank by choosing the other troop. Tombi's choice of the same troop as her superior improved her own rank by correcting the deviation created by Jes. Honey, who occupied an odd rank position, could do just as well by joining either troop. Jes was a very old female and had all of her female and male associates in Darth's Troop, which she chose to join in spite of the consequent loss of one rank position. Crabs' choice of Flash's Troop was only temporary and she later moved to Darth's Troop, where she improved her rank (and joined her associates).

Female baboons and macaques tend to form linear and stable dominance hierarchies, where they associate closely with their kin, who also occupy adjacent ranks (Hausfater et al. 1982; Dunbar 1988). These dominance hierarchies are stabilized through support coalitions within and between dominant matrilineal groups against lower ranking ones (Samuels et al. 1987; Dunbar 1988; Chapais

et al. 1991; de Waal 1991). Troop fission usually occurs when lower ranking matrilineal groups withdraw from the original group, and is therefore horizontal in terms of female rank (Chepko-Sade & Sade 1979; Dunbar 1988; Prud'Homme 1991; A. Whiten, personal communication). The significance of this is assumed to be in retaining the social alliances necessary for successful social functioning (Dunbar 1988; de Waal 1991). Some data suggest that females join the same troop as their male allies (Prud'Homme 1991; Hamilton & Bulger 1993).

Females at Mkuzi did not necessarily choose to retain their social associations. Any splitting of the original group into two distinct new groups would have resulted in breaking some of the 27 female associations that existed prior to fission. If we consider only splits into groups of 11 and 12 females, some would have retained 24 pair-wise associations. The actual split of the group disconnected 10 and retained 17. However, under the assumption of random splitting, the estimated probability of retaining at least 17 associations is 0.1216. (This estimate was obtained by randomly drawing 10 000 splits, out of the $2^{22} - 1 = 4194303$ possible splits, and calculating the proportion of splits that retained at least 17 associations.) The apparently large number of associations that were retained is, therefore, not significantly larger than that one

would expect under the assumption of random splitting.

Eighteen of the females joined a troop where they had at least one male associate, and only five joined a troop where they had none. This seems to indicate the importance of keeping associations with males in deciding which troop to join. However, 17 of the females who kept any of their male associations also used the AYS strategy. Of the six females for whom there was a choice between choosing the AYS and keeping male associates, five adhered to the AYS strategy and abandoned their male associates, while only a single female (Jes) favoured joining her male associate rather than rank promotion. This suggests that females preferred the AYS to keeping male associates.

Thus, improving individual rank seemed to be the major consideration for the Mtshopi Troop females in choosing a new group. This may be explained by the fact that, although high rates of female aggression were recorded at Mkuzi, almost no support coalitions were observed.

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