Dissertation

Paternal kinship among adult female rhesus macaques (*Macaca mulatta*)

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To my parents

with respect and gratitude
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Zusammenfassung

Der Einfluß der mütterlichen Verwandtschaft auf das soziale Verhalten ist eingehend für viele Primatenarten untersucht worden, es ist jedoch schwierig die Bedeutung der Verwandtenselektion auf die Evolution von sozialem Verhalten zu bewerten, wenn Studien auf die mütterliche Verwandtschaft begrenzt sind und die väterliche Verwandtschaft dabei völlig ignorieren. Das Ziel der vorliegenden Dissertation war die Untersuchung des Ausmaßes der väterlichen Verwandtschaft und ihr Einfluß auf die sozialen Beziehungen zwischen adulten Weibchen in einer freilebenden Gruppe von Rhesusaffen (*Macaca mulatta*) auf der Insel Cayo Santiago. Die wichtigsten Resultate können folgendermaßen zusammengefaßt werden:

Erstens, zur Beurteilung des Ausmaßes der väterlichen Verwandtschaft wurde die Vaterschaft der zwischen 1993 und 1998 geborenen Kindern der Studiengruppe bestimmt. Die Resultate zeigten, dass die Reproduktion der Männchen innerhalb der Untersuchungszeit nicht gleich verteilt war; einige wenige Männchen zeugten viele Nachkommen, aber die Mehrzahl der potentiellen Väter reproduzierten sich gar nicht oder nur wenig. Dies führte zu einer Verwandtschaftsstruktur in der fast alle im Untersuchungszeitraum geborenen Kinder mindestens ein väterliches Halbgeschwister mit geringer Altersdifferenz hatten, d.h. entweder im selben Alter (74%) oder maximal zwei Jahre jünger oder älter als es selbst (15%). Wenn auch bei anderen Primatenarten die Reproduktion auf einige wenige Männchen beschränkt ist, dann sollte die Bedeutung der väterlichen Verwandtschaft für Primaten neu bewertet werden. Eine der wichtigsten Konsequenzen der ungleichen Reproduktion der Männchen wäre nämlich, dass viele Individuen mehr väterliche, als mütterliche Halbgeschwister in ihrem Leben haben.

Dies deutet darauf hin, dass Altersnähe einen zusätzlichen regulierenden Einfluß auf affiliatives Verhalten hatte. Beweise dafür, dass sich väterliche Verwandte erkennen können, sind nur in Bezug auf affiliative Interaktionen, nicht aber auf dyadische Aggression gefunden worden, was eine kontextabhängige Verwandtenerkennung annehmen läßt.

Drittens, bei der Einbeziehung weiterer Verwandtschaftskategorien zeigten die Daten, dass mütterliche Verwandte auch bei konstant gehaltenem Verwandtschaftsgrad deutlich gegenüber väterlichen Verwandten bevorzugt wurden. Dies weist darauf hin, dass die mütterliche Verwandtschaft in der untersuchten Gruppe einen größeren Einfluß auf die sozialen Beziehungen adulter Rhesusaffenweibchen hatte als die väterliche Verwandtschaft. Affiliative sowie aggressive Interaktionen nahmen mit sinkendem Verwandtschaftsgrad ab, aber entfernte Verwandte unterschieden einander immer noch von Nichtverwandten, was der Existenz einer Verwandtschaftsschwelle widerspricht.

Viertens, schließlich wurde die väterliche Verwandtschaft in Bezug auf Koalitionsbildungen untersucht. Eine Koalition wird gebildet, wenn ein Individuum in ein laufenden Konflikt zwischen zwei Kontrahenten eingreift, um eine Partei gegen die andere zu unterstützen. Weibliche Rhesusaffen unterstützten am häufigsten ihre mütterliche Halbschwester. Außerdem unterstützten sie Nichtverwandte gleichen Alters häufiger als Nichtverwandte unterschiedlichen Alters. Weibchen unterstützten ihre väterlichen Halbschwestern nicht häufiger als Nichtverwandte, aber die Daten könnten auf einen indirekten Beweis der väterlichen Verwandtenerkennung hinweisen, da Weibchen dazu tendierten gegen ihre väterlichen Halbschwestern seltener zu intervenieren als gegen Nichtverwandte. Dieser Befund könnte durch die Tatsache bedingt sein, dass väterliche Halbschwestern sehr unterschiedliche Dominanzränge einnehmen können, währenddessen mütterliche Halbschwestern immer benachbarte Dominanzränge haben, was zur Folge hat, dass ein rangtiefes Weibchen ihrer väterlichen Halbschwester nicht wirklich helfen kann, da sie ein viel höheres Vergeltungsrisiko auf sich nimmt, wenn sie in einen Konflikt zwischen zwei ranghöhere Kontrahenten interveniert. Als einen Kompromiß könnten Weibchen statt dessen vermeiden gegen ihre väterlichen Halbschwestern zu intervenieren, was darauf hindeuten könnte, dass individuelle Zwänge bezüglich der eigenen Konkurrenzfähigkeit eine bedeutende Rolle bei der Koalitionsbildung spielen. Mütterliche und väterliche Halbschwestern zeigten zudem einen stärkeren Trend zu “reciprocity” und “interchange” als Nichtverwandte und gaben einander einen höheren Anteil an kostenintensiven Unterstützungen.

Schließlich unterstreichen die Ergebnisse dieser Studie deutlich, dass Vertrautheit zwischen Individuen durch frühkindliche Bindungen mindestens auf zwei Wegen erfolgen kann: (i)
Mütter vermitteln Vertrautheit zwischen ihren Kindern (die mütterliche Halbgeschwister sind) aufgrund der durch die Laktation bedingten engen Mutter-Kind Bindung und (ii) Altersnähe vermittelt mehr Vertrautheit zwischen Altersgenossen (die entweder väterliche Halbgeschwister oder Nichtverwandte sind), die wichtige Lebensabschnitte wie z.B. Kindheit, Menstruationsbeginn, Schwangerschaft oder Mutterschaft zu ähnlichen Zeiten durchlaufen, während Weibchen unterschiedlichen Alters dies nicht tun. In jedem Fall brauchen väterliche Halbgeschwister neben der Vertrautheit zu ihren Altersgenossen noch einen zusätzlichen Mechanismus wie z.B. das „phenotype matching“ um innerhalb ihrer Altersgenossen wirklich zwischen väterlichen Halbgeschwistern und Nichtverwandten zu unterscheiden.
1. General introduction

1. Missing the knowledge of paternity is missing half of the knowledge on kinship

Most primates live in groups consisting of several adult males and adult females (Melnick & Pearl 1987). By recording births to known females, relatedness via the maternal line can be reconstructed by human observers. However, when females mate with more than one male, all sexually active males have to be considered as potential sires. Paternity is uncertain to be identified by observation (Inoue et al. 1993), but can be determined using modern genetic techniques. Since paternity analyses were introduced into the field of primatology not earlier than at the beginning of the nineties (e.g., Martin et al. 1992, Inoue & Takenaka 1993), all previous studies on wild or free-ranging primates with multiple mating lacking the knowledge of paternity. For decades, all studies on kinship in primates were limited to maternal kin. Consequently, all individuals not maternally related were considered to be unrelated ignoring the proportion of paternally related individuals (cf. Kummer 1992). However, each individual shares on average 50% of its genes with the mother and the remaining 50% with its father. If we additionally consider the remarkable importance of maternal kinship in shaping female primate behaviour (see chapter 4-6, reviewed in Silk 2001), we still just know half of the story as we miss knowledge about the existence and the importance of paternal kinship. This thesis will investigate whether or not paternal kinship also influences female primate behaviour.

2. The knowledge of paternity allows to investigate new questions

Determining the sire of an individual opens up revolutionary possibilities to answer questions which could not have been addressed before. One question of interest is related to male competition over females. Darwin (1871) already noted this type of sexual selection and named it intrasexual selection. The issue of male reproductive success has attracted researchers (e.g., de Ruiter et al. 1992), but it is still unclear for many primate species whether reproduction is equally distributed among sexually active males or whether reproduction is limited to some males (male reproductive skew) (Pereira et al. 2000). Only the latter situation where few or even one male monopolise/s all receptive females creates paternal kinship. Whether or not paternal kinship is existing among primates will be one of the topics addressed in this thesis.
Another question of enormous interest is to test whether kin selection theory also holds among paternally related individuals (Hamilton 1964). The impact of paternal kinship has been expected to be important (J. Altmann 1979), especially when male reproduction is skewed within the birth cohort considered resulting in paternal cohorts as infant tend to be sired by the same male. Whether paternal cohorts exist and whether the presence of paternal kin is also influencing the social structure has not yet been investigated. From kin selection theory (Hamilton 1964) it is expected, that, assuming costs and benefits being equal, paternal half-siblings should support each other to a similar extent as maternal half-siblings do, as they share the same degree of relatedness. This requires that individuals somehow discriminate their paternal siblings from non-kin, but whether primates are capable of paternal kin discrimination is questionable (Walters 1987).

3. **Factors influencing kinship within a group**

The kinship structure within a social group depends at least upon two variables which also differ among species: (i) **the mating system** of the species and (ii) **the migration system** meaning which sex is the dispersing one.

The study species, the rhesus macaque (*Macaca mulatta*) has a promiscuous mating system, i.e., males and females mate with more than one sexual partner. Clearly, male and female reproductive decisions shape the kinship structure within a group. In other words, a different kin structure will result when the same pair of a male and a female reproduces together each year (resulting in progeny which will be full-siblings), when a female always reproduces with a different male (her offspring will be maternal half-siblings) or when a male fertilises a number of unrelated females (his offspring will be paternal half-siblings).

As in other macaques, the male is the dispersing sex, creating a group which is built by a core of maternally related females and their female descendants structured in matrilineal lineages (Melnick & Pearl 1987). Females live together with their kin and non-kin throughout their life. Males in contrast leave their natal group around puberty and spend most time of their reproductive life among unrelated individuals in a non-natal group. Investigating the effect of kinship, this study is therefore restricted to females which are the social core of a group and assuming male reproduction skew who are likely to have paternal kin to interact with. Therefore, females are likely to interact with both maternal and paternal kin, but also non-kin. Studying paternal kinship may help to complete our understanding of the importance of kinship in primates (cf. Silk 2002). First, the question of the extent of paternal kinship will be investigated in this thesis using paternity data of the study group. Second, in order to evaluate
the importance of paternal kinship, a comparison will be made with respect to maternal kin and non-kin. Therefore, information on maternal and paternal kinship for the whole social group was combined with nearly 700 hours of behavioural observations collected from 34 focal females of the same social group. This is a unique data set combining behavioural and genetic data which allows to address several topics of current interest in behavioural ecology and sociobiology which are outlined in the following chapters.

4. Chapter overview

Chapter 1. General introduction
This is the present one.

Chapter 2. General methods
This chapter will describe the study species, the study population as well as the study group and the focal females which have been studied in detail. Furthermore, it will explain how behavioural data were collected and it will give definitions of behaviour observed. The analyses of these behavioural data will than be described in addition to the statistical tests used. Finally, the technique of paternity analyses will be explained.

Chapter 3. Male reproductive skew, females perspective and paternal birth cohorts
The kinship structure within a social group is the consequence of both male and female mating decisions. Since male and female rhesus macaques mate with more than one sexual partner, reproductive outcome will be analysed from all three perspectives: (i) the sires and their ability to exclude other males from reproduction, (ii) the mothers perspective whether her offspring are sired by the same or by different males across years which effects the kinship relations among her offspring, and (iii) the resulting infants and the relatedness within and across birth cohorts.

Chapter 4. Paternal kin discrimination and age proximity
Among primates, maternal kinship frequently coincides with patterns of grooming and agonistic support, but the extent to which paternal kinship influences female social relationships is still unknown. Here, the effect of paternal kinship on co-operative and competitive interactions among adult female rhesus macaques will be investigated. Since individuals of the same age are known to be more familiar with each other than individuals of a different age, data will also be controlled for age proximity. In addition, likely mechanisms underlying paternal kin discrimination will be discussed.
Chapter 5. Relatedness threshold and the degree of relatedness

Although there is huge evidence that primates bias their behaviour towards their (maternal) kin, less is known about how this bias varies with the degree of relatedness between individuals. For example, kin bias might decrease proportionally with decreasing degree of relatedness or there might also be a relatedness threshold under which distant kin are treated like unrelated individuals. This chapter aims to investigate the importance of the degree of relatedness in regulating social behaviour among both maternal and paternal kin. Furthermore, a comparison will be made between individuals who share the same degree of relatedness but who join a different kin category. To investigate the effect of the degree of relatedness on affiliation and aggression behavioural data are analysed among a wider range of relatedness for both maternal and paternal kinship than presented in the previous chapter.

Chapter 6. Coalition formation with the knowledge of paternal kinship

Previous studies of coalition formation have shown that age, rank and maternal kinship influence the likelihood of an individual interfering in an ongoing fight between two opponents in order to support one of them. Support given (or coalition formation) is thought to be a very costly behaviour since an individual risks to be injured by interfering in a fight. There are three possible theories explaining coalition formation: (i) individuals support kin to enhance their indirect fitness (kin selection), (ii) individuals support non-kin to receive future reciprocal support (reciprocal altruism) or (iii) individuals pursue self-interests and immediately benefit from non-kin support (co-operation). This chapter reinvestigates patterns of agonistic intervention with the knowledge of paternity, because paternal kinship is also expected to shape co-operation during agonistic conflicts.

Parts of this thesis have been already published by the team involved in this project whereas others are in preparation for publication:


2. General methods

1. The Rhesus macaque (Macaca mulatta)

Rhesus macaques have the most extensive geographical range of any non-human primate (Southwick et al. 1996). This species originating from Asia lives in habitats varying from semi-desert, temperate forest to tropical woodland and swamp, from sea level to 3000m (Seth & Seth 1986). Each social group occupies a home range, which is not defended, but is likely to overlap between two neighbouring groups. The home range varies in size between 0.37 and 16 km² (Soutwick et al. 1996). In the wild, the group size varies between 10 to 125 individuals, close to humans they have been observed in groups up to 240 individuals (Seth & Seth 1986, Southwick et al. 1996). Groups are composed either of many small matrilines (definition below) or of a few large matrilines (Melnick & Kidd 1983). After a certain rise in number a large group is likely to fission, e.g., by splitting along matrilines and then pushing the lowest-ranking female with her descendants to the periphery of the group. This subgroup finally splits up and starts a group on its own (Chepko-Sade & Sade 1979, Melnick & Kidd 1983).

Rhesus monkeys live in multi-male, multi-female groups. The females are philopatric, i.e., they stay in their natal group throughout their life and interact with both kin and non-kin (Gouzoules & Gouzoules 1987). As a consequence, females are closely associated with their maternal kin which is called a female-bonded society (Wrangham 1980). Maternal kinship is established via matrilines, with a matriline defined as all descendants by a founder female (Melnick & Pearl 1987). In contrast, male macaques are the dispersing sex (Colvin 1986, Melnick & Pearl 1987). They emigrate from their natal group around puberty to join other social groups (Lindburg 1969, Colvin 1986). This happens especially during the mating season which Lindburg (1969) named mating season mobility. Most males change groups every few years. This behaviour has been interpreted as inbreeding avoidance (Melnick et al. 1984, Pusey 1987, Pusey & Wolf 1996). Although male rhesus were found to join groups into which their elder brothers had immigrated (Meikle & Vessey 1981), males mainly interact with non-kin once they emigrated.

Adult males are dominant to adult females, and females, in addition, are clustered in a strict matrilineal hierarchy. Mothers are dominant to their daughters, and daughters socially inherit
the dominance rank of their mother (Koyama 1967, Berman 1980). The rank order among daughters is inverse to their birth order (Datta 1988). This has three consequences: (i) all daughters rank directly below their mothers in the hierarchy, (ii) all maternal half-siblings occupy adjacent dominance ranks within a troop (Chapais & Schulman 1980), and (iii) the eldest daughter is the lowest ranking among her sisters. High-ranking females are often preferred as social partners (Seyfarth 1980), suggesting that dominance rank is also influencing the social structure among females. Macaques are capable of detecting their own individual dominance relation towards others, but likewise they are capable to detect the rank relation between two other monkeys (reviewed by Cheney & Seyfarth 1990) which is influencing the likelihood of interventions in conflicts among others (see chapter 6).

Females reach **adulthood around 3.5 years** of age, males around 4.5 years of age (Bercovitch & Berard 1993, van Hooff 1988). However, there is probably substantial inter-individual variation in the ages at which the full development is attained (Pereira & Altmann 1985, Bercovitch & Goy 1990).

Rhesus monkeys exhibit a **promiscuous mating system**, males and females mate with several sexual partners. Mating with multiple males has been interpreted as a female reproductive tactic designed to obscure paternity, decrease the risk of infanticide and increase the chance of parental care (Hrdy 1981, Stacey 1982). Female rhesus macaques are found to mate with an average of three males per conception cycle and they tend to conceive on the first cycle of a mating season (Bercovitch 1997). Sexually receptive females form temporary mating bonds (consortships) with males (Carpenter 1942, Lindburg 1971, Chapais 1983). Aggressive competition and male coalitions over access to fertile females are rare in rhesus macaques (reviewed in Bercovitch 1992), but males suffer more wounds during the mating season (Bercovitch 1997). High-ranking males sire more offspring than low-ranking males (Bercovitch & Nürnberg 1996), but females prefer to mate with low-ranking (Manson 1995a) and novel males (Manson 1995a, Bercovitch 1991, 1997, Berard 1999).

2. **The study population of Cayo Santiago**

Cayo Santiago is a 15.2-hectare island situated approximately 1 km off the south-east coast of Puerto Rico (18°09' N, 65°44' W). The climate is subtropical, with average rainfall of 163 cm per annum and mean daily temperatures ranging from 23.8 °C to 27.1 °C (Kessler & Berard 1989). Vegetation on the island ranges from sparsely wooded areas to dense undergrowth, with periodically waterlogged mangrove areas and exposed cliffs.
The island is inhabited by a free-ranging colony of approximately 800 rhesus macaques, which are distributed over the island in several social groups. All individuals are descendants of the founding population of 409 individuals trapped in India in 1938 (more details in Carpenter 1942, Rawlins & Kessler 1986). No individuals have been added on Cayo Santiago since then except through births, but genetic analyses suggest that the island population is not closely inbred (Widdig et al. 2001). Historically seen, this study site is/was important as studies on primates have been restricted to captivity, before studies on wild primates became first successful in the seventies. The advantage of studying kinship in this population is that census records have been kept continuously since 1956, therefore detailed maternal genealogies and male migration histories are known for all individuals. Day of birth and day of death (or removal) are also available for all individuals. In addition, paternity analyses were started with analysing the birth cohort 1989 from group S.

This population lives under so called semi-free conditions and monkeys are habituated to human observers. The animals are provisioned with commercial high protein biscuits distributed once daily in the morning at the three food dispensers located in corrals. Nevertheless, the macaques forage extensively, with an estimated 50% of feeding time spent on natural sources, e.g., foliage, fruits, and insects (Marriot et al. 1986, Marriot 1988). The ingestion of soil is thought to aid against enteric parasites (Knezevich 1998). Available water is supplemented via the collection of rainfall in cisterns and piping of water to drinking basins. Although the primary sources of mortality are starvation and injury (Berard 1990), the lack of natural predators on the island requires an artificial control of the population size. In the past, entire social groups were removed, but since 1996 a proportion of randomly selected 2-year-olds from each social troop has been chosen annually with respect to family membership. Intervention is limited to an annual trapping period (January to March), during which the 1-year-olds are assigned identification codes and blood samples are obtained for paternity analyses.

3. The study group

Like a typical macaque group, the study troop, group R, consists of a stable core of maternally related females with their offspring and adult males who change in number, especially around the mating season where immigration and emigration is at a maximum (Hill 1986). Group R had been formed as the result of a fission event in 1985, whilst group BB subsequently fissioned from R in the period January-February 1996 (Kazem pers. comm.), with the partition being complete prior to the collection of the behavioural data presented here. In the
census provided by the Caribbean Primate Research Center (CPRC), group BB has been considered as a separate group from R since June 1996. Group BB was smaller than group R and mainly formed by the lower-ranking females from R and their offspring. During the behavioural observation period in 1997, group R had a total of 126 core members i.e., 91 natal females and 35 natal males (not involving adult males which are non-natal, see below), but the behavioural analyses were restricted to interactions among adult females and their female descendants (N=91). In addition, the number of adult non-natal males changed between 21 and 31 during the behavioural study due to migration. All males (natal and non-natal) were excluded from the behavioural analyses. After migration males interact more with non-kin than with kin, so for the majority of their adult life they mainly interact with non-kin. However, it could be that males also learn to discriminate paternal kin from non-kin in their natal group. In order to compare interaction between kin (both maternal and paternal) and non-kin, adult females are the appropriate sex to study.

Two data sets will be distinguished in this thesis. The first data set will be used in chapter 3 (reproductive skew) where paternity analyses for all infants born in group R and BB between 1993 and 1998 (N=263) will be presented without additional behavioural observations. The second data set will be used in chapter 4-6 where paternity analyses on all females of group R present in 1997 (N=91) will be presented in combination with behavioural observations. The latter data set, the study group will now be introduced in detail (see also Appendix 1 on the study group).

**Age of the group subjects (N=91)**

Age (date of birth) was known for all group members from the demographic data base of the CPRC. Since age classification differs across studies and inter-individual variation is known (see above), females in this study have been generally categorised as “adults” when they were born in 1994 or before. In other words, they were at least 3 years old during the behavioural study in 1997, because such a female has already given birth to an infant. Further definitions of age classes used in this study are given in Table 2.1.

**Table 2.1: Age categories among the group females (N=91)**

<table>
<thead>
<tr>
<th>Category</th>
<th>Age (in years)</th>
<th>Definition</th>
<th>N females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Infant</td>
<td>0-1</td>
<td>Period between birth and weaning</td>
<td>25</td>
</tr>
<tr>
<td>Juvenile</td>
<td>1-3</td>
<td>Post-weaning until puberty</td>
<td>17</td>
</tr>
<tr>
<td>Adult</td>
<td>≥3</td>
<td>From first oestrous until death</td>
<td>49</td>
</tr>
</tbody>
</table>
The rhesus macaque breeds on a seasonal basis (Lindburg 1971, Drickamer 1974, Bercovitch 1997) with an inter-birth interval of approximately one year (Rawlins & Kessler 1986). The mating season at Cayo Santiago usually lasts from May to October, following the birth season from November to April, with a peak of births in January to February. Thus, individuals can be classified into discrete a **birth cohort**, although individuals born within the same birth season may be born on the same day or up to a maximum of 6 months apart. Individuals born within the same birth season are defined as **peers**, whereas individuals born into different cohorts are **non-peers**. Both age categories were distinguished throughout the study, but in some analyses the exact age differences (in years) are used as a refinement of the non-peer category which includes multiple ages (all age differences except for age mates). More information on age and birth cohorts are given in the Appendix 1 (Study group).

**Kinship of group subjects (N=91)**

Maternal kinship for all subjects was known up to several generations backwards using the demographic database of the CPRC which was started in 1956. During the behavioural study, group R was comprised of three matriline, two smaller (D07: N=11, CS: N=15) and a large one (262: N=65, considering only females). Because the focal group was composed of descendants of only three matriline, a narrow definition of „maternal relatedness“ was adopted which included only close family members. A **family** consisted of the eldest surviving daughter (or granddaughter, if the daughter was deceased) of a matrilineal founder and her offspring (if n≥3 offspring) which is comparable to the definition of a “matriline” used by Dunbar (1984) to distinguish close family relatives from more distant kin in large matriline. Therefore, two elderly maternal half-sisters with multiple offspring could have their own family, even though both were descended from the same founding matriarch. Paternal kinship was defined containing all paternal half-siblings and their descendants. Sirehood was revealed via paternity analyses (see below) and paternal kinship could not be reconstructed for more than 2 generations backwards. However, this seems to be sufficient, as in female-philopatric species adult females are likely to be distant kin, whereas adult males (i.e., potential sires) are likely to be unrelated. For example, de Ruiter & Geffen (1998) found for long-tailed macaques, *Macaca fascicularis*, that the average degree of relatedness among dyads of adult females was much higher than for dyads of adult males (adult female r=0.14 vs. adult males r=−0.10). It was therefore assumed that sires are mainly unrelated.

