### THE STABILITY OF MATRILINEAL DOMINANCE HIERARCHIES IN

VERVET MONKEYS (CERCOPITHECUS AETHIOPS SABAEUS)

by

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#### ABSTRACT

Factors influencing the stability of matrilineal dominance hierarchies were investigated in a feral troop of vervet monkeys (Cercopithecus aethiops sabaeus) in Barbados. Changes in the matrilineal dominance hierarchy were investigated over a 12-year period (1979-1991). Matrilineal ranks remained unchanged for the first 7 years (stable period), reversed on several occasions over the next 3.5 years (unstable period), and have re-stabilised for a further 3.5 years to present date. In stable periods, neither lineage size, nor an index of matrilineal power, was positively correlated with matrilineal rank. In unstable periods, and in the year following emergence from the unstable period, matrilineal rank was correlated with the number of females in the matriline and with the matrilineal power index. Rates of aggression were lower, and fewer aggressions were escalated, in unstable than stable periods. However, more aggressions were met with confrontation and injury rates were higher. In both stable and unstable periods, females escalated more of their aggressions and received more aggressions than males, and females had higher injury rates during unstable periods. Older juveniles were more aggressive than younger juveniles during both stable and unstable periods. These sex- and age-specific aggression differences may partly explain why the number of juvenile females in a matriline, particularly the number of older females, is positively correlated with matrilineal rank during unstable periods and as troops enter new periods of rank stability. Individuals supported matrilineal members more often than non-matrilineal members in aggressive bouts during both stable and unstable periods, and matrilineal support was more common in unstable than stable periods. In unstable periods, females provided more matrilineal support than males, and older juveniles provided more matrilineal support than younger juveniles. Along with the age- and sex-specific differences in aggression noted above, these support differences may explain why matrilineal rank was correlated with the number of juvenile females in the matriline, and with the matrilineal power index which is sensitive to juvenile age and sex, during and at termination of unstable periods in this study. However, age- and sex-specific differences in aggression and support can not explain the ranks of matrilines during stable periods, when rank is not correlated with matrilineal characteristics. Higher ranking matrilines received more non-matrilineal support than lower ranking matrilines during stable periods. This may be a major factor stabilising

matrilineal ranks during stable periods. Non-matrilineal support was less common in unstable than stable periods. The decreased frequency of non-matrilineal support may increase the probability of matrilineal rank reversals, thereby contributing to the continuation of unstable periods. The frequency distribution of non-matrilineal supports in different social contexts, the lower support frequency in unstable than stable periods, and in particular the high reciprocity evident in non-matrilineal support exchanges, suggest that non-matrilineal support is better explained by reciprocal altruism than by mutualism in vervet monkeys.

### RESUMÉ

Les facteurs influençants la stabilité des hiérarchies de dominance matrilinéale fûrent étudiés dans une bande sauvage de singes verts (Cercopithecus aethiops sabaeus) à la Barbade. Les modifications dans la hiérarchie de dominance matrilinéale fûrent suivies pendant une période de 12 ans (1979-1991). Les rangs matrilinéals sont demeurés constants pendant les premiers 7 ans (période stable), se sont renversés plusieurs fois pendant les 3.5 années suivantes (période instable) et se sont restabilisés durant les dernières 3.5 années. Pendant les périodes stables, ni les grandeurs, ni les compositions de sexe et d'âge des lignées, ni un index de pouvoir matrilinéal fûrent corréllés avec le rang matrilinéal. Pendant les périodes instables et pendant l'année suivant la fin de la période instable, le rang matrilinéal était corréllé avec le nombre de femelles dans la lignée et avec l'index de pouvoir matrilinéal. La fréquence et le nombre d'aggressions étaient moins nombreuses pendant les périodes instables que pendant les stables, mais plus d'aggressions étaient violentes et l'incidence de blessures était accrue. Pendant les périodes stables et instables, les femelles ont escaladés et reçu plus d'aggressions que les mâles et les femelles avaient une plus haute fréquence de blessures pendant les périodes instables. Les juvéniles aînés étaient plus aggressifs que les plus jeunes pendant les périodes stables et instables. Ces différences d'aggression reliées au sexe et à l'âge pourraient partiellement expliquer pourquoi le nombre de femelles juvéniles dans une lignée, particulièrement le nombre de femelles aînées, est positivement corréllé avec le rang matrilinéal pendant les périodes instable et lorsque les bandes entrent dans une nouvelle période de stabilité de rangs. Les individus ont appuyé plus souvent des membres de leur lignées matrilinéales que ceux d'autres lignées pendent les périodes stables et instables et le support matrilinéal était plus commun pendant les périodes instables. Pendant les périodes instables, les femelles fournissaient plus de support matrilinéal que les mâles et les juvéniles aînés fournissaient plus de support matrilinéal que les plus jeunes. En association avec les différences d'aggression reliées au sexes at à l'âge nôtées ci-haut, les différences en support matrilinéal pourraient expliquer pourquoi le rang matrilinéal est corréllé avec le nombre de femelles juvéniles dans la lignée ainsi qu'avec l'index de pouvoir matrilinéal, qui est sensible aux âges et sexes des juvéniles, pendant et à la fin des périodes instables dans cette étude. Cependant, les différences d'aggression et de support

reliées au sexe et à l'âge n'expliquent pas les rangs des lignées durant les périodes stables, lorsque les rangs ne sont pas corréllés avec les compositions de sexe ou âge des lignées. Les lignées de haut rang recevaient plus de support non-matrilinéal que les lignées de bas rang pendant les périodes stables. Ceci pourrait être un facteur majeur dans la stabilisation des rangs matrilinéals pendant les périodes stables. Le support non-matrilinéal était moins commun pendant les périodes instables que pendant les périodes stables. La moins grande fréquence de support non-matrilinéal pourrait augmenter la probabilité de renversements des rangs matrilinéals, contribuant ainsi à la continuation des périodes instables. La distribution de fréquences de support non-matrilinéal dans des contextes sociaux différents, le support moins fréquent dans les périodes instables que stables et, en particulier, une grande réciprocité qui est évidente dans les échanges de support non-matrilinéal suggèrent que le support non-matrilinéal est mieux expliqué par de l'altruisme réciproque que par du mutualisme chez les singes verts.

### PREFACE

#### Statement of Contribution

The ideas for this research were developed by myself with input from my supervisor. I was responsible for initial drafts of all chapters. The final draft of this thesis benefited considerably from editorial inputs by my supervisor. Historical data were provided by Dr. J.A. Horrocks.

#### Statement of Originality

This study is the first quantitative investigation of effects of matrilineal characteristics on matrilineal ranks during stable and unstable periods in Old World primates with matrilineal dominance hierarchies. It is the first comparative investigation of frequency and form of aggression in stable and unstable periods, and the first investigation of effects of non-matrilineal support in stabilising matrilineal ranks in feral troops. An attempt to separate the role of mutualism and reciprocal altruism as causal explanations for non-matrilineal support in Old World primates is presented for the first time.

### Thesis Format

This thesis has been prepared as a series of chapters which will form the basis of manuscripts to be submitted for publication in refereed scientific journals. The first chapter has been accepted for publication by the journal *Animal Behaviour*; the format of the other 3 chapters corresponds to that required by this same journal, to which these 3 papers will be submitted.



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### **GENERAL INTRODUCTION**

The most fundamental feature of social organisation in Old World monkeys is a matrilineal dominance hierarchy in which offspring acquire ranks adjacent to but below their mothers, and matrilines rank linearly relative to each other (e.g. Japanese macaques, Macaca fuscata, Kawai 1958; rhesus macaques, M. mulatta, Missakian 1972; stumptail macaques, M. arctoides, Estrada 1978; bonnet macaques, M. radiata, Silk et al. 1981a; longtail macaques, M. fascicularis, Angst 1975; pigtail macaques, M. nemestrina, Bernstein 1969; yellow baboons, Papio cynocephalus, Hausfater 1975; olive baboons, P. anubis, Scott 1984; vervets, Cercopithecus aethiops, Horrocks & Hunte 1983a,b). Long-term studies of matrilineal dominance hierarchies in yellow baboons (Hausfater et al. 1982; Samuels et al. 1987), Japanese macaques (Mori et al. 1989), rhesus macaques (Ehardt & Bernstein 1986), and stumptail macaques (Rhine et al. 1989) indicate that the relative ranks of matrilines remain unchanged for long periods (stable periods), which are interrupted by shorter periods characterised by frequent matrilineal rank reversals (unstable periods). What matrilineal characteristics influence matrilineal rank during stable periods is unclear. For example, Silk & Boyd (1983) and Chapais (1988) suggest that matrilineal rank is a consequence of matrilineal size in macaques, but Ehardt & Bernstein (1986) and Samuels et al. (1987) found no effect of matrilineal size on matrilineal rank in rhesus macaques and yellow baboons respectively. Matrilineal size need not be correlated with matrilineal rank, if the age and sex composition of matrilines also influences their rank; but effects of age and sex composition of matrilines on matrilineal rank have not been specifically investigated. The factors which initiate unstable periods in matrilineal dominance hierarchies are also unclear. Some studies suggest that incapacitation or death of a matriarch may trigger instability (e.g. Bernstein 1972 for pigtail macaques; Gouzoules 1980 for Japanese macaques; Silk et al. 1981a for bonnet macaques; Hausfater et al. 1982 for yellow baboons); but Samuels et al. (1987) suggest that matriarch loss is not a prerequisite for the onset of instability in yellow baboons, and emphasize that no single explanation accounts for the phenomenon. The objectives of Chapter 1 of this thesis are to characterise the matrilineal dominance hierarchy over a 12-year period in a feral troop of vervet monkeys (Cercopithecus aethiops sabaeus) in Barbados, to

investigate effects of matrilineal size and composition on matrilineal rank, to comment on what factors may initiate unstable periods, and to investigate what matrilineal characteristics correlate with matrilineal rank during unstable periods and as troops emerge from unstable periods and enter new periods of matrilineal stability.

Matrilineal composition may influence matrilineal rank if there are age- and sex-specific differences in behaviours which influence matrilineal rank. However, despite the prevalence of matrilineal dominance hierarchies in Old World monkeys, the behaviours which stabilise matrilineal ranks during stable periods, and why they fail to do so during unstable periods, remain unclear (Dunbar 1988; Chapter 1). In macaques, baboons and vervets, individuals are often less aggressive to matrilineal than non-matrilineal members (e.g. Cheney 1977; Kurland 1977; Silk et al. 1981b; Horrocks & Hunte 1983a, but the form of aggression (i.e. whether mild or escalated) is seldom reported. In any case, less aggression towards matrilineals than nonmatrilineals can not explain why certain matrilines remain dominant over others during stable periods. Some studies suggest that high ranking matrilines may be more aggressive towards nonmatrilineals than low ranking matrilines (e.g. Bernstein 1970; Datta 1983; Horrocks & Hunte 1983a), and this may contribute to the prevailing pattern of matrilineal ranks. However, the correlation of aggression with matrilineal rank may be better interpreted as a consequence than cause of higher rank. Information on the form of aggression directed at non-matrilineals by high and low ranking matrilines is not available. Moreover, the distribution and form of aggression to matrilineals and non-matrilineals have not been reported during unstable periods in the matrilineal dominance hierarchy for any Old World monkey. The objectives of Chapter 2 are therefore to characterise the frequency and form of aggression to matrilineals and nonmatrilineals during stable periods in vervet monkeys, to characterise the frequency and form of aggression towards non-matrilineals by matrilines of differing rank and comment on whether the differences are characteristics of the matrilines or consequences of their rank, and to characterise the frequency and form of aggression during unstable periods in the dominance hierarchy, thereby clarifying what behavioural processes may stabilise matrilineal rank in vervets.

In Old World monkeys, individuals typically support matrilineal members over non-matrilineal members in aggressive disputes (e.g. Kaplan 1977, Kurland 1977, Massey 1977, Watanabe 1979, Kaplan *et al.* 1987, Bernstein & Ehardt 1985, Silk 1982, 1992 for macaques; Cheney 1977, Dunbar 1980, 1984 for baboons; Hunte & Horrocks 1987 for vervets), and support frequencies may be higher for higher ranking than lower ranking matrilines (e.g. Berman 1980 for macaques; Cheney 1977, Walters 1980 for baboons; Cheney 1983, Fairbanks & McGuire 1985, Hunte & Horrocks 1987 for vervets). However, the correlation of support frequency with rank may again be a consequence rather than cause of matrilineal rank. If neither matrilineal size, composition, inherent aggressiveness or inherent differences in support tendencies can explain matrilineal ranks during stable periods, the possibile role of the behaviour of non-matrilineals in stabilising matrilineal ranks should be considered. However, effects of the distribution of non-matrilineal support on matrilineal rank stability have not been specifically investigated in feral troops of Old World monkeys. The objectives of Chapter 3 are therefore to determine whether individuals are more supportive of matrilineal than non-matrilineal members, to determine whether higher ranking matrilines support matrilineal members more frequently than lower ranking matrilines and to comment on whether this is a cause or consequence of their ranks, to investigate the distribution of non-matrilineal support and comment on whether it might stabilise prevailing matrilineal hierarchies, and to investigate the frequency and distribution of support during unstable periods in the dominance hierarchy of feral vervet monkeys, and thereby comment on the role of non-matrilineal support in stabilising matrilineal ranks in vervets.

Since individuals within a matriline are genetically related, matrilineal support in Old World monkeys is considered a form of kin altruism (sensu Hamilton 1964; e.g. Massey 1977, de Waal 1978, Kaplan 1978, Datta 1983, Hunte & Horrocks 1987). Since individuals from different matrilines are either unrelated or weakly related, reciprocal altruism (e.g. Seyfarth & Cheney 1984; Hunte & Horrocks 1987; de Waal & Luttrell 1988) and mutualism (e.g. Chapais *et al.* 1991; Chapais 1992) have been suggested as competing causal explanations for nonmatrilineal support. The reciprocal altruism hypothesis for non-matrilineal support in Old World monkeys suggests that an individual supports a recipient in an aggressive dispute, with the expectation of future benefit when the recipient returns the support (Hunte & Horrocks 1987). The value of the recipient as a reciprocator should therefore influence its probability of receiving support. The mutualism hypothesis for non-matrilineal support suggests that an individual supports a recipient in an aggressive dispute because it is seizing the opportunity to reinforce its own rank over the opponent in the dispute. Both individuals therefore benefit at the time of the act, the supporter through rank reinforcement, and the recipient from the support received (Chapais *et al.* 1991; Chapais 1992). The value of the recipient as a reciprocator will not influence its probability of receiving support under the mutualism hypothesis. The reciprocal altruism and mutualism hypotheses therefore make different qualitative predictions on the relative rates and distributions of non-matrilineal support in Old World monkeys. The objective of Chapter 4 is to generate and test three predictions that may allow separation of reciprocal altruism and mutualism as causal explanations for non-matrilineal support in vervet monkeys in Barbados.

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**CHAPTER 1** 

# LONG-TERM STABILITY IN THE MATRILINEAL DOMINANCE HIERARCHY IN A FERAL TROOP OF VERVET MONKEYS (CERCOPITHECUS AETHIOPS SABAEUS)



#### **1.1 ABSTRACT**

Changes in the matrilineal dominance hierarchy were investigated over a 12-year period (1979-1991) in a feral troop of vervet monkeys (Cercopithecus aethiops sabaeus) in Barbados. The relative ranks of matrilines remained unchanged for 7 years. This was followed by a 3.5year unstable period in which rank reversals occurred, and by a new stable period without reversals which has lasted 3.5 years to present date. Matrilines were more cohesive, sensu members occupying adjacent social ranks, in stable than unstable periods. Neither lineage size, lineage age or sex composition, nor an index of matrilineal power (MPI; based on an age/sex tendency to support matrilineal members, summed for all members) explained why high ranking matrilines retained their rank during the 7-year stable period. The tendency of non-matrilineal members to support the higher ranking of the two opponents in dyadic disputes may stabilise matrilineal hierarchies during stable periods. A substantial drop in MPI of the top-ranking matriline, caused by loss of the oldest daughter and incapacitation of the matriarch, initiated the 3.5-year unstable period. Matrilineal rank was not correlated with size or age composition of the matriline during the unstable period. However, it was typically correlated with the number of females in the matriline and also with MPI, since females contribute more per individual to MPI than males. In the year spanning emergence from the unstable period and the onset of the stable period, matrilineal rank was again typically correlated with the number of females and MPI. Matrilineal power, driven primarily by the number of females in the matriline, therefore predicts matrilineal rank in newly structured matrilineal dominance hierarchies.

### **1.2 INTRODUCTION**

The most fundamental feature of social organisation in Old World monkeys is a matrilineal dominance hierarchy in which offspring typically acquire ranks adjacent to but below that of their mothers, and matrilines rank linearly relative to each other (e.g. Japanese macaques, *Macaca fuscata*, Kawai 1958; rhesus macaques, *M. mulatta*, Missakian 1972; stumptail macaques, *M. arctoides*, Estrada 1978; bonnet macaques, *M. radiata*, Silk *et al.* 1981; longtail macaques, *M. fascicularis*, Angst 1975; pigtail macaques, *M. nemestrina*, Bernstein 1969; yellow baboons, *Papio cynocephalus*, Hausfater 1975; olive baboons, *P. anubis*, Scott 1984; vervets, *Cercopithecus aethiops*, Horrocks & Hunte 1983a,b). There are therefore two major characteristics relevant to the stability of matrilineal dominance hierarchies through time; namely, the persistence with which matrilineal members continue to occupy adjacent social ranks (i.e. matrilineal cohesiveness), and the persistence with which the relative ranks of matrilines remain unchanged.

Long-term studies of the stability of matrilineal dominance hierarchies in yellow baboons (Hausfater *et al.* 1982; Samuels *et al.* 1987), Japanese macaques (Mori *et al.* 1989), rhesus macaques (Ehardt & Bernstein 1986), and stumptail macaques (Rhine *et al.* 1989) have indicated that the relative ranks of matrilines remain unchanged for extended periods, the long stable periods being punctuated by shorter periods during which matrilineal rank reversals are common. The issue of changes in matrilineal cohesiveness has received less attention. The only long-term studies of dominance hierarchies in vervet monkeys have been on captive groups (Bernstein 1970; Bramblett *et al.* 1982). One objective of this Chapter is to characterise the matrilineal dominance hierarchy over a 12-year period (1979-1991) in a feral troop of vervet monkeys (*Cercopithecus aethiops sabaeus*) in Barbados, with emphasis on changes in relative ranks of matrilineal cohesiveness.

Although long-term stability of matrilineal dominance hierarchies has now been reported for several species, the behavioural interactions producing stability are less clear (Dunbar 1988). Individuals in many species are now believed to be more frequently aggressive to non-matrilineal members (non-kin) than matrilineal members (typically kin) (e.g. macaques, Silk *et al.* 1981;

baboons, Cheney 1977; vervets, Horrocks & Hunte 1983a); and to support matrilineal members more often than non-matrilineal members in dyadic aggressive disputes (e.g. macaques, Kaplan 1977, Kurland 1977; baboons, Cheney 1977, Walters 1980; vervets, Cheney 1983, Hunte & Horrocks 1987). If aggression towards non-matrilineals and support of matrilineals were the only behaviours contributing to the stability of matrilineal dominance hierarchies, the relative ranks of matrilines should be correlated with lineage size, i.e. with the number of individuals in the matriline. Silk & Boyd (1983) and Chapais (1988) suggest that matrilineal rank may be a consequence of matrilineal size in macaques. However, Ehardt & Bernstein (1986) and Samuels *et al.* (1987) found no effect of matrilineal size on matrilineal rank in rhesus macaques and yellow baboons respectively, and Dunbar (1988) cautioned that whether matrilineal rank is a function of matrilineal size may depend on total group size.

Lineage size alone may not be strongly correlated with matrilineal rank, if the age and sex composition of matrilines also influences their rank. Female juveniles may be more likely than male juveniles to support matrilineal members in aggressive disputes (Fairbanks & McGuire 1985 for vervets; Bernstein & Ehardt 1985 for rhesus macaques). Older juveniles may be more aggressive than younger juveniles to non-matrilineal members (e.g. Horrocks & Hunte 1983a for vervets; Johnson 1987 and Pereira 1989 for baboons) and, at least in the case of females, may be more likely than younger juveniles to support matrilineal members in aggressive disputes (e.g. Massey 1977 for macaques; Hunte & Horrocks 1987 for vervets). However, effects of age and sex composition on matrilineal rank have not been specifically investigated. A second objective of this Chapter is to investigate effects of lineage size and lineage composition on long-term matrilineal rank in vervet monkeys.

The factors contributing to the long-term stability of matrilineal dominance hierarchies require further clarification, but what factors initiate periods of instability are also unclear. A number of studies have suggested that death of a matriarch or her incapacitation through ill health or injury, particularly a high-ranking matriarch, may trigger the onset of unstable periods (e.g. Bernstein 1972 for pigtail macaques; Gouzoules 1980 for Japanese macaques; Silk *et al.* 1981 for bonnet macaques; Hausfater *et al.* 1982 for yellow baboons) and Fairbanks & McGuire (1984) report increased levels of aggression following the deaths of matriarchs in vervets. However, Samuels *et al.* (1987) suggest that matriarch loss is not a prerequisite for the onset

of matrilineal instability in yellow baboons, and emphasize that no single explanation accounts for the phenomenon. Additional phenomena that have been suggested as causing the onset of unstable periods include the simultaneous cycling of several females (Wasser 1983) and the synchronous sexual maturation of a large number of adolescent females (Altmann & Altmann 1970; Chance *et al.* 1977; Chikazawa *et al.* 1979; Samuels & Henrickson 1983; but see Samuels *et al.* 1987). The characteristics of matrilines which may determine their relative ranks as they emerge from periods of instability have not been specifically investigated (Dunbar 1988). The third objective of this Chapter is to comment on what factors may initiate unstable periods, and investigate what matrilineal characteristics may influence matrilineal rank following unstable periods, in a feral troop of vervet monkeys in Barbados.

#### **1.3 METHODS**

Vervet monkeys were introduced to Barbados about 350 years ago, probably from Senegal and Gambia in West Africa (Horrocks 1986). They inhabit wooded gullies and patches of woods, both adjacent to cultivated land and in residential areas, throughout the island. Their recent population size has been estimated at between 5,000 and 8,000 individuals (Horrocks & Baulu 1988).

The vervet troop that is the focus of this study is feral, occupying a home range of approximately 0.5km<sup>2</sup> on the west coast of Barbados. The troop was habituated in 1979, and has been continuously monitored since that time (Horrocks 1982). Observation conditions at the study site are excellent. The genealogy of all natal troop members is known, and all troop members are individually recognizable.