Female rhesus bear only a single offspring in more than 99% of cases (Rawlins & Kessler 1986) suggesting that twins are extremely rare to be found. Assuming that females indeed tend to prefer novel males (Manson 1995a, Bercovitch 1991, 1997, Berard 1999) females are
expected to reproduce with different males rather than always with the same male in consecutive years. This would result in full-siblings to be rarely found, as infants born to the same mother would be **maternal half-siblings** of different ages (i.e., non-peers). Assuming male reproductive skew within the birth season considered, offspring born to different mothers, but sired by the same male, would be **paternal half-siblings** of the same age (i.e., peers) or often in close age proximity.

To investigate the effect of kinship and age proximity on female social relationships (see chapter 4), analyses are restricted to maternal half sisters (same mother, paternally unrelated, coefficient of relatedness \( r = 0.25 \)), paternal half sisters (different family, same father, \( r \approx 0.25 \)), and non-kin (different family and different father, \( r \approx 0.0 \)). For testing the effect of the exact age differences on female social relationships, analyses are restricted to dyads that were either zero (i.e., peers), one, two or three years apart in age.

To investigate the effect of the degree of relatedness on female social relationships (see chapter 5), the analyses were extended to include a wider range of relatedness for both maternal and paternal kinship. In addition to maternal, paternal half-siblings and non-kin used in chapter 4, the following kin categories will be added in chapter 5: mother-daughters (\( r = 0.5 \)), maternal grandmother-granddaughters (\( r = 0.25 \)), maternal aunt-nieces (\( r = 0.125 \)), maternal grandaunt-grandnieces (\( r = 0.0625 \)), maternal cousins (\( r = 0.0625 \)) and paternal aunt-nieces (\( r = 0.125 \)). More information about maternal kinship of the study group is given in the Appendix 1 (Study group).

**Dominance rank of group subjects (N=91)**

Dominance ranks were determined based upon the outcome of dyadic agonistic interactions (ad libitum or continuous data, see below). First, matriline themselves can be arranged in a matrilineal hierarchy which is fairly stable over time. Females from the matriline D07 were highest ranking, followed by matriline CS, and than the large matriline of 262 was lowest ranking. The only exception was the mother-daughter pair 897-J12 from matriline CS, which both ranked lowest within group R, being on the periphery of the group.

Second, females themselves were arranged in an individual hierarchy. All mothers were found to be dominant over their daughters and all maternal half-sisters could also be ranked as predicted from their birth order with the exceptions of the two sister pairs (33C-X34 and X91-T95).

Kawai (1958) distinguished between **dependent rank** where individuals still dependent upon support of a third individual in order to achieve their **basic rank** where they have already acquired their adult rank. However, including all 91 females of the study group in the
hierarchy could bias data if younger females were still dependent in rank upon their mothers. In order to control for this potential bias, hierarchy was restricted to adult females with basic ranks (N=49). The hierarchy of the matriline is given in the Appendix 1 (Study group).

4. **Focal females (N=34)**

From the study group R, 34 out of all 49 adult females were chosen as focal subjects. These females were consistently monitored in respect to their social interactions with other group females (see below). Regarding age, all focal females were adults. All females born between 1994 and 1988 and still present during the behavioural study in 1997 were chosen as focal females regardless of determined paternity. This decision was due to two reasons: First, for adult females born before 1988 it was less likely to establish paternity since the probability that their actual sire was genotyped decreased for elder females. Even though all males on the island were genotyped, systematically blood collection for paternity analyses did not start before 1992 (Nürnberg, pers. comm.). However, for the very old females with undetected paternity the existence of a paternal half-sibling within the study group in 1997 could be excluded (see paternity analysis below). Second, females born in 1995 or later were still dependent in their behaviour upon their mothers and therefore less suitable as focal subjects. All 34 females had 1 to 5 peers and 71 to 82 non-peers. Regarding kinship, all 34 females had a maternal half-sister (ranging from 1 to 6) and 22 out of the 34 focal females had a paternal half-sister (ranging from 1 to 5). Fifteen of these 22 focal females had a paternal half-sister being a peer (range between 1 to 2) and nineteen of these 22 females had a paternal half-sister being a non-peer (range between 1 to 4). Due to trapping (and perhaps early death) individuals lost part of paternal half-siblings which they had at the time of their birth (compare chapter 3 showing that the average number of paternal half-siblings is larger compared to maternal half-siblings). All females had female non-kin in the group, their number varied between 1 to 5 being peers and 64 to 82 non-kin non-peers across focal females. Regarding rank, focal females came from all three matriline and were of high, medium or low maternal rank. Focal females are marked in bold in Appendix 1 (Study group).

5. **Behavioural data taking**

Field work started on the 3rd of May in 1997. After 3 weeks all core members of the group plus most adult males could be distinguished individually. Infants could be identified later, since they were still depending on the mother at the start of the study and could therefore be assigned to their mothers when they went back to suckle. At the same time all observed
behaviour was catalogued and the focal protocol (a written checksheet) was designed. All behavioural data were taken between May 28th and December 23rd of 1997, six days a week between 7 a.m. and 3 p.m. (weekdays) or 7 a.m. and 4.30 p.m. (weekend and holiday), respectively, due to the boat schedule given by the CPRC. Even though there is evidence of seasonal variance in behaviour (e.g. Wilson & Boelkins 1970, D’Amato et al. 1982), most data were taken during the mating season in order to avoid disturbance during the trapping period which finished around the end of March 1997 and started again in January 1998. During the mating season, females were monitored for signs of oestrus (coloration and oedema of the sexual skin, presence of vaginal plug, obvious consort behaviour), because social behaviour may change over the course of these cycles. Whenever the focal female entered the feeding corral, this would be noted in the focal protocol, since increased interactions (especially regarding competition) were expected.

Observations were scheduled in order to achieve an equal distribution per individual over the day, since activity could depend on the time of the day. The sequence of animals observed was determined by randomly selecting a focal from those remaining to be sampled during that particular time block. No individual was observed more than once per day. A focal protocol was interrupted when the focal animal was out of view and continued if this break was less than 5min. Otherwise the protocol was discarded. Census was checked once per observation day including data on group membership, transfers, births and deaths. Where animals appeared to be transferring in or out of the group, their position was continuously checked, until final state was reached. These records were contributed to the census of the CPRC.

A repetition of a behaviour was scored as a new bout if (i) more than 10 seconds had elapsed between occurrences, (ii) at least one partner had switched to a mutually exclusive activity (e.g., from grooming to aggression) or (iii) at least one partner moved out of the 2m radius. The only exception were aggressive events in which a number of different agonistic patterns occur in quick succession. Unless one or both opponents had switched to a mutually exclusive behaviour those bouts were treated as one, but only the most intense kind of aggression was used for the analyses. Acts between mother and their dependent infants were scored as interactions only, when the act was specifically directed towards or initiated by the infant.

6. Behavioural definition

Behavioural data are either states or events (Martin & Bateson 1986). State data are counted as point time sampling (see below). Within a 20min focal protocol, state data were collected
at min 4, 8, 12, 16 and 20. These data include information on the activity of the focal female and all neighbours in spatial proximity (≤ 5 m) at this second (see below).

Event data are sequence data which were either counted as continuous data or ad libitum data (see below). Sequence data were collected on (i) affiliation interactions such as grooming, friendly approach, co-feeding, co-drinking, (ii) agonistic interactions such as agonistic approach, non-physical and physical aggression, and (iii) interventions in conflicts (coalition formation) including both a co-operative and competitive interaction (see below) and (iv) other interactions. All sequences of behaviour included the identity of the initiator and the recipient of a certain interaction which (i) involved always an interaction between a focal female with one of the remaining potential female social partner (N=90) ignoring interactions between the focal and adult males (see continuous data) or (ii) involved an interaction between any group members others than the focal female (see ad libitum data). Behaviour patterns were scored either as affiliative or agonistic interactions or in other contexts. Focal protocols included always the activity of the recipient before the interaction (context) and the response of the recipient following the interaction. All interactions were scored as bouts. Grooming, in addition, was timed as duration (measured in seconds) with one bout lasting at least 5 seconds.

When a third party intervened in an ongoing dyadic conflict (coalition formation), the following information was collected whenever possible: (i) the initiator and recipient of the original dyadic conflict, including kind and context of aggression, response of the recipient, (ii) the sequence of intervening individuals, (iii) the kind of aggression by the intervener/s, (iv) whether the intervener/s supported the aggressor or the victim of the original dyadic conflict, (v) the distance of the supporter towards the dyadic conflict, (vi) whether or not the supporter approached the scene and (vii) the response by the target of support. One possibility to assess the number of potential support by a given female (opportunities of support, see below), all non-silent agonistic interactions were counted ad libitum to determine how often a maternal kin, paternal kin or non-kin of the female considered was involved in a dyadic conflict. A non-silent agonistic interaction was defined as either non-silent aggression including vocal threat, lunge, charge, chase, bite, attack or/and non-silent responses of any aggression such as fleeing and screaming. Silent agonistic interactions as open mouth threat, head-bobbing or displacement were not counted as opportunities of support as they could have been occurred out of sight to potential interveners (e.g., in dense vegetation).

Description of behaviours used in this study are given in the Appendix 2 (Ethogram).
**Point time sampling data**

Two kinds of point time sampling data were collected. First, data on spatial proximity (hereafter: proximity) were based upon point samples taken every 4 min during each focal protocol (Altmann 1974). Here, all neighbours within the 5m radius were identified with their exact distance (in m) towards the focal female including their activity at this time. Where no animal was within 5m of the focal female, the distance (in m) to and identity of the nearest visible individual including their activity were recorded instead, but not used in the analyses. If two neighbours were interacting or in contact they were recorded as social partners. As a second type of point time sampling data, the current activity state of the focal was also noted. (see also Appendix 2 Ethogram).

**Continuous data**

During focal sampling, all behavioural interactions involving the focal female and any of the remaining potential female social partners (N=90) were noted. The behaviour patterns were continuously recorded in the sequence in which they occurred (Altmann 1974).

**Ad libitum data**

Ad libitum data (Altmann 1974) are additional information collected in a focal protocol with interactions not involving the focal animal (non-focal data). Two kinds of ad libitum data were recorded in their sequence whenever they occurred. First, all dyadic and polyadic (coalition formation) agonistic encounters among group members were noted if the identities of the original dyadic conflict were observed. Ad libitum data are expected to be biased towards non-silent agonistic interactions or to conflicts involving individuals which consistently share spatial proximity with the focal female. These data were also used to construct the hierarchy among both males and females. Second, all grooming bouts observed between any group members were recorded in the way described before, but here the duration of a grooming bout is missing.

7. **Behavioural data analyses**

**General analyses**

In total, 645 hours focal sampling of nearly 1000 hours collected were used for analysing interactions of the 34 focal females, with a mean of 1130 min (ranging between 980 to 1180 min) per focal female. All behavioural data collected have later been entered into a complex data base designed in Microsoft Access ©. To answer specific questions, data have been re-
filtered from Access into a two dimensional table which were transferred to Excel. In Excel, the data were arranged in a 34 x 91 matrices (focal female x potential female social partner) to calculate either (i) rates per hour, or (ii) mean duration for each of the 34 females with respect to all potential female social partners within the group. As a general procedure, for each of the focal subjects the observed frequency of a given behaviour per social partner was divided by the observation time, so data on single behaviours are rates per hour.

*Analyses on affiliation and aggression*

Analyses were confined to three affiliative dyadic interactions (spatial proximity, grooming and approach) and two agonistic dyadic interactions (physical and non-physical aggression) because the remaining interactions (co-feeding, co-drinking, passes) were not suitable or did not occur frequently. Dyadic scores for social partners who were related to the focal animal, but who were neither maternal nor paternal half-siblings of the focal female, were excluded from analysis on paternal kin discrimination (chapter 4). Here, the crucial comparison was between non-kin on the one hand, and close kin of identical genetic relatedness (r=0.25), but of different co-parental gender, on the other. In other analyses, dyadic scores for social partners who were maternally or paternally related were calculated in order to compare different degree of relatedness of maternal and paternal kin (chapter 5).

*Analyses on coalition formation*

In chapter 6 data on coalition formation were analysed. A coalition is formed when one individual intervenes in an ongoing conflict between two opponents in order to support one of them. Since support in favour of one party is simultaneously targeting the other party, coalitions are triadic interactions involving a supporter, a recipient and a target (see chapter 6 for more details). Whenever the sequence of intervention by multiple supporters (polyadic support) into the original dyadic conflict was observed, this event was split into single triads each including a target, a recipient and a supporter (cf. Widdig *et al.* 2000).

Different analyses on coalition formation are *all* based on interventions observed over the 8 months study period, either collected ad libitum or in a focal protocol. I assume that these data collection did not bias the sample for the following reasons. Coalitions are relatively long lasting and often noisy events, especially as rhesus macaques tend to redirect aggression they received to other individuals which often produces a series of conspicuous aggressive events (pers. observation). Thus, together with the fact that individuals could be recognised over long distances, it is unlikely that a substantial number of dyadic conflicts followed by coalition
formation were missed (cf. Altmann 1974). As coalitions are based on ad libitum observations data are not rates per hour. Testing the kin selection theory, all coalitions were included where a focal female (N=34) was intervening either in favour of or against a maternal half-sibling, a paternal half-siblings or a non-kin. This implies that the third party in this coalition could be any other individual of group R including adult males. Two different procedures were used to determine whether focal females intervened more on behalf of a particular kin and age category (i.e., maternal half-siblings being non-peers) than expected. The number of observed interventions was either divided (i) by the number of potential partners available in a particular kin and age category (hereafter: availability) or (ii) by the number of opportunities to intervene on behalf of particular kin and age categories (hereafter: opportunities) (cf. Silk et al. 2002). The number of available partners was based on the number of individuals of a particular kin and age categories present during the study period. The number of opportunities to intervene on behalf of a potential recipient were derived from the number of non-silent dyadic conflicts (see above) in which this potential recipient was involved.

Testing reciprocity or interchange, all coalitions were included where an adult female (N=49) was intervening in favour of or against another adult female due to the limitations in the program used for matrix correlation (see below). The third party in this coalition could be any other individual of group R including adult males.

Testing co-operation, all coalitions were included where an adult female (N=49) was intervening either in favour of a maternal half-sibling, a paternal half-siblings or a non-kin. Again, the third party in this coalition could be any other individual of group R including adult males.

8. Statistical Tests
The unit for analyses were either the individual or a dyad units (for the latter see Matrix tests below).

Individual units
However, for most analyses the behaviour of a given focal female, as an individual’s behavioural strategy, was the focus of interest. All interactions in a focal female protocol involved the focal female either as the initiator or the recipient of this particular interaction with any other group female. Females differed in the number of partners in each kin and age classes. For each focal female, her proximity index towards any given social partner was calculated. Then the mean proximity was taken over all female group members meeting a
specific kin and age category with respect to the focal female considered. Analogously, mean indices were calculated for each behaviour. Mean rates per hour for all behaviours (except coalition formation see above) were then compared between kin and age categories by means of paired t-tests applied to the focal females.

If the assumptions of parametric tests were not met (e.g., unequal variance between the categories, data not normally distributed) non-parametric tests such as the Wilcoxon-test were used. In the case of small sample size, the exact instead of the asymptotic p-value was calculated for non-parametric tests (Mundry & Fischer 1998). Exact p-values are indicated as \( P_e \), while asymptotic p-values are given as \( P \).

In order to control the probability of a type I error over multiple statistical tests, the Dunn-Šidák method was adopted for each behaviour (Sokal & Rohlf 1995). The Dunn-Šidák was favoured over the more common Bonferroni correction because the latter is more conservative. Only P-values less than or equal to the corrected significance level (\( P' \)) indicate a significant test result which will be marked in bold.

In contrast, in the next chapter (chapter 3) no behavioural data will be analysed, instead results of the paternity data in comparison with demographic data of potential sires are to be presented.

**Dyadic units**

As a second approach, dyadic units were analysed using the matrix correlation method (Hemelrijk 1990a,b, de Vries 1993) which was restricted to chapter 6 (coalition formation). A relationship between \( N \) individuals of a group is described as a \( N \times N \) Matrix where each cell represents a dyad. Three kinds of questions were analysed: (i) **reciprocity** for the same behaviour among dyads (Hemelrijk 1990a), e.g. is female A grooming female B as often as female B grooms female A, (ii) **interchange** for different behaviours among dyads (Hemelrijk 1990a), e.g. is female A grooming female B as often as female B supports female A and (iii) the correlation between a behaviour and a dyadic attribute (such as rank distance, age distance and degree of relatedness) among dyads, e.g., is an increase in the grooming frequency between dyads associated with an increase in the degree of relatedness between these dyads. The advantages of the matrix correlation method compared to analysis using individual units is that dyadic interdependencies were taken into account. A limitation of this method is that it cannot handle multiple factors (Vervaecke et al. 2000).

Three different matrix tests were used. Firstly, to investigate the correlation between a behaviour (such as grooming, support given or support against) and a dyadic attribute (such as rank distance, age distance or degree of relatedness) on the dyadic level the **Mantel R-test**
was applied. Secondly, to investigate reciprocity or interchange on the individual level the $K_r$-test was used. Finally, (i) to investigate the correlation between a behaviour and the degree of relatedness on the individual level while controlling for rank distance in a third matrix or (ii) to investigate reciprocity or interchange on the individual level while controlling for a dyadic attribute (e.g., maternal sibship) in a third matrix, the partial $K_r$-test was applied (cf. Hemelrijk 1990a,b, de Vries 1993). The Mantel R-test, in contrast to the Mantel Z-test, controls for outliers (cf. Hemelrijk 1990a,b) and investigates whether the sequence of preference among all dyads is correlating between the two matrices. The $K_r$-test, which also controls for outliers, investigates e.g., whether the sequence of preferred partners groomed by individual A is associated with the sequence of partners from whom individual A is being groomed. The partial $K_r$-test is testing the same as the $K_r$-test, but additionally controls for a third dyadic relation which is also described by a NxN matrix. The strength of correlation is measured as a Spearman’s rank correlation coefficient in the case of the Mantel R-test and as a row-wise Kendall correlation coefficient in the case of the $K_r$-test or partial $K_r$-test (cf. de Vries 1993). Matrix correlations were undertaken using the program MatMan by Noldus (licence to Jürgen Streich, IZW). Matrix tests were restricted to females categorised as adults $(N=49)$ using focal and ad libitum data on grooming and support given to a recipient or support against a target. This limitation was necessary, because the program provides only 50 cells.

The significance criterion for all tests was set at alpha=0.05. All statistic tests were two-tailed and taken from Sokal & Rohlf (1995). All these analyses were performed with the SPSS 10.0 package. In order to distinguish degrees of relatedness ($r$) from the Pearson product moment correlation coefficient ($r$) and the Spearman’s rank correlation coefficient ($r$), the former is referred to as $r_p$ and the latter as $r_s$.

9. Paternity analyses

Single locus versus multi-locus approach

DNA typing to identify kinship has mainly been directed at DNA of tandemly repetitive structures, such as (CA)$_n$, (CAG)$_n$, (GATA)$_n$ sequence motifs. They are also referred to as short tandem repeats (STRs). Depending upon the length of the repeat motif and the number of copies tandemly arranged at a single locus, repetitive DNA has been classified by Tautz (1993) as either microsatellites (1-6 bp with 10-100 copies) or minisatellites (9-100 bp with 10-1000 copies). In most cases micro- and minisatellites are characterised by an extreme height of polymorphism (Luty et al. 1990). Polymorphisms are due to mutations such as insertion or
deletion of one or more repeat elements during meiosis resulting in changes of the length of the repeat block. In order to be useful for kinship testing, mutation rate has to be small enough to avoid changes of allele sizes during meiosis to still detect allele sharing between close relatives. Most micro- and minisatellites fulfil this criterion (average mutation rate estimated 10–3 per locus, Edwards et al. 1992). Microsatellites are generally preserved in closely related species (Moore et al. 1991). This allows cross-species amplification of orthologous DNA loci (Kayser et al. 1996). A second approach to kinship analysis uses multi-locus probes. These probes hybridise to multiple sites within the genome which produces a unique pattern of DNA for each individual.

Both, single and multi-locus approaches have advantages and disadvantages which vary depending upon the characteristics of the study species and the population under study (cf. Nürnberg et al. 1998). Paternity assessment by the multi-locus approach was found to have several limitations over microsatellites (ibid.). First, this method requires large amount of DNA, whereas for microsatellites small amount of even degraded DNA are sufficient. Microsatellites also promote non-invasive techniques where samples can be drawn from hair roots or faeces instead of blood (e.g., Launhardt 1998, Smith 2000). Second, data are difficult to compare between gels. Therefore a direct comparison on a single gel including the infant considered, its mother and all the putative candidates (usually 2-4) needs to be available.

At this point two problems related to the present study should be emphasised. The first point of interest is related to the fact that primates in general have a long life span (more than 30 years for rhesus macaques, van Hooff 1988). Paternity might be difficult to assess among the older individuals since it is less likely that their sires have been typed or even sampled. For that reason, it is difficult if not impossible to reconstruct complete patrilineal lineages. Therefore, the main focus of the paternity analyses was restricted to younger individuals. The second point which needs to be considered is the high number of potential sire (i) within the group (up to 62 males in the data set) and (ii) from outside the group because it can not be assumed that sirehood is restricted to resident males. Berard et al. (1993) have demonstrated that a proportion of infants was sired by males from neighbour groups. But since Cayo Sanitago is a close colony (no individuals have been added since 1938 except through births) and because the whole population has been systematically sampled (starting in 1992) it is likely that all potential sires of infants considered were actually genotyped.

Given that (i) the number of microsatellites used is high enough and (ii) that the loci used are polymorphic enough, the best method of choice seems to be a dual approach. In a first step, STR markers are used to reduce the number of potential sires, ideally to N=1. If the number
of potential sires could not been reduced to one sire after testing 15 DNA markers, as a second step, a DNA fingerprinting was undertaken (see below). For the discussion of this combined approach see Nürnberg et al. (1998).

DNA extraction
DNA was available from blood samples which were taken during annual trapping on Cayo Santiago. All samples required for this study were already available as part of the DFG-project of Peter Nürnberg (Nu 50/3-2) which aimed at genotyping the whole population. Genomic DNA was prepared from leukocytes using the Genomix DNA extraction kit (Labortechnik Fröbel GmbH, Lindau, Germany).

Paternity assessment via microsatellites
Primers for the STRs were chosen randomly from the human genome map and their applicability for rhesus macaques was tested on unrelated individuals. Screening of STR markers has earlier been described by Kayser et al. (1996). A total of 14 microsatellites were found to be polymorphic for rhesus macaques with a mean heterozygosity rate of 0.74 (Table 2.2). They comprise di-, tri-, tetr nucleotide repeats. STR markers are as variable as in humans with the mean number of alleles of 8.6 and a slight tendency of shorter alleles in rhesus compared to humans (see Table 2.2).

<table>
<thead>
<tr>
<th>Locus symbol</th>
<th>Repeat motif</th>
<th>Length of PCR product (bp)</th>
<th>N_alleles</th>
<th>H</th>
<th>N_typed</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>D2S367</td>
<td>(CA)_n</td>
<td>115-143 [137-165]</td>
<td>4</td>
<td>0.669</td>
<td>1267</td>
<td>Gyapay et al. 1994</td>
</tr>
<tr>
<td>D5S820</td>
<td>(GATA)_n</td>
<td>181-213 [190-218]</td>
<td>9</td>
<td>0.762</td>
<td>1270</td>
<td>Kayser et al. 1996</td>
</tr>
<tr>
<td>D5S1470</td>
<td>(GATA)_n</td>
<td>195-223 [174-194]</td>
<td>8</td>
<td>0.771</td>
<td>1258</td>
<td>Kayser et al. 1996</td>
</tr>
<tr>
<td>D6S266</td>
<td>(CA)_n</td>
<td>267-285 [268-284]</td>
<td>9</td>
<td>0.852</td>
<td>1262</td>
<td>Weissenbach et al. 1992</td>
</tr>
<tr>
<td>D6S474</td>
<td>(GATA)_n</td>
<td>133-157 [151-167]</td>
<td>7</td>
<td>0.673</td>
<td>1269</td>
<td>Nürnberg et al. 1998</td>
</tr>
<tr>
<td>D6S493</td>
<td>(GATA)_n</td>
<td>256-336 [224-240]</td>
<td>13</td>
<td>0.746</td>
<td>1267</td>
<td>Nürnberg et al. 1998</td>
</tr>
<tr>
<td>D8S271</td>
<td>(CA)_n</td>
<td>261-275 [261-275]</td>
<td>7</td>
<td>0.731</td>
<td>649</td>
<td>Weissenbach et al. 1992</td>
</tr>
<tr>
<td>D8S601</td>
<td>(CA)_n</td>
<td>222-230 [223-236]</td>
<td>10</td>
<td>0.760</td>
<td>691</td>
<td>Xu et al. 1996</td>
</tr>
<tr>
<td>D12S66</td>
<td>(GATA)_n</td>
<td>159-175 [145-177]</td>
<td>6</td>
<td>0.739</td>
<td>647</td>
<td>Kayser et al. 1995</td>
</tr>
<tr>
<td>D12S67</td>
<td>(GATA)_n</td>
<td>108-249 [229-273]</td>
<td>15</td>
<td>0.848</td>
<td>1270</td>
<td>Kayser et al. 1995</td>
</tr>
<tr>
<td>D14S255</td>
<td>(CA)_n</td>
<td>197-211 [197-207]</td>
<td>9</td>
<td>0.699</td>
<td>1269</td>
<td>Kayser et al. 1996</td>
</tr>
<tr>
<td>D20S206</td>
<td>(GATA)_n</td>
<td>154-182 [162-170]</td>
<td>9</td>
<td>0.765</td>
<td>1268</td>
<td>Nürnberg et al. 1998</td>
</tr>
<tr>
<td>D20S476</td>
<td>(GAAT)_n</td>
<td>128-148 [141-157]</td>
<td>7</td>
<td>0.667</td>
<td>702</td>
<td>Sheffield et al. 1995</td>
</tr>
<tr>
<td>SCA1REP</td>
<td>(CAG)_n</td>
<td>163-178 [181-367]</td>
<td>7</td>
<td>0.671</td>
<td>1263</td>
<td>Orr et al. 1993</td>
</tr>
</tbody>
</table>
Abbreviations are as follows: bp is the number of base pairs, numbers in square brackets are human allele length ranges, \( N_{\text{alleles}} \) is the number of alleles found on that locus, \( H \) is the observed heterozygosity, \( N_{\text{typed}} \) is the number of individuals typed on that locus.

In addition to the STR markers listed in Table 2.2, the highly polymorphic DQB1 locus from the major histocompatibility complex (MHC) of rhesus monkeys was analysed as described by Sauermann et al. (1996) and used for paternity determination. Briefly, exon 2 of Mamu-DQB1 was amplified using a single primer pair, followed by digestion of the PCR products with up to ten different restriction endonucleases.

Application of microsatellite markers was favoured by the simple use of the polymerase chain reaction (PCR) has especially promoted microsatellite loci. Unique PCR primers flanking the STR locus of interest were designed. With the amplification of this particular stretch the length of the alleles could identified using gel electrophoresis. The main steps of paternity analysis using microsatellites are summarised in Box 2.1.

**Box 2.1:** Procedure of paternity analysis using a single locus.

<table>
<thead>
<tr>
<th>Paternity analysis using microsatellites:</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Amplification of the locus via PCR</td>
</tr>
<tr>
<td>2. Determination of the allele size using an automatic sequencer (ALF)</td>
</tr>
<tr>
<td>3. Extracting the sire via the program FIND SIRE</td>
</tr>
</tbody>
</table>

**Amplification of the loci via PCR**

PCR was performed in a total volume of 10 µl using a thermal cycler (Trioblock). The reaction mix contained 20-100 ng genomic DNA, 10x buffer (PE), 20 mM dNTP's (Boehringer, Mannheim, Germany), 10 pMol of each Primer (for- and backward), 5 unit Taq Polymerase (Applied Biosystems, except for D8S601 Quiagen), Aqua bidest., 10% Triton, 25 mM MgCl\(_2\). The exact amount of each substance was optimised for each primer pair and is given in Table 2.3. Initial denaturation varied from 2-15 min at 92°C followed by 30-35 cycles of (i) 30-60 s at 94°C, (ii) 30-60s at the annealing temperature (see Table 2.3) and (iii) 90-120 s at 72°C with 10 min at 72°C after the last cycle (elongation). One PCR primer (forward) was labelled by fluorescin for allele size determination. Each PCR included 2 control animals of known allele sizes (positive controls).
Table 2.3: Master-mix for PCR amplification of the 14 microsatellites

<table>
<thead>
<tr>
<th>In µl</th>
<th>H₂O</th>
<th>buffer</th>
<th>Q-sol</th>
<th>dNTP's</th>
<th>Primer</th>
<th>Triton</th>
<th>MgCl₂</th>
<th>Taq</th>
<th>DNA</th>
<th>Tₐ in °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>D2S367</td>
<td>5.8</td>
<td>1</td>
<td>0</td>
<td>0.05</td>
<td>1</td>
<td>0.1</td>
<td>0</td>
<td>0.05</td>
<td>1</td>
<td>58</td>
</tr>
<tr>
<td>D5S820</td>
<td>5.8</td>
<td>1</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>60</td>
</tr>
<tr>
<td>D5S1470</td>
<td>6.3</td>
<td>1</td>
<td>0</td>
<td>0.1</td>
<td>0.75</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>52</td>
</tr>
<tr>
<td>D6S266</td>
<td>3.35</td>
<td>1</td>
<td>2</td>
<td>0.1</td>
<td>1</td>
<td>0</td>
<td>0.5</td>
<td>0.05</td>
<td>1</td>
<td>52</td>
</tr>
<tr>
<td>D6S474</td>
<td>5.8</td>
<td>1</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>54</td>
</tr>
<tr>
<td>D6S493</td>
<td>5.8</td>
<td>1</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>56</td>
</tr>
<tr>
<td>D8S271</td>
<td>5.8</td>
<td>1</td>
<td>0</td>
<td>0.05</td>
<td>1</td>
<td>0.1</td>
<td>0</td>
<td>0.05</td>
<td>1</td>
<td>58</td>
</tr>
<tr>
<td>D8S601</td>
<td>3.35</td>
<td>1</td>
<td>2</td>
<td>0.1</td>
<td>1</td>
<td>0</td>
<td>0.5</td>
<td>0.05</td>
<td>1</td>
<td>52</td>
</tr>
<tr>
<td>D12S66</td>
<td>6.3</td>
<td>1</td>
<td>0</td>
<td>0.1</td>
<td>0.75</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>53</td>
</tr>
<tr>
<td>D12S67</td>
<td>6.3</td>
<td>1</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.5</td>
<td>53</td>
</tr>
<tr>
<td>D14S255</td>
<td>5.8</td>
<td>1</td>
<td>0</td>
<td>0.05</td>
<td>1</td>
<td>0.1</td>
<td>0</td>
<td>0.05</td>
<td>1</td>
<td>53</td>
</tr>
<tr>
<td>D20S206</td>
<td>4.6</td>
<td>1</td>
<td>0</td>
<td>0.2</td>
<td>1</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
<td>1</td>
<td>54</td>
</tr>
<tr>
<td>D20S476</td>
<td>5.8</td>
<td>1</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>1</td>
<td>56</td>
</tr>
<tr>
<td>SCA1REP</td>
<td>7.75</td>
<td>1</td>
<td>0</td>
<td>0.15</td>
<td>0.25</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.5</td>
<td>52</td>
</tr>
</tbody>
</table>

Abbreviations are as follows: Tₐ is the annealing temperature. Note each master-mix was 10 µl per sample, the amount of primers in this table is just given for one of the two.

**Determination of the allele size using an automatic sequencer (A.L.F.)**

Allele sizes were determined using an automatic sequencer (A.L.F., Pharmacia). PCR products were transferred on a 6% polyacrylamide gel and fluorescence labelled fragments were compared against standards in order to determine both alleles of an individual. At first samples were denatured at 95°C. Depending upon the length of the PCR products gels ran at 900V, 45mA, 45W, 45°C between 2 and 4 hours. Peaks of the microsatellites and standards were analysed with a service tool (fragment manager of A.L.F.). More details on chemicals used are given in Voltz (1999).

**Identifying the sire using the program FIND SIRE**

As an individual inherits one allele by its mother (which was genotyped and therefore known by the investigator), the second allele, if the infant is heterozygous at this locus, must come from its father. All homozygous genotypes were at least genotyped twice. If homozygosity was not confirmed, at least two identical results had to be obtained before the genotype was entered in the data base.
Any male 1250 days older than a given infant, and residing on the island 200 days prior to the infant’s birth, was considered a potential sire in the paternity analyses. After the use of a maximum of 15 markers most potential sires could be excluded, except from 1 male. The genotypes were transferred into a data base and genotypes of the infant-mother pair were compared against all potential sires using the FIND SIRE program written by Michael Krawczak (Kiel, Germany).

**Solving individual cases**

Here the point should be made, that paternity for each individual offspring (see paternity data set below) had to be established for every single offspring. In other words, genotyping mother-offspring pairs and all potential sires was only the first step. Any discrepancy between mothers and their offspring had to be re-analysed in order to exclude typing errors. This also revealed systematic typing errors which may have had an influence on the whole data set. Some mutation events could be verified.

**Criteria of established paternity**

Following Krawczak (1999) Log10-likelihood ratios (LR) for paternity vs. unrelatedness were calculated, using the 15 markers for which nearly all animals were genotyped. Paternity was regarded as established when a male fitted into two criterions: (i) he had to reach a LR in favour of paternity that was larger than two (corresponding to a standardised paternity probability of 99%) and (ii) his LR had to be at least one unit larger than the LR of any other male.

Some potential sires have not have been successfully genotyped on all 15 markers and which marker has not been genotyped also varied among potential sires. The LR calculation for a given infant and his potential sire A was based on all marker available for both, but LR calculation for the same infant and his potential sire B may have been based on other markers depending upon which they both shared. However, because the two paternity criterions listed above are very strict, it is unlikely that this was influencing the decision in favour of a male being the actual sire (Krawczak, pers. comm.).

**Paternity assessment via DNA fingerprinting**

If no unequivocal sire could be determined after the use of all 15 DNA markers, DNA fingerprinting was applied to detect paternity. For example, two males had reached a log-likelihood ratio larger than two, but the differences was smaller than one unit. It could have been that these two males were actually father and son themselves as assessed via
microsatellites, but the only way to prove which of the two male sired the considered infant, a comparison of the males DNA fingerprint with whose of the infant-mother dyad was needed. The methodology of DNA fingerprinting using oligonucleotide probes has been described in detail by Epplen (1992). In this study three synthetic oligonucleotide probes (GATA)$_4$, (CA)$_8$ and (GTG)$_5$ were used to produce a specific band pattern per individual. Infant-mother dyads were compared on the same gel with the sires in question in order to avoid problems derived from comparing gels (Nürnberg et al. 1998). DNA samples were digested with the restriction endonuclease Hinf I under standard conditions and DNA fragments were separated on 30 cm 0.7% agarose gels in TAE buffer for up to 48 hours at 1V/cm. $^{32}$P-labeled probes were hybridised to DNA in the dried gels, and exposed to Kodak XAR-5 film over night (cf. Berard et al. 1993, 1994). The DNA fingerprint for each infant were then compared to those of its mother. Bands which the infant did not share with its mother (non-maternal bands) had to be present in the actual sire. All offspring bands of necessarily paternal origin were marked and compared directly to the corresponding mother-infant dyad. A male was regarded as the sire, if he had no mismatches in all three probes for all non-maternal bands, but all other males had at least two mismatches. This techniques was conducted by Ingrid Barth. Band sharing was analysed by visual insepection by myself.

**Paternity data sets**

Paternity analyses have been part of a co-operation aimed at the typing of the whole population of Cayo Santiago. Paternity assessment in groups R and M was undertaken by a team headed by Peter Nürnberg (Charité, Humboldt-University of Berlin), in the remaining groups were analysed by a team headed by Jörg Schmidtke (Medizinische Hochschule, Hannover). This thesis uses two kinds of paternity data sets: (i) all individuals born in group R or its sister group BB between 1993 and 1998 and (ii) all females in group R alive at the time of behavioural study in 1997. While the first data set is only used in chapter 3 (skew), paternity data of females, present in group R in 1997, are used in all remaining chapters 4-6. More information on the paternity results are given in the Appendix 3 (Paternity results).
3. Male reproductive skew, females perspective and paternal birth cohorts

Introduction

Males and females have a conflict of interest, known as sexual conflict, because the investment in offspring differs considerably between the two sexes. Especially among mammals, a male is investing relatively less in each of his sperm compared to a female who produces relatively few large eggs of a limited number and combined with considerable costs during pregnancy and lactation. Males are expected to maximise their reproductive output by fertilising as many females as possible. On the other hand, females are expected to maximise their reproductive success by selecting mating partners of good quality such as good genes or qualities which help to rear their offspring successfully (Krebs & Davies 1993). Females are thought to be the limited resource that males compete for (Bateman 1948, Trivers 1972).

The concept of sexual selection goes back to Darwin (1871) who distinguished between the competition among males over access to oestrous females (male-male competition) and the choice of good-quality mating partners by females (female choice). Although there is this apparent conflict of interest between the sexes, males and females need to co-operate in order to reproduce. This compromise is expected to differ depending upon the mating system of a species.

The study species, the rhesus macaque, lives in groups consisting of many adult males and females who both mate with several partners. This results in a situation where all sexually mature males have to be treated as potential sires for any offspring considered. In species with multiple mating paternity can only be detected with the help of genetic analyses. It should be emphasised that paternity data give no information whether the outcome of reproduction is due to male monopolisation, female choice, both, or other factors. Paternity analyses do not uncover mating decisions; this can only be achieved by behavioural studies but mating strategies were not the aim of the present study. However, paternity analyses reveal kinship relations as a consequence of male and female mating decision.

This chapter aims to investigate kinship relations from three perspectives: the males’ perspective, the females’ perspective and the infants’ perspective. This chapter addresses the question whether the extent of paternal kinship in a social group of primates is pronounced or not (cf. J. Altmann 1979). I will present kinship data from six consecutive birth cohorts (1993-1998) in group R or its sister group BB (see Methods). For paternity analyses all sexual
mature males were regarded as potential sires (see Methods), but in this chapter the number of potential sires will be restricted to the troop males, because including all males from the island will inflate the number of potential sires which addresses another question than asked here. Males from group BB are always treated as nontroop sires with respect to infants born in group R, but whether or not infants born into group BB are included in the analyses depends upon the specific question.

1. Males perspective

Studies across the animal kingdom have found evidence that males compete over access to fertile females using rituals or even overt aggression (Alcock 1984). With the use of paternity analyses it is now possible to demonstrate variation in actual male reproduction. In other words, not only studies investigating whether some males exclude others from mating can be conducted, also studies investigating whether males exclude others from reproducing can now be conducted. Assuming male-male competition, male reproduction is expected to be restricted to a few males which excluded other males from reproducing (hereafter: male reproductive skew). Again, whether the reproductive outcome is exclusively due to male monopolisation or whether female choice is influencing reproductive outcome also, will not be investigated here. The issue here is the degree to which true reproductive success among males is skewed.

Genetic studies of paternity have found that reproduction is restricted to a limited number of males each year, therefore male reproduction seems to be skewed in many primate species (e.g., *Alouatta seniculus*: Pope 1990, *Macaca fascicularis*: de Ruiter et al. 1992, *Madrillus sphinx*: Wickings et al. 1993, *Papio cynocephalus*: Altman, et al. 1996, *Presbytis entellus*: Launhardt 1998, *M. mulatta*: Bercovitch et al. 2000, *Semnopithecus entellus*: Launhardt et al. 2001). Whereas some studies have shown that the highest ranking male sired more offspring than expected by an even distribution (de Ruiter et al. 1992, Launhardt 1998), others have found no evidence of rank influencing the reproductive success (Berard et al. 1993). However, the ability of a male to monopolise receptive females also depends upon the synchrony of female oestrous. If female synchronisation is strong, i.e., all females ovulate within a short time period, then a single male is less likely to be able to monopolise all fertile females. Especially in seasonal breeders, such as rhesus monkeys, where males need to mate guard in order to insure fertilisation, this time investment prevents males from mating elsewhere with other females, too. Here, the extent of skew in male reproduction will be investigated with other variables which may influences this skewness.
2. Females perspective
Contradictory evidence is known about the existence of female choice in primates (Huffman 1991, Manson 1992, 1995b) because it is difficult to separate the two confounding variables: is reproduction due to (i) female choice or (ii) male monopolisation or (iii) a combination of both or additional variables. A female needs to co-operate that the male can mount her, but harassment have been observed in some primate species (Neimeyer & Anderson 1983). As outlined above, investigating female choice is not the aim of the study, we here look only at the female perspective with respect to the kinship relations among her offspring. Are her offspring across years sired by different males or always by the same male? The latter case would increase the degree of relatedness among her offspring to full-siblings sharing on average a degree of relatedness of 0.5, whereas the former case would result in more genetic diversity among her offspring being half-siblings sharing on average a degree of relatedness of 0.25.

3. Infant perspective
When male reproductive success is strongly skewed within the mating season, infants born within the same year (hereafter: age-mates or peers) are likely to be paternal half-siblings (J. Altmann 1979). Because male rhesus only stay a few years in the group before they migrate again (Manson 1995a), paternal half-siblings within a social group are probably sired within a close time window. Depending upon the sharpness of this time window, paternal half-siblings are likely to be found in close age proximity.

Results

1. Males reproductive skew

Male tenure and number of offspring sired
The mating season on Cayo Santiago usually starts in May and ends in October (see Methods). Census data from group R were available from the mating seasons of 1992-1997. All males greater than or equal to 5 years of age who were observed as group members in R for at least one of the six months of the mating season were counted as potential troop sires for the following birth cohort, i.e., a male present during the mating season of 1992 is a potential troop sire of any offspring born in 1993 regardless whether or not he was observed mating. Due to male inter-troop movement, group R had between 29 and 63 adult males during the of 1992 to 1997 mating seasons. Males who immigrated into group R during the
mating season spend most of the whole mating season in the group (Table 3.1). Sires could also come from outside the group (see extra-group paternities below), but only troop males are considered in Table 3.1. Infants born in the sister group BB which fissioned during the mating season of 1996 (see Methods) are excluded here, so only infants born in group R and sired by potential troop sires were analysed.

Table 3.1: Male tenure and number of offspring sired

<table>
<thead>
<tr>
<th>Months in group R</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>N potential troop sire</th>
<th>N offspring considered</th>
<th>r_s tenure vs. N off prod</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>8</td>
<td>5</td>
<td>7</td>
<td>1</td>
<td>3</td>
<td>10</td>
<td>34 (30)*</td>
<td>30</td>
<td>0.357</td>
<td>P=0.053</td>
</tr>
<tr>
<td>1994</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>2</td>
<td>14</td>
<td>29</td>
<td>23</td>
<td>0.264</td>
<td>P=0.167</td>
</tr>
<tr>
<td>1995</td>
<td>13</td>
<td>9</td>
<td>2</td>
<td>5</td>
<td>10</td>
<td>24</td>
<td>63 (62)*</td>
<td>35</td>
<td>0.311</td>
<td>P=0.014</td>
</tr>
<tr>
<td>1996</td>
<td>10</td>
<td>3</td>
<td>4</td>
<td>12</td>
<td>4</td>
<td>21</td>
<td>54</td>
<td>30</td>
<td>0.049</td>
<td>P=0.726</td>
</tr>
<tr>
<td>1997</td>
<td>12</td>
<td>6</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>16</td>
<td>46</td>
<td>28</td>
<td>0.280</td>
<td>P=0.060</td>
</tr>
<tr>
<td>1998</td>
<td>7</td>
<td>1</td>
<td>13</td>
<td>3</td>
<td>4</td>
<td>17</td>
<td>45</td>
<td>30</td>
<td>0.242</td>
<td>P=0.109</td>
</tr>
<tr>
<td>Sum</td>
<td>56</td>
<td>25</td>
<td>29</td>
<td>30</td>
<td>29</td>
<td>102</td>
<td>271 (266)</td>
<td>176</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

All potential troop sires (5 year olds and older) were considered who spend 1, 2, 3 or all 6 months in group R during the mating season when infants were conceived, but born 6 months later (resulting in birth cohorts 1993-1998). Abbreviation are as follows: number of potential troop sires (N potential troop sire), *five potential troop sires could not been genotyped for unknown reasons and are therefore missing in the remaining analyses, number of infants with known paternity who were (i) sired by potential troop males and (ii) born in group R (N offspring considered), Spearman’s rank correlation coefficient (r_s) between the proportion of time spent in the group and the number of offspring sired is given for each year with the corresponding P-value.

For three birth cohorts (1995, with a trend in 1993 and 1997) the data revealed a positive relationship between the proportion of time spent in the group during this mating season and the number of offspring sired. Manson (1995a) found in the same population as studied here, that male tenure is positively related with male rank, but the present study had just limited data on male rank (see male rank below). In some years (e.g., 1995) the number of potential troop sires was nearly twice as high as the number of infants born in group R indicating that some males will be excluded from reproducing because the number of males is higher than the number of offspring sired.
Actual sires

Most sires identified came from group R, but between 3.23 to 36.73 % of infants were sired from males outside of group R (hereafter: extra-group paternities), with most of them from neighbouring groups (see Table 3.2).

Table 3.2: Number of group paternities vs. extra-group paternities

<table>
<thead>
<tr>
<th>Cohort</th>
<th>N group paternities</th>
<th>N extra-group paternites</th>
<th>% extra-group paternities</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>30</td>
<td>1</td>
<td>03.23 %</td>
</tr>
<tr>
<td>1994</td>
<td>23</td>
<td>13</td>
<td>36.11 %</td>
</tr>
<tr>
<td>1995</td>
<td>34</td>
<td>8</td>
<td>19.05 %</td>
</tr>
<tr>
<td>1996</td>
<td>36</td>
<td>4</td>
<td>10.00 %</td>
</tr>
<tr>
<td>1997</td>
<td>31</td>
<td>18</td>
<td>36.73 %</td>
</tr>
<tr>
<td>1998</td>
<td>31</td>
<td>18</td>
<td>36.73 %</td>
</tr>
<tr>
<td>Sum</td>
<td>185</td>
<td>62</td>
<td>247</td>
</tr>
<tr>
<td>Mean</td>
<td>30.83</td>
<td>10.33</td>
<td>23.64 %</td>
</tr>
</tbody>
</table>

Note the total number of offspring is higher than in Table 3.1, because all infants (with solved paternity) born in group R or BB between 1993 and 1998 are included.

The values of extra-group paternities were extremely high in birth cohort 1997 and 1998, where a high proportion of sires came from the sister group BB, which fissioned from group R in June 1996. In other words, even though these two groups completely fissioned and these males joined BB, they still sired offspring in group R during the mating season of 1996 and 1997.

Male reproductive skew among troop sires

If male reproduction is skewed the skew is either positive or negative. Positive skew describes a distribution, where few males have sired a higher number of offspring, but the majority of potential sires has no or few offspring. Negative skew, in contrast, describes a distribution, where few males have no or few offspring, but the majority of males has a higher number of offspring.

Two different skews among troop males were calculated. First, skew includes all potential troop sires, both sires and nonsires. Second, skew includes only troop sires, ignoring the number of nonsires. In the first skew calculation, nontroop sires and infants born in group R, but sired by nontroop sires, will be excluded, because a skew calculation using both troop and
nontroop sires would have to include all potential troop and nontroop sires on the island which would inflate the number of potential sires to approximately 300-400 males. Therefore, the question is restricted to measure the degree of skew among troop males. Over 20 different ways to measure reproductive skew have been proposed (e.g., Cant 1998, Nonacs 2000, see review in Kokko et al. 1999), but the conditions and assumptions of the models do not fit most primates societies (cf. Clutton-Brock 1998). As a consequence, I used the standard measure of statistical skew (Sokal & Rohlf 1995) as a means of measuring the asymmetry in male reproductive success. The advantage of this measurement is that skew values can be compared across species. Table 3.3 gives a number of different variables which may have an effect on male reproductive skew.