As a component of the monitoring program, all births, deaths, emigrations of natal males, successful and unsuccessful challenges for troop tenure by non-natal males, and durations of male tenure have been recorded. Troop composition is therefore continuously known for the past 12 years. Throughout this time, the troop has been essentially uni-male, i.e. single breeding males are sequentially replaced following relatively brief periods of competitive interactions for troop tenure (Horrocks & Hunte 1993); and there have been four persistent matrilines.

The social rank of all troop members has been continuously recorded throughout the 12year monitoring program by scoring the outcomes of dyadic aggressive/submissive interactions (see Horrocks & Hunte 1983a for the repertoire of aggressive and submissive behaviours used in rank assignment). The outcomes of spontaneous dyadic aggressive disputes were the typical means of assigning rank during the routine monitoring periods. However, if interactions between any troop members over any time period were not observed frequently enough to record relative ranks, interactions were induced by throwing a preferred food item between two individuals, and recording the outcome of the competition for access to the item.

The small number of matrilines and individuals in this troop, characteristics common to all vervet troops in Barbados, greatly facilitated the ease with which relative ranks of individuals, relative matrilineal rank, and cohesiveness of matrilines, could be determined and recorded throughout the 12-year monitoring program.

### **1.4 RESULTS**

### 1.4.1 Demographic Characteristics of the Study Troop

All demographic events in the troop over the 12-year monitoring program are provided in 6-month time periods from January 1980 to December 1991 in Table 1. The demographic events are provided separately for each matriline. Matrilines A, B, C and D were ranked 1, 2, 3 and 4 respectively at the time of habituation of the troop in 1979 and the onset of the monitoring program in 1980.

A number of demographic events are worthy of specific comment. Although troop size varied somewhat during the 12-year monitoring period, it has remained remarkably constant in the longer-term; troop size was 12 in the first and last of the 6-month periods of the monitoring program (Table 1). Only 1 female born into the troop reached sexual maturity and gave birth with her mother still alive in the troop. This occurred in Matriline A (the then top-ranking matriline) in Period 7 (early 1983), the oldest daughter of the matriarch giving birth to a daughter. This primiparous female and her daughter were killed just over 1 year later in Period 10. The event has therefore not been represented as the formation of a new matriline (Table 1). A female born into matriline B reached sexual maturity and gave birth in Period 19 (early 1989), but this was 2 years after her mother's death (Period 14, late 1986; Table 1). Similarly, 2 females born into Matriline C reached sexual maturity and gave birth in Period 21 (early 1990), but this was 1 year after their mother's death (Period 19, early 1989; Table 1). These females have remained in the troop and continue to breed. Since they were the only 2 members of Matriline C in the troop at the time they gave birth, this event was considered as the formation of 2 new matrilines from original Matriline C, matrilines which have been termed  $C_1$  and  $C_2$ (Table 1). The formation of these matrilines would have brought the total number of matrilines in the troop to 5. Interestingly, at this time, the sole remaining member of Matriline B (a young matriarch; Table 1) emigrated from the troop and, accompanied by a young non-natal adult male, has begun the formation of a new troop in a home range adjacent to the study troop.

Seven natal males reached sexual maturity and emigrated from the troop during the 12year monitoring period (Table 1). Two of these males were from Matriline A (Periods 16, 22), **Table 1.** Demographic events (births, deaths, emigrations, troop composition, troop size) in the study troop from January 1980 to June 1991, presented in 6-month time periods. B-Birth, D-Death, E-Emigration, C-Composition, M<sub>4</sub>-Matriarch, F-Juvenile Female, M-Juvenile Male. \* Birth by primiparous female. \*\* New matriarch.

ſ					3	MATRI	ILINE A					MATRI	LINE B				1	MATRI	LINE C				]	MATRI	LINE D		
	TI	IME NOD	SIZE	В	D	E		С		B	D	E		С		B	D	E		С		B	D	E		С	
	FE	KIUD					Μ.	F	М	1			М,	F	М				M,	F	М				M,	F	М
	1980	1	12	0	0	0	1	1	0	1(M)	0	0	1	0	2	0	0	0	I	1	0	1(F)	0	0	1	1	2
		2	12	0	0	0	1	1	0	0	0	0	1	0	2	0	0	0	1	1	0	0	0	0	1	1	2
	1981	3	15	1(F)	0	0	1	2	0	1(F)	0	0	1	1	2	1(M)	0	0	1	1	1	1(F)	1(M)	0	1	2	1
		4	14	1(M)	1(F)	0	1	1	1	0	1(M)	0	1	1	1	0	0	0	1	1	1	0	0	0	1	2	1
	1982	5	16	0	1(M)	0	1	1	0	0	0	0	1	1	1	1(M)	0	0	ł	1	2	1(F)	0	0	1	3	1
		6	17	1(M)	0	0	1	1	1	1(F)	0	0	1	2	1	0	0	0	I	1	2	0	1(F)	0	1	2	1
	1983	7	16	1(F)	0	0	1	2	1	1(M)	2(F)	0	1	0	2	0	0	0	1	1	2	1(F)	1(F)	0	1	2	1
		8	13	1(M)	1(M)	0	1	2	1	0	1(M)	1(M)	1	0	0	0	0	0	1	1	2	0	0	1(M)	1	2	0
	1984	9	15	1(M)	0	0	1	2	2	0	0	0	1	0	0	1(M)	0	0	1	1	3	1(F)	0	0	1	3	0
5		10	11	0	3(FFM)	0	1	0	1	0	0	0	1	0	0	0	1(F)	0	1	0	3	0	2(F)	0	1	1	0
	1985	11	14	1(F)	0	0	1	1	1	1(M)	0	0	1	0	1	1(F)	0	0	1	1	3	1(M)	0	0	1	1	1
		12	14	0	0	0	1	1	1	1(F)	0	0	1	1	1	0	0	1(M)	1	1	2	0	0	0	1	1	1
	1986	13	18	1(M)	0	0	1	1	2	1(M)	0	0	1	1	2	1(F)	0	0	1	2	2	1(M)	0	0	1	1	2
		14	16	0	0	0	1	1	2	0	1(M,)	0	0	1	2	0	0	1(M)	1	2	1	0	0	0	1	1	2
	1987	15	16	0	1(M_)	0	0	1	2	0	1(M)	0	0	1	1	1(M)	0	0	1	2	2	1(M)	0	0	1	1	3
		16	13	0	0	1(M)	0	1	1	0	0	0	0	1	1	0	2(M)	0	1	2	0	0	0	0	1	1	3
	1988	17	14	0	0	0	0	1	1	0	0	0	0	1	1	1(F)	0	0	1	3	0	1(F)	1(F)	0	1	1	3
		18	14	0	0	0	0	1	1	0	0	0	0 .*	1	1	0	0	0	1	3	0	0	0	0	1	1	2
	1989	19	11	0	0	0	0	1	1	1(M)	2(M)	0	I	0	0	1(F)	3(M_FF)	) ()	0	2	0	0	0	0	1	1	3
		20	- 11	0.	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0 ++	2	0	0	0	0	1	1	3
	1990	21	12	1(F)	0	0	1	1	1	0	0	0	1	0	0	2 (M)	0	0	2 ++	0	2	0	1(M)	1(M)	1	1	1
		22	11	0	0	1(M)	1	1	0	0	0	1( <b>M</b> ,)	0	0	0	0	0	0	2	0	2	1(M)	0	0	1	1	2
						Matri	iline A			1		Matril	ine C <sub>1</sub>					Matri	line C <sub>2</sub>			Matriline D					
	1991	23	12	0	0	0	1	I	0	1(M)	0	0	1	0	2	0	0	0	1	0	1	0	0	0	1	1	2
		24	12	0	0	0	1	1	0	0	1(M)	0	1	0	1	0	0	0	1	0	1	0	0	0	1	1	2

one from Matriline B (Period 7), two from Matriline C (Periods 12, 14), and two from Matriline D (Periods 8,21) (Table 1).

#### 1.4.2 Long-term Changes in the Rank and Cohesiveness of Matrilines

The relative ranks of matrilines remained unchanged from at least the onset of habituation of the troop in early 1979 until Period 11 (1985), i.e. for about a 7-year period (Fig. 1A,B). This period is referred to as the Stable Period. Periods 12 to 19 are characterised by a series of matrilineal rank reversals, the first reversal occurring in Period 12 (late 1985) and the last in Period 19 (early 1989). This 3.5-year period is referred to as the Unstable Period. From Period '20 (late 1989) onwards to the present, there have been no further matrilineal rank reversals, i.e. the troop has entered a new stable period with respect to the structure of the matrilineal dominance hierarchy.

In Figure 1A, matrilineal rank is presented as the mean rank of the individuals in the matriline. This has the advantage of indicating times when the ranks of any 2 matrilines are converging or diverging, and hence times when the probability of rank reversal between the 2 matrilines may be lower or higher (e.g. divergence between Matrilines C and D between Periods 13 and 16; the convergence between Matrilines A and B during Periods 16 to 18 which continued into rank reversal between the matrilines in Period 19; Fig. 1A). The temporal variation observed for each matriline in the mean rank of its matrilineal members during the stable period (Periods 1-11) merely reflects changes in the numbers of individuals in matrilines. In Figure 1B, matrilineal rank is ordered as either 1, 2, 3 or 4, depending on the relative values of the mean rank of matrilineal members in each matriline. This has the advantage of making the stable and unstable periods more visually evident.

Matrilineal dominance hierarchies are characterised, not only by a linear dominance ranking between matrilines, but also by the fact that matrilineal members occupy adjacent social ranks, i.e. by cohesiveness of matrilines. One way to characterise the cohesiveness of a matriline is to calculate the variance in rank of the matrilineal members. If matrilineal members occupy adjacent social ranks (matrilineal cohesiveness high), variance in matrilineal rank will be low; if matrilineal members occupy very different social ranks (matrilineal cohesiveness low),

### Figure 1

Matrilineal ranks of the 4 matrilines (A,B,C,D), presented in 6-month periods from January 1980 to June 1991, as mean rank of the matrilineal members (A), and ordered 1, 2, 3 or 4 by mean rank of the matrilineal members (B).



## Figure 2

Variance in rank of matrilineal members, presented separately for each of Matrilines A, B, C and D in 6-month periods from January 1980 to June 1991.


variance in matrilineal rank was low for all matrilines, indicating that matrilineal members were occupying adjacent social ranks, i.e. matrilines were cohesive. During Periods 12 to 19 (unstable period), variance in matrilineal rank rose substantially, indicating that matrilineal members were not occupying adjacent social rank, i.e. matrilines were much less cohesive. From Period 20 onwards, when the troop had entered a new stable period with respect to relative rank of matrilines, variance in matrilineal rank dropped sharply for all matrilines, indicating a return to matrilineal cohesiveness, i.e. matrilineal members were again occupying adjacent social ranks (Fig. 2). The sharp difference between stable and unstable periods in variance in matrilineal rank indicated by Figure 2, suggests that this parameter may be a valuable means of identifying and characterising stable and unstable periods in primates with matrilineal dominance hierarchies.

#### 1.4.3 Factors Affecting Matrilineal Rank during the Stable Period

The number of individuals in a lineage (lineage size), the number of male offspring in the lineage, the number of female offspring in the lineage, the number of older offspring in the lineage, and the number of younger offspring in the lineage were considered as factors that might affect the rank of matrilines in the stable period. Since mean age to sexual maturity for females is 4 years, females > than 2 years were considered old and females < 2 years young. Since mean age to sexual maturity for males is 5 years, males > 2.5 years were considered old and males < 2.5 years young. Finally, an index, termed the Matrilineal Power Index, was calculated and considered as a factor that might affect matrilineal rank. The Index considers the fact that the tendency to aid matrilineal members varies with sex and age, and that total support available to a matriline should therefore be a function of both matrilineal composition and size. Data from the 12-year monitoring program on vervets in Barbados suggest that the overall mean percent support to matrilineal members (i.e. Supports/Aggressive Disputes x 100) is 6.1% from old female juveniles, 5.9% from matriarchs, 2.6% from young female juveniles, 2.3% from young male juveniles, and 1.2% from old male juveniles. This is a ratio of 5 : 4.9 : 2.1 : 1.9 : 1, and can be considered to indicate units of matrilineal support power available from each of the 5 categories respectively. The Matrilineal Power Index in any time period is therefore the number of matrilineal members in each of the 5 categories, multiplied by the number of support power units appropriate to that category, summed across the categories (see Dunbar 1988 for similar assumption that power within coalitions is additive). Matrilineal Power Indices for each of the 4 matrilines, provided in 6-month time periods for the 10-year period 1980 to 1990, are shown in Table 2.

In 9 of the 11 6-month stable periods (i.e. Periods 1-11; Stable Period), the Spearman Rank Correlation Coefficient ( $r_s$ ; N=4) between matrilineal rank (as mean rank of matrilineal members) and lineage size was negative (Table 3), suggesting that higher ranking matrilines did not have larger lineages.

In 10 of the 11 6-month periods, the r, value (N=4) between matrilineal rank and number of female juveniles in the matriline was negative (Table 3), suggesting that higher ranking matrilines did not have more female juveniles in the matriline. In 6 of the 11 periods, the r, value (N=4) between matrilineal rank and number of male juveniles in the matriline was negative (Table 3), suggesting that higher ranking matrilines did not have more male juveniles in the matriline.

In 10 of the 11 periods, the  $r_s$  value (N=4) between matrilineal rank and number of young juveniles in the matriline was negative (Table 3), suggesting that higher ranking matrilines did not have more young juveniles in the matriline. In 6 of the 11 periods, the  $r_s$  value (N=4) between matrilineal rank and number of old juveniles in the matriline was negative (Table 3), suggesting that higher ranking matrilines did not have more old juveniles in the matriline.

	MAT	RILINEAL POW	ER INDEX	
Time Period	Matriline A	Matriline B	Matriline C	Matriline D
(1980) 1	7.0	8.7	7.0	9.9
2	8.4	8.2	7.0	9.9
3	12.0	9.9	10.3	10.1
4	11.8	8.0	11.8	10.1
5	9.9	8.9	13.7	12.2
6	11.8	13.0	13.7	13.0
7	13.9	7.8	12.8	10.1
8	13.9	4.9	12.8	9.1
9	15.3	4.9	13.8	11.2
10	5.9	4.9	8.8	7.0
11	8.0	6.8	10.9	8.9
12	5.6	8.9	9.9	11.8
13	6.0	10.8	11.1	13.7
14	5.0	5.9	10.1	13.2
15	7.9	4.5	14.9	14.7
16	6.6	6.0	13.7	13.5
17	6.0	6.0	17.0	10.9
18	6.0	6.0	17.0	10.6
19	6.0	5.0	10.0	10.0
20	6.0	5.0	10.0	10.0
(1990) 21	6.0	5.0	10.0	8.0

**Table 2.** Matrilineal Power Indices (see text for calculation) for each of the 4 matrilines (A, B, C, D) presented in 6-month periods for the 10-year period from January 1980 to June 1990.

**Table 3.** Spearman Rank Correlation Coefficients  $(r_s)$  between matrilineal rank (as mean rank of matrilineal members) and: Lineage size, Number of female juveniles in matriline, Number of male juveniles in matriline, Number of older juveniles in matriline, Number of younger juveniles in matriline, and the Matrilineal Power Index (MPI) for the matriline; presented separately for each 6-month period from January 1980 to December 1985 (Periods 1-11, the stable period; Fig. 1). N=4 in each correlation analysis. Old and Young as defined in text.

Period	Lineage	Female	Male	Old	Young	M.P.I.
	Size	Juveniles	Juveniles	Juveniles	Juveniles	
1	-0.63	-0.26	-0.45	-0.78	-0.48	-0.63
2	-0.63	-0.26	-0.45	-0.78	-0.48	-0.20
3	-0.48	0	-0.32	+0.26	-0.78	+0.40
4	-0.78	-0.78	-1.0	-1.0	-0.78	+0.22
5	-1.00	-0.78	-0.63	-1.0	-1.00	-0.60
6	-0.78	-0.45	-0.26	-0.45	-0.26	-0.63
7	-0.26	-0.11	+0.21	-0.26	0	+0.40
8	+0.21	-0.11	+0.21	+0.21	-0.11	+0.40
9	+0.21	-0.40	+0.21	+0.21	-0.11	+0.40
10	-0.32	-0.78	+0.21	+0.21	-0.89	-0.60
11	-0.32	-0.26	-0.26	+0.21	-0.89	-0.60



Finally, in 6 of the 11 periods, the  $r_{s}$  value (N=4) between matrilineal rank and the Matrilineal Power Index for the matriline was negative (Table 3), suggesting that higher ranking matrilines did not have higher Matrilineal Power Indices.

Together the results indicate that neither lineage size, nor any aspect of lineage composition, can explain the relative ranks of matrilines during stable periods in vervet monkeys in Barbados. This suggests that behavioural interactions other than those involving matrilineal members may be instrumental in maintaining matrilineal ranks during stable periods in vervets.

## 1.4.4 Factors Initiating Instability and Characterisation of the Unstable Period

During Periods 1-9 (Fig. 1), the matriarchs in all 4 matrilines appeared healthy and active. In Period 10, the matriarch of Matriline A (the highest ranking matriline) lost her oldest daughter. Although this sharply decreased the Matrilineal Power Index of the matriline (Table 2), it had no immediate effect on matrilineal rank. However, in Period 11, this matriarch (Matriarch A) developed a cataract on one eye which impaired her vision, and she began to show visual signs of rapid ageing. Individuals from Matrilines B and C increased the intensity of their aggression towards the matriarch's two offspring (old male, young female), and she appeared increasingly unable to support them. Her intervention frequency on behalf of her offspring dropped from about 5% at the start of Period 11 to about 2.5% in Period 12 and about 1% by Period 13; resulting in a continuing decline in the Matrilineal Power Index of the matriline (Table 2). During this time, Matriarch A directed most of her aggression at Matriline C. By the beginning of Period 12, the 2 offspring in Matriline A had fallen in rank below Matriline B; this began the decline in mean rank of the matriline and the increase in variance in matrilineal rank witnessed in Period 12 (Figs. 1A and 2, respectively). Toward the end of Period 12, Matriarch A began to defer to the members of Matriline B and matrilineal rank reversal was complete.

The rank reversal between Matrilines A and B was followed by a period of intense aggression by Matriline C against both A and B. This was a period of frequent injuries to members of Matrilines A, B, and C. It was noticeable that individuals from Matriline D did not involve themselves in the rank disputes, and remained injury-free throughout. The mean rank of matriline A continued to fall during this period, dropping below that of matriline C in Period 12 (Fig. 1A). The variance in rank of Matriline A continued to be high during this process (Fig. 2), as the old male juvenile in the lineage was able to maintain a higher social rank than Matriarch A, who maintained a substantially higher social rank than her daughter.

Matrilineal ranks might have stabilised in the sequence occurring at the end of Period 14 (i.e. B > C > A > D; Fig. 1), but towards the end of Period 14, Matriarch B was killed, leaving an old son and young daughter as the only lineage members. The death of this matriarch caused a sharp decrease in the Matrilineal Power Index of the matriline (Table 2; compare Period 13 with 14). The mean rank of Matriline B began to decline, falling below that of Matriline C during Period 15 (Fig. 1A). As had occurred with Matriline A, the variance in matrilineal rank of Matriline B was high during this process, since the old male juvenile was able to retain a substantially higher rank than the young female juvenile. The relative matrilineal ranks that emerged at the end of Period 15 remained unchanged until the end of Period 18 (2.5 years), but the mean ranks of matrilines A and B were clearly converging between Periods 16 and 18 (Fig. 1A), and variances in the ranks of both matrilines remained high, indicating little matrilineal cohesiveness, i.e. lineage members were not occupying adjacent social ranks. At the beginning of Period 19, the male in Matriline B was killed, and mean rank of Matriline A rapidly rose above that of Matriline B (Fig. 1A). By the end of Period 20, the sole remaining member of Matriline B emigrated (see previous Section).

The relative ranks of matrilines have remained unchanged from the end of Period 19/onset of Period 20 until the present, in spite of the death of Matriarch C in Period 19. This death led to a within-lineage rank reversal of her older daughter over her younger, but no matrilineal rank reversal. The death of the matriarch did drop the Matrilineal Power Index of the matriline (Table 2; compare Period 18 with 19), but the Power Index remained high relative to Matrilines A and B, given the presence of 2 older juvenile females in Matriline C, and the fact that Matriarchs A and B were already dead. The splitting of Matriline C in Period 22 into top-ranking Matriline  $C_1$  (older daughter of Matriarch C) and second-ranking Matriline  $C_2$  (younger daughter of Matriarch C) had no effect on relative ranks of matrilines (Fig. 1).

# 1.4.5 Factors Affecting Matrilineal Rank during the Unstable Period and Emergence of the New Matrilineal Hierarchy

In contrast to Matrilines A, B and C which reversed ranks in the unstable period (Periods 12-19), Matriline D remained the lowest ranking matriline throughout the 12-year monitoring program (Fig. 1). Moreover, field observations indicated that members of Matriline D did not involve themselves in the escalated rank-order disputes that were characteristic of Matrilines A, B, and C in the unstable period. Matriline D has therefore been excluded from the investigation of factors affecting matrilineal rank during the unstable period.

In 4 of the 8 six month unstable periods, the Spearman Rank Correlation Coefficient  $(r_s)$ between matrilineal rank and lineage size was negative (Table 4), suggesting that higher ranking matrilines did not have larger lineages. In 6 of the 8 periods, the r, value between matrilineal rank and the number of old juveniles in a matriline was negative (Table 4); in 6 of the 8 periods, the r, value between matrilineal rank and the number of young juveniles in the matriline was negative (Table 4). These results suggest that higher ranking matrilines did not have either more old or more young juveniles in the matriline. In all 8 periods, the r, value between matrilineal rank and the number of male juveniles in a matriline was negatively correlated (Table 4), clearly indicating that higher ranking matrilines do not have more male juveniles. However, in 7 of the 8 periods, the r, value between matrilineal rank and the number of juvenile females in the matriline was positive, suggesting that higher ranking matrilines had more juvenile females in the matriline (Table 4). Consistent with this, since females contribute more to the Matrilineal Power Index than males, in 7 of the 8 periods, the r, value between matrilineal rank and the Matrilineal Power Index was positive (Table 4). This suggests that higher ranking matrilines had higher Matrilineal Power Indices. It is of interest in this context that both the number of females in a matriline and the Matrilineal Power Index, also appear to predict the relative ranks of competing matrilines as they emerge from the unstable period and enter the new stable period. In Periods 19 to 21 (i.e. the 1-year period spanning emergence from the unstable period until the splitting of Matriline C into  $C_1$  and  $C_2$  (Fig. 1), matrilineal rank was again positively correlated with the number of females in the matriline and with the Matrilineal Power Index.