### Table 3.3: Male reproductive skew and variables which may effect male reproductive skew

<table>
<thead>
<tr>
<th>Cohort</th>
<th>N off troop</th>
<th>N pot troop sire</th>
<th>N trop non sire</th>
<th>N trop sire</th>
<th>N non-troop sire</th>
<th>% top sire</th>
<th>N ad females</th>
<th>Syni</th>
<th>Synii</th>
<th>Skewi</th>
<th>Skewii</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>30</td>
<td>30</td>
<td>21</td>
<td>9</td>
<td>1</td>
<td>30.00</td>
<td>42</td>
<td>147</td>
<td>4.74</td>
<td>2.589</td>
<td>1.248</td>
</tr>
<tr>
<td>1994</td>
<td>23</td>
<td>29</td>
<td>20</td>
<td>9</td>
<td>13</td>
<td>21.74</td>
<td>46</td>
<td>112</td>
<td>3.03</td>
<td>1.968</td>
<td>1.578</td>
</tr>
<tr>
<td>1996</td>
<td>36</td>
<td>54</td>
<td>38</td>
<td>16</td>
<td>4</td>
<td>27.18</td>
<td>56</td>
<td>125</td>
<td>3.05</td>
<td>4.168</td>
<td>2.586</td>
</tr>
<tr>
<td>1997</td>
<td>31</td>
<td>46</td>
<td>32</td>
<td>14</td>
<td>18</td>
<td>20.00</td>
<td>61</td>
<td>140</td>
<td>2.55</td>
<td>2.652</td>
<td>1.913</td>
</tr>
<tr>
<td>1998</td>
<td>31</td>
<td>45</td>
<td>31</td>
<td>14</td>
<td>18</td>
<td>19.35</td>
<td>55</td>
<td>223</td>
<td>4.65</td>
<td>2.499</td>
<td>1.984</td>
</tr>
</tbody>
</table>

Abbreviations are as follows: birth cohort considered (cohort), number of offspring sired by troop males and born in group R or BB (N off troop), number of potential troop sires (N pot troop sire), number of troop males who did not reproduce (N non sire), number of different troop sires (N trop sire), number of different nontroop sires (N non-troop sire), percent of offspring sired by the top sire (% top sire), number of adult females in the group (N ad females), female cycle synchrony (Syni and Synii in days, see below), statistical skew including troop sires and nonsires (Skewi) and statistical skew including only troop sires (Skewii).

As evident from Table 3.3, both measurements on male reproductive skew were positive, indicating that when sires and nonsires were considered the majority of males produced no or few offspring, whereas considering only sire, the majority of males produced one or few offspring. One the other hand, both skew calculations imply that few males also sired a higher number of offspring. The troop male which produced the highest number of offspring during a mating season (hereafter: top sire) was responsible for siring between 19.35 and 30.00% (mean ± SD=24.22 ± 4.44%) of infants born into the 1993-1998 birth cohorts. The remaining reproduction was shared by 8 to 15 other troop males. However, the number of nonsires
varied between 20 to 51 males across years.
Male reproductive skew might be expected to be less pronounced when birth clustering is tighter, because more males have an opportunity to mate when more females are cycling at the same time. Assuming approximately similar gestation length, infants born around the same days are likely to be conceived around the same days which means that females were more or less synchronised in their ovulation. Male reproductive skew was not associated with female cycle synchrony calculated (i) as the interval between the first and the last birth of the cohort ($r_s=-0.143$, $n=6$, $P=0.787$) or (ii) as the mean interval over all consecutive births within a cohort ($r_s=-0.086$, $n=6$, $P=0.872$).

Three points should be mentioned with respect to other variables investigated even though their interpretation is limited because of the sample size. First, the higher the percentage of offspring produced by the top sire, the lower the number of nontroop sires ($r_s=-0.943$, $N=6$, $P=0.005$) as well as the number of offspring produced by nontroop sires ($r_s=-0.986$, $N=6$, $P<0.001$). Both associations may indicate that a top sire was not only excluding potential troop sires from reproduction (indicated by the percent of offspring produced by a single male), he also excluded potential nontroop sires.

Second, the more potential troop sires were in the group, the higher the number of offspring sired by troop males ($r_s=0.928$, $N=6$, $P=0.008$) which may suggest that the top sire was not be able to monopolise as many females as with less male-male competition, but also that less nontroop sires were successful in sneaky reproducing (cf. Berard et al. 1994).

Third, the higher the number of adult females in the group, the higher the number of troop sires ($r_s=0.883$, $N=6$, $P=0.020$). On the other hand, the number of adult females was neither associated with the number of nontroop sires ($r_s=0.257$, $N=6$, $P=0.623$) nor the percent of offspring sired by the top sire ($r_s=-0.486$, $N=6$, $P=0.329$). In other words, when more females were available they tended not to be fertilised by nontroop sires or by the top sire. Instead, the number of females was positively associated with the skew among sires ($r_s=0.829$, $N=6$, $P=0.042$), not with the skew calculated among both sires and nonsires ($r_s=0.486$, $N=6$, $P=0.329$) indicating that some troop sires probably had some success in reproducing few offspring each, when the number of females increased (shifting the positive skew curve a bit more to the right).

**Top sires**
The most reproductively successful male per season (top sire) differed across years. However, in 1994 two males (E05 and I37) sired the highest number of offspring, with E05 being also the top sire in 1993 (see Table 3.4). In addition, I78 and K85 were twice the top sire with a
year in between where a different male was the most successful sire (see Table 3.4).

Table 3.4: Top sires and number of offspring they produced

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Top sire</td>
<td>N_{offspring}</td>
<td>N_{offspring}</td>
<td>N_{offspring}</td>
<td>N_{offspring}</td>
<td>N_{offspring}</td>
<td>N_{offspring}</td>
<td>N_{offspring}</td>
</tr>
<tr>
<td>E05</td>
<td>9</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>I37</td>
<td>6</td>
<td>5</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>I78</td>
<td>0</td>
<td>0</td>
<td>9</td>
<td>8</td>
<td>9</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td>K85</td>
<td>0</td>
<td>1</td>
<td>6</td>
<td>10</td>
<td>6</td>
<td>6</td>
<td>29</td>
</tr>
</tbody>
</table>

Values represent reproductive outcome of top sires including all infants born in group R, or its sister group BB between 1993 and 1998. The number of offspring sired by the top sire per season is marked in bold, with two top sires in 1994.

What are the attributes of these top sires? Regarding rank, none of the top sires was the highest-ranking male of the troop at the time of reproduction. In fact, they were mid-ranking and rose in rank later in the season (Bercovitch unpubl. data, Kazem pers. comm., Widdig unpubl. data). Regarding age, the top sires varied in age between 8 and 11 years (mean ± SD=9.57 ± 1.27) at the time of reproduction, so they were in their “best” years with respect to body condition. Regarding natal status, all males were non-natal, i.e., none of the top sires was born in group R. Regarding kinship, the demographic database of the CPRC revealed, that only male I37 had a younger maternal half-brother (S19), but he did not join group R during the years investigated. Regarding group tenure, life history patterns of top sires seemed to differ from each other. For male E05, there was a peak in reproduction after which the number of offspring produced goes down, followed by a decreasing proportion of time spent in group R. In other words, he left the group as his reproductive success decreased. Similar, after his drop in reproduction, male I37 left the group but came back without being successful anymore in group R. In contrast, male I78 was never completely resident of group R for any mating season, but he sired a huge proportion of infants in the group. K85 was the most successful sire ever measured in group R with a total of 29 offspring produced and he was still in the group in 2000.

Male rank and age at the time of reproduction

No detailed data on male rank were available in the present study, but for the mating season of 1997, all potential troop sires (N=45) could been categorised by the outcome of dyadic agonistic interactions as either high-, middle- or low-ranking (each rank class including 15 males). High-ranking males sired 22 out of all 31 offspring (70.97%) born cohort 1998,
middle-ranking males produced 8 out of 31 offspring (25.81%) whereas low-ranking males sired 1 out of 31 offspring (3.23%). In Table 3.5 a comparison was made between the number of sires and nonsires found in each rank class which revealed a significant association between sirehood and rank class ($\chi^2 = 6.429$, d.f.=2, $P=0.040$).

Table 3.5: The association between sirehood and rank class

<table>
<thead>
<tr>
<th>Rank class</th>
<th>High</th>
<th>Middle</th>
<th>Low</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>N sires</td>
<td>7</td>
<td>6</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>N nonsires</td>
<td>8</td>
<td>9</td>
<td>14</td>
<td>31</td>
</tr>
<tr>
<td>Total</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>45</td>
</tr>
</tbody>
</table>

Number of sires and nonsires found in each rank class (high, middle and low). Data are restricted to mating season 1997 (and birth cohort 1998).

Testing the number of offspring as a function of the sires’ rank class revealed a marginal difference among the three rank classes (Kruskal-Wallis Test, $\chi^2 = 5.836$, d.f.=2, $P=0.054$). Berard at al. (1994) found in the same population that high-ranking males sired 55% of offspring by forming long-term consorts, while low-ranking males sired 45% of offspring by sneaking (i.e., quick and hidden) copulations. No clear advantage of one single mating tactic could be detected, but consortships might be most effective for high-ranking males (ibid.). Sneaking copulation is a reproductive tactic mainly used by younger males (Kuester & Paul 1992).

With respect to male age, results of the present study indicated that nontroop sires were indeed much younger than troop sires including only males older than 5 years of age (mean years ± SD: nontroop=10.13 ± 4.06, N=39 vs. troop sire=12.33 ± 4.26, N=73, Mann-Whitney U-test, $z=-2.826$, $P=0.005$). The extent of sneaky mating among troop sires cannot be evaluated, because of the lack of mating data. However, data suggest that male mating tactics were probably related to age. In contrast, age of troop sires did not differ from the age of troop nonsires (mean years ± SD: troop sires=12.33 ± 4.26, N=73 vs. troop nonsires=12.14 ± 4.54, N= 197, Mann-Whitney U-test, $z=-0.359$, $P=0.720$). Age-related male reproduction is illustrated in Fig. 3.1. Taking potential troop sires (5 years and older) between 1993 and 1998 into account, the graph represents the proportion between the number of infants and the number of males over age classes.
Fig. 3.1: Age-related male reproduction
The graph represents the proportion between the number of infants and the number of males over age classes. With respect to the number of potential troop males per age class, only males between 9 and 11 years of age produced a higher number of infants than the number of potential troop sires available per age class. The same peak of reproduction was suggested by Bercovitch (1997) after analysing paternity in group R of one birth cohort. This result is also similar to that reported among male Barbary macaques (cf. Kuester et al. 1995).

2. Females Perspective

Continuity of paternity

From the females perspective it was measured whether females show continuity of paternity among their offspring. Given that a female gave birth to six offspring during the six cohorts investigated (1993-1998), paternity continuity would be high if a female conceived her offspring from the same sire each year. In contrast, paternity continuity would be low if she conceived her offspring from a different sire each year. By reproducing with the same male her offspring are full-siblings (degree of relatedness=0.5) whereas by reproducing always with a different male her offspring are maternal half-siblings (degree of relatedness=0.25). The proportion between the number of different fathers divided by the number of offspring would be one when the female always chose a different father (low paternity continuity) or the proportion would be close to zero when the female often or nearly always chose the same father again (high paternity continuity). As Fig. 3.2 illustrates, nearly 70% of mothers showed low paternity continuity as they always reproduced with a different father, the remaining percentage of females sometimes reproduced with the same father, but there was no single case where a female always reproduced with the same sire regarding all her offspring. This distribution differed significantly from a uniform distribution (Komogorov-Smirnov-test,
Therefore, low paternity continuity seemed to be the general pattern for females of this group over the six years investigated.

Fig. 3.2: Continuity of paternity for reproducing females
The number of mothers (N=52) in relation to the number of different sires per number of offspring. The graph shows that 36 out of 52 mothers (69%) reproduced with a different sire across consecutive years.

**Number of full-siblings**
Only 16 out of all 324 sibling dyads who shared the same mother and were born into group R or BB between 1993 to 1998 were full- not half-siblings. In other words, only 4.94% of all sibling dyads shared both the same mother and the same father. Fourteen of these 16 dyads were full-siblings born in consecutive years. There was only one case in which the same male sired the offspring of a female in three consecutive years. These results strongly suggest that (i) females reproduce with different males in consecutive years, therefore most individuals born to the same female will tend to be maternal half-siblings and (ii) if they are full-siblings (which is extremely rare), they show a tendency to be born in consecutive years, i.e., they are in close age proximity. Among the adult females investigated in the behavioural study (see chapter 4-6), there was none case of a full-sibling. Therefore, this kin category will not be included in the chapters that follow.

**Number of maternal and paternal half-siblings vs. full-siblings**
Including all infants born between 1993 and 1998 in R or BB with solved paternity (N=247) the number of maternal half-siblings, paternal half-siblings and full-siblings per individual was calculated over the six years. Results revealed that individuals had on average more paternal half-siblings (mean ± SD=9.887 ± 9.71, range=0-28) than maternal half-siblings (mean ± SD=2.623 ± 1.44, range=0-5) or full-siblings (mean ± SD=0.138 ± 0.38, range=0-2).
Likewise the number of maternal half-siblings per individual was higher than the number of full-siblings (see Table 3.6).

Table 3.6: Number of maternal and paternal half-siblings vs. full-siblings

<table>
<thead>
<tr>
<th>Test</th>
<th>Paired t-test</th>
<th>N</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>PS vs. MS</td>
<td>t=11.718</td>
<td>N=247</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>PS vs. Full-sibs</td>
<td>t=15.972</td>
<td>N=247</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>MS vs. Full-sibs</td>
<td>t=-26.041</td>
<td>N=247</td>
<td>P&lt;0.001</td>
</tr>
</tbody>
</table>

Paired t-tests with respect to the number of paternal half-siblings (PS), maternal half-siblings (MS) and full-siblings (full-sibs) per individual born between 1993 to 1998 in group R with solved paternity (N=247).

This result was expected as the maximum number of maternal half-siblings and full-siblings in the six consecutive years is five, given that females bear only a single offspring per year (cf. Rawlins & Kessler 1986). In contrast, the maximum number of paternal half-siblings over six years can theoretically be much higher assuming male reproductive skew. However, it should be pointed out, that due to death and colony management the situation among the focal females in group R in 1997 was different (see below).

3. Paternal birth cohorts

The paternity data solved between 1993 to 1998 revealed that almost all individuals in the study group have paternal half-siblings because male reproductive success is strongly skewed. At least 73.96% of individuals had one paternal half-sibling of the same age. In addition, at least 15.02% of individuals had a paternal half-sibling within a two-year age difference. Hence, at most only 11.02% of individuals lacked a paternal half-sibling at all or in close age proximity within the troop (Table 3.7). These values were the lower limits of numbers or paternal half-siblings as paternity data of birth cohort 1999 and 2000 were not yet available. In sum, at least 88.98% of all individuals had (at least) a paternal half-sibling either of the same age or within a two year age difference.
<table>
<thead>
<tr>
<th>Cohort</th>
<th>N pat peer</th>
<th>N pat sib ≤ 2 years</th>
<th>N no pat sib or ≥ 3 years</th>
<th>Total = Solved</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>26 (83.87%)</td>
<td>4 (12.90%)</td>
<td>1 (3.23%)</td>
<td>31</td>
</tr>
<tr>
<td>1994</td>
<td>24 (66.67%)</td>
<td>7 (19.44%)</td>
<td>5 (13.89%)</td>
<td>36</td>
</tr>
<tr>
<td>1995</td>
<td>35 (83.33%)</td>
<td>3 (7.14%)</td>
<td>4 (9.52%)</td>
<td>42</td>
</tr>
<tr>
<td>1996</td>
<td>26 (65.00%)</td>
<td>8 (20.00%)</td>
<td>6 (15.00%)</td>
<td>40</td>
</tr>
<tr>
<td>1997</td>
<td>38 (77.55%)</td>
<td>7 (14.29%)</td>
<td>4 (8.16%)</td>
<td>49</td>
</tr>
<tr>
<td>1998</td>
<td>33 (67.35%)</td>
<td>8 (16.33%)</td>
<td>8 (16.33%)</td>
<td>49</td>
</tr>
<tr>
<td>Sum</td>
<td>182</td>
<td>37</td>
<td>28</td>
<td>247</td>
</tr>
<tr>
<td>Mean</td>
<td>73.96%</td>
<td>15.02%</td>
<td>11.02%</td>
<td></td>
</tr>
</tbody>
</table>

Cell values show the number of infants who had paternal half-siblings (% are given in brackets). Abbreviations are as follows: number of individuals with at least one paternal peer (N pat peer), number of individuals with at least one paternal half-sibling born within two years of itself (N pat sib ≤ 2 years), number of individuals with either no paternal half-siblings or a paternal half-sibling at least three years older or younger than themselves (N no pat sib or ≥ 3 years), number of infants with solved paternity (Total = Solved). Note individuals counted in one category were not counted elsewhere, e.g., individuals with a paternal peer were not considered in the 2nd category (paternal half-sibling born with two years of itself), therefore the number of individuals is equal to the number of infants with solved paternity.

These results demonstrate, that paternal sibships was very common in the study group during the six years investigated, because nearly all individuals had (i) at least one paternal half-sibling and (ii) paternal half-siblings were almost exclusive in close age proximity (see also Fig. 3.3)
The data presented in this chapter investigate kinship relations as a consequence of male and female reproductive decisions from three perspectives: the males, the females and the infants perspective. These three perspectives will be discussed in more detail below.

Reproductive skew

The most important result found from the male perspective can be summarised as follows. First, in the study group male reproduction among troop males is skewed within birth cohorts with few males producing a higher number of offspring whereas the majority of males produced no or few offspring. Male skew among potential troop sires was not associated with indirect measurements of female cycle synchrony, because skew was not decreasing when birth clustering is tighter, although more males should have an opportunity to mate when more females are cycling at the same time. Second, 24% of infants were sired by males from
outside the troop (extra group paternities) meaning that these males were not excluded from reproduction by potential troop sires. Other studies found 36.4% of extra group paternities in rhesus macaques on Cayo Santiago (Berard et al. 1993) and 33% of extra group paternities in Japanese macaques, *M. fuscata*, (Soltis et al. 2001), but paternity data were restricted to a small number of infants. The high proportion of extra group paternities might be a consequence of female choice as females seem to prefer novel males (Manson 1995a, Bercovitch 1991, 1997, Berard 1999) and nontroop sires were significantly younger than troop sires. In addition, nontroop sires tended to come from adjacent troops and when male rhesus macaques enter a new group they start at the bottom of hierarchy and move up only as higher-ranking males leave or die (Vessey & Meikle 1987). As nontroop sires occupy no dominance rank, these results indicate that factors in addition to male-male competition must influence male reproductive success. Third, on average 24% of offspring born per season were sired by the top sire (which was never the highest-ranking males of the group) whereas 20 to 51 troop males were excluded from reproducing at all. Fourth, limited rank data suggest that high-ranking males sired the majority of offspring born (71%) in one birth season whereas Berard at al. (1994) found in the same population high-ranking males siring 55% of offspring. Sixth, the peak of male reproduction was between 9-11 years comparing the number of infants with the number of potential sires per age class available which supports earlier findings on the same group after one year of paternity analysis (Bercovitch 1997). Studies on male Barbary macaques suggested a peak between 8.5-9.5 years of age (von Segesser et al. 1994) or found a positive correlation between male age and reproductive success (Paul & Kuester 1996).

The theory of reproductive skew was introduced by Vehrencamp (1983a,b) suggesting that reproduction is expected to be highly skewed when access to limited resources (e.g., fertile females) can be monopolised by only a subset of individuals. In other words, the dominant has complete control when settling alone or becoming a dominant is difficult for a subordinate (optimal skew models). Later versions of the model developed by Keller & Reeve (1994) added peace incentives (to forego challenging the dominant) and staying incentives (allowing subordinates to reproduce). Here reproductive skew is expected to increase with increasing relatedness between dominant and subordinate, as kin compensate loss in direct fitness with gains in indirect fitness (concession model). Most recent models on reproductive skew (Reeve et al. 1998) assume an influence on reproductive decisions by the subordinate suggesting an incomplete control by the dominant (incomplete control model). However, models of reproductive skew have mainly been developed to explain the variation in the
distribution of reproductive opportunities among social insects (e.g., Keller & Nonacs 1993) and in co-operative breeders of birds or mammals (e.g., reviewed in Emlen 1997, Packer et al. 1991, Cooney & Bennett 2000, Allainé 2000). It seems unlikely that a single model will account for all eusocial invertebrates and co-operative vertebrates which show fundamental differences (Clutton-Brock 1998) and no available model applies to primate societies (cf. Emlen 1995, Sterck 2002).

There is evidence that competition between males primates over fertile females is strong and that there is a corresponding strong skew in the reproductive output (reviewed in van Hooff 2000). Skew in male reproduction has inferred in primate species based upon the finding that dominance rank is related to a larger proportion of mating opportunities (e.g., rhesus macaques: Chapais 1983, Hill 1987, Manson 1992, Savannah baboons: Hausfater 1975, Bulger 1993, see Cowlishaw & Dunbar 1991, 1992 for review), but no correlation between male rank and number of matings was found in other studies (e.g., rhesus macaques: McMillan 1989, Savannah baboons: Bercovitch 1986). This contradiction gave cause for a huge debate about the importance of male dominance rank and whether or not dominant males achieve indeed a higher reproductive output. However, more recent studies using paternity data could confirm that high-ranking males indeed monopolise the majority of mates as they produce more offspring than low-ranking males (e.g., rhesus macaques: Smith 1993, Berard et al. 1993, Bercovitch & Nürnberg 1996, long-tailed macaques: de Ruiter et al. 1992, de Ruiter & van Hooff 1993, Barbary macaques: Paul et al. 1993, stump-tailed macaques: Bauers & Hearn 1994, toque macaques: Keane et al. 1997, Japanese macaques: Soltis et al. 2001, Savannah baboons: Altmann et al. 1996, sooty mangabeys: Gust et al. 1998, Hanuman langurs: Launhardt 1998, red howler monkey: Pope 1990). Smith (1993), Berard (1999) and Alberts et al. (2002) showed by using long-term data that a positive correlation between male rank and number of mating opportunities occurs only in some years within a single population. The present study has only limited data on male rank, but they indicate that high-ranking males sired a higher proportion of offspring than both middle- and low-ranking males, although the alpha male in none of the six years investigated was the most successful sire (cf. Smith 1993 for captive rhesus macaques). Therefore, male dominance rank influenced reproduction, but not as a linear function.

To date, no quantitative study on male reproductive skew in primates has used paternity data and only two studies according to my knowledge have examined male reproductive skew in mammals using genetic data. First, reproduction among male African lions is more skewed with increasing coalition size and non-reproductive helpers, in these coalitions are often close
relatives (Packer et al. 1991). As a second example, reproduction among male spotted hyenas (Crocuta crocuta) was also skewed as non-natal males over a 10 year study sired 97% of all offspring even though they are of lower rank than natal males, indicating female choice in this species, where females are dominant over males, has an impact on the degree of male reproductive skew (Engh et al. 2002). The present study is the first study in primates quantitatively investigating male reproductive skew measuring number of offspring sired by potential sires for six separated birth cohorts. The combination of both mating behaviour and paternity data would be necessary to answer the question whether skew in male reproduction is due to male monopolisation or female choice.

**Female reproductive decisions**

As females tend to conceive their offspring from different males in consecutive years, paternity continuity from the females’ perspective is low. An important consequence of this is that most siblings sharing the same mother will therefore be maternal half-siblings, not full-siblings, which are very rarely in the study group. This has also been found in paternity studies on other macaque species (Japanese macaques: Inoue et al. 1991, toque macaques: Keane et al. 1997). By reproducing with different males across years, females reduced the degree of relatedness among their offspring from $r=0.5$ (full-siblings) to $r=0.25$ (half-siblings). Female reproductive decisions might be explained in the sense of optimal out-breeding (Bateson 1982) accepting a lower degree of relatedness towards the benefit of genetic diversity among their offspring. Recent research on juvenile Atlantic salmon has reported that juvenile Atlantic salmon (Salmo salar) have a heterogenous advantage that outweighs the benefits of kin-biased behaviour, both at the individual and population level (Griffiths & Armstrong 2001). The theories of kin selection and heterogeneous advantage predict diametrically opposite effects. In other words, the latter suggests that competition is low with high genetic diversity (i.e., among non-kin) and high with low genetic diversity (i.e., among kin). In contrast, Hamilton’s kin selection theory (1964) predicts less aggression among kin. The presented data raise questions about whether lineage specific mate choice characterises rhesus macaques (Silk & Boyd 1983, McMillan 1986), because females are not maximising the degree of relatedness among their offspring.