Table 4. Spearman Rank Correlation Coefficients  $(r_s)$  between matrilineal rank (as mean rank of matrilineal members) and: Lineage size, Number of female juveniles in matriline, Number of male juveniles in matriline, Number of older juveniles in matriline, Number of younger juveniles in matriline, and the Matrilineal Power Index (MPI) for the matriline; presented separately for each 6-month period from July 1985 to June 1989 (Periods 12-19, the unstable period; Fig. 1). Old and Young as defined in text.

Period	Lineage	Female	Male	Old	Young	M.P.I.
	Size	Juveniles	Juveniles	Juveniles	Juveniles	
12	-0.87	+0.50	-0.87	-0.87	-0.50	+0.50
13	-0.87	-0.87	-0.50	-0.12	-0.87	-0.50
14	-0.62	+0.12	-0.62	-0.62	-0.62	+0.62
15	+0.50	+0.62	-0.12	+0.50	-0.50	+0.50
16	-0.50	+0.62	-0.87	-0.50	-0.12	+0.50
17	+0.62	+0.62	-0.87	-0.50	+0.62	+0.62
18	+0.62	+0.62	-0.87	-0.50	+0.62	+0.62
19	+0.62	+1.00	-0.12	+0.62	-0.50	+1.00

#### **1.5 DISCUSSION**

Two major features characterise matrilineal dominance hierarchies; first, matrilines rank linearly relative to each other, and second, matrilineal members occupy adjacent social ranks, i.e. matrilines are cohesive. Long-term studies of matrilineal dominance hierarchies have confirmed the persistence of the first characteristic through time. For example, Samuels *et al.* (1987) reported a 10-year period without matrilineal rank reversals in yellow baboons, followed by a 9-month period of rapid change and a 27-month period of slower change and matrilineal restabilisation. A similar pattern of long stable periods interspersed with shorter periods of rapid change has been reported for macaques (e.g. Ehardt & Bernstein 1986; Mori *et al.* 1989). The persistence of matrilineal cohesiveness through time has received less quantitative attention.

The relative ranks of vervet matrilines in this study remained unchanged for at least 7 years. This was followed by a 3.5-year period in which matrilineal rank reversals occurred, and by a new stable period without rank reversals that has so far lasted for 3.5 years. Changes from periods in which relative ranks of matrilines were stable to periods in which rank reversals occurred were accompanied by changes in the cohesiveness of matrilines. In stable periods, matrilineal members tended to occupy adjacent social ranks, i.e. matrilines were cohesive. In unstable periods, matrilineal members were less likely to occupy adjacent social ranks, i.e. matrilines were less cohesive. Matrilines which were falling in rank were least cohesive. The loss of cohesiveness results from the fact that, as matrilineal rank falls, matrilineal members with high individual agonistic power (e.g. older juvenile males) can retain a relatively high social rank, but those with less individual power (e.g. younger juvenile females) fall further in rank. This tendency toward loss of matrilineal cohesiveness may be aggravated by the fact that it is those matrilineal members with highest individual power (older males) who may be least inclined toward support of matrilineal members (Fairbanks & McGuire 1985). Ehardt & Bernstein (1986) reported that, unlike other matrilineal members, adolescent males in rhesus macaques were not cohesive with their relatives when matrilineal rank was falling, and did not defend them.

The factors which maintain the relative ranks of matrilines during the extended periods over which matrilineal rank reversals do not occur, remain unclear. The most obvious causal candidate is lineage size. However, whereas Sade (1972), Silk & Boyd (1983) and Chapais

(1988) have suggested that matrilineal rank is correlated with matrilineal size in macaques, Ehardt & Bernstein (1986) found no such correlation in rhesus macaques; and Samuels *et al.* (1987) found no effect of matrilineal size on matrilineal rank in yellow baboons.

Since the tendency to aid matrilineal members is age- and sex-dependent, in particular older juvenile females are more likely to aid matrilineal members than are males and younger females (Fairbanks & McGuire 1985, for vervets; Bernstein & Ehardt 1985, for macaques), the age and sex composition of matrilines may be as important in maintaining matrilineal rank in stable periods as lineage size; but this does not appear to have been specifically examined. Since both lineage size and composition may influence matrilineal rank, a simple index of matrilineal power which incorporates both characteristics was calculated in this study (see Results). From January 1980 to June 1985 (the stable period monitored in this study), matrilineal rank appeared not to be influenced by the number of male juveniles in the matriline, the number of old juveniles in the matriline, nor the Matrilineal Power Index of the matriline; and was typically negatively correlated with lineage size and with the number of female juveniles in the matriline. The results indicate that neither lineage size, composition, nor the overall index of matrilineal power computed, can explain why high ranking matrilines were able to maintain their rank during the stable period of this study. It suggests that the behaviour of non-matrilineal members may be instrumental in maintaining matrilineal ranks during stable periods in vervets. In this context, Hunte & Horrocks (1987) have suggested that, in feral vervets, non-kin (non-matrilineal members) are more likely to aid the higher ranking of the two opponents in dyadic disputes, and have commented that the cumulative effect of this behaviour will be to stabilise the existing matrilineal hierarchy. A similar tendency to support higher-ranking over lower-ranking opponents has been reported for rhesus macaques by Datta (1981, 1983), and for Japanese macaques by Chapais et al. (1991). This issue is further explored in Chapter 3 of this thesis.

Given the possible effect of non-matrilineal members in stabilising matrilineal hierarchies, a substantial drop in the matrilineal power of a high ranking matriline may be required to move matrilineal hierarchies from stable periods to periods of matrilineal rank reversal. Samuels *et al.* (1987) suggest that the factors initiating periods of instability remain unclear, and they emphasize that several factors may be responsible for their onset. Nevertheless, a number of studies have reported that incapacitation or death of a matriarch has coincided with the onset of unstable periods (e.g. Bernstein 1972; Gouzoules 1980; Silk *et al.* 1981; Hausfater *et al.* 1982). Particularly in troops with small matrilines, the reduction in matrilineal power accompanying death of a matriarch may often be enough to trigger instability. In this study, Matriline A, the top-ranking matriline during the stable period, suffered a substantial drop in matrilineal power prior to and at the onset of the unstable period - first through the loss of the oldest juvenile female and then through incapacitation of the matriarch. The consequence was that rank of the matriline fell below that of Matrilines B and C. The next matrilineal power resulting from death of a matriarch. Indeed, the sequential deaths of matriarchs may have been largely responsible for the relatively extended duration of the unstable period observed in this study. It is nevertheless important to note that whether death of a matriarch leads to matrilineal rank reversal will depend on the power of the matriline after her death, relative to that of challenging matrilines. The death of the matriarch in Matriline C in this study did not lead to matrilineal rank reversal, presumably because matrilineal power following her death remained greater than that of Matrilines A and B.

Two points are worthy of further comment in the context of the initiation of matrilineal rank reversal. First, any event which sharply increases aggression levels in the troop may increase the probability of rank reversal, simply because it may force the relative power of matrilines to be actually tested. This might explain why simultaneous cycling of several females (Wasser 1983) and synchronous sexual maturation of a large number of adolescent females (Chance *et al.* 1977; Altmann & Altmann 1979; Chikazawa *et al.* 1979; Samuels & Henrickson 1983) have been reported as initiating unstable periods. Second, if non-matrilineal support is less frequent in unstable than stable periods, the magnitude of change in matrilineal power required to cause change in matrilineal rank during unstable periods will be less than that necessary to initiate unstable periods. Hunte & Horrocks (1987) suggest that support of non-matrilineal members (non-kin) is a form of reciprocal altruism, higher ranking individuals receiving more support because they are more valuable reciprocators (see also Datta 1983). Since reciprocation, and hence the benefit to the supporting animal, is realised at some future time, the rank uncertainty characteristic of unstable periods may decrease the probability of providing non-

matrilineal support. Non-matrilineal support frequency in stable and unstable periods is investigated in Chapter 3.

The importance of matrilineal power in influencing matrilineal rank during unstable periods is supported by the results of the investigation of factors affecting matrilineal rank during the 3.5-year unstable period in this study. Matrilineal rank did not appear to be affected by lineage size, by the number of older juveniles in the matriline, nor by the number of younger juveniles in the matriline, suggesting that neither sheer lineage size nor age composition predict matrilineal rank during unstable periods. However, matrilineal rank was typically positively correlated with the number of juvenile females, and consistent with this since females contribute more to matrilineal power than males, was also typically positively correlated with the Matrilineal Power Index. Finally, in the 1-year period spanning emergence from the unstable period and the onset of the new stable period, matrilineal rank again appeared to be positively correlated with both the number of females in the matriline and with the Matrilineal Power Index. This suggests that matrilineal power, driven primarily by the number of females in the matriline, may be a strong predictor of the relative ranks of matrilines as they emerge from unstable periods and enter new periods of matrilineal rank stability.

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## CHAPTER 2

## THE DISTRIBUTION AND FORM OF AGGRESSION DURING STABLE AND UNSTABLE PERIODS IN THE MATRILINEAL DOMINANCE HIERARCHY OF FERAL VERVET MONKEYS (CERCOPITHECUS AETHIOPS SABAEUS)

## 2.1 ABSTRACT

The distribution and form of aggression during two stable (September 1982 - March 1983; January 1991 - June 1991) and two unstable (January 1987 - March 1987; May 1989 -July 1989) periods in the matrilineal dominance hierarchy of a troop of feral vervet monkeys (Cercopithecus aethiops sabaeus) were investigated. Rates of aggression were lower, and fewer aggressions were escalated, in unstable than stable periods; but in the former, more aggressions were met with confrontation and injury rates were higher. Individuals were more often aggressive and escalated more of their aggressions to other matrilines than to members of their own matriline. During stable periods, higher ranking matrilines were more aggressive than lower ranking matrilines. This is better perceived as a consequence than cause of rank, but may contribute to the maintenance of rank once rank is established. In both stable and unstable periods, female juveniles escalated more of their aggressions and received more aggressions than males, and females had significantly higher injury rates during unstable periods. Older juveniles were more aggressive than younger juveniles during both stable and unstable periods. These sexand age-specific differences in aggressiveness may partly explain why the number of juvenile females in a matriline, particularly the number of older females, was typically positively correlated with matrilineal rank during unstable periods and as troops enter new periods of matrilineal rank stability (Chapter 1). However, the differences can not explain observed patterns of matrilineal rank during stable periods, since rank was not correlated with the age or sex composition of matrilines during these periods. This suggests that the behaviour of nonmatrilineals may be important in maintaining matrilineal ranks during stable periods (Chapter 3). The best predictor of the distribution of aggression was its cost as indicated by the probability that the aggression would be met with confrontation. Higher ranking matrilines (contrast lower), older juveniles (contrast younger) and males (contrast females) were more confrontational and received less aggression, and aggression rates were lower during unstable periods when confrontation probability was high.

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## **2.2 INTRODUCTION**

A matrilineal dominance hierarchy in which offspring acquire ranks adjacent to their mothers, and matrilines rank linearly relative to each other, is a fundamental characteristic of social organisation in Old World monkeys (e.g. Kawai 1958, Bernstein 1969, Missakian 1972, Estrada 1978, Silk *et al.* 1981a for macaques; Hausfater 1975, Scott 1984 for baboons; Cheney *et al.* 1981, Horrocks & Hunte 1983a,b for vervets). Several studies now suggest that the relative ranks of matrilines remain unchanged for long periods, these stable periods being interrupted by shorter unstable periods during which matrilineal rank reversals occur (e.g. Hausfater *et al.* 1982, Samuels *et al.* 1987 for baboons; Ehardt & Bernstein 1986, Mori *et al.* 1989, Rhine *et al.* 1989 for macaques; Bramblett *et al.* 1982, Chapter 1 for vervets).

Despite the prevalence of matrilineal dominance hierarchies, the behaviours which stabilise matrilineal ranks during stable periods, and why they fail to do so during unstable periods, remain unclear (Dunbar 1988; Chapter 1). In macaques, baboons and vervets, individuals are often less aggressive to matrilineal than non-matrilineal members (e.g. Cheney 1977; Kurland 1977; Silk *et al.* 1981b; Horrocks & Hunte 1983a; but see Bernstein & Ehardt 1986), but the form of aggression (i.e. whether mild or escalated) is seldom reported. One objective of this Chapter is to characterise the frequency and form of aggression to matrilineal and non-matrilineal members during stable periods in vervet monkeys.

Less aggression towards matrilineals than non-matrilineals indicates that matrilines tend to act as cohesive units, but does not explain why certain matrilines remain dominant over others during stable periods. High ranking matrilines may be more aggressive towards non-matrilineals than low ranking matrilines (e.g. Bernstein 1970; Datta 1983; Horrocks & Hunte 1983a), and this may contribute to the prevailing pattern of matrilineal ranks. However, the tendency of higher ranking matrilines to be more aggressive to non-matrilineals may be better perceived as a consequence than a cause of higher rank, perhaps resulting from a lower retaliatory cost of aggression for higher ranking than lower ranking matrilines (Hunte & Horrocks 1987; Dunbar 1988). Information on the form of aggression directed at non-matrilineals by high and low ranking matrilines is not available. The second objective of this Chapter is to characterise the frequency and form of aggression towards non-matrilineals by matrilines of differing rank, and to comment on whether the differences are characteristics of the matrilines or consequences of their rank.

Since matrilines tend to act as cohesive units, and if the tendency of high ranking matrilines to be more aggressive is a consequence rather than cause of high rank, matrilineal rank might be expected to correlate with matrilineal size during stable periods, i.e. larger matrilines may be able to maintain higher rank. However, Ehardt & Bernstein (1986) and Samuels *et al.* (1987) found no such effect in macaques and baboons respectively, and there was no correlation of matrilineal rank with either matrilineal size or matrilineal power (based on an age/sex tendency to aid matrilineal members summed for all members) during stable periods in vervet monkeys in this study (Chapter 1). This may suggest that the behaviour of non-matrilineal members is important in stabilising the relative ranks of matrilines. A third objective of this Chapter is to investigate whether matrilines are more aggressive, in frequency or form, to the lower ranking than higher ranking of any pair of matrilines when the pairs of matrilines rank either below or above them, thereby contributing to maintaining the relative ranks of the recipient matrilines.

The distribution and form of aggression to matrilineals and non-matrilineals have not been reported during unstable periods in the matrilineal dominance hierarchy for any Old World monkey. The final objective of this Chapter is to characterise the distribution and form of aggression during unstable periods in the dominance hierarchy of feral vervet monkeys, and by comparison with the patterns observed during stable periods, to assist in clarifying the behavioural processes which stabilise matrilineal rank in vervets.





## **2.3 METHODS**

## 2.3.1 Subjects

The colonisation of Barbados by vervets, and their distribution on the island, are described by Horrocks (1986), and population size estimates are provided by Horrocks & Baulu (1988). The vervet troop studied in this Chapter is feral, occupying a home range of approximately 0.5m<sup>2</sup> on the west coast of Barbados. It was habituated in 1979, and has been continuously monitored since (Horrocks 1982; Chapter 1). Observation conditions at the study site are excellent, and most troop members can be approached to within 1m. The genealogy of all natal troop members is known and all troop members are individually recognizable.

## 2.3.2 Chronology of Data Collection

For this Chapter, 2 data sets were collected during stable periods and 2 during the unstable period in the matrilineal dominance hierarchy of the study troop (see Chapter 1 for the time and duration of stable and unstable periods). Data for Stable Period 1 were collected between September 1982 and March 1983. The troop consisted of 4 matrilines whose relative ranks were stable during the period. Within matrilines, offspring ranked immediately below their mothers (i.e. matrilines were cohesive sensu Chapter 1) and younger female offspring outranked older. Data for Stable Period 2 were collected between January 1991 and June 1991. As for Stable Period 1, the troop consisted of 4 matrilines whose relative ranks were unchanged during the period. Data for Unstable Period 1 were collected between January 1987 and March 1987. Four matrilines were again present, 3 of which changed rank during the period. Within matrilines, offspring did not necessarily rank adjacent to their mothers, i.e. matrilines were not cohesive sensu Chapter 1. Data for Unstable Period 2 were collected between Sensu Chapter 3. July 1989. Four matrilines were again present, 2 of which reversed rank during the period. As for Unstable Period 1, matrilines were not cohesive. Troop size, age and sex composition are provided for all 4 study periods in Chapter 1.

## 2.3.3 Method of Data Collection

Behaviour-dependent sampling was used to collect data on the frequency, distribution and form of aggressive acts. Data were typically collected at the same time every day, between 0900 to 1100h and 1600 to 1800h. Observation sessions were therefore usually of 2h duration. Total observation time was 229h for Stable Period 1, 326h for Stable Period 2, 82h for Unstable Period 1, and 108h for Unstable Period 2. The time that each individual was present during each observation session was recorded, and rates of aggression were calculated based on individual time present. This sampling protocol was possible because the troop is small and observation conditions are good. Adult males were excluded from the study. Threat and lunge were recorded as mild aggressive behaviours; chase, hit, grab, bite, and hold down and bite as escalated aggressive behaviours. A confrontational aggression was defined as one in which the recipient of the aggression retaliated, sensu through a counter-threat, counter-lunge, or physical contact response (hit-back, grab-back, bite-back). The outcomes of dyadic aggressive/submissive interactions were used to determine social rank throughout the study (see Chapter 1).

## 2.3.4 Data Analysis

Data on aggression rates were non-normal and could not be normalised using standard transformations. Differences in aggression rates have therefore been compared non-parametrically using Kruskal-Wallis tests, Mann-Whitney tests and Wilcoxon Matched-Pairs Signed-Ranks tests as appropriate; correlations between rank and aggression given and received were analysed using Spearman Rank Correlations. Differences in the distributions of aggressions given or received have been analysed by  $\chi^2$  Goodness of Fit, and differences in proportions of aggressions that were escalated or confrontational have been analysed by  $\chi^2$  Contingency tests. All  $\chi^2$  analyses have been conducted on count data, and have been adjusted for continuity where appropriate (Zar 1984).



## **2.4 RESULTS**

#### **2.4.1 Distribution and Form of Aggression in Stable Periods**

## 2.4.1.1 Frequency of Aggression Towards Matrilineals vs Non-matrilineals

In both stable periods, troop members directed more aggression at other matrilines (nonmatrilineals) than at matrilineal members (Table 1; Period 1, 88.8% at non-matrilineals > the 80.0% expected if probability of aggressing matrilineals and non-matrilineals is equal,  $\chi^2$ =59.78, P<0.001; Period 2, 91.7% at non-matrilineals > 80.4% expected,  $\chi^2$ =231.81, P<0.001). Consistent with this, the rate of aggression (no/h) towards non-matrilineals was significantly higher than towards matrilineals (Table 1; Wilcoxon Matched-Pairs Signed-Ranks Test, paired by individuals; Period 1, T=0, N=16, P<0.001; Period 2, T=2.41, N=11, P<0.02).

#### 2.4.1.2 Form of Aggression Towards Matrilineals vs Non-matrilineals

Not only was there more aggression towards non-matrilineals than matrilineals in stable periods, but a higher percentage of the aggressive acts towards non-matrilineals was escalated in both stable periods (Table 2; Period 1,  $\chi^2 = 7.68$ , P<0.006; Period 2,  $\chi^2 = 6.57$ , P<0.01). The percentage of aggressive acts that were met with confrontation did not differ between matrilineal and non-matrilineal aggression in either stable period (Table 2; Period 1,  $\chi^2 = 0.19$ , P=0.66; Period 2,  $\chi^2 = 0.22$ , P=0.64).

## 2.4.1.3 Aggression Towards Non-matrilineals

## 2.4.1.3.1 Effects of Rank on Frequency of Aggression

Both matrilines and matriarchs differed significantly in number of aggressive acts directed at non-matrilineals (Table 3; distributions different from those expected if non-matrilineal aggression by matrilines and matriarchs were equal; Period 1: matrilines,  $\chi^2 = 521.53$ , P < 0.001, matriarchs,  $\chi^2 = 282.40$ , P < 0.001; Period 2: matrilines,  $\chi^2 = 1372.56$ , P < 0.001, matriarchs,  $\chi^2 = 2749.38$ , P < 0.001). Consistent with this, the rate of aggression directed at non-matrilineals differed significantly between matrilines and matriarchs (Table 3; Kruskal-Wallis Test; Period Table 1. The percentage and rate (no/h) of aggressive acts directed at matrilineals and nonmatrilineals during the two stable and two unstable periods. Obs % is the percentage of aggressive acts directed at non-matrilineals; Exp % is the percentage expected to be directed at non-matrilineals on the null hypothesis of equivalent probability of aggressing non-matrilineals and matrilineals in the ratio of non-matrilineals to matrilineals in the troop. Mean aggression rate is the mean number of aggressions/h directed by troop members at non-matrilineals and matrilineals. N is number of aggressive acts; n is number of individuals.

Period	Obs %	Exp %	N	n	Non-matrilineal	Matrilineal
					Mean Rate	Mean Rate
Stable 1	88.8	80.0	1218	16	0.64	0.09
Stable 2	91.7	80.4	1338	11	0.50	0.06
Unstable 1	90.7	80.0	216	16	0.21	0.03
Unstable 2	79.4	66.7	194	10	0.14	0.04

Table 2. The percentage of aggressive acts that were escalated and confrontational, presented separately for matrilineal and nonmatrilineal aggressions in each of the stable and unstable periods. N is number of aggressive acts.

PERIOD	NON-MATRI	LINEAL AGGRESSIO	N	MATRILINEA	MATRILINEAL AGGRESSION					
	% Escalated	% Confrontational	N	% Escalated	% Confrontational	N				
Stable 1	40.7	10.4	1082	27.9	8.8	136				
Stable 2	49.2	12.4	1227	36.0	14.4	111				
Unstable 1	28.1	15.3	196	10.0	5.0	20				
Unstable 2	44.2	29.2	154	12.5	15.0	40				

Table 3. The percentage and rate (no/h) of non-matrilineal aggressions by matrilines and matriarchs, presented separately for the two stable and two unstable periods. For matrilines, Obs % is the percentage of all acts given by each matriline; for matriarchs, Obs % is the percentage of matriarchal aggressions given by each matriarch; Exp % is the percentage on the null hypothesis of equivalent probability of aggression by each aggressor category and on the number of individuals in each aggressor category. N is number of aggressive acts.