**Paternal cohorts**

This study revealed that from the infants perspective, at least 74% of individuals have one paternal half-sibling of the same age and at least 15% of individuals have a paternal half-sibling within a two-year age difference. Hence, at most only 11% of individuals either lacked
a paternal half-sibling at all or in close age proximity within the troop. In fact, nearly 90% of infants will have at least a paternal half-sibling either of the same age or within two-years of age difference. In addition, the average number of paternal half-siblings per individual was much higher than the average number of maternal half-siblings. The presence of such a large number of paternal half-siblings which also tend to be in close age proximity, should have evolutionary consequences in terms of paternal kin discrimination (cf. J. Altmann 1979), since animals are expected to benefit supporting a paternal half-sibling to a similar extent as supporting a maternal half-sibling. A second implication of these results is, that even in large troops, such as group R, where many males compete over a limited number of oestrous females within a mating season, male reproductive skew creates cohorts of paternal half-siblings.

Summary
When access to limited resources (e.g., fertile females) is monopolised by only a subset of individuals, than conditions are created which are conducive to reproductive skew among potential sires. Paternity studies in primates have found that reproduction is restricted to a limited number of males each year, therefore male reproduction seems to be skew, but to date statistical analyses of skew in the actual reproductive success of males has not yet been published. The results of the present chapter suggest that reproduction among males was skewed over six years investigated, indicating that some males monopolise the high proportion of mates by excluding others from reproducing. The factors most likely to account for male reproductive skew in this study are female choice and male-male competition, because high-ranking males had a higher reproductive success, but low paternity continuity and a high proportion of nontroop sires may also suggest female choice. The extreme skew in male reproduction yielded a kinship structure where 74% of infants had a paternal half-sibling within the same cohort. Given that male reproductive success is probably skewed in other primate species, then J. Altmann’s (1979) suggestion that paternal sibships are important in primate societies, should be re-emphasised. One of the most important consequences of reproductive skew in primate societies is that many individuals will have more paternal, than maternal, half-siblings during their life time.
4. Paternal kin discrimination and age proximity

Introduction

1. Mechanisms of kin discrimination

Kin selection is expected to promote the evolution of social behaviour that increases the survival and reproductive success of close relatives (Hamilton 1964, Maynard Smith 1964). One prerequisite for kin selection is that individuals have the ability to discriminate between kin and non-kin (Grafen 1990). There are four possible mechanisms underlying kin recognition (Box 4.1).

Box 4.1: Mechanisms of kin recognition.

- **Spatial distribution**: If relatives are distributed predictably in space, nepotism (favouring kin) occurs as a result of location-specific behaviour, e.g., in reed warbler (cit. Krebs & Davies 1993).
- **Familiarity via prior association**: Relatives must predictably interact in unambiguous social circumstances, in which kinship is rarely confused due to the mixing of equally related individuals (social learning), e.g., in house mice (Kareem & Barnard 1982).
- **Phenotype matching**: An individual learns its own phenotypic attributes (odour, appearance, vocalisations etc.) or those of known relatives and matches this learned template against a potential kin in order to assess kinship (recognition in the absence of familiarity), e.g., in ground squirrels (Holmes 1986a).
- **Recognition alleles or green beard effect**: Genes that cause a unique phenotypic effect (e.g., green beard) enable the bearer to recognise them in other individuals, one case reported in the fire ant (Keller & Ross 1998).

Note, recent work suggested to drop spatial distribution and recognition alleles as mechanisms of kin recognition and combined familiarity via association and phenotype matching as one mechanism as both are based on learning (Tang-Martinez 2001).

Among mammals, maternal kinship is detectable for human observers as lactation reveals mother-infant relationships. These close mother-infant bonds produce a social system in which maternal kinship and familiarity are tightly associated. Familiarity is therefore thought to be the most important mechanism of maternal kin recognition in primates (Gouzoules &
Gouzoules 1987, Walters 1987, Bernstein 1991, Chapais et al. 2001). However, maternal
kinship frequently coincides with patterns of spatial proximity and a higher frequency of
grooming and agonistic aiding among female primates, making it difficult to distinguish the
effects of kinship from those of familiarity on structuring social relationships. Therefore it is
also unclear, whether primates recognise indeed shared genes in terms of the actual degree of
relatedness or whether they just recognise the degree of familiarity.

In multi-male societies with unknown paternity, where rank, age or other factors may
influence male reproduction, paternal sibship is expected to be found (e.g., as a result of male
reproductive skew, see chapter 3). Paternal kin are probably not familiar to each other as
fathers are not likely to mediate familiarity among their offspring. Among primates it remains
questionable whether paternal kin can be identified in the absence of familiarity or whether
they use alternative mechanisms such as phenotype matching to recognise each other.

To be more precise, kin discrimination among primates is most likely to arise if individuals
either classify relatives due to shared family traits, via phenotype matching (Holmes &
Sherman 1983, Lacy & Sherman 1983) or identify relatives due to frequent association

2. Defining kin discrimination vs. kin recognition

It is necessary to define relevant terms used in this chapter, as they have often been
confounded in the literature. I will mainly follow the definitions given by Tang-Martinez
(2001). Kin discrimination refers to the differences in the behavioural responses that an
individual shows toward its kin compared to non-kin, based on conspecific labels or cues that
are correlated with kinship (Tang-Martinez 2001). Kin discrimination therefore only implies
to behavioural responses and not necessarily to cognitive processes. Kin recognition, on the
other hand, refers to the cognitive mechanisms (i.e., neural processing) which allow animals
to classify conspecifics as either kin or non-kin (see Byers & Bekoff 1986, Waldman et al.
1988).

The behavioural discrimination of kin may allow one to infer kin recognition, but the latter
can never be observed directly because it is a neural process. For simplification kin
discrimination and kin recognition will be used interchangeably in this thesis as in other
studies (Lacy & Sherman 1983, Sherman et al. 1997), because I will examine discrimination
in behaviour but not recognition abilities. A lack of discrimination in one context does not
imply its absence in another (Waldman et al. 1988, Barnard & Aldhous 1991, Sherman et al.
1997) suggesting that kin discrimination operates in a context-dependent fashion.

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3. Evidence of kin discrimination

Whether or not individuals can recognise their kin has been studied across the entire animal kingdom from social amoeba (Strassmann et al. 2000) to humans (e.g. Porter & Moore 1981). Most detailed evidence of kin recognition comes from social insects (review e.g. in Breed & Bennett 1987, Bourke & Ratnieks 1999) which are of particular interest due to their variable degree of relatedness caused by haplo-diploidy. However, broad evidence of kin discrimination has also been reported for a variety of vertebrate species, e.g., rainbowfish, *Melanotaenia eachamensis*, (Arnold 2000), cascades frog tadpoles, *Rana cascadae* (Blaustein & O’Hara 1981, 1982), long-tailed tits, *Aegithalos caudatus* (Hatchwell et al. 2001), house mice, *Mus musculus* (Kareem & Barnard 1982), white-footed mice, *Peromyscus leucopus* (Grau 1982), spiny mice, *Acomys cahirinus* (Porter et al. 1983), Belding’s ground squirrels, *Spermophilus beldingi* (Holmes & Sherman 1982, 1983), beavers, *Castor canadensis* (Sun & Müller-Schwarze 1997), and chimpanzees, *Pan troglodytes* (Parr & de Waal 1999, see also review for vertebrates in Blaustein et al. 1987a).

As most studies on kin recognition have focused on the discrimination of maternal (i.e., familiar) kin versus non-kin, less is known whether paternal (i.e., unfamiliar) kin can recognise each other. Only a few studies have been able to test paternal half-siblings against non-kin, e.g., house mice (Kareem & Barnard 1982), Belding’s ground squirrels (Holmes 1986b), peacocks, *Pavo cristatus* (Petrie et al. 1999), golden hamsters, *Mesocricetus auratus* (Todrank et al. 1998), and savanna baboons, *Papio cynocephalus* (Alberts 1999, Smith 2000). Paternal kin discrimination is most likely to evolve when paternal sibships occur in a social species. This happens (i) when unrelated females live together in a social group and (ii) when these females conceive their offspring by the same male (male reproductive skew). Both conditions are likely to be found in many primate societies.

The importance of maternal kinship in primates has been extensively studied (reviewed in more detail in chapter 5), studies including paternal kin are, however, still very limited. One captive study has investigated paternal kin discrimination in primates (Wu et al. 1980). They concluded that pigtailed macaques, *Macaca nemestrina*, exhibit kin recognition in the absence of familiarity, based upon their finding that unfamiliar juvenile peers prefer to sit closer to their paternal half-siblings than to non-kin. However, all subsequent studies of the same species not only failed to replicate the original findings, but inferred that familiarity rather than paternal kinship affected social preferences (Fredrickson & Sackett 1984, Sackett & Fredrickson 1987). Furthermore, captive studies of long-tailed macaques, *M. fascicularis* (Welker et al. 1987), and savanna baboons, *Papio cynocephalus* (Erhart et al. 1997) have
reported that primates do not recognise paternal kin and that familiarity regulates social relationships. Nepotism (preferential treatment of kin) is thought to develop among primates as a consequence of familiarity and matrilineal, but not patrilineal, relatedness (Gouzoules & Gouzoules 1987, Walters 1987, Bernstein 1991, Chapais et al. 2001). Paternal kin discrimination has therefore been thought to be unlikely among primates for the last 20 years, but recent studies in wild baboons have resurrected the interest in the prospect that paternal kin recognition occurs in primates (Alberts 1999, Smith 2000).

4. Hypothesis

In species with multiple mating, sirehood has been found to be restricted to a limited number of males each year (e.g., M. fascicularis: de Ruiter et al. 1992, P. cynocephalus: Altmann, et al. 1996, M. sinica: Keane et al. 1997, M. mulatta: Bercovitch et al. 2000). When male reproductive success is strongly skewed, peers are likely to be paternal half-siblings (J. Altmann 1979). On the other hand, peers are rarely maternal half-siblings because most female primates give birth to only a single offspring. Therefore, maternal half-siblings are at least one, but often two or more, years apart. Under this type of demographic structure, maternal half-siblings would be members of different age cohorts (i.e. non-peers), while paternal half-siblings would often be members of the same age cohort (i.e. peers).

One way of trying to distinguish familiarity from phenotype matching in primates is to examine patterns of social relationships among paternal half-siblings. If male reproduction is skewed within a season, if age mates are more familiar with each other than non-age mates, and if familiarity per se promotes social relationships, then one would expect individuals to associate more frequently with (often paternally related) peers than with non-peers. However, if relatedness per se regulates social relationships, then one would expect individuals to associate as often with maternal as with paternal kin.

5. Aim of this chapter

This chapter will examine the influence of both maternal and paternal kinship, as well as age proximity, on patterns of affiliation and aggression among semi free-ranging adult female rhesus macaques. In rhesus macaques, male reproductive success is skewed (see chapter 3) and age mates play more often with each other than animals of different ages do (Janus 1992), so peers are probably frequently playing with paternal siblings. Adult female rhesus macaques from the same age cohort, therefore, have a strong likelihood of having the same sire, but the extent to which shared paternity influences adult female social relationships is unknown.
Both age proximity and paternal kinship influence mating behaviour in savanna baboons. Alberts (1999) found that paternal half-siblings were engaged in lower levels of affiliative and sexual behaviour than non-kin. Alberts also found that individuals from the same cohort tended to avoid mating with each other, but a limited sample size precluded simultaneous examination of age proximity and kinship. Here, Alberts’s hypothesis will be significantly expanded by scrutinising the influence of maternal and paternal kinship, as well as age proximity, on affiliative and aggressive relationships among adult female rhesus macaques.

**Results**

1. **The effect of kinship and age proximity on affiliation and aggression**

Kin selection theory (Hamilton, 1964) suggests that the cost-benefit ratio of behaviours, whether they are affiliative or aggressive, will be proportional to the degree of relatedness of the actor and recipient, respectively. In other words, affiliation is expected to increase as the degree of relatedness increases, but likewise aggression is expected to decrease along with relatedness. Under conditions promoted by kin selection (Hamilton 1964) affiliation should be more pronounced among kin (both maternal and paternal) than among non-kin, whereas aggression should be less pronounced among kin than among non-kin. Here, data on affiliation and aggression are listed for maternal half-siblings, paternal half-siblings, and non-kin, the two latter being either peers or non-peers (Table 4.1). Note that maternal half-siblings can only be non-peers (see Methods). Definition on affiliative and aggressive interactions can be found in the Appendix 2. Definitions on the kin and age categories used are described in detail in the Methods.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS-NP</td>
<td>34</td>
<td>2.117 ± 1.087</td>
<td>0.372 ± 0.301</td>
<td>1.581 ± 0.754</td>
<td>0.017 ± 0.022</td>
<td>0.050 ± 0.041</td>
</tr>
<tr>
<td>PS-P</td>
<td>15</td>
<td>0.588 ± 0.419</td>
<td>0.088 ± 0.119</td>
<td>0.521 ± 0.330</td>
<td>0.007 ± 0.018</td>
<td>0.029 ± 0.072</td>
</tr>
<tr>
<td>PS-NP</td>
<td>19</td>
<td>0.450 ± 0.302</td>
<td>0.012 ± 0.026</td>
<td>0.308 ± 0.160</td>
<td>0.002 ± 0.007</td>
<td>0.024 ± 0.040</td>
</tr>
<tr>
<td>NK-P</td>
<td>34</td>
<td>0.360 ± 0.160</td>
<td>0.024 ± 0.030</td>
<td>0.327 ± 0.137</td>
<td>0.005 ± 0.008</td>
<td>0.019 ± 0.020</td>
</tr>
<tr>
<td>NK-NP</td>
<td>34</td>
<td>0.350 ± 0.111</td>
<td>0.011 ± 0.007</td>
<td>0.232 ± 0.054</td>
<td>0.003 ± 0.002</td>
<td>0.013 ± 0.006</td>
</tr>
</tbody>
</table>

Cell values are mean frequencies per hour (± SD) for proximity, grooming, approach (affiliative interactions), physical and non-physical aggression (agonistic interactions). Abbreviations are as follows: number of individuals tested (N), maternal half-sisters, non-peer (MS-NP), paternal half-sisters, peer (PS-P) or non-peer (PS-NP) and non-kin, peer (NK-P) or
non-peer (NK-NP). Dyads that fit in more than one category (e.g., being paternal half-siblings and maternal aunt-niece) were excluded in all analyses.

Regarding kinship, the three kin groups differed from each other in rates of affiliative and aggressive interactions. Maternal half-siblings were generally more affiliative, but also more aggressive than either paternal half-siblings or non-kin. Paternal half-siblings exhibited about 1.5 to 4 times higher rates of affiliation than non-kin, but likewise rates of aggression exceeded the one found for non-kin. Regarding age, rates of both affiliation and aggression were higher among peers than among non-peers both among paternal half-siblings and non-kin. Variation in the data was higher among paternal half-sisters than non-kin and was even more pronounced among peers, indicating that some females frequently exhibit affiliation and/or aggression towards paternal peers while others do not. For statistical tests see below.

Testing age proximity controlling for kinship

Given that peers are more familiar than non-peers (Janus 1992), one might expect that affiliative interactions are more frequent among peers than among non-peers. In addition, peers are likely to compete for the same resources at the same time of their lives, resulting in more frequent aggressive interactions among peers than among non-peers (Janus 1991). It was already suggested by Alexander (1974) that the closest competitor will also be the closest in co-operator. Therefore, affiliation and aggression between peers and non-peers were first compared in order to test for effects of age proximity on affiliation. Possible kinship effects were eliminated by restricting this comparison to non-kin. The results are summarised in Table 4.2.

Table 4.2: Testing age proximity controlling for kinship

<table>
<thead>
<tr>
<th>Paired t-tests</th>
<th>N</th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>NK-P</td>
<td>34</td>
<td>t=0.350</td>
<td>t=2.560</td>
<td>t=4.266</td>
<td>t=1.627</td>
<td>t=1.874</td>
</tr>
<tr>
<td>vs. NK-NP</td>
<td></td>
<td>P=0.728</td>
<td>P=0.015</td>
<td>P&lt;0.001</td>
<td>P=0.113</td>
<td>P=0.070</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P’=0.017</td>
<td>P’=0.006</td>
<td>P’=0.006</td>
<td>P’=0.007</td>
<td>P’=0.009</td>
</tr>
</tbody>
</table>

Paired t-tests using data from Table 4.1. P’ represents the Dunn-Šidák correction for multiple testing undertaken for 10 simultaneous tests, i.e., per single behaviour for Table 4.2-4.4 this chapter and Table 5.3-5.4 chapter 5 (see Methods). Recall from the Methods that only P-values less than or equal to the corrected P-value (P’) indicate a significant test result which will be marked in bold.
Unrelated adult females affiliated more with their peers than with their non-peers. Peers groomed and approached each other significantly more often than non-peers, but no such difference emerged from patterns of proximity. Regarding aggression, peers tended to exhibit more non-physical aggression than non-peers, but no such difference was found for physical aggression. Overall, the results show that age proximity had a significant effect on rates of affiliation and aggression between adult female rhesus macaques. Therefore, all subsequent analyses will differentiate between peers and non-peers.

**Testing maternal vs. paternal half-siblings and non-kin controlling for age proximity**

Most studies on kinship in primates have compared maternal kin against maternal unrelated individuals, ignoring the proportion of paternal kin. As only few studies were able to separate paternal half-sibling from non-kin, a comparison was made between maternal and paternal half-siblings on the one hand, and maternal half-siblings and non-kin on the other hand (Table 4.3). Analyses were restricted to non-peers as maternal half-siblings are rarely peers (see Methods).

<table>
<thead>
<tr>
<th>Paired t-tests</th>
<th>N</th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS-NP</td>
<td>34</td>
<td>t=9.799</td>
<td>t=6.977</td>
<td>t=10.493</td>
<td>t=5.437</td>
<td>t=3.754</td>
</tr>
<tr>
<td>vs. NK-NP</td>
<td></td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P'=0.005</td>
<td>P'=0.005</td>
<td>P'=0.005</td>
<td>P'=0.005</td>
<td></td>
</tr>
<tr>
<td>MS-NP</td>
<td>19</td>
<td>t=6.344</td>
<td>t=5.291</td>
<td>t=6.565</td>
<td>t=1.960</td>
<td>t=3.078</td>
</tr>
<tr>
<td>vs. PS-NP</td>
<td></td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P=0.066</td>
<td>P=0.006</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P'=0.005</td>
<td>P'=0.005</td>
<td>P'=0.005</td>
<td>P'=0.006</td>
<td></td>
</tr>
</tbody>
</table>

Paired t-tests using data from Table 4.1. See Table 4.2 for more details.

When compared among non-peers, maternal half-siblings were more affiliative and more aggressive towards each other in all interactions examined than either paternal half-siblings or non-kin, with the exception that maternal half-siblings showed only a trend towards more aggression than paternal half-siblings.
Testing paternal half-siblings vs. non-kin controlling for age proximity

As age proximity influenced affiliation and aggression among non-kin, it is expected that both age proximity and paternal kinship influence female social relationships. Here, a comparison was made between affiliation and aggression of paternal half-siblings vs. non-kin being either peers or non-peers (Table 4.4).

Table 4.4: Testing paternal half-siblings vs. non-kin controlling for age proximity

<table>
<thead>
<tr>
<th>Paired t-tests</th>
<th>N</th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>PS-P</td>
<td>15</td>
<td>t=-2.963</td>
<td>t=-2.136</td>
<td>t=-3.170</td>
<td>t=0.139</td>
<td>t=0.553</td>
</tr>
<tr>
<td>vs. NK-P</td>
<td>P=0.010</td>
<td>P=0.051</td>
<td>P=0.007</td>
<td>P=0.891</td>
<td>P=0.589</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P'=0.009</td>
<td>P'=0.007</td>
<td>P'=0.010</td>
<td>P'=0.025</td>
<td>P'=0.025</td>
<td></td>
</tr>
<tr>
<td>PS-NP</td>
<td>19</td>
<td>t=-1.263</td>
<td>t=0.011</td>
<td>t=-2.096</td>
<td>t=-0.582</td>
<td>t=-1.244</td>
</tr>
<tr>
<td>vs. NK-NP</td>
<td>P=0.222</td>
<td>P=0.991</td>
<td>P=0.051</td>
<td>P=0.568</td>
<td>P=0.230</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P'=0.013</td>
<td>P'=0.050</td>
<td>P'=0.013</td>
<td>P'=0.006</td>
<td>P'=0.013</td>
<td></td>
</tr>
</tbody>
</table>

Paired t-tests using data from Table 4.1. See Table 4.2 for more details.

To examine the effects of both paternal kinship and age proximity, affiliative and aggressive interactions were first analysed within a given birth cohorts. Among peers, paternal half-siblings were significantly more affiliative (with grooming as a trend after the Dunn-Šidák correction), but showed similar rates of aggression than non-kin. As a second step, affiliative and aggressive interactions were compared across birth cohorts. Among non-peers, paternal half-siblings showed a trend of approaching each other more often than non-kin, according the Dunn-Šidák correction, but the results were inconsistent, which was probably a consequence of including multiple ages in the non-peer category (see below). In sum, the results indicate that adult female rhesus macaques discriminate paternal half-siblings from non-kin, with paternal kin discrimination pronounced among peers in terms of affiliative interactions, but less visible regarding aggressive interactions.
Testing kinship and age proximity simultaneously

A two-way analysis of variance was applied to simultaneously examine the influence of both paternal kinship and age proximity on all affiliative and agonistic behaviours. In other words, it was investigated whether both parameters produce an interaction effect for any of the behaviours considered. Here, indices of the same focal animal with social partners of different levels of relatedness were treated as independent. (Table 4.5).

<table>
<thead>
<tr>
<th>ANOVA Two-way</th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kin (d.f.=1)</td>
<td>F=11.071</td>
<td>F=9.395</td>
<td>F=14.855</td>
<td>F=0.115</td>
<td>F=2.352</td>
</tr>
<tr>
<td>PS vs. NK</td>
<td><strong>P=0.001</strong></td>
<td><strong>P=0.003</strong></td>
<td>P&lt;0.001</td>
<td>P=0.735</td>
<td>P=0.128</td>
</tr>
<tr>
<td>Age (d.f.=1)</td>
<td>F=2.265</td>
<td>F=17.864</td>
<td>F=19.286</td>
<td>F=3.299</td>
<td>F=0.525</td>
</tr>
<tr>
<td>P vs. NP</td>
<td>P=0.136</td>
<td><strong>P&lt;0.001</strong></td>
<td><strong>P&lt;0.001</strong></td>
<td>P=0.072</td>
<td>P=0.470</td>
</tr>
<tr>
<td>Kin*Age (d.f.=1,98)</td>
<td>F=1.700</td>
<td>F=8.909</td>
<td>F=2.818</td>
<td>F=0.415</td>
<td>F=0.012</td>
</tr>
<tr>
<td></td>
<td><strong>P=0.004</strong></td>
<td>P=0.096</td>
<td>P=0.521</td>
<td>P=0.914</td>
<td></td>
</tr>
</tbody>
</table>

Two-way analysis of variance treating values of proximity, grooming, approach, physical and non-physical aggression of the same focal animal with social partners from different classification levels as independent. Dyads present either paternal half-siblings (PS) or non-kin (NK) with respect to kinship and either peers (P) or non-peers (NP) with respect to age. Mean, SD and sample size of the data used in this analyses are shown in Table 4.1.

When tested by means of two-way analysis of variance, both paternal kinship and peerage had a significant effect on affiliation with the exception of age on patterns of proximity. The interaction between paternal kinship and age was only found to be statistically significant for grooming. However, neither paternal kinship nor peerage had an effect on both type of aggression analysed. Referring to Table 4.1 again, a comparison of the means between paternal half-sisters and non-kin, being either peers and non-peers suggests that paternal half-sibling born into the same cohort showed consistently the highest means on all affiliative interactions, while non-kin born into different cohorts showed consistently the lowest means on all affiliative interactions. The same trend emerged for physical and non-physical aggression.
2. The effect of kinship and the exact age differences on affiliation and aggression

The analysis of age proximity and kinship was refined by considering the exact age difference (in years) between maternal half sisters, paternal half sisters and non-kin, using individuals either zero (i.e., peers), one, two or three years apart in age. While all 34 focal females had non-kin of all three age classes, the number of (at least one) maternal and/or paternal half siblings per focal female varied, resulting in a total N for maternal half-siblings of 43 (Table 4.6), paternal half-siblings of 39 (Table 4.7) and non-kin of 102 (Table 4.8).

| Table 4.6: The effect of maternal kinship and exact age differences on affiliation and aggression |
|---------------------------------------------------------------|------------------------------------------------|------------------|------------------|
| Proximity | Grooming | Approach | Physical Aggression | Non-physical Aggression |
| MS-1 (N=14) | 1.662 ± 0.648 | 0.376 ± 0.401 | 1.173 ± 0.651 | 0.017 ± 0.024 | 0.043 ± 0.086 |
| MS-2 (N=12) | 1.966 ± 1.182 | 0.280 ± 0.206 | 1.363 ± 1.128 | 0.013 ± 0.023 | 0.056 ± 0.060 |
| MS-3 (N=17) | 2.403 ± 1.371 | 0.452 ± 0.417 | 2.002 ± 0.962 | 0.026 ± 0.035 | 0.067 ± 0.070 |
| Pearson corr. | r_p=0.278 | r_p=0.098 | r_p=0.368 | r_p=0.154 | r_p=0.141 |
| N_total=43 | P=0.071 | P=0.530 | **P=0.015** | P=0.323 | P=0.368 |

Pearson correlation coefficient for focal females who had at least one maternal half-siblings (MS) with an exact age difference of either 1, 2 or 3 years apart. The exact age difference was correlated with proximity, grooming, approach, physical or non-physical aggression, respectively. Cell values are mean frequencies per hour (± SD). For 43 focal females the Pearson correlation coefficient (r_p) was calculated, treating the same focal animal with social partners from different classification levels as independent.

As the age differences between maternal half siblings increased, rates of approach also increased, but no such association was found for aggression or grooming. A trend to increased proximity with increased age difference was also apparent.
Table 4.7: The effect of paternal kinship and exact age differences on affiliation and aggression

<table>
<thead>
<tr>
<th></th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>PS-P (N=15)</td>
<td>0.588 ± 0.419</td>
<td>0.088 ± 0.119</td>
<td>0.521 ± 0.330</td>
<td>0.007 ± 0.018</td>
<td>0.029 ± 0.072</td>
</tr>
<tr>
<td>PS-1 (N=15)</td>
<td>0.491 ± 0.320</td>
<td>0.026 ± 0.093</td>
<td>0.390 ± 0.240</td>
<td>0.006 ± 0.016</td>
<td>0.036 ± 0.049</td>
</tr>
<tr>
<td>PS-2 (N=9)</td>
<td>0.404 ± 0.250</td>
<td>0.014 ± 0.026</td>
<td>0.255 ± 0.149</td>
<td>0.000 ± 0.000</td>
<td>0.009 ± 0.018</td>
</tr>
<tr>
<td>Pearson corr.</td>
<td>( r_p = -0.208 )</td>
<td>( r_p = -0.313 )</td>
<td>( r_p = -0.372 )</td>
<td>( r_p = -0.166 )</td>
<td>( r_p = -0.120 )</td>
</tr>
<tr>
<td>N total=39</td>
<td>P=0.204</td>
<td>P=0.052</td>
<td>P=0.019</td>
<td>P=0.313</td>
<td>P=0.468</td>
</tr>
</tbody>
</table>

Pearson correlation coefficient for paternal half-siblings (PS) between the exact age difference (0, 1, or 2 years apart) and proximity, grooming, approach, physical and non-physical aggression, respectively. For 39 focal females the Pearson correlation coefficient (\( r_p \)) was calculated, treating the same focal animal with social partners from different classification levels as independent. For more details see Table 4.6.

As the exact age differences between paternal half siblings increased, rates of grooming (trend) and approaches declined consistently. However, no such association was found for proximity, physical and non-physical aggression.

Table 4.8: The effect of non-kinship and exact age differences on affiliation and aggression

<table>
<thead>
<tr>
<th></th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>NK-P (N=34)</td>
<td>0.360 ± 0.160</td>
<td>0.024 ± 0.030</td>
<td>0.327 ± 0.137</td>
<td>0.005 ± 0.008</td>
<td>0.019 ± 0.020</td>
</tr>
<tr>
<td>NK-1 (N=34)</td>
<td>0.383 ± 0.118</td>
<td>0.020 ± 0.020</td>
<td>0.313 ± 0.097</td>
<td>0.003 ± 0.004</td>
<td>0.019 ± 0.017</td>
</tr>
<tr>
<td>NK-2 (N=34)</td>
<td>0.390 ± 0.154</td>
<td>0.015 ± 0.019</td>
<td>0.286 ± 0.088</td>
<td>0.003 ± 0.005</td>
<td>0.019 ± 0.010</td>
</tr>
<tr>
<td>Pearson corr.</td>
<td>( r_p = 0.085 )</td>
<td>( r_p = -0.151 )</td>
<td>( r_p = -0.157 )</td>
<td>( r_p = -0.123 )</td>
<td>( r_p = 0.023 )</td>
</tr>
<tr>
<td>N total=102</td>
<td>P=0.394</td>
<td>P=0.131</td>
<td>P=0.114</td>
<td>P=0.219</td>
<td>P=0.820</td>
</tr>
</tbody>
</table>

Pearson correlation coefficient for unrelated females (NK) between the exact age difference (0, 1, or 2 years apart) and proximity, grooming, approach, physical and non-physical aggression, respectively. For 102 focal females the Pearson correlation coefficient (\( r_p \)) was calculated, treating the same focal animal with social partners from different classification levels as independent. For more details see Table 4.6.

The exact age differences between unrelated females had no significant effect on either affiliative or aggressive interactions.
In sum, only levels of affiliation between paternal half sisters increased gradually with decreasing age difference, while maternal half sisters tended to display the opposite pattern. Affiliation and aggression among non-kin showed no association regarding the exact age differences.

3. **The effect of kinship and age proximity on affiliation and aggression controlling for spatial proximity**

Individuals who spend a large amount of time in close spatial proximity are much more likely to interact with each other in both co-operative and competitive ways than individuals who are rarely found in spatial proximity (cf. Alexander 1974). In addition, Chapais (2001) discussed a confounding effect between spatial proximity and matrilineal kinship on the evolution of nepotism, as the persistence of mother-daughter preferential bonds into adulthood generates a structure of spatial proximity among maternal kin, which reflects genetic relatedness. Correlation between degree of relatedness and time spent in proximity was reported for Japanese macaques by Kurland (1977) and rhesus macaques by Kapsalis & Berman (1996a). As shown above, spatial proximity rates in this study also differed depending upon genetic relatedness and/or age proximity. In order to control for this possible confounding effect between proximity and relatedness, data were corrected for spatial proximity by dividing the frequency of a certain behavioural interaction (e.g., grooming) within each individual dyad by the frequency of proximity within the same dyad. The data presented above will be re-analysed after controlling them for spatial proximity (see Table 4.9). The test results which follow will be compared in respect to analyses with or without the control for spatial proximity.

<table>
<thead>
<tr>
<th>Mean frequency</th>
<th>N</th>
<th>Grooming cp</th>
<th>Approach cp</th>
<th>Physical Aggression cp</th>
<th>Non-physical Aggression cp</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS-NP</td>
<td>34</td>
<td>0.046 ± 0.034</td>
<td>0.199 ± 0.057</td>
<td>0.002 ± 0.002</td>
<td>0.008 ± 0.008</td>
</tr>
<tr>
<td>PS-P</td>
<td>15</td>
<td>0.027 ± 0.033</td>
<td>0.250 ± 0.168</td>
<td>0.001 ± 0.003</td>
<td>0.012 ± 0.028</td>
</tr>
<tr>
<td>PS-NP</td>
<td>19</td>
<td>0.005 ± 0.011</td>
<td>0.226 ± 0.178</td>
<td>0.002 ± 0.005</td>
<td>0.016 ± 0.034</td>
</tr>
<tr>
<td>NP-P</td>
<td>34</td>
<td>0.012 ± 0.016</td>
<td>0.258 ± 0.111</td>
<td>0.005 ± 0.010</td>
<td>0.023 ± 0.045</td>
</tr>
<tr>
<td>NK-NP</td>
<td>34</td>
<td>0.005 ± 0.003</td>
<td>0.207 ± 0.048</td>
<td>0.003 ± 0.004</td>
<td>0.013 ± 0.007</td>
</tr>
</tbody>
</table>

Cell values are mean frequencies (± SD) for grooming, approach (affiliative interactions), physical and non-physical aggression (agonistic interactions) which are controlled for proximity indicated by cp. Abbreviations as in Table 4.1.
When controlled for spatial proximity, the three kin groups differed less from each other in respect to affiliation and aggression. Maternal half-siblings still exhibited the highest rates of grooming, followed by paternal half-siblings and then non-kin, with grooming more frequent among peers than among non-peers. However, controlling for spatial proximity seemed to decrease the bias in behaviour towards maternal half-siblings.

Testing age proximity controlling for kinship and spatial proximity
Affiliation and aggression between peers and non-peers will first be compared, and possible kinship effects were eliminated by restricting this comparison to non-kin. The results are summarised in Table 4.10.

<table>
<thead>
<tr>
<th>Paired t-tests</th>
<th>N</th>
<th>Grooming&lt;sub&gt;cp&lt;/sub&gt;</th>
<th>Approach&lt;sub&gt;cp&lt;/sub&gt;</th>
<th>Physical Aggression&lt;sub&gt;cp&lt;/sub&gt;</th>
<th>Non-physical Aggression&lt;sub&gt;cp&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>NK-P</td>
<td>34</td>
<td>t=2.595</td>
<td>t=2.645</td>
<td>t=1.172</td>
<td>t=1.336</td>
</tr>
<tr>
<td>vs. NK-NP</td>
<td></td>
<td><strong>P=0.014 (=)</strong></td>
<td><strong>P=0.012 (=)</strong></td>
<td><strong>P=0.250 (=)</strong></td>
<td><strong>P=0.191 (=)</strong></td>
</tr>
<tr>
<td></td>
<td></td>
<td>P’=0.017</td>
<td>P’=0.010</td>
<td>P’=0.013</td>
<td>P’=0.013</td>
</tr>
</tbody>
</table>

Paired t-tests using data from Table 4.9. P’ represents the Dunn-Šidák correction for multiple testing undertaken for 5 simultaneous tests, i.e., per single behaviour for Table 4.10-4.12 of this chapter (see Methods). Recall from the Methods that only P-values less than or equal to the corrected P-value (P’) indicate a significant test result which will be marked in bold. The equal sign (=) indicates that the test did not change whether or not one controlled for spatial proximity, i.e., a test either remained significant or non-significant.

When controlled for spatial proximity, the results revealed that unrelated females groomed and tended to approach their peers more often than their non-peers as they did in the previous analyses, but no differences emerged with respect to aggression.
Testing maternal vs. paternal half-siblings and non-kin controlling for age proximity and spatial proximity

Analyses were restricted to non-peers, comparing maternal half-siblings with non-kin on the one hand and maternal half-siblings with paternal half-siblings on the other hand (Table 4.11).

Table 4.11: Testing maternal vs. paternal half-siblings and non-kin controlling for age proximity and spatial proximity

<table>
<thead>
<tr>
<th>Paired t-tests</th>
<th>N</th>
<th>Grooming_{cp}</th>
<th>Approach_{cp}</th>
<th>Physical Aggression_{cp}</th>
<th>Non-physical Aggression_{cp}</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS-NP</td>
<td>34</td>
<td>t=7.113</td>
<td>t=-0.843</td>
<td>t=-0.897</td>
<td>t=-3.131</td>
</tr>
<tr>
<td>vs. NK-NP</td>
<td>P&lt;0.001 (=)</td>
<td>P=0.406</td>
<td>P=0.376</td>
<td>P'=0.010</td>
<td>P'=0.004 (=)</td>
</tr>
<tr>
<td></td>
<td>P'=0.010</td>
<td>P'=0.017</td>
<td>P'=0.017</td>
<td>P'=0.010</td>
<td></td>
</tr>
<tr>
<td>vs. PS-NP</td>
<td>19</td>
<td>t=4.667</td>
<td>t=-0.545</td>
<td>t=0.420</td>
<td>t=-1.051</td>
</tr>
<tr>
<td></td>
<td>P&lt;0.001 (=)</td>
<td>P=0.593</td>
<td>P=0.680 (=)</td>
<td>P=0.307</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P'=0.013</td>
<td>P'=0.050</td>
<td>P'=0.050</td>
<td>P'=0.025</td>
<td></td>
</tr>
</tbody>
</table>

Paired t-tests using data from Table 4.9. See Table 4.10 for more details. Note, no equal sign in a non-significant result indicates that this test was significant before.

When compared among non-peers and controlled for spatial proximity, maternal half-siblings still differed significantly in grooming and non-physical aggression from non-kin as in the previous analyses, but the previous differences found in approach and physical aggression did not hold when data were controlled for spatial proximity. On the other hand, maternal half-siblings still differed significantly in grooming from paternal half-siblings than in the previous analyses, but the previous differences found in approach and non-physical aggression did not hold when data were controlled for spatial proximity.

Testing paternal half-siblings vs. non-kin controlling for age proximity

Here, the comparison is re-analysing affiliation and aggression among paternal half-siblings vs. non-kin being either peers or non-peers (Table 4.12).
Table 4.12: Testing paternal half-siblings vs. non-kin controlling for age proximity and spatial proximity

<table>
<thead>
<tr>
<th></th>
<th>Grooming (_{cp})</th>
<th>Approach (_{cp})</th>
<th>Physical Aggression (_{cp})</th>
<th>Non-physical Aggression (_{cp})</th>
</tr>
</thead>
<tbody>
<tr>
<td>PS-P</td>
<td>15</td>
<td>(t=1.192)</td>
<td>(t=-0.900)</td>
<td>(t=-1.655)</td>
</tr>
<tr>
<td>vs. NK-P</td>
<td>P=0.253 (=)</td>
<td>P=0.383</td>
<td>P=0.120 (=)</td>
<td>P=0.270 (=)</td>
</tr>
<tr>
<td></td>
<td>P'=0.025</td>
<td>P'=0.013</td>
<td>P'=0.010</td>
<td>P'=0.017</td>
</tr>
<tr>
<td>PS-NP</td>
<td>19</td>
<td>(t=-0.053)</td>
<td>(t=0.774)</td>
<td>(t=-0.575)</td>
</tr>
<tr>
<td>vs. NK-NP</td>
<td>P=0.958 (=)</td>
<td>P=0.449 (=)</td>
<td>P=0.572 (=)</td>
<td>P=0.508 (=)</td>
</tr>
<tr>
<td></td>
<td>P'=0.050</td>
<td>P'=0.025</td>
<td>P'=0.025</td>
<td>P'=0.050</td>
</tr>
</tbody>
</table>

Paired t-tests using data from Table 4.9. See Table 4.10 for more details. Note, no equal sign in a non-significant result indicates that this test was significant before.

Recall from the previous analyses, that the comparison among peers revealed that paternal half-siblings tended to groom and approach each other more often than non-kin. When controlled for spatial proximity, paternal half-siblings showed similar rates of affiliation and aggression as non-kin, both among peers and among non-peers. In other words, relative to proximity, paternal half-siblings and non-kin interact with each other at similar rates.

Testing kinship and age proximity simultaneously

Referring to Table 4.9 again, a comparison was made including paternal kinship and age proximity simultaneously in order to investigate whether both parameters interact with each other (Table 4.13).

Table 4.13: Testing kinship and age proximity simultaneously

<table>
<thead>
<tr>
<th></th>
<th>Grooming (_{cp})</th>
<th>Approach (_{cp})</th>
<th>Physical Aggression (_{cp})</th>
<th>Non-physical Aggression (_{cp})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kin (d.f.=1)</td>
<td>F=4.183</td>
<td>F=0.040</td>
<td>F=2.840</td>
<td>F=0.348</td>
</tr>
<tr>
<td>PS vs. NK</td>
<td>P=0.044 (=)</td>
<td>P=0.841</td>
<td>P=0.095 (=)</td>
<td>P=0.556 (=)</td>
</tr>
<tr>
<td>Age (d.f.=1)</td>
<td>F=17.858</td>
<td>F=2.118</td>
<td>F=0.432</td>
<td>F=0.173</td>
</tr>
<tr>
<td>P vs. NP</td>
<td>P&lt;0.001 (=)</td>
<td>P=0.149</td>
<td>P=0.513 (=)</td>
<td>P=0.678 (=)</td>
</tr>
<tr>
<td>Kin*Age (d.f.=1,98)</td>
<td>F=4.686</td>
<td>F=0.276</td>
<td>F=0.795</td>
<td>F=1.161</td>
</tr>
<tr>
<td></td>
<td>P=0.033 (=)</td>
<td>P=0.600 (=)</td>
<td>P=0.375 (=)</td>
<td>P=0.284 (=)</td>
</tr>
</tbody>
</table>

Two-way analysis of variance treating values of grooming, approach, physical and non-physical aggression of the same focal animal with social partners from different classification levels as independent. Values were controlled for spatial proximity. Dyads present either paternal half-siblings (PS) or non-kin (NK) with respect to kinship and either peers (P) or
non-peers (NP) with respect to age. Mean, SD and sample size of the data used in this analyses are shown in Table 4.9.

Controlling for spatial proximity had no effect on grooming which stayed significant when tested for paternal kinship, age and their interaction, but influenced the outcome of other interactions measured. In other words, regardless of whether proximity was controlled for or not, kinship and age proximity interact to regulate grooming frequency between females.

In summary, when controlled for spatial proximity peers still affiliated with each other more than with non-peers. Maternal half-siblings still groomed each other more than either non-kin or paternal half-siblings, and exhibited more non-physical aggression than non-kin.

4. The correlation between affiliation and aggression

Finally, an attempt was made to correlate affiliation with aggression for the three kin categories investigated in this chapter. This comparison was performed to test Alexander’s (1974) suggestion that pairs who are most affiliative are also most aggressive towards each other. The three kin groups will be analysed among non-peers (Table 4.14) and two kin groups among peers (Table 4.15).

Table 4.14: The correlation between affiliation and aggression among non-peers

<table>
<thead>
<tr>
<th></th>
<th>MS-NP (N=34)</th>
<th>PS-NP (N=19)</th>
<th>NK-NP (N=34)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Physical Aggression</td>
<td>Non-physical Aggression</td>
<td>Physical Aggression</td>
</tr>
<tr>
<td>Proximity</td>
<td>rs=0.018</td>
<td>rs=-0.129</td>
<td>rs=0.033</td>
</tr>
<tr>
<td></td>
<td>P=0.920</td>
<td>P=0.467</td>
<td>P=0.894</td>
</tr>
<tr>
<td>Grooming</td>
<td>rs=-0.015</td>
<td>rs=0.125</td>
<td>rs=0.287</td>
</tr>
<tr>
<td></td>
<td>P=0.931</td>
<td>P=0.482</td>
<td>P=0.234</td>
</tr>
<tr>
<td>Approach</td>
<td>rs=-0.084</td>
<td>rs=-0.052</td>
<td>rs=0.339</td>
</tr>
<tr>
<td></td>
<td>P=0.636</td>
<td>P=0.768</td>
<td>P=0.156</td>
</tr>
</tbody>
</table>

Spearman’s rank correlation coefficient between affiliation (proximity, grooming or approach) and aggression (physical or non-physical) among non-peers including maternal half-siblings (MS-NP), paternal half-siblings (PS-NP) or non-kin (NK-NP).

Among non-peers, a correlation between affiliation and aggression was not apparent, neither for maternal half-siblings nor paternal half-siblings, but was evident for non-kin. Females directed significantly more physical aggression to non-kin, the more these females shared spatial proximity with each other. Females also directed more non-physical aggression to non-
kin, the more these females groomed each other. These results revealed a positive relation between affiliation and aggression only among non-kin, not among maternal and paternal kin.

Table 4.15: The correlation between affiliation and aggression among peers

<table>
<thead>
<tr>
<th></th>
<th>PS-P (N=15)</th>
<th>NK-P (N=34)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Physical Aggression</td>
<td>rs=0.590</td>
<td>rs=0.079</td>
</tr>
<tr>
<td>P=0.021</td>
<td>P=0.779</td>
<td>P=0.083</td>
</tr>
<tr>
<td>Non-physical Aggression</td>
<td>rs=0.301</td>
<td>rs=-0.041</td>
</tr>
<tr>
<td>Physical Aggression</td>
<td>rs=-0.096</td>
<td>rs=0.291</td>
</tr>
<tr>
<td>Grooming</td>
<td>rs=0.431</td>
<td>rs=0.064</td>
</tr>
<tr>
<td>P=0.109</td>
<td>P=0.735</td>
<td>P=0.094</td>
</tr>
<tr>
<td>Non-physical Aggression</td>
<td>rs=0.309</td>
<td>rs=0.053</td>
</tr>
<tr>
<td>Approach</td>
<td>rs=0.592</td>
<td>rs=0.821</td>
</tr>
<tr>
<td>P=0.020</td>
<td>P=0.821</td>
<td>P=0.766</td>
</tr>
</tbody>
</table>

Spearman’s rank correlation coefficient between affiliation (proximity, grooming or approach) and aggression (physical or non-physical) among peers being either paternal half-siblings (PS-P) or non-kin (NK-P).

Among peers, paternal half-siblings directed significantly more physical aggression towards each other, the more they shared spatial proximity or approached each other. Maternal half-siblings could not be analysed because they are not peers (see Methods). Unrelated peers showed no association between affiliation and aggression.

In summary, the results revealed no correlation between affiliation and aggression among maternal half-siblings. Although maternal half-siblings exhibited the highest frequency of both affiliation and aggression, these measurements did not correlate with each other. In other words, some focal females showed high levels of affiliation, but not of aggression, towards their maternal half-siblings, while other focal females showed high levels of aggression, but not of affiliation, towards their maternal half-siblings. The data support Alexander’s hypothesis (1974) that high affiliative individuals are also engaged in a high level of aggression, but only among some kinship and age categories.

**Discussion**

The results of this chapter confirm that the closest social bonds among adult female rhesus macaques follow maternal relatedness. Maternal half-siblings are both more affiliative and aggressive towards each other than either paternal half-siblings or non-kin. The present study also provides the first evidence that both paternal relatedness and age proximity exert a significant impact upon affiliation patterns among adult female rhesus macaques. Paternal
half-siblings prefer to affiliate with each other in comparison with non-kin, but patterns of aggressive activity show no kin discrimination according to paternal relatedness. Among paternal half-siblings, rates of affiliation, but not of aggression, increased with decreasing age difference whereas among unrelated females neither patterns of affiliation nor aggression were influenced by exact age difference. Among maternal half-siblings, increasing age difference had no impact on patterns of aggressive interactions, but decreasing exact age differences were associated with significant decreases in rates of approach. Data of this study demonstrate that (i) adult female rhesus macaques are capable of discriminating between paternal kin and non-kin, with kin discrimination more pronounced among peers than among non-peers and inversely related to age proximity, (ii) paternal kin discrimination is context-dependent because it is exhibited during affiliative, not aggressive, interactions, (iii) kin discrimination is asymmetric because maternal and paternal half-siblings interact differently, and (iv) both familiarity and phenotype matching probably drive kin discrimination in rhesus macaques. These points will now be discussed in more detail.

Peer effect

The bias towards peers in both affiliation and aggression (hereafter: peer effect) was already described among immature rhesus macaques for both sexes (Janus 1991, 1992). Peers were more affiliate and more aggressive towards each other than non-peers. Strong affiliative partners also exhibit more aggression, but aggression directed towards strong affiliate partners was less severe (ibid.). This suggests that familiarity not only favours affiliation, as aggression among age mates may reflect that they compete for the same resources at the same time in their life. In another study on the same population as studied here, Colvin & Tissier (1985) distinguished between strong and weak relationship of 3-year-old male rhesus macaques with strong peer relations defined as those in which each partner was involved for more than 15% of the total peer proximity and with reciprocity among strong but not among weak peer relations. However, paternity was not available in this earlier study, but paternal kinship was also not suggested as a likely explanation for the differences found between strong and weak peer relations.