AGGRESSOR	STAB	LE PER	IOD 1		STAB	LE PER	IOD 2		UNSTABLE PERIOD 1				UNSTABLE PERIOD 2			
	Obs %	Exp %	N	Rate	Obs %	Exp %	N	Rate	Obs %	Exp %	N	Rate	Obs %	Exp %	N	Rate
Matriline 1	51.2	25	554	4.87	30.0	18.2	368	1.67	16.9	26.7	33	0.44	51.9	20.0	80	0.75
Matriline 2	30.1	25	326	2.78	53.5	18.2	656	2.78	12.2	20.0	24	0.47	2.0	10.0	3	0.03
Matriline 3	10.2	25	110	1.56	3.4	27.3	42	0.20	54.0	26.7	106	1.66	18.2	20.0	28	0.26
Matriline 4	8.5	25	92	1.09	13.1	36.3	161	0.81	16.9	26.7	33	0.59	27.9	50.0	43	0.40
Matriarch 1	60.6	25	218	1.34	22.2	25.0	174	0.55	14.8	33.3	4	0	-	-	-	-
Matriarch 2	25.6	25	92	0.95	72.3	25.0	567	2.30	-	-	-	-	100	50.0	3	0.03
Matriarch 3	11.6	25	42	0.23	3.1	25.0	24	0.13	85.2	33.3	23	0.37	-	-	-	-
Matriarch 4	2.2	25	8	0.13	2.4	25.0	19	0.10	0	33.3	0	0	0	50.0	0	0

1: matrilines, H=65.20, N=192, P<0.001, matriarchs, H=19.57, N=48, P<0.001; Period 2: matrilines, H=24.05, N=90, P<0.001, matriarchs, H=14.63, N=37, P<0.003). The 2 higher ranking matrilines and matriarchs were more aggressive towards non-matrilineals, both by number and rate of acts, than the 2 lower ranking matrilines and matriarchs (Table 3). Considering all troop members, the rate of aggression towards non-matrilineals was significantly correlated with individual rank in both stable periods (Spearman Rank Correlation Coefficient; Period 1,  $r_s=0.68$ , N=16, P<0.005; Period 2,  $r_s=0.66$ , N=11, P<0.04).

The distribution of Matriline 1's aggression among Matrilines 2, 3 and 4 differed significantly in both stable periods (Table 4; Period 1,  $\chi^2$ =42.86, P<0.001; Period 2,  $\chi^2$ =36.98, P<0.001), more aggression than expected being directed towards matrilines ranking closest to Matriline 1 in both cases (Table 4). The distribution of Matriline 2's aggression did not differ among Matrilines 3 and 4 in Stable Period 2; but Matriline 2 was more aggressive towards Matriline 3 than 4 in Stable Period 1 (Table 4; Period 1,  $\chi^2$ =17.88, P<0.001; Period 2,  $\chi^2$ =1.99, P=0.16). Matriline 3 was more aggressive towards Matriline 2 than 1 in Stable Period 1, but was too rarely aggressive towards Matrilines 1 and 2 in Stable Period 2 to justify analysis (Table 4; Period 1,  $\chi^2$ =13.25, P<0.001). The distribution of Matriline 4's aggressions among Matrilines 1, 2 and 3 differed significantly in both stable periods (Table 4; Period 1;  $\chi^2$ =43.08, P<0.001; Period 2,  $\chi^2$ =20.64, P<0.001), most aggression being directed towards the matriline ranking closest to Matriline 4 in both cases (Table 4).

## 2.4.1.3.2 Effects of Rank on Form of Aggression

Matrilines differed in the percentage of aggressive acts towards non-matrilineals that were escalated in both stable periods (Table 5; Period 1,  $\chi^2$ =43.79, P<0.001; Period 2,  $\chi^2$ =22.83, P<0.001), more aggression by the highest ranking matriline and less aggression by the lowest ranking matriline being escalated (Table 5). Matriarchs did not differ significantly in the percentage of aggressive acts towards non-matrilineals that were escalated (Table 5; Period 1,  $\chi^2$ =1.40, P=0.71; Period 2,  $\chi^2$ =2.61, P=0.46), but the trend with rank was similar to that for matrilines (Table 5). Both matrilines and matriarchs differed in the percentage of non-matrilineal aggressive acts that were confrontational (Table 5; Period 1: matrilines,  $\chi^2$ =20.20, P<0.001; matriarchs,  $\chi^2$ =8.41, P<0.04; Period 2: matrilines,  $\chi^2$ =150.97, P<0.001, matriarchs,

Table 4. The distribution of aggressions by individual matrilines among groups of matrilines which rank either above or below them, presented separately for the two stable periods. Obs % is the percentage of the aggressor matriline's aggressions directed at each of the recipient matrilines; Exp % is the percentage on the null hypothesis of equivalent probability of aggression to each group of recipient matriline and on the number of individuals in each recipient category. () is number of aggressive acts by the aggressor matriline to the recipient matrilines ranking either above or below them.

AGGRESSOR	Τ	RECIPIENT MATRILINES												
MATRILINE				Stable	Period 1									
		1		2		3		4						
	Obs %	Exp %	Obs % Exp %		Obs %	Exp %	Obs %	Exp %						
1 (554)	-	-	45.7	33.3	31.0	33.3	23.3	33.3						
2 (290)	-	-	-	-	62.4	50.0	37.6	50.0						
3 (55)	25.5	50.0	74.5	50.0	-	-	-	_						
4 (92)	13.0	33.3	21.7	33.3	65.2	33.3	-	-						
	<b>_</b>	<u></u>		Stable	Period 2									
1 (368)	-	-	35.3	22.2	29.3	33.3	35.3	44.5						
2 (616)	-	-	-	-	45.3	42.9	54.7	57.1						
3 (3)	-	-	-	-	-	-	-	-						
4 (161)	14.4	28.6	27.3	28.6	58.4	42.8		-						

Table 5. The percentage of non-matrilineal aggressions given by matrilines and matriarchs that were escalated and confrontational.% Esc is the percentage of aggressive acts that were escalated; % C is the percentage of aggressive acts that were confrontational.N is number of aggressive acts.

AGGRESSOR	STABLE PERIOD 1			<b>STABLE PERIOD 2</b>			<b>UNSTABLE PERIOD 1</b>			UNSTABLE PERIOD 2		
	% Esc	% C	N	% Esc	% C	N	% Esc	% C	N	% Esc	% C	N
Matriline 1	48.2	8.7	554	56.8	9.0	368	6.1	15.2	33	58.8	17.5	80
Matriline 2	35.3	9.5	326	49.1	6.6	656	37.5	29.2	24	66.7	100	3
Matriline 3	40.9	10.0	110	38.1	23.8	42	30.2	10.4	106	21.4	32.1	28
Matriline 4	14.1	23.9	92	35.4	41.0	161	36.4	21.2	33	30.2	44.2	43
Matriarch 1	40.4	5.5	218	50.0	2.3	174	0	0	4	-	-	-
Matriarch 2	39.1	2.2	92	46.9	5.8	567	_	-	-	66.7	100	3
Matriarch 3	33.3	4.8	42	33.3	20.8	24	30.4	17.4	23	-	-	-
Matriarch 4	25.0	25.0	8	42.1	47.4	19	0	0	0	0	0	0

 $\chi^2$ =65.77, P<0.001); more of the aggression by lower ranking matrilines and matriarchs being met with confrontation (Table 5).

The percentage of Matriline 1's aggressions towards Matrilines 2, 3 and 4 that were escalated did not differ between the recipient Matrilines in either stable period (Table 6; % values too close to justify analysis). Similarly, the percentage of Matriline 2's aggressions that were escalated towards Matrilines 3 and 4, the percentage of Matriline 3's towards 1 and 2, and the percentage of Matriline 4's towards 1, 2 and 3 did not differ in either stable period (Table 6; % values too close to justify analysis).

## 2.4.1.3.3 Effects of Juvenile Age and Sex on Frequency of Aggression

Given the effect of matrilineal rank on frequency of aggression to non-matrilineals, effects of age and sex on aggression towards non-matrilineals were analysed separately for high ranking (Matrilines 1 and 2 combined) and low ranking (Matrilines 3 and 4 combined) juveniles. To increase the sample size, data from Stable Periods 1 and 2 were pooled. High ranking males and females did not differ in frequency of aggression towards non-matrilineals (Table 7;  $\chi^2=0.06$ , P=0.81). However, low ranking males were more aggressive towards non-matrilineals than low ranking females (Table 7;  $\chi^2=79.89$ , P<0.001). For both high ranking and low ranking juveniles, older individuals were more aggressive towards non-matrilineals than younger individuals (Table 7; high rank,  $\chi^2=75.31$ , P<0.001; low rank,  $\chi^2=48.44$ , P<0.001).

## 2.4.1.3.4 Effects of Juvenile Age and Sex on Form of Aggression

Given the effect of matrilineal rank on form of aggression towards non-matrilineals, effects of age and sex on form of aggression were analysed separately for high ranking (Matrilines 1 and 2) and low ranking (Matrilines 3 and 4) juveniles, pooled for the two stable periods. Females escalated a higher percentage of their aggressive acts than males (Table 8; high rank,  $\chi^2=23.42$ , P<0.001; low rank,  $\chi^2=3.47$ , P=0.06). Males and females did not differ in the percentage of their bouts that were met with confrontation (Table 8; high rank,  $\chi^2=0.86$ , P=0.35; low rank,  $\chi^2=0.35$ , P=0.55). Young and old juveniles did not differ significantly in the percentage of their aggressive acts that they escalated (Table 8; high rank,  $\chi^2=2.16$ , Table 6. The percentage of aggressions by individual matrilines to matrilines which rank either above or below them that were escalated (% Esc), presented separately for the two stable periods. N is the number of aggressive acts by the aggressor matriline to the recipient matriline.

AGGRESSOR		RECIPIENT MATRILINES												
MATRILINE				Stab	le Period 1									
		1		2		3		4						
	% Esc	Ν	% Esc	N	% Esc	N	% Esc	N						
1	-	-	47.8	253	46.5	172	46.9	129						
2	-	-	-	-	39.2	181	41.2	119						
3	35.7	14	36.6	41	-	-	-	-						
4	16.7	12	15.0	20	13.3	60	-	-						
				Stab	le Period 2									
1	-	-	56.9	130	57.4	108	58.5	130						
2	-	-	-	-	50.5	279	48.7	337						
3	-	2	-	1	-	-	-	-						
4	39.1	23	31.8	44	35.1	94	-	-						

Table 7. The percentage of non-matrilineal aggressions given by different categories of aggressors (for females, old is > 2yrs; for males, old > 2.5yrs; categorisation based on mean age to sexual maturity of 4yrs for females and 5yrs for males), presented separately for the stable and unstable periods. Obs % is the percentage of aggressive acts given by each category of aggressor; Exp % is the percentage expected to be given by each category of aggressor on the null hypothesis of equivalent probability of aggression by each aggressor category and on the number of individuals in each aggressor category. N is number of aggressive acts.

AGGRESSOR	STABLE	PERIODS		AGGRESSOR	UNSTABL	UNSTABLE PERIODS			
	Obs %	Exp %	N		Obs %	Exp %	N		
High Ranking Male	49.6	50.0	423	Male	52.5	52.4	168		
High Ranking Female	50.4	50.0	430						
Low Ranking Male	79.8	54.6	249	Female	47.5	47.6	152		
Low Ranking Female	20.2	45.4	63						
High Ranking Old	37.9	25.0	323	Old	59.1	35.0	189		
High Ranking Young	62.1	75.0	530						
Low Ranking Old	59.3	40.0	185	Young	40.9	65.0	131		
Low Ranking Young	40.7	60.0	127						

Table 8. The percentage of non-matrilineal aggressions given by different categories of aggressors that were escalated and confrontational (old and young as in Table 7), presented separately for the stable and unstable periods. % Esc is the percentage of aggressive acts that were escalated; % C is the percentage of aggressive acts that were confronational. N is number of aggressive acts.

AGGRESSOR	STABLE	PERIODS		AGGRESSOR	UNSTABLE PERIODS			
	% Esc	% C	N		% Esc	% C	N	
High Ranking Male	39.7	13.2	423	Male	23.8	25.6	168	
High Ranking Female	56.5	10.9	430					
Low Ranking Male	37.0	28.5	249	Female	48.7	14.5	152	
Low Ranking Female	50.8	33.3	63					
High Ranking Old	45.5	13.6	323	Old	42.9	15.3	1 <b>89</b>	
High Ranking Young	50.9	11.7	530					
Low Ranking Old	40.0	30.3	185	Young	25.2	27.5	131	
Low Ranking Young	34.7	26.0	127					

P=0.14; low rank,  $\chi^2$ =0.70, P=0.40), nor in the percentage of aggressions that were met with confrontation (Table 8; high rank,  $\chi^2$ =0.52, P=0.47; low rank,  $\chi^2$ =0.48, P=0.49).

## 2.4.1.4 Aggression Received from Non-matrilineals

## 2.4.1.4.1 Effects of Rank on Frequency of Aggression

Both matrilines and matriarchs differed significantly in the number of aggressive acts received from non-matrilineals (Table 9; Period 1: matrilines,  $\chi^2=262.47$ , P<0.001, matriarchs,  $\chi^2=42.68$ , P<0.001; Period 2: matrilines,  $\chi^2=193.39$ , P<0.001, matriarchs,  $\chi^2=103.64$ , P<0.001). Consistent with this, the rate of aggression received from non-matrilineals differed between matrilines and matriarchs, although the differences were not statistically significant in Period 2 (Table 9; Kruskal-Wallis; Period 1: matrilines, H=31.12, N=192, P<0.001, matriarchs, H=11.84, N=48, P<0.002; Period 2: matrilines, H=7.13, N=90, P=0.07, matriarchs, H=6.25, N=37, P=0.10). The highest ranking matriline and matriarch received the least aggression both by number and rate of acts (Table 9). Considering all troop members, the rate of aggression received from non-matrilineals was significantly correlated with individual rank in Stable Period 1 (Spearman Rank Correlation Coefficient; r<sub>s</sub>=0.73, N=16, P<0.005), but the correlation was not statistically significant in Stable Period 2 (r<sub>s</sub>=0.49, N=11, P=0.12).

## 2.4.1.4.2 Effects of Rank on Form of Aggression

Matrilines differed significantly in the percentage of aggressive acts received from nonmatrilineals that were escalated in Period 1 but not in Period 2 (Table 10; Period 1, matrilines,  $\chi^2 = 18.01$ , P < 0.001; Period 2,  $\chi^2 = 1.88$ , P = 0.60). The difference in Period 1 was due to a lower percentage of aggressions received by the highest ranking matriline being escalated (Table 10). The highest ranking matriarchs received virtually no aggression from non-matrilineals; and for the remaining matriarchs, there was no apparent trend with rank in percentage of aggressions received that were escalated (Table 10). Matrilines differed significantly in their tendency to be confrontational when aggressed by non-matrilineals (Table 10; Period 1,  $\chi^2 = 44.79$ , P < 0.001; Period 2,  $\chi^2 = 91.18$ , P < 0.001), a higher percentage of the aggressions received by higher **Table 9.** The percentage and rate (no/h) of non-matrilineal aggressions received by matrilines and matriarchs, presented separately for the two stable and two unstable periods. Obs % is the percentage of aggressive acts received by each category of recipient; Exp % is the percentage on the null hypothesis of equivalent probability of aggression by each recipient category and on the number of individuals in each aggressor category. N is number of aggressive acts.

RECIPIENT	STAB	LE PER	IOD 1		STAB	LE PER	IOD 2		UNSTABLE PERIOD 1				UNSTABLE PERIOD 2			
	Obs %	Exp %	N	Rate	Obs %	Exp %	N	Rate	Obs %	Exp %	N	Rate	Obs %	Exp %	N	Rate
Matriline 1	4.8	25.0	52	0.77	5.2	18.2	65	0.34	29.6	26.7	58	0.98	6.5	20.0	10	0.09
Matriline 2	29.0	25.0	314	4.20	14.3	18.2	175	0.87	24.0	20.0	47	0.51	36.4	10.0	56	0.52
Matriline 3	38.2	25.0	413	4.74	38.9	27.3	477	2.36	16.8	26.7	33	0.89	23.4	20.0	36	0.34
Matriline 4	28.0	25.0	303	3.92	41.6	36.3	510	1.60	29.6	26.7	58	1.45	33.7	50.0	52	0.49
Matriarch 1	0	25.0	0	0	0.7	25.0	1	0.01	52.9	33.3	9	0.12	-	-	-	-
Matriarch 2	39.6	25.0	42	0.35	47.7	25.0	71	0.33	-	-	-	-	96.6	50.0	56	0.52
Matriarch 3	37.7	25.0	40	0.44	43.6	25.0	65	0.20	5.9	33.3	1	0.02	-	-	-	-
Matriarch 4	22.6	25.0	24	0.41	8.0	25.0	12	0.10	41.2	33.3	7	0.11	3.4	50.0	2	0.02
Table 10. The percentage of non-matrilineal aggressions received by matrilines and matriarchs that were escalated and confrontational. % Esc is the percentage of aggressive acts that were escalated; % C is the percentage of aggressive acts that were confrontational. N is number of aggressive acts.

RECIPIENT	STABL	E PERIC	<b>)D</b> 1	STABL	E PERIO	DD 2	UNSTAB	LE PER	IOD 1	UNSTA	BLE PE	RIOD 2
	% Esc	% C	N	% Esc	% C	N	% Esc	% C	Ν	% Esc	% C	Ν
Matriline 1	19.2	32.7	52	41.5	47.7	65	36.2	13.8	58	10.0	40.0	10
Matriline 2	42.0	10.8	314	51.4	18.3	175	29.8	25.5	47	50.0	19.6	56
Matriline 3	37.3	9.7	413	49.3	9.9	477	15.2	9.1	33	41.7	27.8	36
Matriline 4	47.5	6.9	303	49.4	8.2	510	25.9	12.1	58	46.2	38.5	52
Matriarch 1	-	-	0	-	-	1	0	0	9	-	-	-
Matriarch 2	28.6	4.8	42	53.5	14.1	71	-	-	-	50.0	19.6	56
Matriarch 3	35.0	10.0	40	30.8	7.7	65	0	100	1	-	-	-
Matriarch 4	25.0	16.7	24	66.7	8.3	12	14.3	0	7	50.0	50.0	2

ranking matrilines being met with confrontation (Table 10). There was no apparent trend with rank in the percentage of aggressions received by matriarchs that were met with confrontation (Table 10).

#### 2.4.1.4.3 Effects of Juvenile Age and Sex on Frequency of Aggression

High ranking males and females did not differ in aggression received from nonmatrilineals (Table 11;  $\chi^2=0.52$ , P=0.47). However, low ranking females received more aggression from non-matrilineals than low ranking males (Table 11;  $\chi^2=69.47$ , P<0.001). For both high ranking and low ranking juveniles, younger individuals received more aggression from non-matrilineals than older individuals (Table 11; high rank,  $\chi^2=11.10$ , P<0.001; low rank,  $\chi^2=343.76$ , P<0.001).

#### 2.4.1.4.4 Effects of Juvenile Age and Sex on Form of Aggression

A higher percentage of the aggression received by females was escalated than that received by males for both high ranking and low ranking juveniles (Table 12; high rank,  $\chi^2=4.52$ , P<0.04; low rank,  $\chi^2=9.05$ , P<0.003). Males were more likely to be confrontational when receiving aggression than females (Table 12; high rank,  $\chi^2=41.37$ , P<0.001; low rank,  $\chi^2=26.06$ , P<0.001). Young and old juveniles did not differ significantly in the percentage of aggressions they received that were escalated (Table 12; high rank,  $\chi^2=1.47$ , P=0.23; low rank,  $\chi^2=2.56$ , P=0.11). Young and old high ranking juveniles did not differ significantly in their tendency to be confrontational when receiving aggression (Table 12;  $\chi^2=0.33$ , P=0.57), but old low ranking juveniles were more likely to be confrontational when receiving aggression than young low ranking juveniles (Table 12;  $\chi^2=27.68$ , P<0.001).

#### 2.4.1.5 Injury Rates

Injury rates (no/individual/wk) during the stable periods were too low to justify analysis, but no differences were apparent by matrilineal rank, age or sex (Table 13).

Table 11. The percentage of non-matrilineal aggressions received by different categories of recipients (old and young as in Table 7), presented separately for the stable and unstable periods. Obs % is the percentage of aggressive acts recieved by each category of recipient; Exp % is the percentage expected to be received by each category of recipient on the null hypothesis of equivalent probability of aggression by each recipient category and on the number of individuals in each category. N is number of aggressive acts.

RECIPIENT	STABLE	PERIODS		RECIPIENT	UNSTAI	BLE PERIC	DDS
	Obs %	Exp %	Ν		Obs %	Exp %	N
High Ranking Male	48.4	50.0	238	Male	30.6	52.4	84
High Ranking Female	51.6	50.0	254				
Low Ranking Male	44.1	54.6	689	Female	69.4	47.6	191
Low Ranking Female	55.9	45.4	873				
High Ranking Old	18.5	25.0	91	Old	32.7	35.0	90
High Ranking Young	81.5	75.0	401				
Low Ranking Old	17.0	40.0	266 Young		67.3	65.0	185
Low Ranking Young	83.0	60.0	1296				

Table 12. The percentage of non-matrilineal aggressions received by different categories of recipients that were escalated and confrontational (old and young as in Table 7), presented separately for the stable and unstable periods. % Esc is the percentage of aggressive acts that were escalated; % C is the percentage of aggressive acts that were confrontational. N is number of aggressive acts.

RECIPIENT	STABLE	<b>PERIOD</b>	5	RECIPIENT	UNSTABLE PERIODS			
	% Esc	% C	N		% Esc	% C	N	
High Ranking Male	37.0	31.1	238	Male	32.1	33.3	84	
High Ranking Female	46.9	6.9 7.9 25						
Low Ranking Male	43.0	13.5	689	Female	34.6	17.8	191	
Low Ranking Female	50.7	5.8	873					
High Ranking Old	38.5	27.5	91	Old	28.9	21.1	90	
High Ranking Young	46.1	23.9	401					
Low Ranking Old	51.1	15.4	266	Young	36.2	23.2	185	
Low Ranking Young	45.5	5.9	1296					

Table 13. Injury rate (mean no/individual/wk) during the stable (combined) and unstable (combined) periods, presented for all individuals (overall) and separately by matriline, sex and age.

	STABLE PERIODS	UNSTABLE PERIODS
Matriline 1	0.034	0.118
Matriline 2	0.020	0.125
Matriline 3	0.015	0.116
Matriline 4	0.024	0.077
Males	0.025	0.052
Females	0.037	0.136
Old	0.041	0.146
Young	0.023	0.047
Overall	0.032	0.099



#### 2.4.2 Distribution and Form of Aggression in Unstable Periods

#### 2.4.2.1 Frequency of Aggression Towards Matrilineals vs Non-matrilineals

As for stable periods, troop members directed more aggression at non-matrilineals than at matrilineals in both unstable periods (Table 1; Period 1,  $\chi^2 = 15.36$ , P<0.001; Period 2,  $\chi^2 = 14.46$ , P<0.001). Consistent with this, the rate of aggression (no/h) towards nonmatrilineals was significantly higher than towards matrilineals (Table 1; Wilcoxon Matched-Pairs Signed-Ranks Test, paired by individuals; Period 1, T=8, N=16, P<0.05; Period 2, T=2, N=10, P<0.008).

A notable difference between stable and unstable periods was that the rates of matrilineal and non-matrilineal aggression (no/h) were lower in unstable than stable periods, but the difference was not statistically significant for matrilineal aggression (Table 1; Mann-Whitney Test, data pooled for the two stable and two unstable periods; matrilineal, Z=0.58, N=27, P=0.56; non-matrilineal, Z=3.29, N=26, P<0.001).

#### 2.4.2.2 Form of Aggression Towards Matrilineals vs Non-matrilineals

As for stable periods, a higher percentage of aggressive acts towards non-matrilineals was escalated than towards matrilineals (Table 2; Period 2,  $\chi^2 = 12.24$ , P<0.001; number of escalated matrilineal aggressions in Period 1 too few for analysis). The percentage of bouts that were met with confrontation was twice as high for aggression directed at non-matrilineals than matrilineals, but the difference was not statistically significant (Table 2; Period 2,  $\chi^2 = 0.66$ , P=0.42; number of matrilineal aggressions in Period 1 too few for analysis).

Not only was the frequency of aggression lower in unstable than stable periods, but the percentage of aggressions that were escalated tended to be lower in unstable than stable periods for both non-matrilineal and matrilineal aggression (Table 2; matrilineal, Stable 2 vs Unstable 2,  $\chi^2 = 6.70$ , P<0.01; number of matrilineal aggressions in Unstable 1 too few for analysis; non-matrilineal, Stable 1 vs Unstable 1,  $\chi^2 = 10.58$ , P<0.001; but note Stable 2 vs Unstable 2,  $\chi^2 = 1.21$ , P=0.27). A higher percentage of aggressive acts towards non-matrilineals was met with confrontation in unstable than stable periods (Table 2; Period 1,  $\chi^2 = 3.64$ , P<0.05; Period 2,  $\chi^2 = 30.34$ , P<0.001). The percentage of aggressions towards matrilineals that were met with

confrontation did not differ between stable and unstable periods (Table 2; Period 2,  $\chi^2 = 0.01$ , P=0.93; number of matrilineal aggressions in Period 1 too few for analysis).

# 2.4.2.3 Aggression Towards Non-matrilineals

# 2.4.2.3.1 Effects of Rank on Frequency of Aggression

As for the stable periods, both matrilines and matriarchs differed in number of aggressions towards non-matrilines in unstable periods (Table 3; Period 1: matrilines,  $\chi^2 = 75.15$ , P<0.001, matriarchs,  $\chi^2 = 33.56$ , P<0.001; Period 2: matrilines,  $\chi^2 = 102.36$ , P<0.001; number of aggressions by matriarchs too small to justify analysis in Period 2). Consistent with this, the rate of aggression directed at non-matrilineals differed significantly between matrilines and matriarchs (Table 3; Kruskal-Wallis Test; Period 1: matrilines, H=13.81, N=192, P<0.001; Period 2: matrilines, H=15.99, N=66, P<0.002; aggression by matriarchs too rare to justify analysis). However, in contrast to stable periods, matrilines and matriarchs that were high ranking at the onset of the observation period were not more aggressive towards non-matrilineals by number or rate of acts than lower ranking matrilines and matriarchs (Table 3). Moreover, considering all troop members, the rate of aggression towards non-matrilineals was not significantly correlated with individual rank (Spearman Rank Correlation Coefficient; Period 1, r<sub>s</sub>=0.18, N=16, P=0.48; Period 2, r<sub>s</sub>=0.53, N=10, P=0.08).

#### 2.4.2.3.2 Effects of Rank on Form of Aggression

Matrilines differed in the percentage of their aggressions directed at non-matrilineals that were escalated (Table 5; Period 1,  $\chi^2=10.34$ , P<0.02; Period 2,  $\chi^2=16.77$ , P<0.001) and confrontational (Table 5; Period 1,  $\chi^2=6.43$ , P=0.09; Period 2,  $\chi^2=17.35$ , P<0.001). However, in contrast to stable periods, there was no apparent trend for either the percentage of aggressions escalated or the percentage confrontational to be related to matrilineal rank (Table 5). Aggressions by matriarchs towards non-matrilineals in unstable periods were too few to justify analysis (Table 5).

#### 2.4.2.3.3 Effects of Juvenile Age and Sex on Frequency of Aggression

Since rank did not predict aggression towards non-matrilineals in unstable periods, effects of age and sex on aggression towards non-matrilineals were analysed for juveniles from all matrilines combined. Males and females did not differ in frequency of aggression towards nonmatrilineals in unstable periods (Table 7;  $\chi^2 = 0.001$ , P=0.97). However, as was true for stable periods, older juveniles were more aggressive towards non-matrilineals than younger juveniles in unstable periods (Table 7;  $\chi^2 = 81.44$ , P<0.001).

#### 2.4.2.3.4 Effects of Juvenile Age and Sex on Form of Aggression

Since rank did not predict the form of aggression towards non-matrilineals in unstable periods, effects of age and sex on form of aggression were analysed for juveniles from all matrilines combined. Females escalated a higher percentage of their aggressions towards nonmatrilineals than males (Table 8;  $\chi^2=20.46$ , P<0.001), and a lower percentage of the aggressions by females were met with confrontation (Table 8;  $\chi^2=5.43$ , P<0.02). Older juveniles escalated a higher percentage of their aggressions towards non-matrilineals than younger juveniles (Table 8;  $\chi^2=9.77$ , P<0.005), and a lower percentage of the aggressions by older juveniles were met with confrontation (Table 8;  $\chi^2=6.31$ , P<0.01).

#### 2.4.2.4 Aggression Received from Non-matrilineals

#### 2.4.2.4.1 Effects of Rank on Frequency of Aggression

Matrilines differed significantly in the number of aggressive acts received from nonmatrilineals (Table 9; Period 1,  $\chi^2$ =9.97, P<0.02; Period 2,  $\chi^2$ =135.22, P<0.001), and the rate of aggression received from non-matrilineals differed significantly between matrilines (Table 9; Period 1: Kruskal-Wallis Test; matrilines, H=11.27, N=192, P<0.001; Period 2: matrilines, H=14.99, N=66, P<0.002). However, there was no tendency for lower ranking matrilines to receive most aggression by number or rate of acts (Table 9). Aggression received by matriarchs appeared to differ, but was not apparently related to rank (Table 9; statistical analyses not warranted). Considering all troop members, the rate of aggression received from non-matrilineals was not significantly correlated with individual rank (Spearman's Rank Correlation Coefficient; Period 1,  $r_s=0.03$ , N=16, P=0.92; Period 2,  $r_s=0.42$ , N=10, P=0.23).

## 2.4.2.4.2 Effects of Rank on Form of Aggression

Matrilines did not differ significantly in the percentage of aggressions they received from non-matrilineals that were escalated (Table 10; Period 1,  $\chi^2 = 4.84$ , P=0.18; Period 2,  $\chi^2 = 5.68$ , P=0.13) or confrontational (Table 10; Period 1,  $\chi^2 = 5.35$ , P=0.15; Period 2,  $\chi^2 = 5.23$ , P=0.16). Aggressions received by matriarchs from non-matrilineals were too few to justify analysis (Table 10).

### 2.4.2.4.3 Effects of Juvenile Age and Sex on Frequency of Aggression

Since rank did not predict aggression received from non-matrilineals in unstable periods, effects of age and sex on aggression recieved from non-matrilineals were analysed for juveniles from all matrilines combined. Females received significantly more aggression from non-matrilineals than males in unstable periods (Table 11;  $\chi^2$ =52.48, P<0.001), but younger and older juveniles did not differ in frequency of aggression received (Table 11;  $\chi^2$ =0.58, P=0.45).

#### 2.4.2.4.4 Effects of Juvenile Age and Sex on Form of Aggression

Females and males did not differ significantly in the percentage of aggressions received from non-matrilineals that were escalated (Table 12;  $\chi^2=0.06$ , P=0.80), but males were more likely to be confrontational when receiving aggression than females (Table 12;  $\chi^2=7.20$ , P<0.008). Older and younger juveniles did not differ significantly in the percentage of aggressions received that were escalated (Table 12;  $\chi^2=1.14$ , P=0.28), nor in their tendency to be confrontational when receiving aggression (Table 12;  $\chi^2=0.06$ , P=0.81).

#### 2.4.2.5 Injury Rates

Despite lower rates of aggression during unstable than stable periods, the injury rate of individuals was higher during unstable periods (Table 13; Mann-Whitney Test, data pooled for the two stable and two unstable periods; Z=3.72, N=53, P<0.001), indicating a higher probability that an aggressive interaction will result in injury during unstable than stable periods.

Injury rates during unstable periods were significantly higher for females than for males, and for older than for younger juveniles (Table 13; sex, Z=5.09, N=20, P<0.001; age, Z=5.21, N=20, P<0.001).

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#### **2.5 DISCUSSION**

#### 2.5.1 Stable Periods

During both periods in which the matrilineal dominance hierarchy was stable in this study, vervets were more often aggressive, and escalated more of their aggressions, to individuals from other matrilines than to members of their own matriline. Cheney (1977), Kurland (1977) and Silk *et al.* (1981b) have previously reported higher rates of aggression towards non-matrilineals in baboons, Japanese macaques, and bonnet macaques respectively, but Bernstein & Ehardt (1986) reported higher rates to matrilineals in captive troops of rhesus macaques. The distribution of aggression observed in most studies is therefore consistent with the perspective that matrilines act as cohesive units within troops, but this observation can not explain why certain matrilines remain dominant over others during the extended stable periods characteristic of matrilineal dominance hierarchies in Old World monkeys.

A more pertinent observation re the maintenance of matrilineal ranks is that higher ranking matrilines and matriarchs aggressed non-matrilineals more frequently, and escalated more of their aggressions, than lower ranking matrilines and matriarchs during stable periods. Conversely, the highest ranking matrilines and matriarchs received the least aggression and the lowest proportion of escalated aggressive acts. Although these patterns of aggression could contribute to the maintenance of matrilineal ranks once ranks are established, the results of this study strongly suggest that they are better perceived as a consequence than cause of the prevailing pattern of matrilineal rank. If the probability of aggression being met with confrontation is an index of its cost, the simplest explanation for the higher rates and more escalated aggression of higher ranking matrilines is that their aggression has a lower retaliatory cost (see also Dunbar 1988). A lower percentage of the aggression by higher ranking matrilines and matriarchs was met with confrontation, and higher ranking matrilines were more likely to be confrontational when receiving aggression than lower ranking matrilines in this study. Moreover, and most significantly, higher ranking matrilines were more aggressive, by frequency and form, than lower ranking matrilines in both stable periods, even though the stable periods were interspersed by an unstable period in which matrilineal rank reversals were common. The consequence of the reversals was that the highest ranking matriline in Period I was a low ranking matriline in Period 2, and one of the lower ranking matrilines in Period 1 was the highest ranking matriline in Period 2. These results strongly suggest that the tendency of higher ranking matrilines to be more aggressive, and lower ranking matrilines to be less aggressive, is the consequence of their rank rather than an intrinsic characteristic of the specific matrilines.

High ranking male and female juveniles did not differ significantly in frequency of aggression received from non-matrilineals in this study, although a higher percentage of the aggression received by females was escalated. Low ranking females received significantly more aggression than low ranking males, and again a higher percentage of the aggression received was escalated. Several studies have previously reported that juvenile females receive more aggression than juvenile males, although the form of aggression is not usually reported (e.g. Cheney 1978, Pereira 1988 for baboons; Dittus 1977, 1979 for toque macaques; Berman 1980a,b for rhesus macaques; Silk et al. 1981b,c for bonnet macaques; Horrocks & Hunte 1983a for vervets). A typical explanation is that, since females remain in natal troops but males leave at puberty, troop members should attempt to control the rank of females more than that of males (e.g. Dittus 1979; Horrocks & Hunte 1983a; Silk & Boyd 1983; Pereira 1988). This may well influence aggression, but a more proximate cause could simply be that the cost of aggressing juvenile males may be higher than that of aggressing juvenile females. Juvenile males were more likely to be confrontational when receiving aggression than juvenile females in this study. This sex difference is probably a consequence of sexual dimorphism in size. In vervets, males are larger than females and may have greater individual agonistic power (Chapter 1; see also Lee & Oliver 1979, Pereira 1988). Consistent with this, males were more frequently aggressive than females under circumstances in which individual agonistic power could be expected to strongly influence the tendency to be aggressive (i.e. for low ranking juveniles); but males and females did not differ in frequency of aggressions under circumstances in which social rank may more strongly influence the tendency to be aggressive than individual agonistic power (i.e. for high ranking juveniles).

The effects of juvenile age on aggression observed in this study support the suggestion that the probability of a recipient of aggression being confrontational strongly influences its likelihood of being aggressed; and that the probability of the recipient being confrontational can be influenced by its size and hence individual agonistic power. Older (larger) juveniles were more often confrontational when receiving aggression than younger juveniles, the difference being statistically significant only for low ranking juveniles. Consistent with this, older juveniles received less aggression from non-matrilineals than younger juveniles. Moreover, older juveniles were more aggressive to non-matrilineals than younger juveniles, a difference that again may reflect the difference in size and hence in individual agonistic power.

The influence of confrontational probability on the distribution of aggression can therefore largely explain the effects of rank, age and sex on the distribution of aggressions observed during stable periods in this study. Higher ranking matrilines were more confrontational when receiving aggression, and received less aggression; males were more confrontational than females, and received less aggression; and older juveniles were more confrontational than younger juveniles, and received less aggression. However, none of these rank-, age- and sex-specific differences in confrontational probability and aggression frequency can explain why certain matrilines remain dominant over others during stable periods in this study. The tendency of high ranking matrilines to be more confrontational and receive less aggression may contribute to the maintenance of rank once rank is established, but is more appropriately perceived as a consequence than cause of high rank. Moreover, matrilineal rank was not correlated with either the age composition or sex composition of the matriline during stable periods in this study (Chapter 1). Matrilineal rank was also not correlated with matriline size during stable periods, suggesting that rank is not determined by sheer numbers in the matriline (Chapter 1). Ehardt & Bernstein (1986) and Samuels et al. (1987) also found no correlation between matrilineal rank and size in rhesus macaques and yellow baboons respectively (but see Silk & Boyd 1983 and Chapais 1988 for suggesting a correlation in macaques).

The fact that characteristics of matrilines during stable periods do not predict matrilineal ranks may suggest that the behaviour of non-matrilineals is important in stabilising matrilineal ranks. For example, if a matriline is more aggressive to the lower than higher ranking of any pair of matrilines which rank either above or below it, this could contribute to maintaining the relative ranks of the recipient matrilines. However, the distribution of aggression observed in this study does not suggest that this typically occurs. The best predictor of the distribution of aggression by individual matrilines was proximity of rank, i.e. rank distance. For both "uprank"

(the recipient matrilines outranked the aggressor matriline) and "downrank" aggressions (the recipient matrilines were outranked by the aggressor matriline), matrilines were most aggressive to those matrilines ranking adjacent to themselves (see Bernstein 1968, Mazur 1973, Clutton-Brock & Harvey 1976, Huffman 1987, Johnson 1989, and de Waal 1991 for similar observations). For downrank aggressions, this implies that the higher ranking of any pair of recipient matrilines receives most of the aggression. For uprank aggressions, it does imply that the lower ranking of any pair of recipient matrilines receives most of the aggressions (only 10% of aggressions were uprank in this study troop). If non-matrilineals are important in stabilising the relative ranks of imatrilines during stable periods in vervets, the effect must therefore be through their distribution of support rather than distribution of aggression (Chapter 3).

#### **2.5.2 Unstable Periods**

The distribution of aggression during unstable periods in the matrilineal dominance hierarchy was similar to that during stable periods in several respects. First, vervets were more often aggressive, and escalated more of their aggressions, to individuals from other matrilines than to members of their own matriline. Second, females escalated a higher proportion of their aggressions than males and received more aggression than males; and males were more likely to be confrontational when receiving aggression. Third, older juveniles were more aggressive than younger juveniles.

A major difference between stable and unstable periods was that during the latter, neither the frequency or form of aggression, either given or received, was correlated with the ranks of matrilines at the onset of the unstable periods. This is consistent with previous suggestions that the tendency of high ranking matrilines to be more aggressive, and lower ranking matrilines to be less aggressive, is not a characteristic of the matriline but is the consequence of the matriline's rank. The ranks of matrilines are, by definition, changing during unstable periods.

A notable difference between stable and unstable periods was that rates of aggression were significantly lower in the latter, and fewer aggressions were escalated. This was surprising since unstable periods are typically perceived as aggressive periods. However, a higher percentage of aggression was met with confrontation in unstable than stable periods. This again suggests that the probability of an aggression being met with confrontation is a good index of its cost, and hence is a good predictor of aggression frequency. Although aggression rates were lower in unstable than stable periods, injury rates were significantly higher. This indicates that the probability of an aggressive encounter resulting in injury is appreciably higher in unstable periods. Injury probability is clearly a good index of aggression cost, and the high injury rates observed in unstable periods are consistent with the low rates of aggression in this context.

The sex- and age-specific differences in injury rates observed during unstable periods in this study indicate that involvement in aggression during unstable periods significantly increases injury probability. Females escalated more of their aggressions than males and received more aggressions, and injury rates were significantly higher for females than males during unstable periods. Older juveniles were more aggressive than younger juveniles, and had significantly higher injury rates during unstable periods.

These sex- and age-specific differences in aggression rates and injury rates during unstable periods may suggest that the behaviour of females, particularly older juvenile females, is important in influencing the ranks of matrilines during unstable periods and as troops emerge from unstable periods and enter new periods of matrilineal rank stability. It is of interest in this context that the number of juvenile females in a matriline was typically positively correlated with matrilineal rank during unstable periods in this study, and predicted the relative ranks of the matrilines as they entered new periods of rank stability (Chapter 1). Further clarification of the role of matrilineals and non-matrilineals in influencing matrilineal rank in vervet monkeys requires an investigation of sex-specific and age-specific differences in support during stable and unstable periods in the matrilineal dominance hierarchy (see Chapter 3).

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**CHAPTER 3** 

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# THE DISTRIBUTION OF SUPPORT IN AGGRESSIVE DISPUTES DURING STABLE AND UNSTABLE PERIODS IN THE MATRILINEAL DOMINANCE HIERARCHY OF FERAL VERVET MONKEYS (*CERCOPITHECUS AETHIOPS SABAEUS*)

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#### **3.1 ABSTRACT**

The distribution of support during two stable and two unstable periods in the matrilineal dominance hierarchy of a feral troop of vervet monkeys was investigated. During both stable and unstable periods, individuals supported members of their own matriline more often than those from other matrilines. However, this does not explain why certain matrilines remain dominant over others during stable periods, since matrilineal rank during stable periods did not appear to be influenced by matriline size, composition, or matrilineal power. Higher ranking matrilines provided more matrilineal support than lower ranking matrilines during stable periods, but this is a consequence rather than cause of matrilineal rank. Higher ranking matrilines received more non-matrilineal support than lower ranking matrilines during stable periods, perhaps because higher ranking matrilines are more valuable as support reciprocators. The suggestion that value as a reciprocator influences the distribution of non-matrilineal support is supported by the fact that older juveniles receive more non-matrilineal support than younger juveniles, and males (larger) receive more support than females (smaller). The tendency for higher ranking matrilines to receive more non-matrilineal support than lower ranking matrilines may be a major factor stabilising matrilineal ranks during stable periods. Non-matrilineal support was less common m unstable than stable periods, perhaps because reciprocation predictability is lower. The lower support frequency increases the probability of matrilineal rank reversals, thereby contributing to the continuation of the unstable period. By contrast, matrilineal support was more common in unstable than stable periods. In unstable periods, female juveniles provided more matrilineal support than male juveniles, and older juveniles provided more support than younger juveniles. This is consistent with the observation that matrilineal rank was typically positively correlated with the number of juvenile females in the matriline, and with an index of matrilineal power, during unstable periods. These results suggest that the characteristics of matrilines and behaviour of matriline members, in particular the number and behaviour of older juvenile females, are important in determining matrilineal rank as troops emerge from unstable periods and enter new periods of matrilineal rank stability.

#### **3.2 INTRODUCTION**

There are few long-term studies of stability in matrilineal dominance hierarchies in Old World monkeys. However, it is now evident that matrilineal ranks in Old World monkeys typically remain unchanged for extended periods (stable periods), with unstable periods characterised by matrilineal rank reversals being relatively rare and of shorter duration (e.g. Hausfater *et al.* 1982, Samuels *et al.* 1987 for baboons; Mori *et al.* 1989, Rhine *et al.* 1989 for macaques; Bramblett *et al.* 1982, Chapter 1 for vervets). Studies of matrilineal composition during stable periods have provided little insight into the processes stabilising rank. For example, matrilineal rank may not be correlated with matrilineal size in macaques (Sugiyama & Ohsawa 1982; Ehardt & Bernstein 1986; but see Silk & Boyd 4983 and Chapais 1988), baboons (Altmann 1980; Samuels *et al.* 1987), or vervets (Chapter 1), nor with matrilineal age composition, sex composition or power (based on an age/sex tendency to support summed for all matrilineal members; Chapter 1).

Differences between matrilines in aggressiveness could explain differences in matrilineal rank during stable periods. In macaques (Datta 1983), baboons (Seyfarth 1976) and vervets (Horrocks & Hunte 1983; Chapter 2), higher ranking matrilines are more often aggressive than lower ranking matrilines. However, at least in vervets, this is a consequence of rank rather than an inherent characteristic of matrilines, and hence is not a causal factor explaining why certain matrilines maintain dominance over others during stable periods (Chapter 2).

The fact that neither matrilineal size, composition nor inherent aggressiveness can explain the relative ranks of matrilines during stable periods in vervets may suggest that the behaviour of non-matrilineals is important in stabilising ranks. For example, if matrilines are more aggressive to the lower than higher ranking of any pair of matrilines which rank either above or below them, the behaviour of the aggressor matriline could be contributing to the maintenance of the relative ranks of the recipient matrilines. However, the distribution of aggression in vervets does not suggest that this typically occurs. The best predictor of the distribution of nonmatrilineal aggression was proximity of rank, i.e. matrilines were most aggressive to those matrilines ranking adjacent to themselves (Chapter 2; see Bernstein 1968, Mazur 1973, Clutton-Brock & Harvey 1976 and de Waal 1991 for similar observations). This suggests that, if nonmatrilineals stabilise matrilineal ranks during stable periods in vervets, the effect must be through the distribution of supports rather than distribution of aggressions.