Evidence for a peer effect has also been found in other species. Play among Japanese macaques was most frequently observed between peers at the age of one (Koyama 1985). In general, play was observed more often than expected among age mates until the age of 4 years, but also among individuals with disparity of age less than one year (Koyama 1985). Familiarity among play mates could influence mating decisions as adults. Alberts (1999) found among savanna baboons that peers were less likely to be engaged in sexual consort than
non-peers, suggesting that familiarity could result in mating avoidance. Additional support for my findings comes from Smith (2000), studying the same baboon population as Alberts. Smith (2000) found that unrelated peers are more affiliative than unrelated non-peers. These studies support the hypothesis that familiarity among individuals can arise through association in early development by at least two alternatives: (i) mothers mediating familiarity among her offspring (which are maternal half-siblings) and (ii) age proximity is mediating familiarity among age mates (including both paternal related and unrelated peers) which spend more time together than individuals of different ages do due to the formation of play groups among peers.

It should be emphasised that familiarity among peers cannot explain why paternally related peers are more affiliative than unrelated peers. In other words, as both groups of individuals are likely to be familiar to a similar extent, the higher frequency of affiliation among paternal half-sisters than among unrelated females must have been evolved through a different mechanism than familiarity. Controlling for the age differences this test was indeed restricted to compare different degrees of genetic relatedness. Smith (2000) noted that being similarly aged has two important consequences in promoting familiarity. First, barring death and group fission, female peers are likely to interact their entire lives (especially in species where females do not leave their natal group), while very different aged individuals do not. Second, female peers go through important life history stages at similar times, e.g., infancy, menarche, pregnancy, motherhood, while differently-aged females do not. This applies to all age cohort members, regardless of the variation in relatedness.

The behavioural differences found between paternal sisters and non-kin of different ages (non-peers) were not very clear comparing single behaviours, as the only significant difference found was that paternal half-siblings approached each other more other than non-kin. In contrast, combining affiliative measurements to a single affiliation index (cf. Widdig et al. 2001) there was a significant differences found between peers and non-peers. The advantage of using single behaviours is that they can show context-dependent kin discrimination (cf. Widdig et al. 2002) whereas the advantage of using an affiliation index is that it can reveal general patterns of behaviour. The less pronounced differences found among non-peers might be due to the fact that the non-peer category include individuals of multiple ages, i.e., unrelated non-peers varied in age between 1-10 years, while paternal sisters being non-peers varied in age between 1-3 years (with the exception of one pair of paternal half-siblings being 4 years apart in age). Therefore the exact age difference was used showing that affiliation is increasing the closer paternal half-siblings are in age, but the reverse effect
appeared for maternal half-siblings, affiliation decreased the closer they are in age. However, unrelated females show no association between exact age difference and affiliation.

*Context-dependent kin discrimination*

Another important result from the present study is that female rhesus macaques bias their behaviour towards paternal half-siblings, but they did so in only some contexts, e.g., affiliation and not aggression. Context-dependent kin discrimination (Waldman et al. 1988, Barnard & Aldhous 1991, Sherman et al. 1997) was reported among other vertebrates. For example, spadefoot toad tadpoles, *Scaphiopus bombifrons*, occur in two morphs with omnivores preferentially associating with siblings and carnivores preferentially associating with non-siblings (Pfennig et al. 1993). Carnivores avoid eating kin, but they become less selective when hungry, suggesting that their level of kin discrimination is context-dependent (ibid.). While female white-footed mice, *Peromyscus leucopus*, prefer the odour of males of intermediate relatedness when they are in oestrus, non-oestrus females show no preference (Keane 1990). In savanna baboons Alberts (1999) found that pairs of paternal brothers and sisters were just as likely to be in sexual consort as unrelated pairs, but consorts of paternal half-siblings were less affiliative and sexual than that of non-kin. In the same baboon population Smith (2000) reported that paternal half-sisters of different age groomed each other more than unrelated females of different age, but no distinction was found with respect to the nearest neighbour while resting.

Kin discrimination seems to be detected only when behaviours most linked to fitness are examined under relevant conditions. For example, studies on prairie voles, *Microtus ochrogaster*, had found a breakdown of incest avoidance after 8-15 days of sibling isolation, but a re-evaluation using amicable and agonistic interactions of same sex individuals suggested that sibling recognition is still present when isolation was less than 20 days (Paz y Mino & Tang-Martinez 1999). Again, this emphasises the importance of studying multiple behaviours under different conditions. However, Paz y Mino & Tang-Martinez (1999) suggested from their findings that kin recognition can be detected at different time intervals using different approaches. The current finding that affiliation, not aggression, is associated with kin discrimination in adult female rhesus macaques would be expected if co-operative interactions had a greater impact on fitness than competitive interactions (Jolly 1999).

*Asymmetry in behaviour between maternal and paternal half-siblings*

The data of the present study show a strong asymmetry in both affiliation and aggression between maternal and paternal half-siblings in favour of the former even though they share on
average the same degree of relatedness. Given that maternal half-sibling are of adjacent rank whereas paternal half-sibling and non-kin may considerably vary in dominance rank (unpubl. data), the bias towards maternal kin may be a by-product of the attraction to similar ranking females as suggested by de Waal (1991), Kapsalis & Berman (1996a,b) and Chapais et al. (1991, 1994). Silk also noted (2001) that paternal kinship may play a less salient role than maternal kinship because there is always some degree of uncertainty about paternity. In addition, because male reproductive skew is fare from being perfect sharing the same peer group does not necessary mean that individuals also share the same sire.

However, the only study available which also compares maternal half-siblings vs. paternal half-siblings and paternal half-siblings vs. non-kin is the one on wild baboons in Amboseli by Smith (2000) using similar affiliative measurements as my study. Like the present study female baboons also exhibit paternal kin discrimination, as paternal half-sister affiliate more with each other than non-kin. However, in contrast to the present study, baboons did not differentiate between maternal and paternal half-sisters, as they were equally likely to affiliate. Interestingly, in one measurement (total number of counts of affiliation) paternal half-siblings directed more affiliation towards each other than maternal half-siblings, i.e., the opposite trend than found in the present study. There are at least two demographic explanations for the difference between the baboon and the rhesus study. First and probably most important, Smith also found a bias towards peers, but she did not distinguish peers from non-peers. In other words, she did not control for age when testing kinship between maternal and paternal half-siblings probably due to limited sample size. This adds familiarity through peerage to genetic relatedness in the case of paternal half-siblings which maternal half-siblings, typically of different ages, are missing. Second, Chapais (2001) noted that kin-bias should strongly be affected by the number of kin per kin classes. Thus population difference may be responsible for the discrepancy, as Smith pooled data over three small group with paternal half-sisters being equally distributed among groups, but a single family from one group disproportionately contributed data for maternal half-sibling. The number of maternal half-siblings per individual was also much higher in the present study than in the baboon study. However, Smith herself pointed out some confounding factors that may influence her analyses as the relative proportion of close kin to non-kin, i.e., the female with the highest frequency of grooming found for all pairs of paternal half-sisters had no maternal kin in the group and in addition her paternal half-sister was the only peer in the group. In contrast, the present study used always paired tests, meaning that each focal female had at least one kin per kin class tested.
Mechanisms of kin recognition

One prerequisite for kin selection is that individuals have the ability to discriminate between kin and non-kin (Grafen 1990). As outlined above, kin discrimination among primates is most likely to arise by one of the two following mechanisms. First, individuals learn the phenotypes of related individuals during early development and later discriminate these familiar relatives from unfamiliar individuals, i.e., familiarity due to prior association (Walters 1987, Tang-Halpin 1991). Second, individuals learn their own phenotypes and/or those of their familiar kin, and later compare or match the phenotypes of unknown individuals with this learned template, i.e., phenotype matching (Holmes & Sherman 1983, Lacy & Sherman 1983). Unfortunately, phenotype matching is often used as a proxy for genetic mechanisms, and familiarity denotes learning processes and some studies did not separate familiarity and relatedness. For example, recent work by Tang-Martinez (2001) suggests to combine familiarity via association and phenotype matching to one mechanism as both are based on learning. However, it is still under discussion whether these two mechanisms are mutually exclusive or overlapping (Heth et al. 1998). Although both mechanisms involve a comparison between encountered phenotypes and recognition templates, familiarity leads to recognition of previously encountered familiar individuals, whereas phenotype matching permits recognition of unfamiliar kin, through generalisation of learned templates (Holmes & Sherman 1982, Sherman et al. 1997). This distinction suggested to Mateo (2002) has implications for the evolution of kin-directed behaviours because phenotype matching permits more refined kin-differentiated behaviour than familiarity. Hamilton himself (1964, p. 22) proposed that one possible mechanism mediating kin selection could be “familiarity of appearance…being (that) relatives must tend to look alike…”. Heth et al. (1998) have expanded this concept by noting that association patterns during ontogeny, i.e., familiarity, could be the critical variable fostering phenotype matching mechanisms. It seem possible that familiarity and phenotype matching can be alternative mechanisms under some conditions as suggested by Heth et al. (1998), but the data of the present study suggest that paternal kin discrimination arises from an interaction between familiarity and phenotype matching that is expressed in an asymmetric, context-dependent fashion. In other words, the primary mechanisms used for paternal kin discrimination is familiarity through peerage and that phenotype matching is used to distinguish paternal half-siblings from non-kin.

The most frequently mentioned mechanism of kin recognition across species is phenotype matching, which depends upon comparing shared traits within a lineage to a reference template using visual, vocal or olfactory cues (Holmes & Sherman 1983, Lacy & Sherman
Mechanisms of kin discrimination are probably not identical across species. Differences are to be expected because recognition mechanisms must function within the confines set by a species phylogenetic history and reflect key sensory modalities used in communication, as well as mating and demographic structure. Co-operation between adult female rhesus macaques seems to be promoted by paternal kinship, but the mechanisms underlying paternal kin discrimination found in this study remain unknown.

One possible explanation could be that females nurture co-operation among their patrilineally related offspring by encouraging infants to play with offspring of females who have mated with the same male. Maternal affiliation patterns partly drive the development of infant affiliation patterns among peers (Berman & Kapsalis 1999) so that, if mothers who have conceived infants from the same male were closely associated, their offspring could develop affiliations with same-age paternal relatives. The hypothesis of maternal behavioural cues was tested by comparing mothers who were unrelated non-peers, but whose infants were either same-age paternal half-siblings or same-age non-kin. In the study population, however, mothers of paternal half-siblings who were peers had proximity scores similar to mothers of non-kin peers, as no difference emerged from these two sets of mothers (mean proximity per hour (± SE) between mothers of same-age paternal half-siblings 0.464 ± 0.065 vs. mothers of non-kin peers 0.451 ± 0.027, paired t=-0.233, d.f. 15, P=0.819). Therefore, mothers do not appear to mediate affiliation between their infants as a function of shared paternity. Instead, adult females tend to associate with their own kin and/or peers regardless of the identity of the sire of their offspring.

A second possible explanation for paternal kin discrimination could be that dominance rank influences affiliation patterns. In rhesus macaques, as in other cercopithecine primates, maternal half-sisters do not only affiliate with each other at high rates, but tend to occupy adjacent dominance ranks within a troop (Chapais & Schulman 1980). In order to test whether dominance rank was a confounder in the analysis, the mean rank difference between focal females and their paternal half-siblings was compared with the mean rank difference between focal females and their non-kin, controlling for age proximity. No significant differences in mean rank difference were observed, neither for peers (mean rank difference (± SE) between paternal half-siblings=33 ± 5 vs. non-kin=32 ± 3, Wilcoxon-test, z=-0.031, d.f. 14, P=0.987) nor for non-peers (paternal half-siblings=35 ± 3 vs. non-kin=32 ± 1, Wilcoxon-test, z=-0.322, d.f. 18, P=0.748). However, including all females in the analysis could bias results if younger females were dependent in rank upon their mothers. In order to control for this potential bias,
the analysis was repeated by excluding younger females for which the social rank could still be dependent upon their mothers’ rank (N=42). Of the nineteen focal subjects with paternal half-sibling, non-peers, three of them were removed from the analysis because all of their paternal siblings were immature animals. Results remained consistent with no significant differences noted, neither among peers (mean rank difference (± SE) between focal and paternal half-siblings=18 ± 3 vs. 17 ± 1 for non-kin, Wilcoxon-test, z=-0.114, d.f. 14, P=0.934) nor among non-peers (paternal half-siblings=20 ± 2 vs. non-kin=18 ± 1, Wilcoxon-test, z=-0.724, d.f. 15, P=0.469). In conclusion, although paternal half-siblings and non-kin had a similar rank in relation to the focal females, the latter still affiliated more with paternal half-sisters than non-kin, implying that differences in affiliation are unlikely to be caused by differences in relative dominance rank.

A third explanation for paternal kin discrimination could be that the differences found between paternal half-siblings and non-kin are due to differences in age proximity among peers. Recall from the Methods that individuals born into the same birth season, i.e., peers can be born on the same day or up to 6 months apart. Comparing the mean birthdate difference between peers revealed the opposite trend. Peer non-kin were actually closer in age to each other than peer paternal half-siblings (mean birthday difference in days (± SE) between peer paternal half-siblings=45 ± 7 vs. peer non-kin=33 ± 6, paired t=2.199, d.f. 14, P=0.045). Therefore, the preference of paternal half-siblings for each other within the peer group is not a consequence of close proximity of date of birth.

A fourth explanation for paternal kin discrimination could be phenotype matching, using shared characteristics within lineages, such as appearance, odour, or vocalisations, against a reference template (Holmes & Sherman 1983, Lacy & Sherman 1983, Tang-Halpin 1991, Dawkins 1982, Blaustein et al. 1987a,b). The data presented here are compatible with the phenotype matching hypothesis because paternal kin discrimination was most pronounced among peers, but was still trendy among non-peers. However, phenotype matching cannot account for the preference of peers over non-peers (peer effect), and the observed interaction between kinship and age proximity suggests that familiarity among age mates also contributes to paternal kin discrimination.

Given the crucial importance of vision among cercopithecine primates, the most likely sensory mechanism presenting cues for phenotype matching is visual recognition, as suggested for chimpanzees by Parr & de Waal (1999). However, in contrast to chimpanzees, Old World monkeys have consistently failed mirror self-recognition tests (Gallup 1997, De Veer & van den Bos 1999) and long-tailed macaques, M. fascicularis, do not seem to perceive
physical resemblance between relatives (Dasser 1988). Furthermore, for the age proximity effect to be regulated by visual cues, adult females would need to be able to distinguish same-age peers from those who are a couple of years older or younger than themselves. Therefore, it seems to be unlikely that paternal kin discrimination in rhesus macaques is visually-mediated.

Among rodents, olfactory cues have been implicated in kin discrimination (e.g., Todrank et al. 1998, Mateo & Johnston 2000). New World monkeys scent mark and discriminate both sex and reproductive state of conspecifics (e.g., Converse et al. 1995, Smith & Abbott 1998), but Old World monkeys do not scent mark and have a poorly developed olfactory sense (Martin 1990). Most olfactory inspection among rhesus macaques occurs when males sniff the anogenital region of females (Bercovitch, pers. comm.), but sniffing is not necessary to perceive odour. Olfactory cues among mice are used to detect dissimilarity in the major histocompatibility complex (MHC) region as a means of mate choice (Yamazaki et al. 1976) and humans prefer the odour of MHC-dissimilar individuals (Wedekind et al. 1995, Wedekind & Füri 1997). However, unlike the situation with house mice, no reproductive advantage was found in the same population studied here as dissimilar and similar mates in terms of MHC type (Mamu-DQB locus) were equally likely to be found, even though heterozygous males overall sired more offspring than homozygous males (Sauermann et al. 2001). It seems unlikely that females adjust social behaviour with female conspecifics according to MHC type when their reproductive success is not dependent upon adjusting mating behaviour according to MHC type. However, inbreeding avoidance may still be an outcome of kin recognition that is depended upon other MHC loci and olfactory discrimination can still regulate female social relationship, even though self-recognition by odour has not yet been shown in rhesus macaques.

Auditory cues provide signals indicating maternal relatedness in both rhesus macaques (Hauser 1996, Rendall et al. 1996) and Savannah baboons (Cheney & Seyfarth 1999). However, in these species matrilineal relatedness corresponds with familiarity (Grafen 1990) and these studies did not separate maternal unrelated individuals into paternal kin and non-kin. For vocal cues to mediate kin discrimination among adult females, they would need to match paternal half-sibling utterances to self utterances, and distinguish them from non-kin calls, but auditory matching to self is difficult because the sounds emitted by an individual are perceived differently by the sender than they are by the receiver. Again, paternal kin discrimination in rhesus macaques seems therefore to be unlikely for mediating via auditory channels.
In conclusion, in the case of paternal kin discrimination discussed here, individual A is interacting more with (paternal half-sibling) B than with (non-kin) C, which must involve a self-referential phenotype matching system. No studies of non-human primates have yet examined prospects for matching-to-self in either the auditory or olfactory realms, and a “phylogenetic gap” between monkeys and apes is apparent in the visual realm because the former fail to display self-recognition (de Veer & van den Bos 1999, Hauser et al. 2001). Hence, although the most likely sensory modality mediating kin discrimination in rhesus macaques is vision, unless this species is capable of matching-to-self, then phenotype matching using visual cues cannot explain the current findings. Heth et al. (1998) proposed that self-referential phenotype matching provides the best means for guiding kin discrimination, but no solid evidence for such a process exists among non-hominoid primates.

As a result of the present study a novel mechanism of phenotype matching in primates was suggested (Widdig et al. 2001). We hypothesise that phenotype matching in rhesus macaques, and other cercopithecine species, is guided by behavioural traits, such as personality and temperament rather than by morphological or physiological attributes. Non-human primates develop and display distinct personality profiles (Clarke & Boinski 1995, Bolig et al. 1992, Sapolsky & Ray 1989). In rhesus macaques, some personality traits, such as increased impulsivity and aggressiveness, are closely associated with diminished concentrations of cerebrospinal fluid monoamine metabolites, which have a significant paternal genetic component (Higley et al. 1993, Clarke et al. 1995) and are fairly stable throughout life (Higley et al. 1996, Stevenson-Hinde et al. 1980). About 30-50% of the variance in personality traits among people is thought to be due to genetic factors (Kagan 1994, Loehlin 1992). Hence, shared paternally inherited personality attributes could be modulating social relationships and provide a mechanism fostering behavioural phenotype matching. One prediction of this hypothesis is that if individuals choose social partners on the basis of age and personality traits, and if these traits are partly determined by paternal genes, then preferred social partners will share paternity and age proximity more often than expected by chance alone. Comparing the relatedness and personalities of playmates within and across cohorts should be the next step in testing this hypothesis.

**Summary**

Paternal kin discrimination influences the structure of social relationships in female rhesus macaques as a function of both age proximity and shared paternity. It is proposed that paternal relatedness and age proximity regulate the development of social relationships through an ontogenetic process of phenotype matching using behavioural cues modulated by inherited
personality traits. In cercopithecine primates both mating and social preferences could be a function of paternal kinship and age proximity acting via a mechanism involving personality phenotype matching. Baboons tend to avoid mating with paternal kin of the same cohort (Alberts 1999), and rhesus macaques prefer associating with paternal kin of the same age (this study). The proposed mechanism for paternal kin discrimination suggests that fitness consequences resulting from kin selection favouring nepotism (Hamilton 1967, West Eberhard 1975) and mate selection favouring inbreeding avoidance share a common foundation. In both circumstances, female reproductive success is maximised through the development of kin recognition devices that emerge during ontogeny when females develop the capacity to match their own personality template with that of conspecifics who share the same sire. Kin discrimination in primates is expressed in a context-dependent fashion with those behaviours most relevant to reproductive success the ones that extract the expression of kin discrimination.
5. Relatedness threshold and the degree of relatedness

Introduction
Sociality reflects a balance between co-operation and competition (Alexander 1974, Silk 1987, Walters & Seyfarth 1987). Kinship has had an important effect on the structure of social relationships among primates, especially in female-bonded groups with male dispersal (Gouzoules & Gouzoules 1987). Maternal kinship in primates frequently coincides with proximity patterns and a higher frequency of grooming with grooming being reciprocal among kin (e.g., Kurland 1977, Gouzoules & Gouzoules 1987, Kapsalis & Berman 1996a, reviewed by Dugatkin 1997). Relatives tolerate each other more often at feeding sites than non-kin (Kawai 1958, Stewart & Harcourt 1987, Pastor-Nieto 2001, Belisle & Chapais 2001.) and food sharing is more common among kin than among non-kin (Goodall 1968, Silk 1978, 1979). Female primates also prefer to support their kin in aggressive interactions against non-kin and take more risk on behalf of close kin (e.g., Kurland 1977, Kaplan 1977, 1978, Massey 1977, Walters 1980, Silk 1982, Bernstein & Ehardt 1985a, reviewed in Gouzoules & Gouzoules 1987). On the other hand, agonistic interactions of immature rhesus monkeys are more frequent among strongly affiliated partners (i.e., maternal half-siblings) than among weakly affiliated partners (i.e., non-siblings) (Janus 1991). Female relatives do not refrain from acting aggressively toward kin, and are often disproportionately more aggressive towards maternal kin than non-kin (Kurland 1977; Bernstein & Ehardt 1986a), but Silk et al. (1981) found that female bonnet macaques, *M. radiata*, direct more severe aggression towards non-kin than towards kin.

Although there is a lot of evidence that primates bias their social behaviour towards their (maternal) kin, less is known about how this bias varies with the degree of relatedness between individuals. Some scientists have suggested that kin bias might decrease proportionally with the degree of relatedness and in addition, a relatedness threshold may be expected under which distant kin are treated like unrelated individuals (Chapais et al. 1997). Others have suggested that the distribution of social behaviour may asymptotically decrease with the degree of relatedness, as it pays more to give as much as possible to the closest kin to gain the highest possible benefit as predicted from the probability theory (S. Altmann 1979). However, data from the same population as studied here, suggest that adult female rhesus macaques behave preferentially toward close maternal kin compared to distant maternal kin,
but do not discriminate between distant maternal kin \((r<0.125)\) and non-kin, suggesting that a relatedness threshold limits nepotism (Kapsalis & Berman 1996a). Among captive Japanese macaques, mothers and sisters supported their daughters and younger sisters to outrank peers (Chapais 1988a). Likewise, in the presence of their grandmother, granddaughters were able to outrank all dominant peers, but in the presence of their aunt, nieces were not. These results also point to a relatedness threshold for effective nepotistic aiding above the aunt–niece level of relatedness (again \(r<0.125\)) (Chapais et al. 1997). In addition, Japanese macaque great-grandmothers support great-grandsons more often than aunts support nephews, despite identical levels of relatedness (Chapais et al. 2001) indicating that kin category in addition to the degree of relatedness modifies primate behaviour. Again, nothing is known about the degree of relatedness with respect to paternal kinship.

One means of examining more precisely how relatedness affects affiliative and agonistic interactions is to scrutinise the role of both paternal and maternal relatedness, given that offspring are equally related to their mothers as to their fathers. Establishing the role of paternal kinship is problematic because females tend to mate with multiple males. Therefore, this chapter aims to investigate the effect of the degree of relatedness on affiliation and aggression among a wider range of relatedness for both maternal and paternal kinship than presented in the previous chapter. The existence of a relatedness threshold will be tested and a comparison will be made between individuals who share the same degree of relatedness but belong to a different kin category (e.g., dyads of maternal half-siblings vs. grandmother-granddaughter). Finally, data on both kin lineage will be compared.
Results

1. **Testing the effect of the degree of relatedness on affiliation and aggression**

Table 5.1 shows data on affiliation and aggression for a number of kinship categories (see Methods) which were restricted to non-peer dyads in order to control for familiarity among peers which has been demonstrated in the previous chapter.