In Gid World monkeys, individuals typically support matrilineal members over nonmatrilineal members in aggressive disputes (e.g. Kaplan 1977, Kurland 1977, Massey 1977, Watanabe 1979, Bernstein & Ehardt 1985, Kaplan et al. 1987, Silk 1982, 1992 for macaques; Cheney 1977, Dunbar 1980, 1984 for baboons; Hunte & Horrocks 1987 for vervets). Moreover, some studies suggest that higher ranking matrilines support matrilineal members more frequently than do lower ranking matrilines (e.g. Berman 1980 for macaques; Cheney 1977, Walters 1980 for baboons; Cheney 1983, Fairbanks & McGuire 1985, Hunte & Horrocks 1987 for vervets). However, as is the case for aggression, this behaviour may be the consequence rather than the cause of matrilineal rank. Finally, there is some evidence to suggest that non-matrilineals preferentially support the higher ranking of the two opponents in aggressive disputes, a tendency which would stabilise prevailing ranks of the opponents (Hunte & Horrocks 1987; Chapais et al. 1991). However, effects of the distribution of non-matrilineal support on matrilineal rank stability have not been specifically investigated in feral troops. Objectives of this chapter are therefore to determine whether individuals are more supportive of matrilineal than nonmatrilineal members in feral vervet monkeys in Barbados, to determine whether higher ranking matrilines support matrilineal members more frequently than lower ranking matrilines and to comment on whether this difference is a characteristic of the matrilines or a consequence of their ranks, and to investigate the distribution of non-matrilineal support and comment on whether such support may stabilise prevailing matrilineal hierarchies. Support patterns in unstable periods have not been reported for any Old World monkey. The final objective of this chapter is to investigate the frequency and distribution of support during unstable periods in the dominance hierarchy of feral vervet monkeys, and by comparison with patterns observed during stable periods, to comment on the role of support in stabilising matrilineal ranks in vervets.

#### **3.3 METHODS**

#### **3.3.1 Subjects**

The feral vervet troop investigated in this study was habituated in 1979 and has been continuously monitored since (Horrocks 1982; Chapter 1). The genealogy of troop members is known, all are individually recognizable and most can be approached to within 1m by regular observers (see Chapters 1 and 2). The colonisation of Barbados by vervets, and their intra-island distribution and life history characteristics, are provided by Horrocks (1986).

# 3.3.2 Chronology of Data Collection

The time and duration of stable and unstable periods in the matrilineal dominance hierarchy of the study troop is described in Chapter 1.

The chronology of data collection for the present study was the same as that used for acquiring the data on aggression, and is described in Chapter 2. Briefly, two data sets were collected during stable periods and two during unstable periods. Stable Period 1 was between September 1982 and March 1983, Stable Period 2 between January 1991 and June 1991, Unstable Period 1 between January 1987 and March 1987, and Unstable Period 2 between May 1989 and July 1989. Matrilineal and troop characteristics and composition are provided for each of these periods in Chapters 1 and 2.

#### **3.3.3 Method of Data Collection**

Most supports were by single individuals in dyadic disputes, and only these were considered in this study. Supports in aggressive disputes between individuals from the same matriline are not considered. Matrilineal support therefore refers to the situation in which the supporting animal belongs to the same matriline as the recipient of the support, but to a different matriline than the opponent. Non-matrilineal support refers to the supporting animal belonging to a different matriline than either the recipient or the opponent. Mild aggressive behaviours included threat and lunge; escalated aggressive behaviours included chase, hit, grab, bite, and hold down and bite. A confrontational aggression was defined as one in which the recipient of the aggression retaliated, sensu through a counter-threat, counter-lunge, or physical contact response (hit-back, grab-back, bite-back).

The method of data collection was the same as that used for acquiring the aggression data, and is described in Chapter 2. Behaviour-dependent sampling was used to collect all data on matrilineal and non-matrilineal supports. Data were typically collected between 0900 and 1100hrs, and between 1600 and 1800hrs. The time that each individual was present during each observation session was recorded. Total observation time was 229h for Stable Period 1, 326h for Stable Period 2, 82h for Unstable Period 1, and 108h for Unstable Period 2. The outcomes of dyadic aggressive/submissive disputes were used to determine social rank throughout the study (see Chapter 1).

#### 3.3.4 Data Analysis

Differences in the distributions of numbers of supports given or received by different categories of supporters or recipients have been analysed by  $\chi^2$  Goodness of Fit, and differences in percent support in aggressive disputes (supports/disputes x 100) have been analysed by  $\chi^2$  Contingency tests. All  $\chi^2$  analyses have been conducted on count data, and have been adjusted for continuity where appropriate (Zar 1984).

#### **3.4 RESULTS**

#### 3.4.1 Support in Stable Periods

# 3.4.1.1 Frequency of Support by Matrilineals vs Non-matrilineals

Supports occurred in 220 (20.3%) of the 1082 between-matriline dyadic aggressive disputes observed in Stable Period 1, and in 305 (24.9%) of the 1227 disputes observed in Stable Period 2. Supports by matrilineals were more common than by non-matrilineals, allowing for the higher number of non-matrilineals than matrilineals for each individual in the troop (Table 1; Period 1,  $\chi^2$ =215.03, P<0.001; Period 2,  $\chi^2$ =45.83, P<0.001). On only one occasion in Stable Period 1 (<0.5% of supports) and 3 occasions in Stable Period 2 (<1% of supports) was an individual observed to support a non-matrilineal against a matrilineal member in an aggressive dispute.

# 3.4.1.2 Effects of Rank, Age and Sex on Support Given by Matrilineals

Higher ranking matrilines and matriarchs provided more matrilineal supports than lower ranking matrilines and matriarchs in both stable periods (Table 2; Period 1: matrilines,  $\chi^2$ =115.08, P<0.001, matriarchs,  $\chi^2$ =72.46, P<0.001; Period 2: matrilines,  $\chi^2$ =113.21, P<0.001, matriarchs,  $\chi^2$ =77.71, P<0.001). Given this effect of matrilineal rank on supports, support differences between male and female juveniles, and between young and old juveniles, were analysed separately for high ranking and low ranking individuals. The data were pooled for Periods 1 and 2 to increase sample size. For high ranking juveniles, females provided more matrilineal supports than males, and older juveniles provided more matrilineal supports than supports than males,  $\chi^2$ =27.59, P<0.001; age,  $\chi^2$ =47.36, P<0.001). Age and sex differences in matrilineal supports were small for low ranking juveniles, and supports were too rare to justify analysis (Table 3).

Matrilineal support was more likely when matrilineal members were involved in escalated than mild aggressions (Periods 1 and 2 combined; supports in 12.6% of escalated aggressions; in 8.4% of mild aggressions;  $\chi^2 = 10.79$ , P < 0.001); and more likely when matrilineal members were involved in confrontational than non-confrontational aggressions (Periods 1 and 2 Table 1. The number and percent of matrilineal and non-matrilineal supports in between-lineage dyadic aggressive disputes, presented separately for the two stable and two unstable periods. Obs N is number of supports observed; Exp N is number of supports expected on the null hypothesis of equivalent probability of matrilineal and non-matrilineal support and on the ratio of matrilineals to non-matrilineals in the troop. n is the number of between-lineage aggressive disputes observed. % is supports/disputes x 100.

PERIOD	MATRIL	INEAL SUPP	ORTS		NON-MATRILINEAL SUPPORTS					
	Obs N	Exp N	n	%	Obs N	Exp N	n	%		
Stable 1	131	44	1082	12.1	89	176	1082	8.2		
Stable 2	107	60	1227	8.7	198	245	1227	16.1		
Unstable 1	51	13	196	27.5	12	53	196	6.1		
Unstable 2	41	17	154	26.6	9	33	154	5.8		

# Table 2. The number and proportion of matrilineal supports given by the 4 matrilines and matriarchs presented separately for each of the stable and unstable periods. Obs is the proportion of total supports by each supporter category; Exp is the proportion expected on the null hypothesis of equivalent probability of support by the supporter categories, given the numbers of individuals in each category. N is number of supports.

SUPPORTER	STABL	E 1		STABL	E 2		UNSTABLE 1			UNSTA	BLE 2	
	Obs	Exp	N	Obs	Exp	N	Obs	Exp	N	Obs	Exp	N
Matriline 1	0.64	0.25	84	0.47	0.18	50	0.06	0.27	3	0.37	0.20	15
Matriline 2	0.22	0.25	29	0.38	0.18	41	0.29	0.20	15	0.02	0.10	1
Matriline 3	0.07	0.25	9	0.01	0.27	1	0.65	0.27	33	0	0.20	0
Matriline 4	0.07	0.25	9	0.14	0.37	15	0	0.27	C	0.61	0.50	25
Matriarch 1	0.75	0.25	39	0.69	0.25	45	0.06	0.33	1	-	-	-
Matriarch 2	0.17	0.25	9	0.26	0.25	17	-	-	-	0	0.50	0
Matriarch 3	0.08	0.25	4	0.02	0.25	1	0.94	0.33	15	-	-	-
Matriarch 4	0	0.25	0	0.03	0.25	2	0	0.33	0	0	0.50	0

Table 3. The number and proportion of matrilineal supports given by different categories of supporters, presented separately for the stable and unstable periods (for females, old > 2yrs; for males, old > 2.5yrs; categorisation based on mean age to sexual maturity of 4yrs for females and 5yrs for males). Obs is the proportion of total supports given by each category of supporter; Exp is the proportion expected by each category of supporter on the null hypothesis of equivalent probability of support by each category and on the number of individuals in each category. N is number of supports.

SUPPORTER	STABLE	PERIODS		SUPPORTER	<b>UNSTABLE PERIODS</b>			
	Obs	Ехр	N		Obs	Exp	N	
High Ranking Male	0.23	0.50	23	Male	0.42	0.52	32	
High Ranking Female	0.77	0.50	75					
Low Ranking Male	0.52	0.55	12	Female	0.58	0.48	44	
Low Ranking Female	0.48	0.45	11					
High Ranking Old	0.55	0.25	54	Old	0.53	0.35	40	
High Ranking Young	0.45	0.75	44					
Low Ranking Old	0.52	0.40	12	Young	0.47	0.65	36	
Low Ranking Young	0.48	0.60	11					

combined; supports in 16.2% of confrontational aggressions; in 9.5% of non-confrontational aggressions;  $\chi^2_c = 10.63$ , P < 0.001).

#### 3.4.1.3 Effects of Rank, Age and Sex on Support Received by Matrilineals

By definition, matrilines receive the same number of matrilineal supports that they provide. Higher ranking matrilines therefore received significantly more matrilineal support than lower ranking matrilines (see Table 2 and subsection above). For high ranking juveniles, males and females did not differ significantly in either the number or percent (supports/disputes) of matrilineal supports they received (Table 4; number,  $\chi^2 = 1.15$ , P=0.28; percent,  $\chi^2_e = 2.99$ , P=0.08). For high ranking juveniles, older individuals received significantly more matrilineal supports than younger individuals (Table 4;  $\chi^2 = 4.59$ , P<0.04). However, this may be driven by the fact that older juveniles are involved in substantially more aggressive disputes than younger juveniles (Chapter 2), since the percentage of aggressive disputes in which matrilineal support was received did not differ between young and old juveniles (Table 4;  $\chi^2 = 0.18$ , P=0.67). Low ranking juveniles received too few matrilineal supports to justify analysis by age and sex (Table 4).

#### 3.4.1.4 Effects of Rank, Age and Sex on Support Given by Non-matrilineals

Higher ranking matrilines and matriarchs provided more support to non-matrilineals than lower ranking matrilines and matriarchs in both stable periods (Table 5; Period 1: matrilines,  $\chi^2$ =11.63, P<0.01, matriarchs,  $\chi^2$ =12.0, P<0.001; Period 2: matrilines,  $\chi^2$ =278.0, P<0.001, matriarchs,  $\chi^2$ =177.0, P<0.001). Given this effect of rank, differences between male and female juveniles, and between young and old juveniles, in the provision of non-matrilineal support were analysed separately for high ranking and low ranking individuals, pooled for Periods 1 and 2. High ranking males and females did not differ in the number of non-matrilineal supports provided, but low ranking males provided significantly more non-matrilineal supports than low ranking females (Table 6; high rank,  $\chi^2$ =0.01, P=0.92; low rank,  $\chi^2$ =4.78, P<0.03). Older juveniles provided more non-matrilineal supports than younger juveniles, but the difference was only statistically significant for high ranking individuals (Table 6; high rank,  $\chi^2$ =146.8, P<0.001; low rank,  $\chi^2$ =1.33, P=0.25). Table 4. The number, proportion and % (supports/disputes) of matrilineal supports received by different categories of recipients (old and young as in Table 3), presented separately for the stable and unstable periods. Obs is the proportion of total supports received by each category of recipient; Exp is the proportion expected by each category of recipient on the null hypothesis of equivalent probability of receiving support and on the number of individuals in each recipient category. N is number of supports.

RECIPIENT	STABL	E PERICI	DS	•	RECIPIENT	UNSTA	BLE PER	RIODS	
	Obs	Exp	N	%		Obs	Ехр	N	%
High Ranking Male	0.46	0.50	67	8.8	Male	0.55	0.52	44	17.5
High Ranking Female	0.54	0.50	80	11.7					
Low Ranking Male	0.68	0.55	13	1.4	Female	0.45	0.48	36	10.5
Low Ranking Female	0.32	0.45	6	0.6					
High Ranking Old	0.33	0.25	48	11.6	Old	0.60	0.35	48	17.2
High Ranking Young	0.67	0.75	99	10.6					
Low Ranking Old	0.37	0.40	7	1.6	Young	0.40	0.65	32	10.1
Low Ranking Young	0.63	0.60	12	0.8					

Table 5. The number and proportion of non-matrilineal supports given by the 4 matrilines and matriarchs presented separately for each of the stable and unstable periods. Obs is the proportion of total supports by each supporter category; Exp is the proportion expected on the null hypothesis of equivalent probability of support by the supporter categories, given the numbers of individuals in each category. N is number of supports.

SUPPORTER	STABL	E 1		STABL	.E 2		UNSTABLE 1			UNSTABLE 2		
	Obs	Ехр	N	Obs	Exp	N	Obs	Exp	<u>N</u>	Obs	Exp	N
Matriline 1	0.28	0.25	25	0.56	0.18	111	0.33	0.27	5	0.33	0.20	3
Matriline 2	0.38	0.25	34	0.34	0.18	68	0.07	0.20	1	0.22	0.10	2
Matriline 3	0.19	0.25	17	0.02	0.27	4	0.20	0.27	3	0	0.20	0
Matriline 4	0.15	0.25	13	0.08	0.36	15	0.40	0.27	6	0.45	0.50	4
Matriarch 1	0.58	0.25	7	0.61	0.25	73	1.00	0.33	1	-	-	
Matriarch 2	0.42	0.25	5	0.39	0.25	47	-	-	-	0	0.50	0
Matriarch 3	0	0.25	0	0	0.25	0	0	0.33	0	-		-
Matriarch 4	0	0.25	0	0	0.25	0	0	0.33	0	0	0.50	0

Table 6. The number and proportion of non-matrilineal supports given by different categories of supporters, presented separately for the stable and unstable periods (old and young as in Table 3). Obs is the proportion of total supports given by each category of supporter; Exp is the proportion expected by each category of supporter on the null hypothesis of equivalent probability of support by each category and on the number of individuals in each category. N is number of supports.

SUPPORTER	STABLE	PERIODS		SUPPORTER	UNSTAE	BLE PERIO	DS
	Obs	Ехр	N		Obs	Ехр	N
High Ranking Male	0.51	0.50	53	Male	0.57	0.52	13
High Ranking Female	0.49	0.50	52				
Low Ranking Male	0.70	0.55	35	Female	0.43	0.48	10
Low Ranking Female	0.30	0.45	15				
High Ranking Old	0.76	0.25	80	Old	0.44	0.35	10
High Ranking Young	0.24	0.75	25				
Low Ranking Old	0.48	0.40	24	Young	0.57	0.65	13
Low Ranking Young	0.52	0.60	26				

Non-matrilineal support was more likely when individuals were involved in escalated than mild aggressions (Periods 1 and 2 combined; supports in 17.2% of escalated aggressions; in 8.5% of mild aggressions;  $\chi^2$ =39.55, P<0.001); and more likely when individuals were involved in confrontational than non-confrontational aggressions (Periods 1 and 2 combined; supports in 20.4% of confrontational aggressions; in 11.4% of non-confrontational aggressions;  $\chi^2$ =16.56, P<0.001).

#### 3.4.1.5 Effects of Rank, Age and Sex on Support Received by Non-matrilineals

High ranking matrilines received more non-matrilineal supports, and a higher percentage of non-matrilineal supports in aggressive disputes, than low ranking matrilines in both stable periods (Table 7; Period 1: number,  $\chi^2 = 16.75$ , P<0.001, percent,  $\chi^2 = 7.28$ , P=0.06; Period 2: number,  $\chi^2 = 219.66$ , P<0.001, percent,  $\chi^2 = 79.24$ , P<0.001). Similarly, high ranking matriarchs received more non-matrilineal supports, and a higher percentage of non-matrilineal supports in aggressive disputes, than low ranking matriarchs (Table 7; Period 2: number,  $\chi^2 = 177.02$ , P<0.001, percent,  $\chi^2_c = 13.16$ , P<0.005; supports of matriarchs too few in Period 1 to justify analysis).

High ranking males and females did not differ in either the number or percent (supports/disputes) of non-matrilineal supports they received (Table 8; number,  $\chi^2 = 0.20$ , P=0.66; percent,  $\chi^2_c = 0.47$ , P=0.49); but low ranking males received more non-matrilineal support than low ranking females by number and percent (Table 8; number,  $\chi^2 = 5.90$ , P<0.02; percent,  $\chi^2_c = 16.56$ , P<0.001). For high ranking juveniles, older individuals received more non-matrilineal support, by number and percent, than younger individuals (Table 8; number,  $\chi^2 = 7.17$ , P<0.01; percent,  $\chi^2_c = 22.82$ , P<0.001). For low ranking juveniles, older and younger individuals did not differ significantly in the number of supports received (Table 8;  $\chi^2 = 0.52$ , P=0.47); but this may have been driven by the fact that younger juveniles received almost five times as many aggressions as older juveniles (1296 vs 266). Older low ranking juveniles received non-matrilineal support in a significantly higher percentage of their aggressions than younger low ranking juveniles (Table 8;  $\chi^2_c = 32.93$ , P<0.001).

Individuals who outranked their opponents were more likely to receive non-matrilineal support than individuals who were outranked by their opponents (81.7% of 89 supports was on

Table 7. The number, proportion and % (supports/disputes) of non-matrilineal supports received by matrilines and matriarchs, presented separately for each of the stable and unstable periods. Obs is the proportion of total supports received by each category of recipient; Exp is the proportion expected by each category of recipient on the null hypothesis of equivalent probability of receiving support and on the number of individuals in each recipient category. N is number of supports.

RECIPIENT	STAI	BLE 1			STAB	LE 2			UNSTABLE 1				UNSTABLE 2			
	Obs	Ехр	N	%	Obs	Ехр	N	%	Obs	Ехр	N	%	Obs	Exp	N	. %
Matriline 1	0.27	0.25	24	4.0	0.26	0.18	52	12.0	0.13	0.27	2	2.2	0.57	0.20	5	5.6
Matriline 2	0.41	0.25	36	5.6	0.55	0.18	109	13.1	0.33	0.20	5	7.0	0.11	0.10	1	1.7
Matriline 3	0.22	0.25	20	3.8	0.12	0.27	23	4.4	0.40	0.27	6	4.3	0	0.20	0	0
Matriline 4	0.10	0.25	9	2.3	0.07	0.36	14	2.1	0.13	0.27	2	2.2	0.33	0.50	3	3.2
Matriarch 1	0.54	0.25	7	3.2	0.25	0.25	32	18.3	0	0.33	0	0	-	-	-	-
Matriarch 2	0.31	0.25	4	3.0	0.73	0.25	94	14.7	-	-	-	-	0	0.50	0	0
Matriarch 3	0.15	0.25	2	2.4	0.02	0.25	3	3.4	1.00	0.33	1	4.2	-	-	-	-
Matriarch 4	0	0.25	0	0	0	0.25	0	0	0	0.33	0	0	0	0.50	0	0

**Table 8.** The number, proportion and % (supports/disputes) of non-matrilineal supports received by different categories of recipients (old and young as in Table 3), presented separately for each of the stable and unstable periods. Obs is the proportion of total supports received by each category of recipient; Exp is the proportion expected by each category of recipient on the null hypothesis of equivalent probability of receiving support and on the number of individuals in each recipient category. N is number of supports.

RECIPIENT	STABL	E PERIOD	S		RECIPIENT	UNSTA	BLE PE	RIODS	
	Obs	Ехр	Ν	%		Obs	Exp	N	%
High Ranking Male	0.52	0.50	43	18.1	Male	0.61	0.52	14	5.6
High Ranking Female	0.48	0.50	39	15.4					
Low Ranking Male	0.70	0.55	44	6.4	Female	0.39	0.48	9	2.6
Low Ranking Female	0.30	0.45	19	2.2					
High Ranking Old	0.38	0.25	31	34.1	Old	0.65	0.35	15	5.4
High Ranking Young	0.62	0.75	51	12.7					
Low Ranking Old	0.44	0.40	28	10.5	Young	0.35	0.65	8	2.5
Low Ranking Young	0.56	0.60	35	2.7					•
behalf of the higher ranking contestant in Period 1; 88.9% of 198 supports in Period 2; distributions significantly uneven at P < 0.001 by chi-square analyses in both cases).

#### **3.4.2 Support in Unstable Periods**

#### 3.4.2.1 Frequency of Support by Matrilineals vs Non-matrilineals

Supports occurred in 66 (33.7%) of the 196 between-matriline dyadic aggressive disputes observed in Unstable Period 1, and in 50 (32.5%) of the 154 disputes observed in Period 2. Supports by matrilineals were more common than by non-matrilineals (Table 1; allowing for the ratio of matrilineals to non-matrilineals for each individual in the troop,  $\chi^2 = 157.64$ , P<0.001 for Period 1;  $\chi^2 = 51.34$ , P<0.001 for Period 2). No individuals were observed to support a non-matrilineal against a matrilineal member in either unstable period.

Rates of aggression were substantially lower in unstable than stable periods (Chapter 2), and consequently opportunities for support are lower in unstable periods. However, the percentage of aggressive disputes in which matrilineal support was provided was significantly higher in unstable than stable periods (Table 1; Periods 1 and 2 combined; stable vs unstable,  $\chi^2_c = 58.32$ , P<0.001). By contrast, the percentage of aggressive disputes in which nonmatrilineal support was provided was significantly lower in unstable z than stable periods (Table 1; Periods 1 and 2 combined; stable vs unstable,  $\chi^2_c = 16.64$ , P<0.001).

### 3.4.2.2 Effects of Rank, Age and Sex on Support Given by Matrilineals

Matrilines differed significantly in the number of matrilineal supports provided during both unstable periods (Table 2; Period 1,  $\chi^2 = 51.79$ , P<0.001; Period 2,  $\chi^2 = 17.01$ , P<0.001), but there was no apparent effect of matrilineal rank on support provided (Table 2). Matrilineal support by matriarchs was too rare to justify analysis (Table 2). Since there was no effect of matrilineal rank on supports, juveniles were pooled to investigate support differences by age and sex. As for stable periods, female juveniles tended to provide more matrilineal support than male juveniles, and older juveniles gave more support than younger juveniles (Table 3; sex,  $\chi^2 = 3.21$ , P=0.07; age,  $\chi^2 = 10.39$ . P<0.005).

#### 3.4.2.3 Effects of Rank, Age and Sex on Support Received by Matrilineals

By definition, matrilines receive the same number of matrilineal supports that they provide. Consequently, although matrilines differed significantly in matrilineal support received, there was no apparent effect of matrilineal rank on support received (see Table 2 and sub-section above). Males and females did not differ significantly in the number of matrilineal supports received during unstable periods (Table 4;  $\chi^2=0.22$ , P=0.64). However, this may be driven by the fact that females receive substantially more aggression in unstable periods than males (Chapter 2), since the percentage of aggressive disputes in which matrilineal support was received was significantly lower for females than males in unstable periods (Table 4;  $\chi^2_c=5.47$ , P<0.02). Older juveniles received more matrilineal support than younger juveniles in unstable periods, both by number and percent support (Table 4; number,  $\chi^2=21.98$ , P<0.001; percent,  $\chi^2_c=5.78$ , P<0.02).

#### 3.4.2.4 Effects of Rank, Age and Sex on Support Given by Non-matrilineals

The numbers of non-matrilineal supports provided in Unstable Periods 1 and 2 were too few to justify analysis by matrilineal rank, but there was no apparent effect of rank on support provided (Table 5). Given the rarity of non-matrilineal supports in unstable periods, no significant differences between male and female juveniles, nor between old and young juveniles, could be detected in the number of supports provided (Table 6; sex,  $\chi^2=0.16$ , P=0.69; age,  $\chi^2=0.73$ , P=0.39).

#### 3.4.2.5 Effects of Rank, Age and Sex on Support Received by Non-matrilineals

Non-matrilineal supports received in unstable periods were too few to justify analysis by matrilineal rank, but there was no apparent effect of rank on support received (Table 7). Male and females did not differ significantly in the number of non-matrilineal supports received during unstable periods (Table 8;  $\chi^2=0.66$ , P=0.42); but there was a weak tendency for the percentage of aggressive disputes in which non-matrilineal support was received to be lower for females than males (Table 8;  $\chi^2_c=2.62$ , P=0.10). Older juveniles received more non-matrilineal supports than younger juveniles in unstable periods (Table 8;  $\chi^2=9.23$ , P<0.003), and tended to receive supports in a higher percentage of their aggressive disputes (Table 8;  $\chi^2_c=2.57$ , P=0.10).

#### **3.5 DISCUSSION**

#### **3.5.1** Stable Periods

During both periods in which the matrilineal dominance hierarchy was stable in this study, individuals supported members of their own matriline more often than those from other matrilines. They rarely supported an individual from another matriline in an aggressive dispute against a matrilineal member. The tendency to preferentially support matrilineal members has previously been reported for several macaques (e.g. Kaplan 1977; Kurland 1977; Massey 1977; Silk 1992), for chacma and yellow baboons (Cheney 1977; Walters 1980) and for vervets (Cheney 1983; Hunte & Horrocks 1987). This behaviour, and the observation that Old World monkeys are typically more aggressive towards individuals from other matrilines than towards matrilineal members (Kurland 1977, Silk et al. 1981 for macaques; Cheney 1977 for baboons; Chapter 2 for vervets), confirms that matrilines act as cohesive units, and mignt suggest that matrilineal rank should be correlated with matrilineal size during stable periods in the dominance hierarchy. However, matrilineal rank did not appear to be correlated with matrilineal size during stable periods in this study troop (Chapter 1), and Ehardt & Bernstein (1986) and Samuels et al. (1987) reported no correlation between matrilineal size and rank in rhesus macaques and yellow baboons, respectively (but see Silk & Boyd 1983 and Chapais 1988 for suggestion of a correlation in macaques).

The age and sex composition of matrilines could in principle influence matrilineal rank during stable periods, if there are age- and sex-specific differences in aggressiveness towards non-matrilineals and/or in the tendency to support matrilineals during aggressive disputes. Female vervets escalate a higher proportion of their aggressions towards non-matrilineals than males; and older juveniles are more frequently aggressive than younger juveniles (Chapter 2). Moreover, the results of this Chapter suggest that female juveniles provide more matrilineal support than males, and older juveniles provide more matrilineal support than younger juveniles. Despite these age- and sex-specific differences in aggression and support, matrilineal rank did not appear to be correlated with matrilineal age composition, sex composition or matrilineal power (based on an age/sex tendency to provide matrilineal support summed for all matrilineal members) in this study troop (Chapter 1). Matrilineal rank during stable periods may not be

predicted by lineage size, age or sex composition if there are inherent differences between matrilines in aggressiveness towards non-matrilineals and/or in the tendency to provide matrilineal support. Higher ranking matrilines were more frequently aggressive, and escalated a higher proportion of their aggressions, than lower ranking matrilines in this study troop (Chapter 2). Similar results for frequency of aggression have been reported for other Old World monkeys (e.g. Bernstein 1970; Datta 1983). In vervets, the greater aggressiveness of higher ranking matrilines appears to result from a lower cost of aggression, and is better considered a consequence than cause of high matrilineal rank (Chapter 2; see a'so Hunte & Horrocks 1987; Dunbar 1988). The present results indicate that higher ranking matrilines provide more matrilineal support during stable periods than lower ranking matrilines, and a similar pattern has been reported for baboons (e.g. Cheney 1977; Walters 1980) and macaques (e.g. Berman 1980). However, as was the case for aggression, the more frequent support by higher ranking matrilines is better perceived as a consequence than cause of higher rank, the cost of matrilineal support being lower for higher ranking matrilines (see also Hunte & Horrocks 1987). The best evidence for this perspective is that higher ranking matrilines provided more matrilineal support in both stable periods, even though the relative ranks of the matrilines differed in the two stable periods because of the matrilineal rank reversals which occurred during the intervening unstable period.

The fact that matrilineal characteristics do not appear to predict matrilineal ranks during stable periods suggests that the behaviour of non-matrilineal members may be important in stabilising matrilineal ranks. For example, if non-matrilineals are preferentially aggressive towards the lower ranking than higher ranking of any pair of matrilines when the pair ranks either above or below them, they might contribute to the maintenance of the relative ranks of the recipient matrilines. However, the distribution of aggression observed in this study troop is not consistent with this (Chapter 2). The best predictor of the distribution of aggression was "rank distance", i.e. matrilines were most aggressive to those matrilines ranking immediately adjacent to themselves (Chapter 2; see Bernstein 1968, Mazur 1973, Clutton-Brock & Harvey 1976 and de Waal 1991 for similar results). The distribution of non-matrilineal aggression does not therefore suggest that it would stabilise matrilineal ranks, but the distribution of non-matrilineal supports could have this effect. Higher ranking matrilines both gave and received significantly more non-matrilineal support than lower ranking matrilines in both stable periods

of this study. Cheney (1983) and Hunte & Horrocks (1987) have previously suggested this for vervets, and similar results have been reported for yellow baboons by Walters (1980). Consistent with the tendency for higher ranking matrilines to receive more non-matrilineal support, about 85% of all non-matrilineal supports in the present study were on behalf of the higher ranking of the contestants in a dyadic aggressive dispute, and Chapais *et al.* (1991) reported a similar tendency in Japanese macaques. Since there are typically fewer matrilineal supports received by an individual in a troop, the total number of non-matrilineal supports received by an individual over any time period is often greater than the total number of matrilineal supports, typically on behalf of higher ranking contestants and consequently favouring higher ranking over lower ranking matrilines, may therefore be a major factor stabilising the relative ranks of matrilines during stable periods in vervet monkeys.

Several authors have suggested that support to non-matrilineals (non-kin) is a form of reciprocal altruism (e.g. Kurland 1977; Packer 1977; Hunte & Horrocks 1987), and this is discussed further in Chapter 4. The question of why higher ranking matrilines both give and receive more non-matrilineal supports than lower ranking matrilines merits comment in this context. High ranking matrilines may give more non-matrilineal supports for the same reason that they give more matrilineal supports, i.e., since they are likely to outrank the individual against whom the support is directed, the probability of retaliation, and hence the cost of support is low. High ranking matrilines may receive more non-matrilineal supports because they are more valuable as reciprocators, i.e. their rank will allow them to reciprocate the current supporter over a wide range of potential conflicts in which he/she becomes involved. For any given contest, the probability of future reciprocation is higher if an individual supports the higher ranking rather than the lower ranking of the contestants.

The suggestion that value as a reciprocator influences the probability that an individual will receive non-matrilineal support is supported by the age- and sex-specific differences in receipt of non-matrilineal support observed in this study. High ranking males and females did not differ in non-matrilineal support received, suggesting that they are equivalently valuable as reciprocators, and this is supported by the fact that they did not differ in the number of non-matrilineal supports which they provided. Low ranking males received more non-matrilineal

support than low ranking females. The sexual dimorphism in size characteristic of vervets may make males increasingly more valuable as reciprocators than females as juveniles age (see Hunte & Horrocks 1987 for similar suggestion); and this is supported by the fact that low ranking males provided more non-matrilineal support than low ranking females in this study. The suggestion that size influences the value of individuals as reciprocators is supported by the observation that older juveniles both received and gave more non-matrilineal support than younger juveniles in this study.

#### **3.5.2 Unstable Periods**

The tendency of non-matrilineals to support higher ranking over lower ranking matrilines may be a major factor stabilising the relative ranks of matrilines during stable periods, and may thereby ensure that matrilineal characteristics such as lineage size, age composition and matrilineal power, do not predict matrilineal rank during stable periods (Chapter 1). Given this stabilising effect of non-matrilineals, a substantial drop in the matrilineal power of a high ranking matriline may be required to move matrilineal hierarchies from stable periods to periods of matrilineal rank reversals. Once this occurs, the present results suggest that non-matrilineal support, and hence its effect of stabilising matrilineal ranks, decreases, thereby tending to increase the duration of the unstable period by increasing the probability of further matrilineal rank reversals. A major difference between unstable and stable periods in this study was that the number of non-matrilineal supports provided, as well as the percentage of aggressive disputes in which supports were provided, were substantially lower in the former than latter periods. This was despite the fact that the percentage of aggressive bouts which were met with confrontation was higher in unstable than stable periods (Chapter 2), and non-matrilineals were more likely to provide support in confrontational than non-confrontational disputes in this study. The reduced non-matrilineal support in unstable periods may result from the fact that the relative ranks of matrilines are less certain over time, and hence the value of an individual as a future reciprocator is less predictable.

The reduction in the importance of non-matrilineal support as a stabilising effect during unstable periods may suggest that the characteristics of matrilines, and the behaviour of matrilineal members, become increasingly important in determining the ranks of matrilines

during unstable periods and as troops emerge from unstable periods and enter new periods of matrilineal rank stability. The potential importance of matrilineal members in determining matrilineal rank during unstable periods is amplified by the fact that matrilineal support was provided in a higher percentage of aggressive disputes in unstable than stable periods in this study. The increased importance of matrilineal characteristics in determining matrilineal rank in unstable periods, a change which occurs through an increase in the relative importance of matrilineal to non-matrilineal support in unstable periods, is suggested by the observation that matrilineal rank was typically correlated with the number of juvenile females in the matriline. and with the Matrilineal Power Index, during and at the termination of unstable periods in this study troop (Chapter 1). During unstable periods, females escalated more of their aggressions than males, and had higher injury rates; and older juveniles were more aggressive than younger juveniles (Chapter 2). Moreover, female juveniles provided more matrilineal support than male juveniles, and older juveniles provided more than younger juveniles, during unstable periods in this study. These results suggest that the behaviour of females, particularly older juvenile females, is important in determining matrilineal rank during unstable periods; and this is consistent with the observation that matrilineal rank is typically correlated with the number of females in the matriline, and with the Matrilineal Power Index, as troops emerge from unstable periods and enter new periods of matrilineal rank stability. Once relative ranks remain unchanged for long enough through perpetuation of the differences in matrilineal characteristics, non-matrilineal support favouring higher ranking over lower ranking matrilines will increase in frequency, thereby increasing matrilineal rank stability in the emergent dominance hierarchy. Once the stabilising effect of non-matrilineal support is established, subsequent changes in matrilineal characteristics need not result in matrilineal rank changes, and a correlation between matrilineal rank and matrilineal characteristics will decrease in strength over time. The consequence is that, whether matrilineal rank is correlated with matrilineal characteristics in any study, will depend on what temporal segment of the cyclical change between stable and unstable periods the study has focused on.

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## **CHAPTER 4**

# NON-MATRILINEAL SUPPORT IN VERVET MONKEYS: MUTUALISM OR RECIPROCAL ALTRUISM ?

#### **4.1 ABSTRACT**

Non-matrilineal support was investigated in feral vervet monkeys to determine whether mutualism or reciprocal altruism better explains observed patterns of non-matrilineal support in Old World monkeys. The frequency distribution of supports in the six different social contexts that can be generated by altering the relative ranks of supporter, recipient and opponent, and hence altering the costs and benefits of support, fell into the three frequency groups predicted by the reciprocal altruism hypothesis. Supports were most frequent when costs were low and benefits were high, occurred with intermediate frequency when benefits were low and costs were low, or benefits high and costs high, and were infrequent when benefits were low and costs were high. The mutualism hypothesis strictly predicts only two frequency groups of non-matrilineal supports, but with a plausible modification that incorporates changes in support costs with changes in the relative ranks of recipients and opponents, the same trimodal frequency distribution of supports is predicted by the mutualism hypothesis as by the reciprocal altruism hypothesis. Support frequency was lower during unstable than stable periods in the matrilineal dominance hierarchy, as predicted by the reciprocal altruism hypothesis but not by the mutualism hypothesis. Under reciprocal altruism, the benefits of support should be lower in unstable periods, since the future rank of recipients, and hence their value as reciprocators, is uncertain. The benefits of support should be higher under mutualism since the benefits of rank reinforcement should be higher. Most importantly, for 13 of the 16 individuals investigated in this study, the proportion of an individual's support given to different troop members was significantly correlated with the proportion of its support received from troop members. This is predicted by reciprocal altruism but not by mutualism. The results therefore suggest that reciprocal altruism is a better model for non-matrilineal support in vervet monkeys than is mutualism.

#### **4.2 INTRODUCTION**

In Old World monkeys, individuals often support conspecifics in dyadic aggressive disputes by forming a cooperative coalition with one of the contestants. The social structure of Old World monkeys is characterised by a matrilineal dominance hierarchy, and support is typically on behalf of members of the same matriline against individuals from other matrilines (matrilineal support; e.g. Massey 1977, Silk 1992 for macaques; Cheney 1977, Walters 1980 for baboons; Hunte & Horrocks 1987, Chapter 3 for vervets). Since individuals within the same matriline are genetically related, matrilineal support is considered a form of kin altruism (sensu Hamilton 1964; e.g. Massey 1977, de Waal 1978, Kaplan 1978, Datta 1983, Hunte & Horrocks 1987). However, support also occurs in disputes between individuals both of whom are from matrilines other than that of the supporter (non-matrilineal support; see Chapter 3). Studies of non-matrilineal support are less common than matrilineal support, but emerging characteristics are that higher ranking matrilines give and receive more non-matrilineal support than lower ranking matrilines (e.g. Chapais et al. 1991 for macaques; Walters 1980 for baboons; Cheney 1983, Chapter 3 for vervets), that older juveniles give and receive more non-matrilineal support than younger juveniles (Chapter 3 for vervets), and that low ranking males give and receive more non-matrilineal support than low ranking females (Chapter 3 for vervets; but see Chapais et al. 1991 for macaques). The tendency for individuals to provide more non-matrilineal support to higher ranking than lower ranking matrilines may be the major factor stabilising matrilineal ranks during stable periods in the matrilineal dominance hierarchy of vervet monkeys (Chapters 1, 3).

Since the cooperation evident in non-matrilineal support is between unrelated or weakly related individuals, reciprocal altruism (e.g. Seyfarth & Cheney 1984; Hunte & Horrocks 1987; de Waal & Luttrell 1988) and mutualism (e.g. Chapais *et al.* 1991; Chapais 1992) have both been suggested as causal explanations for the behaviour. In this Chapter, cooperation is considered to be a jointly executed act which occurs because more than one individual obtains a net benefit from the act. If the benefit to the cooperating individuals occurs at the time of the act, and requires no prior or subsequent interactions between the individuals, the cooperative behaviour is termed mutualism (e.g. Boyd 1988; Rothstein & Pierotti 1988). If one individual

(the supporter) assists a second individual (the recipient) at a cost to the supporter, but with the expectation of benefit when the support is subsequently returned, the cooperative behaviour is referred to as reciprocal altruism. This behaviour therefore requires subsequent, and typically prior interactions between the individuals (Trivers 1971; Hemelrijk 1990a; see Boyd 1988 for argument that the Repeated Prisoner's Dilemma game of Axelrod & Hamilton 1981 remains a good model for the evolution of reciprocal altruism).

The reciprocal altruism hypothesis for non-matrilineal support in Old World monkeys is therefore that an individual supports a recipient in an aggressive dispute with the expectation of future benefit when the recipient returns the support (Hunte & Horrocks 1987). The value of the recipient as a reciprocator should therefore influence its probability of receiving support. Consequently, the identity and characteristics of the recipient that influence its value as a reciprocator, including its prior record of support exchanges with the supporter, should influence its receipt of support. The mutualism hypothesis for non-matrilineal support suggests that, in supporting a recipient in an aggressive dispute, an individual is taking the opportunity to reinforce its own rank over the opponent in the dispute. Both individuals therefore derive immediate benefits from the cooperative behaviour, the supporter by benefits obtained through rank reinforcement, and the recipient from the support received (Chapais et al. 1991; Chapais 1992; but note that Chapais refers to this as the cooperation (not mutualism) hypothesis). Since the value of the recipient as a reciprocator should not influence its probability of receiving support under the mutualism hypothesis, the identity and characteristics of the recipient which influence its value as a reciprocator, including its prior record of support exchanges with the supporter, should not influence receipt of support.

Reciprocal behaviour in primate social relationships is potentially complex (de Waal & Luttrell 1988; Hemelrijk 1990a,b). Quantitative tests of reciprocity theory are particularly difficult, given the problems of quantifying costs and benefits of different behaviours, and of relating these to individual fitness (Seyfarth & Cheney 1988). Nevertheless, the reciprocal altruism and mutualism hypotheses for non-matrilineal support in Old World monkeys do make different qualitative predictions about the relative rates and distributions of non-matrilineal support. The objective of this Chapter is to generate and test three predictions that may allow

separation of reciprocal altruism and mutualism as causal explanations for non-matrilineal support in vervet monkeys in Barbados.

#### 4.3 METHODS

#### 4.3.1 Data Collection

The feral troop used in this study has been described by Horrocks (1982, 1986) and in Chapters 1, 2 and 3 of this thesis. The database on dyadic aggressive disputes and nonmatrilineal supports used for this Chapter is the same as that used in Chapters 2 and 3. Briefly, the data were collected by behaviour-dependent sampling during four observation periods. These were: Stable Period 1, September 1982 to March 1983, 229h of observation; Unstable Period 1, January 1987 to March 1987, 82h of observation; Stable Period 2, January 1991 to June 1991, 326h of observation; Unstable Period 2, May 1989 to July 1989, 108h of observation. Troop characteristics during each of the four observation periods are provided in Chapters 1 and 2. A stable period is defined as one in which no matrilineal rank reversals occurred; an unstable period as one in which matrilineal rank reversals were frequent (Chapters 1, 2, 3). As in Chapter 2, non-matrilineal support refers to the situation in which the supporting animal (supporter) belongs to a different matriline than either of the two individuals (recipient; opponent) in the aggressive dispute.

#### 4.3.2 Predictions of the Reciprocal Altruism and Mutualism Hypotheses

## 4.3.2.1 <u>Prediction 1: On the Frequency Distribution of Non-matrilineal Support as a Function</u> of Social Context

#### 4.3.2.1.1 Reciprocal Altruism

It is assumed that non-matrilineal support will occur most frequently in social contexts in which the benefit of supporting is high and the cost of supporting is low, from the perspective of the supporter; and that the cost of support will be low when the supporter outranks the opponent (low retaliation probability) and the benefit of support will be high when the recipient outranks the opponent (high reciprocation probability).

There are six possible social contexts for non-matrilineal support, depending on the relative ranks of the supporter (S), recipient (R) and opponent (O). These are (where > means ranks higher than): S>R>O, R>S>O, S>O>R, R>O>S, O>R>S, anc O>S>R. The reciprocal altruism hypothesis predicts that, during stable periods when relative ranks are

predictable, the six forms of non-matrilineal support should occur in three frequency groups (Fig. 1A). S > R > O and R > S > O should occur with high frequency, since the benefits of support are high and the costs of support are low. S > O > R and R > O > S should occur with intermediate frequency, the former because the costs of support are low, but the benefits of support are high, the latter because the benefits of support are high, but the costs are also high. O > R > S and O > S > R should occur with low frequency, since the benefits of support are low and the costs of support are high.

#### 4.3.2.1.2 Mutualism

It is again assumed that non-matrilineal support will occur most frequently in social contexts in which the benefit of supporting is high and the cost of supporting is low, from the perspective of the supporter. Under the mutualism hypothesis, the cost of support should be low when the supporter outranks the opponent (low retaliation probability), and the benefit of support should be realised whenever the supporter outranks the opponent (reinforcement of rank). In its strictest interpretation, the mutualism hypothesis therefore predicts that the six forms of non-matrilineal support should occur in two frequency groups (Fig. 1B). S > R > O, R > S > O, and S > O > R should occur with high frequency since the costs of support are low and the benefits of support accrue. R > O > S, O > R > S, and O > S > R should occur with low frequency since the costs of support are high and there can be no benefit through rank reinforcement.

### 4.3.2.2 Prediction 2: On Reciprocity in Non-matrilineal Support

#### 4.3.2.2.1 Reciprocal Altruism

Prior patterns of support exchange between individuals should influence the probability of current support if they provide honest information on the probability that current support will subsequently be reciprocated. Under the actor-receiver model of reciprocity (see Hemelrijk 1990a), the reciprocal altruism hypothesis therefore predicts that the percentage of an individual's non-matrilineal support given to each troop member determines what percentage of that individuals's support it receives from each troop member, i.e. individuals will give most often to those from whom they receive most often.

## Figure 1

Frequency distribution of non-matrilineal support as a function of social context. Frequency groups predicted by the reciprocal altruism hypothesis (A), and by the mutualism hypothesis (B) (see text for explanation). S-Supporter, R-Recipient, O-Opponent. > means ranks higher than.

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#### 4.3.2.2.2 Mutualism

The probability of support in aggressive disputes will not vary with prior patterns of support exchange between the recipient and supporter, since the benefit of support does not depend on the probability of subsequent reciprocation but on reinforcement of the supporter's rank over the opponent. The mutualism hypothesis therefore predicts that the percentage of an individual's non-matrilineal support given to each troop member will not be correlated with the percentage of that individual's support it receives from each troop member.

#### 4.3.2.3 Prediction 3: On Non-matrilineal Support in Stable and Unstable Periods

#### 4.3.2.3.1 Reciprocal Altruism

Non-matrilineal support will be more common during stable than unstable periods in the matrilineal dominance hierarchy of Old World monkeys, since in unstable periods, the future social rank of the recipient, and hence its value as a reciprocator, is less certain.

#### 4.3.2.3.2 *Mutualism*

Non-matrilineal support will be more common during unstable periods in the matrilineal dominance hierarchy, since rank reversals are more probable, and hence the benefits of using available opportunities to reinforce rank over lower ranking opponents are greater.

### 4.4.1 Prediction 1: On the Frequency Distribution of Non-matrilineal Support as a Function of Social Context

The frequency distributions of non-matrilineal supports during Stable Periods 1 and 2 are shown in Figures 2 and 3 respectively. In both cases, non-matrilineal support in the six social contexts possible in terms of relative ranks of supporter, recipient and opponent (Section 4.3.2.1.1) fell into the three frequency groups predicted by the reciprocal altruism hypothesis (Fig. 1A for predicted distribution; Figs. 2 & 3 for observed distributions). Supports occurred most frequently when both the supporter and the recipient outranked the opponent, i.e. reciprocation probability (benefit) high, and retaliation probability (cost) low. Supports occurred with intermediate frequency when the supporter outranked the opponent who outranked the recipient, i.e. retaliation probability (cost) low, but reciprocation probability (benefit) low; and when the recipient outranked the opponent who outranked the supporter, i.e. retaliation probability (cost) high, but reciprocation probability (benefit) high. Supports occurred with lowest frequency when the opponent outranked both the supporter and the recipient, i.e. reciprocation probability (benefit) how and retaliation probability (cost) high.

The observed distributions of the six forms of non-matrilineal support (Figs. 2 & 3) differed substantially from the two frequency groups predicted by the mutualism hypothesis (Fig. 1B). The mutualism hypothesis predicted that supports in social contexts in which the supporter outranked the opponent who outranked the recipient should occur with high frequency (Fig. 1B; retaliation probability, and hence cost, low; full benefit of rank reinforcement), but these were observed to occur with intermediate frequency (Figs. 2 & 3). Supports in social contexts in which the recipient outranked the opponent who outranked the supporter were predicted to occur with low frequency (Fig. 1B; retaliation probability, and hence cost, high; no benefit through rank reinforcement), but were observed to occur with intermediate frequency (Figs. 2 & 3).

### 4.4.2 Prediction 2: On Reciprocity in Non-matrilineal Support

For 8 of the 9 vervets who both gave and received significant numbers of non-matrilineal supports during Stable Period 1, individuals received the highest percentage of their

## Figure 2

Observed frequency distribution (%) of non-matrilineal support in Stable Period 1 as a function of social context. S-Supporter, R-Recipient, O-Opponent. > means ranks higher than.

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## Figure 3

Observed frequency distribution (%) of non-matrilineal support in Stable Period 2 as a function of social context. S-Supporter, R-Recipient, O-Opponent. > means ranks higher than.

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supports from the troop member to whom they gave the highest percentage of their supports (Fig. 4). This was also true for 6 of the 7 individuals who gave and received significant numbers of non-matrilineal supports during Stable Period 2 (Fig. 5). Moreover, for all individuals in Stable Period 1, and for 5 of the 7 individuals in Stable Period 2, the percentage of an individual's supports received from each troop member was significantly correlated with the percentage of the individual's supports given to each troop member (Figs. 4 & 5). This strongly supports the prediction of the reciprocal altruism hypothesis that support to troop members is allocated on the basis of support received from troop members. The results are inconsistent with the mutualism hypothesis which predicts no correlation between support given and support received.

#### 4.4.3 Prediction 3: On Non-matrilineal Support in Stable and Unstable Periods

As predicted by the reciprocal altruism hypothesis, non-matrilineal support rates were substantially higher in stable (mean 0.50 supports/h) than unstable periods (mean 0.11 supports/h), but this could reflect fewer opportunities to support, since aggression rates were significantly lower in unstable than stable periods in this study (Chapter 2). However, the percentage of aggressive disputes in which non-matrilineal support was provided was significantly lower in unstable (5.9%) than stable periods (12.2%) in this study ( $\chi^2_{\chi} = 16.64$ , P < 0.001). These results are inconsistent with the mutualism hypothesis which predicts that non-matrilineal support should be more common in unstable than stable periods, since behaviour which reinforces individual rank should be particularly beneficial in unstable periods (Section 4.3.2.3.2).

## Figure 4

The percentage of each individual's non-matrilineal supports given to other troop members and received from other troop members in Stable Period 1. r, is the Spearman Rank Correlation Coefficient; P is the level of probability.

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## Figure 5

The percentage of each individual's non-matrilineal supports given to other troop members and received from other troop members in Stable Period 2.  $r_s$  is the Spearman Rank Correlation Coefficient; P is the level of probability.



**Recipients** 



#### **4.5 DISCUSSION**

Under the reciprocal altruism hypothesis for non-matrilineal support in Old World monkeys, benefit to the supporter is envisaged to occur through subsequent support reciprocated by the recipient (e.g. Packer 1977; Hunte & and Horrocks 1987). Benefit to the supporter should therefore be higher when the recipient outranks the opponent than when the recipient is outranked by the opponent, since in the former case, the probability of future reciprocation by the recipient is higher. It also seems reasonable to assume that the cost of support is either immediate or subsequent retaliation by the opponent; and that this cost will be higher when the opponent outranks the supporter. Using only these crude indices of costs and benefits, the reciprocal altruism hypothesis predicted the frequency distribution of non-matrilineal supports in different social contexts accurately in this study. In both of two data collection periods, separated by enough time that several troop members had changed, non-matrilineal supports occurred with highest frequency when benefits were high and costs were low, with intermediate frequency when benefits were high but costs were high, or when benefits were low but costs were low, and with low frequency when benefits were low and costs were high. This frequency distribution therefore suggests that the primary benefit of non-matrilineal support has been accurately identified, i.e. the benefit occurs through subsequent reciprocation by the recipient. The results are clearly consistent with the assertion that reciprocal altruism is an appropriate model for non-matrilineal support in vervet monkeys. The observed frequency distribution of non-matrilineal support differs from that expected under the mutualism hypothesis. This predicts only two principal frequency groups for non-matrilineal supports. Supports should occur frequently whenever the supporter outranks the opponent, regardless of the relative rank of the recipient, since costs will be low (supporter outranks opponent) and benefits accrue (supporter outranks opponent; rank reinforcement can occur). Supports should occur infrequently whenever the opponent outranks the supporter, regardless of the relative rank of the recipient, since costs will be high and benefits through rank reinforcement can not occur. However, the mutualism hypothesis can be made consistent with the observed trimodal frequency distribution of nonmatrilineal supports by assuming that the rank of the recipient relative to the opponent influences the cost of support. If in the basically low cost bouts that occur when the supporter outranks the

opponent (see Fig. 1B), the support cost is raised if the opponent outranks the recipient, the observed lower frequency of S > O > R support compared to S > R > O and R > S > O supports (Figs. 2 & 3) could materialise. Similarly, if in the basically high cost bouts that occur when the supporter is outranked by the opponent (see Fig. 1B), the support cost is lowered if the recipient outranks the opponent, the observed higher frequency of R > O > S supports compared to O > R > S and O > S > R supports (Figs. 2 & 3) could materialise. The frequency distribution of non-matrilineal supports observed in different social contexts in this study therefore does not allow clear separation of the reciprocal altruism and mutualism hypotheses as causal explanations for non-matrilineal support in vervets.

Hemelrijk (1990a) has stressed that our comprehension of reciprocity has been constrained by ad hoc approaches to defining and testing the relevant processes, and in particular has emphasised the need to differentiate between actor-reactor models and actor-recipient models in studies of reciprocity. In actor-reactor models, supporters give relatively more to those recipients who return to them relatively more than the recipients give to others. This implies that the supporter must consider, not only what the recipient gives to the supporter, but what the recipient gives to others. In actor-recipient models, individuals give more to those individuals from whom they receive more, and the supporter therefore need not consider what recipients give to others. Hemelrijk (1990a) argues convincingly that actor-recipient reciprocation requires less complex cognitive abilities, is less time consuming, and is less vulnerable to deceit than actor-reactor reciprocation, and hence is a more plausible model for reciprocity studies. The actor-recipient approach to reciprocation has been used in this study.

Eight of 9 individuals during Stable Period 1 and 6 of 7 individuals during Stable Period 2, received the highest percentage of their supports from troop members to whom they gave the highest percentage of their supports. Moreover, for all individuals in Stable Period 1, and for 5 of the 7 individuals in Stable Period 2, the percentage of an individual's support received from each troop member was correlated with the percentage of the individual's support given to each troop member. This is strong support for the reciprocal altruism hypothesis, since it suggests that non-matrilineal support given by an individual to other troop members in vervets is carefully allocated on the basis of support received by the individual from those troop members. The results are inconsistent with the mutualism hypothesis which predicts opportunistic support when

low cost opportunities for rank reinforcement arise, independently of the identity of the recipient and hence of past patterns of support exchange between the recipient and supporter. The results therefore strongly suggest that reciprocal altruism is a better model for the evolution of nonmatrilineal support in vervet monkeys than is mutualism. Reciprocation has previously been suggested to be the basis of cooperation between non-kin in rhesus macaques (Colvin & Tissier 1985; de Waal & Luttrell 1988), stumptail macaques (de Waal & Luttrell 1988), baboons (Packer 1977; Bercovitch 1988) and chimpanzees (de Waal & Luttrell 1988). By contrast, Chapais et al. (1991) reported little evidence of reciprocity in non-kin alliances in a captive troop of Japanese macaques. They concluded, on the basis of rank correlation analyses, that in most cases individuals did not distribute their support among non-kin in proportion to the amount of support they received from the latter. In vervets, the great majority of non-matrilineal support by any individual is provided to only a few troop members, the amount of support to the remaining troop members being negligible (see Figs. 4 & 5). It is important to determine whether the support given to the "preferred" individuals is reciprocated, but frequency distributions of support given and received are not provided by Chapais et al. (1991). Since rank correlation analyses were used in their study, the correlation between support given and received by an individual across all troop members may be emerging as statistically insignificant because of differences generated by troop members with whom negligible amounts of support are exchanged, and in spite of the fact that the great majority of support which is provided by the individual and targets only a few "preferred" troop members, may be strongly reciprocated.

In the present study, the percentage of aggressive disputes in which non-matrilineal support was provided was significantly lower in unstable than stable periods. In unstable periods, rank reversals are frequent, and the need to reinforce rank over opponents should therefore be high. If rank reinforcement were the primary benefit of non-matrilineal support, as suggested by the mutualism hypothesis, support should be more, not less frequent, in unstable periods. However, the observed reduction in support during unstable periods is expected if, as suggested by the reciprocal altruism hypothesis, the primary benefit of non-matrilineal support is future reciprocation by the recipient. In unstable periods when future ranks are uncertain, the value of a recipient as a reciprocator is also uncertain, and hence the benefits of non-matrilineal support may be low.

An alternative explanation to reduced benefit for the lower support frequency observed in unstable periods is that the cost of support may be higher. The explanations are not mutually exclusive. However, it should be noted that the frequency of matrilineal (kin) support increased in unstable periods in this study (Chapter 3), suggesting that constraints on support frequency arising through increased support costs in unstable periods may be small. A primary benefit of matrilineal support is the maintenance of matrilineal rank. The increased matrilineal support frequency in unstable periods therefore supports the suggestion that behaviours which facilitate the maintenance of rank are particularly beneficial during unstable periods. It therefore seems likely that, if rank reinforcement were the primary benefit of non-matrilineal support as suggested by the mutualism hypothesis, non-matrilineal support frequency should also increase during unstable periods, even if support costs are higher. The observed decrease in nonmatrilineal support frequency during unstable periods therefore remains more consistent with the reciprocal altruism than mutualism hypothesis. Under reciprocal altruism, reduced support frequency is definitively predicted, since the benefits of support through future reciprocation may be lower, and any increase in support cost will further decrease the probability of support.

In summary, the data are consistent with all three predictions of the reciprocal altruism hypothesis for non-matrilineal support in vervets generated in this Chapter. However, the predictions vary in their ability to separate the reciprocal altruism and mutualism hypotheses for non-matrilineal support. The frequency distribution of non-matrilineal supports in different social contexts is exactly as predicted by the reciprocal altruism hypothesis, but can be made consistent with the predictions of the mutualism hypothesis if the latter are relaxed to incorporate possible changes in support costs as a function of the relative rank of recipients and opponents. The reduced support frequency in unstable periods is definitively predicted by the reciprocal altruism hypothesis. It could possibly occur under the mutualism hypothesis if support costs are higher in unstable periods and are large relative to the benefits of rank maintenance in unstable periods, but data on matrilineal supports suggest that benefits of rank maintenance behaviours during unstable periods are high. The non-matrilineal supports observed in this study were highly reciprocal, individuals giving most support to those from whom they receive most support. This is predicted by the reciprocal altruism hypothesis, but not by the mutualism hypothesis, and is the strongest evidence favouring the former as the better model for non-matrilineal support. The
reciprocal altruism hypothesis, but not the mutualism hypothesis, can explain all observed patterns of non-matrilineal support by feral vervet monkeys in Barbados.

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## SUMMARY

The thesis investigated factors influencing the stability of matrilineal dominance hierarchies in a feral troop of vervet monkeys (Cercopithecus aethiops sabaeus) in Barbados. In Chapter 1, changes in the matrilineal dominance hierarchy were followed over a 12-year period (1979-1991), and correlates of matrilineal rank were examined. The relative ranks of matrilines remained unchanged for the first 7 years of the study. This was followed by a 3.5year period in which rank reversals occurred, and by a new stable period without reversals which has lasted 3.5 years to present date. Matrilines were more cohesive in stable than unstable periods, in the sense that matrilineal members occupied adjacent social ranks during stable periods. Neither lineage size, lineage age or sex composition, nor an index of matrilineal power based on an age/sex tendency to aid matrilineal members summed for all members, explained why high ranking matrilines retained their rank during the 7-year stable period. This suggests that the behaviour of non-matrilineal members may be important in stabilising matrilineal ranks during stable periods. A substantial drop in the matrilineal power index of the top-ranking matriline, caused by the loss of the oldest daughter and the incapacitation of the matriarch, initiated the 3.5-year unstable period. Matrilineal rank was not correlated with size or age composition of the matriline during the unstable period. However, it was typically correlated with the number of females in the matriline and with the matrilineal power index. This dual correlation is not surprising, since females contribute more per individual to the matrilineal power index than males. In the year spanning emergence from the unstable period and the onset of the stable period, matrilineal rank was again typically correlated with the number of females and with the matrilineal power index. The results of Chapter 1 therefore suggest that matrilineal power, driven primarily by the number of females in the matriline, predicts matrilineal rank in newly structured matrilineal dominance hierarchies.

In Chapter 2, the distribution and form of aggression during two stable periods (September 1982 - March 1983; January 1991 - June 1991) and two unstable periods (January 1987 - March 1987; May 1989 - July 1989) in the matrilineal dominance hierarchy of the study troop were investigated. Rates of aggression were lower, and fewer aggressions were escalated, in unstable than stable periods; but more aggressions were met with confrontation and injury

rates were higher in unstable periods. Individuals were more frequently aggressive and escalated a higher proportion of their aggressions to individuals in other matrilines than to members of their own matriline. During stable periods, higher ranking matrilines were more aggressive than lower ranking matrilines. However, the results of this study suggest that the higher aggression is a consequence of higher rank, not an inherent characteristic of matrilines which causes them to acquire and maintain high rank. In both stable and unstable periods, female juveniles escalated a higher proportion of their aggressions and received more aggressions than male juveniles, and females had significantly higher injury rates during unstable periods. Older juveniles were more frequently aggressive than younger juveniles during both stable and unstable periods. These sexand age-specific differences in aggressiveness may partly explain why the number of juvenile females in a matriline, particularly the number of older females, is typically positively correlated with matrilineal rank during unstable periods and as troops enter new periods of matrilineal rank stability (Chapter 1). However, the differences can not explain why certain matrilines remained dominant over others during stable periods, since rank was not correlated with the age or sex composition of the matrilines during stable periods. This again suggests that the behaviour of non-matrilineals may be important in maintaining matrilineal ranks during stable periods. However, aggression by non-matrilineals was not directed more frequently at the lower ranking than higher ranking members of pairs of matrilines ranking either above or below the aggressor matriline; suggesting that the distribution of non-matrilineal aggression does not stabilise matrilineal ranks during stable periods. If the behaviour of non-matrilineals is important in stabilising matrilineal ranks, the effect must be through the distribution of non-matrilineal supports (Chapter 3). The best predictor of the distribution of aggression in this study was the cost of aggression as indicated by the probability that the aggression would be met with confrontation. Higher ranking matrilines (contrast lower), older juveniles (contrast younger), and males (contrast females) were more confrontational when receiving aggression, and received less aggression, and aggression rates were lower during unstable periods when confrontation probability was higher.

In Chapter 3, the distribution of supports in aggressive disputes was investigated during the same two stable and two unstable periods in the matrilineal dominance hierarchy of the study troop (see Chapter 2). During both stable and unstable periods, individuals supported members of their own matriline more often than individuals from other matrilines. However, this behaviour does not explain why certain matrilines remained dominant over others during stable periods, since matrilineal rank was not correlated with lineage size, lineage age or sex composition, or matrilineal power in stable periods (Chapter 1). Higher ranking matrilines provided more matrilineal support than lower ranking matrilines during stable periods. However, the results suggest that this is a consequence of higher rank, not an inherent characteristic of matrilines which causes them to retain high rank. Higher ranking matrilines received more nonmatrilineal support than lower ranking matrilines during stable periods, perhaps because the high ranking matrilines are more valuable as support reciprocators. The suggestion that value as a reciprocator influences the distribution of non-matrilineal support is supported by the observation that older juveniles received more non-matrilineal support than younger juveniles, and males received more non-matrilineal support than females in this study. Given sexual dimorphism in size in vervets, males, particularly older males, will tend to be larger than females at a given age. The tendency for higher ranking matrilines to receive more non-matrilineal support than lower ranking matrilines may be a major factor stabilising matrilineal ranks during stable periods in vervet monkeys. Non-matrilineal support was less common in unstable than stable periods, perhaps because the future rank of recipients, and hence future reciprocation probability, is less certain. The lower frequency of non-matrilineal support in unstable periods will increase the probability of matrilineal rank reversals, thereby contributing to the continuation of the unstable period. In contrast to non-matrilineal support, matrilineal support was more common in unstable than stable periods. In unstable periods, female juveniles provided more matrilineal support than male juveniles, and older juveniles provided more matrilineal support than younger juveniles. These results are consistent with the observation that matrilineal rank is typically correlated with the number of juvenile females in the matriline, and with a Matrilineal Power Index that is influenced by age and sex, during unstable periods (Chapter 1). The results of the study therefore suggest that the characteristics of matrilines and behaviour of matrilineals, in particular the number and behaviour of older juvenile females, are important in determining matrilineal ranks as troops emerge from unstable periods and enter new periods of matrilineal rank stability.

In Chapter 4, the distribution of non-matrilineal support was investigated in the study troop to comment on whether mutualism or reciprocal altruism better explains patterns of non-

matrilineal support in Old World monkeys. Under the reciprocal altruism hypothesis, the benefit of non-matrilineal support comes through future support reciprocation by the recipient; under the mutualism hypothesis, the benefit comes through immediate re-enforcement of the supporter's rank over the opponent. The frequency distribution of supports in the six different social contexts that can be generated by altering the relative ranks of supporter, recipient and opponent, and hence altering the costs and benefits of support, fell into the three frequency groups predicted by the reciprocal altruism hypothesis. Supports were most frequent when costs were low (supporter outranks opponent; retaliation probability low) and benefits were high (recipient outranks opponent; reciprocation probability high). They occurred with intermediate frequency when benefits were low (opponent outranks recipient) and costs were low (supporter outranks opponent) or when benefits were high (recipient outranks opponent) and costs were high (opponent outranks supporter). They occurred infrequently when benefits were low and costs were high (opponent outranks both supporter and recipient). A strict interpretation of the mutualism hypothesis predicts only two frequency groups of non-matrilineal supports. Supports should occur frequently whenever the supporter outranks the opponent (low cost, benefits accrue), and infrequently whenever the opponent outranks the supporter (high cost, no benefits of rank re-enforcement). However, if the mutualism hypothesis is modified to allow for possible changes in support costs as a consequence of changes in the relative ranks of recipients and opponents, it makes a similar prediction for the frequency distribution of supports as does the reciprocal altruism hypothesis. Support frequency was lower during unstable than stable periods in the matrilineal dominance hierarchy in this study. This is predicted by the reciprocal altruism hypothesis but not by the mutualism hypothesis. Under reciprocal altruism, the benefits of support should be lower in unstable periods, since the future rank of the recipient, and hence its future value as a reciprocator is uncertain. Under mutualism, the benefits of support should be higher in unstable periods, since benefits arising through rank re-enforcement should be higher. The strongest support for the reciprocal altruism hypothesis emerged in studies of reciprocity in non-matrilineal support exchanges. In 14 of the 16 individuals investigated in this study, the proportion or an individual's support given to troop members was significantly correlated with the proportion of its support received from the troop members. This is predicted by the reciprocal altruism but not by the mutualism hypothesis. Under mutualism, nonmatrilineal supports should occur opportunistically whenever low cost opportunities for rank reenforcement appear. Supports should therefore be unaffected by the identity of the recipient and the probability of future reciprocation. The results of the study therefore suggest that reciprocal altruism is a better model for non-matrilineal support in vervet monkeys than is mutualism.