Table 5.1: The effect of degrees of relatedness on affiliation and aggression in different kin categories

<table>
<thead>
<tr>
<th>r</th>
<th>N</th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>MD</td>
<td>0.5</td>
<td>32</td>
<td>6.060 ± 2.112</td>
<td>2.070 ± 0.978</td>
<td>3.896 ± 1.281</td>
<td>1.117 ± 0.151</td>
</tr>
<tr>
<td>MS</td>
<td>0.25</td>
<td>34</td>
<td>2.117 ± 1.087</td>
<td>0.372 ± 0.301</td>
<td>1.581 ± 0.754</td>
<td>0.017 ± 0.022</td>
</tr>
<tr>
<td>MGMD</td>
<td>0.25</td>
<td>10</td>
<td>1.437 ± 1.194</td>
<td>0.446 ± 0.456</td>
<td>1.109 ± 0.895</td>
<td>0.021 ± 0.036</td>
</tr>
<tr>
<td>MAN</td>
<td>0.125</td>
<td>34</td>
<td>0.927 ± 0.480</td>
<td>0.095 ± 0.156</td>
<td>0.645 ± 0.345</td>
<td>0.010 ± 0.017</td>
</tr>
<tr>
<td>MGAN</td>
<td>0.0625</td>
<td>25</td>
<td>0.510 ± 0.331</td>
<td>0.031 ± 0.077</td>
<td>0.349 ± 0.193</td>
<td>0.006 ± 0.014</td>
</tr>
<tr>
<td>MC</td>
<td>0.0625</td>
<td>28</td>
<td>0.488 ± 0.310</td>
<td>0.020 ± 0.025</td>
<td>0.352 ± 0.168</td>
<td>0.004 ± 0.007</td>
</tr>
<tr>
<td>PS</td>
<td>0.25</td>
<td>19</td>
<td>0.450 ± 0.302</td>
<td>0.012 ± 0.026</td>
<td>0.308 ± 0.160</td>
<td>0.002 ± 0.007</td>
</tr>
<tr>
<td>PAN</td>
<td>0.125</td>
<td>19</td>
<td>0.352 ± 0.274</td>
<td>0.029 ± 0.065</td>
<td>0.258 ± 0.243</td>
<td>0.001 ± 0.003</td>
</tr>
<tr>
<td>NK</td>
<td>~0.0</td>
<td>34</td>
<td>0.350 ± 0.111</td>
<td>0.011 ± 0.007</td>
<td>0.232 ± 0.054</td>
<td>0.003 ± 0.002</td>
</tr>
</tbody>
</table>

Cell values are mean frequencies per hour (± SD) for proximity, grooming, approach, physical or non-physical aggression. Abbreviations are as follows: dyads of mother-daughters (MD), maternal half-siblings (MS), maternal grandmother-granddaughters (MGMD), maternal aunt-nieces (MAN), maternal grandaunt-grandnieces (MGAN), maternal cousins (MC), paternal half-siblings (PS), paternal aunt-nieces (PAN), non-kin (NK), degree of relatedness (r), sample size (N). Data were based on all of the 34 focal females who had at least one kin in a specified kin class, e.g., 32 out of the 34 females had a mother-daughter relation, 10 out of 34 females had a grandmother-granddaughter relation etc. All categories include only data for female non-peer dyads to control for familiarity among peers. Dyads that fit in more than one category (e.g., being paternal half-siblings and maternal aunt-niece) were excluded in all analyses.

Not surprisingly, the highest rates of affiliation were found in mother-daughter dyads, while the lowest rates occurred among non-kin. There is a proportional decrease with degree of relatedness among maternal and paternal kin, even though values of paternal kin were always
lower than the equivalent maternal degree of relatedness. Note, some paternal cousins existed in the study group, but as these females were not adults they were not focal subjects.

Data from Table 5.1 were tested for a possible correlation between degree of relatedness and frequency of affiliation or aggression respectively. From kin selection theory (Hamilton 1964) one predicts that an increase in the degree of relatedness will result in an increase in affiliation and a decrease in aggression. Spearman’s rank correlation coefficient is presented in Table 5.2 using only maternal degrees of relatedness introduced in Table 5.1, because just two paternal degrees of relatedness were available.

Table 5.2: Correlation between various maternal degrees of relatedness and affiliation or aggression, respectively

<table>
<thead>
<tr>
<th>Maternal kin</th>
<th>N</th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maternal kin</td>
<td>163</td>
<td>$r_s=0.840$</td>
<td>$r_s=0.844$</td>
<td>$r_s=0.860$</td>
<td>$r_s=0.413$</td>
<td>$r_s=0.352$</td>
</tr>
<tr>
<td></td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
</tr>
</tbody>
</table>

Spearman’s rank correlation coefficient ($r_s$) between various maternal degrees of relatedness and affiliation or aggression, respectively. Data were the same presented in Table 5.1 using only non-peers. N is the number of focal females tested treating the same focal female with social partners from different kin categories as independent.

The maternal degree of relatedness was significantly associated with the frequency of affiliation and aggression in such a way that there was an increase in affiliation the closer females were related, but different from what was expected, there was also an increase in aggression the closer females were related.

2. Testing the relatedness threshold concept on affiliation and aggression

Table 5.3 presents data testing the relatedness threshold concept. This concept predicts that distant kin and non-kin are treated alike below a certain degree of relatedness. Furthermore, it supposes that depending upon the cost-benefit ratio different behaviours may differ in respect to their relatedness threshold.
Table 5.3: Testing the relatedness threshold concept on affiliation and aggression

<table>
<thead>
<tr>
<th>Kin class</th>
<th>R</th>
<th>N</th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>MGAN vs. NK</td>
<td>0.52</td>
<td>25</td>
<td>t=-3.044</td>
<td>t=-1.413</td>
<td>t=-3.183</td>
<td>t=-1.318</td>
<td>t=-1.046</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P=0.006</td>
<td>P=0.171</td>
<td>P=0.004</td>
<td>P=0.200</td>
<td>P=0.306</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P'=0.006</td>
<td>P'=0.009</td>
<td>P'=0.009</td>
<td>P'=0.009</td>
<td>P'=0.017</td>
</tr>
<tr>
<td>MC vs. NK</td>
<td>0.06</td>
<td>28</td>
<td>t=-2.773</td>
<td>t=-2.073</td>
<td>t=-4.111</td>
<td>t=-0.948</td>
<td>t=-2.384</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P=0.010</td>
<td>P=0.048</td>
<td>P&lt;0.001</td>
<td>P=0.351</td>
<td>P=0.024</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P'=0.007</td>
<td>P'=0.006</td>
<td>P'=0.007</td>
<td>P'=0.013</td>
<td>P'=0.006</td>
</tr>
<tr>
<td>PAN vs. NK</td>
<td>0.12</td>
<td>19</td>
<td>t=0.101</td>
<td>t=-1.103</td>
<td>t=-0.599</td>
<td>t=3.112</td>
<td>t=1.632</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P=0.921</td>
<td>P=0.284</td>
<td>P=0.557</td>
<td>P=0.005</td>
<td>P=0.120</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P'=0.050</td>
<td>P'=0.013</td>
<td>P'=0.025</td>
<td>P'=0.005</td>
<td>P'=0.010</td>
</tr>
<tr>
<td>PS vs. PAN</td>
<td>0.25</td>
<td>14</td>
<td>t=-3.466</td>
<td>t=-1.140</td>
<td>t=-5.005</td>
<td>t=0.012</td>
<td>t=-2.061</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P=0.004</td>
<td>P=0.275</td>
<td>P=0.001</td>
<td>P=0.991</td>
<td>P=0.060</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P'=0.006</td>
<td>P'=0.010</td>
<td>P'=0.006</td>
<td>P'=0.050</td>
<td>P'=0.007</td>
</tr>
</tbody>
</table>

Testing the relatedness threshold concept on affiliation and aggression using paired t-tests between kin groups of various degree of relatedness. Data and abbreviations are from Table 5.1, but include only matched samples, i.e., focal females who had a kin in both test groups. P' represents the Dunn-Šidák correction for multiple testing undertaken for 10 simultaneous tests, i.e., per single behaviour for Table 4.2-4.4 chapter 4 and Table 5.3-5.4 this chapter (see Methods). Recall from the Methods that only P-values less than or equal to the corrected P-value (P') indicate a significant test result which will be marked in bold.

Maternal grandaunt-grandniece dyads (r=0.0625) had higher rates of proximity and approach, but not of grooming, than non-kin dyads (r~0.0). No difference between them was found for aggressive interactions. Maternal cousins (r=0.0625) differed in approach from non-kin (r~0.0), with a trend evident in proximity, grooming and non-physical aggression. Paternal aunt-niece dyads (r=0.125) showed similar rates of affiliative interactions, but significantly less physical aggression, than non-kin (r~0.0). In addition, it was tested whether paternal half-siblings differ in their behaviour from paternal aunt nieces, as predicted by the higher degree of relatedness. Indeed, paternal half-siblings (r=0.25) exhibited higher rates of proximity and approach, and tended to express less non-physical aggression, than paternal aunt-nieces (r=0.125).
3. **Testing the effect of different kin categories on affiliation and aggression controlling for degree of relatedness**

A comparison will be made between individuals who share the same degree of relatedness but belong to different kin categories (Table 5.4). For example, dyads of maternal grandmother-granddaughters and dyads of maternal half-siblings both share on average 0.25 of their genes, but the former are direct descendants (direct line) while the latter are collateral kin (cf. Chapais *et al.* 2001). As a second example, dyads of maternal grandaunt-grandniece and maternal cousins both share on average 0.0625 of their genes, but both are collateral kin.

Table 5.4: The effect of kin category on affiliation and aggression

<table>
<thead>
<tr>
<th>Kin class</th>
<th>r</th>
<th>N</th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>MGMD</td>
<td>both</td>
<td>10</td>
<td>t=1.323</td>
<td>t=-0.248</td>
<td>t=-0.155</td>
<td>t=-1.057</td>
<td>t=2.202</td>
</tr>
<tr>
<td>vs. MS</td>
<td>0.25</td>
<td></td>
<td>P=0.219</td>
<td>P=0.810</td>
<td>P=0.154</td>
<td>P=0.318</td>
<td>P=0.055</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P’=0.010</td>
<td>P’=0.025</td>
<td>P’=0.017</td>
<td>P’=0.010</td>
<td>P’=0.006</td>
</tr>
<tr>
<td>MGAN</td>
<td>both</td>
<td>22</td>
<td>t=-0.288</td>
<td>t=-1.060</td>
<td>t=-0.373</td>
<td>t=-0.789</td>
<td>t=0.059</td>
</tr>
<tr>
<td>vs. MC</td>
<td>0.0625</td>
<td></td>
<td>P=0.776</td>
<td>P=0.301</td>
<td>P=0.713</td>
<td>P=0.439</td>
<td>P=0.954</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>P’=0.025</td>
<td>P’=0.017</td>
<td>P’=0.050</td>
<td>P’=0.017</td>
<td>P’=0.050</td>
</tr>
</tbody>
</table>

The effect of kin category on affiliation and aggression using paired t-tests between different kin categories who share the same degree of relatedness. Data and abbreviations are from Table 5.1, but include only matched samples, i.e., focal females who had a kin in both test groups. P’ represents the Dunn-Šidák correction for multiple testing (see Methods).

Both comparisons reveal that kin category (neither direct vs. collateral nor collateral vs. collateral) did not influence the extent of affiliation and aggression, when they share the same degree of relatedness.

4. **Testing the effect of kin lineage and degree of relatedness on affiliation and aggression**

A two-way analysis of variance was applied to simultaneously examine the influence of both kin lineage (either maternal or paternal) and degree of relatedness (either half-siblings with r=0.25 or aunt-nieces with r=0.125) on all affiliative and agonistic behaviours. For maternal half-siblings I used data on 34 focal females, for paternal half-siblings 19 focal females, for maternal aunt-nieces 34 focal females and for paternal aunt-nieces 19 focal females. Indices of the same focal animal with social partners of different levels of relatedness were treated as independent. Two kin categories for both kin lineages could be tested, because these two were only available for paternal kin (Table 5.5).
Table 5.5: Testing the effect of kin lineage and degree of relatedness on affiliation and aggression

<table>
<thead>
<tr>
<th>ANOVA Two- way</th>
<th>Proximity</th>
<th>Grooming</th>
<th>Approach</th>
<th>Physical Aggression</th>
<th>Non-physical Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kin lineage (d.f.=1)</td>
<td>F=63.074</td>
<td>F=28.979</td>
<td>F=70.664</td>
<td>F=13.609</td>
<td>F=8.985</td>
</tr>
<tr>
<td>Maternal vs. Paternal</td>
<td>( P&lt;0.001 )</td>
<td>( P&lt;0.001 )</td>
<td>( P&lt;0.001 )</td>
<td>( P&lt;0.001 )</td>
<td>( P&lt;0.003 )</td>
</tr>
<tr>
<td>r (d.f.=1)</td>
<td>F=20.803</td>
<td>F=10.892</td>
<td>F=24.959</td>
<td>F=1.686</td>
<td>F=12.669</td>
</tr>
<tr>
<td>0.25 vs. 0.125</td>
<td>( P&lt;0.001 )</td>
<td>( P=0.001 )</td>
<td>( P&lt;0.001 )</td>
<td>( P=0.197 )</td>
<td>( P&lt;0.001 )</td>
</tr>
<tr>
<td>Kin lineage * r (d.f.=1,102)</td>
<td>F=14.949</td>
<td>F=13.893</td>
<td>F=20.162</td>
<td>F=0.660</td>
<td>F=0.962</td>
</tr>
<tr>
<td></td>
<td>( P&lt;0.001 )</td>
<td>( P&lt;0.001 )</td>
<td>( P&lt;0.001 )</td>
<td>( P=0.418 )</td>
<td>( P&lt;0.329 )</td>
</tr>
</tbody>
</table>

Data from Table 5.1. Kin lineage was either maternal or paternal kin, \( r \) is the degree of relatedness either 0.25 or 0.125 and kin lineage * \( r \) represents the interaction, d.f. are the degrees of freedom. All data on non-peers.

Kin lineage had a significant impact on all affiliative and aggressive interactions investigated and likewise the degree of relatedness with the exception on physical aggression. However, the interaction between kin lineage and degree of relatedness was significant for all three affiliative interaction, but for none of the two aggressive interactions (see also Fig. 5.1).
Fig. 5.1 Mean frequency of proximity, grooming, approach, physical and non-physical aggression as a function of the degree of relatedness for maternal kin (squares) and paternal kin (triangle). The interaction between kin lineage and degree of relatedness is significant when the lines for maternal and paternal kin are different from parallel.

Discussion
Using a wider range of degree of relatedness for both maternal and paternal kinship than just half-siblings (see chapter 4), there emerge four main results from this chapter. First, affiliation and aggression both increase as the degree of maternal relatedness among females increases supporting findings of other studies. Second, no evidence was found in this study for the existence of a relatedness threshold, because distant kin could still be differentiated from non-kin. Third, females from different kin categories sharing the same degree of relatedness do not differ in affiliation and aggression, suggesting that kin category is not as important as reported by other studies. Fourth, there emerged an asymmetry in affiliation and aggression between maternal and paternal kin lineage, with the maternal kin lineage being both more affiliate and aggressive than the paternal kin lineage. These points will now be discussed in more detail.

Degree of relatedness
The results of the present chapter suggest that affiliation, but likewise aggression increase proportionally with an increase in the degree of maternal relatedness. Few studies have investigated how nepotism varied according to the degree of relatedness, but they all report that frequencies of affiliation or tolerated co-feeding increase with an increase in the degree of maternal relatedness (Kurland 1977, Berman 1982, Beckerman Glick et al. 1986, Singh et al. 1992, Kapsalis & Berman 1996a, Belisle & Chapais 2001). The latter study further indicates that patterns of spatial proximity decreased asymptotically with decreasing degree of relatedness, while grooming decreased proportionally with decreasing degree of relatedness.
which may also indicate context-dependent kin discrimination among maternal kin (cf. Kapsalis & Berman 1996a, Fig. 4). However, Kapsalis & Berman (1996a) concluded from their study that distinguishing close kin \((r \geq 0.125)\) from non-kin explains better the distribution of behaviour than using the all degrees of relatedness.

Hamilton’s kin selection theory (1964) predicts that the more individuals are related the more they should direct affiliation towards each other, but likewise, the less they should direct aggression towards each other (cf. Hamilton 1987). The first prediction was met by the data presented, but aggression was in contrast to what is predicted. Nevertheless, the data seem plausible, as close kin spend an enormous time in close spatial proximity, that the likelihood of aggression, both initiated and received, is higher too. High levels of aggression among close kin were also reported from other studies on Japanese macaques (Kurland 1977) and rhesus macaques (Bernstein & Ehardt 1986a). Silk et al. (1981) found that female bonnet macaques direct more severe aggression towards non-kin than towards kin, but the present study suggests that less affiliative dyads (i.e., distant kin and non-kin) direct less physical aggression than non-physical aggression towards each other (cf. Table 5.1). The most frequent aggression in the present study was found in mother-daughter pairs, directed from mother to their daughters, which reflects the importance of aggression in the socialisation of rhesus macaques (Bernstein & Ehardt 1986a) given the fact that this species has the most despotic hierarchy among all macaques species. Bernstein & Ehardt (1986a) noted that aggression received from kin declined as individuals matured, with females of all ages directing aggression more to kin than non-kin, whereas males involvement in kin aggression decreases with age.

**Relatedness threshold**

As a second result, distant maternal kin with a degree of relatedness of \(r=0.0625\) still affiliate more than unrelated females, but no difference was found in respect to aggression. On the other hand, paternal kin sharing a degree of relatedness of \(r=0.125\) show no difference in affiliation in comparison to unrelated females, but show significantly less physical aggression than unrelated females. These results contradict previous studies (Kapsalis & Berman 1996a, Chapais et al. 1997, 2001) which found no difference between distant kin and non-kin for any behaviour measured concluding the existence of a relatedness threshold (but cf. also Silk et al. 2002). As mentioned above, the concept of a relatedness threshold predicts that, despite differences in the degree of relatedness, distant kin and non-kin do not differ in the extent of their behavioural interactions. However, maternal and paternal kin in the present study differed in comparison to non-kin, but the context expressing this differences was not the
same, as there emerged a higher level of affiliation among maternal kin in comparison to non-kin, but a reduced level of aggression among paternal kin in comparison to non-kin. The contradictions found across studies could be due to different behaviour examined, as the concept of a relatedness threshold predicts that depending upon their cost-benefit ratio different behaviours may have a *different* relatedness threshold (cf. Chapais 2001). From experimental study on captive Japanese macaques, Chapais *et al.* (2001) suggested a relatedness threshold among direct kin at $r=0.125$ (great-grandmothers) and among collateral kin at $r=0.25$ (half-siblings), because effective kin support was only observed at or above this degree of relatedness and never below. Chapais *et al.* (1997, 2001) studied the concept of relatedness threshold on coalition formation, a behaviour which can be very costly for the actor compared to the behaviours I used here. However, analyses on coalition formation (see next chapter) need to consider the observed and expected frequency of support, as the opportunities of interventions depend upon the likelihood that certain individuals (e.g., kin) are involved in aggressive conflicts. In other words, if one has only one paternal half-sister who tends to be rarely involved in dyadic aggression, then one rarely has the chance to support her. Chapais *et al.* (1997, 2001), in contrast, induces experimental conditions by isolating kin of certain degrees of relatedness to study coalition formation which is not comparable with studying coalition formation in free-ranging animals.

A second study on the same population than studied here concluded that a relatedness threshold among maternal kin might operate at the level of $r=0.125$ (Kapsalis & Berman 1996a) investigating similar affiliative interactions than the present study. First, it seems likely that the discrepancy between Kapsalis & Berman (1996a) and the present study is influenced by the number of kin available, as the former study group had up to 320 individuals which may exceed the natural ability of a monkey to recognise such a high number of individuals and/or kin. Second, due to the lack of paternity data in their study, paternal kin were not differentiated from non-kin so both were pooled as maternally unrelated individuals. Third, Kapsalis & Berman (1996a) found that extremely distant kin ($r \geq 0.0005$) were treated similarly to non-kin. As the present study was unable to investigate extremely distant kin (with $r<0.0625$), then contradictions may have arose due to the use of different degrees of relatedness. With respect to the importance of paternal kinship and age proximity on female social relationships (see previous chapter), as well as methodological differences among studies, the idea of a relatedness threshold should be re-evaluated in more detail.

Finally, it should also be emphasised, that the absence of nepotism may also reflect limits of kin recognition. Because any female would benefit from supporting any of her relatives that
are within the relatedness threshold, two alternatives for the absence of nepotism between distant kin are likely: (i) females recognise their distant kin, but they do not derive a net benefit from helping them and (ii) females do not recognise their distant kin even though they are within the relatedness threshold and nepotism might still be profitable (cf. Beecher 1991, Mateo 2002).

*Kin categories*

As a third result, no significant difference was found for maternal kin who shared the same degree of relatedness but belonged to different kin categories (e.g., for $r=0.25$ between maternal grandmother-granddaughters vs. maternal half-siblings). This also contrasts the results found by Chapais *et al.* (2001) who suggested that kinship category (e.g., direct or collateral), in addition to the degree of relatedness, is a key variable affecting the occurrence of altruistic behaviour. Chapais *et al.* (2001) concluded this from their study on female Japanese macaques who provided support to maternal kin. They found that great-grandmothers ($r=0.125$, direct kin) provided constantly support to their great-grandchildren, but aunts ($r=0.125$, collateral kin), grandaunts and cousins (both $r=0.0625$, collateral kin) abstained from doing so (ibid.). Although it seems likely that direct kin are more familiar than collateral kin, rank is inherited in a vertical way, with direct kin occupying adjacent ranks. It is therefore likely that competition over rank is higher among collateral kin than among direct kin, since in the latter case the higher-ranking individual (e.g., mother) passes on its own rank towards the other individual of the dyad (e.g., daughter) with the mother having a self-interest that her daughter acquires the rank predicted from birth in order to develop strong alliances with her in the future.

*Kin lineage*

As a fourth result revealed from the data, kin lineage either maternal or paternal was influencing all measurements of affiliation and aggression. In addition, the degree of relatedness (whether $r=0.25$ or $r=0.125$) was significantly influencing all measurements of affiliation and non-physical aggression and the interaction between kin lineage and degree of relatedness was significantly influencing all measurements on affiliation. Again, a context-dependent impact emerged from the data, but likewise a strong asymmetry between maternal and paternal kin. Given that maternal kin are generally closer in rank than paternal kin or non-kin (unpubl. data), the bias towards maternal kin may be a by-product of the attraction to similar ranking females as suggested by de Waal (1991), Kapsalis & Berman (1996a,b) and Chapais *et al.* (1991, 1994).
Summary
The results of this chapter extend earlier findings demonstrating that paternal kin discrimination regulates affiliative and aggressive interactions among adult female rhesus macaques (Widdig et al. 2001 and previous chapter). Both affiliation and aggression declined with decreasing degrees of relatedness among maternal kin. Distant kin still differentiated each other from non-kin, contradicting the existence of a relatedness threshold. Furthermore, individuals sharing the same degree of relatedness but belonging to different kinship category (direct vs. collateral) seemed not to differ in exhibiting social behaviour. Individuals who were maternally related adjusted their affiliation and aggression according to their degree of relatedness, this trend was not as clear for paternal kin with only two kin categories available for testing. This asymmetry in social relationships when the degree of relatedness was held constantly suggests that maternal kinship was more important than paternal kinship in the study group.
6. Coalition formation with the knowledge of paternal kinship

Introduction

A coalition\(^1\) is formed when one individual intervenes in an ongoing conflict between two opponents in order to support one of them. Since support in favour of one party is simultaneously targeting the other party, coalitions are triadic interactions involving a supporter, a recipient and a target. The adaptive function of altruistic behaviour such as sterile insect benefiting the family was a headache for Darwin (1859) when he realised that altruistic behaviour contradicted his theory of natural selection since an individual should only help another when it is likely to benefit from the support it provides. In other words, selection is not expected to favour individuals who reduce their own fitness to increase the fitness of others. Ever since there are two possible explanations for the function of support: (i) intervention is of altruistic or (ii) even of selfish origin. Altruistic behaviour is associated with costs to the altruist (i.e., time, energy, risk of injury and retaliation) and benefits to the recipient (i.e., access to a limited resource, suffering less injury in an attack). If coalition formation is altruistic, it is expected to be directed towards kin or reciprocal partners.

The theory of **kin selection** (ref. Maynard Smith 1964) predicts that individuals who support kin enhance their indirect fitness, because they share genes with the recipient of support (Hamilton 1964). Selection is expected to favour altruism among kin the closer individuals are related, the lower the costs to the altruist, and the greater the benefits to the recipient.

In **reciprocal altruism**, however, the altruistic act incurs costs and no immediate benefits, but the altruist receives future benefits from the recipient (Trivers 1971, Axelrod & Hamilton 1981). Since the benefits to the recipient are expected to be greater than the costs to the altruist, both partners enhance their direct fitness over a longer period of time even when unrelated. Following Hemelrijk (1990a) repayment by the former recipient can be given in the same currency (**reciprocity**: e.g., support for support) or in different currencies (**interchange**: e.g., grooming for support). Both terms will be distinguished throughout the chapter.

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\(^1\)In the literature several terms have been used to describe the same behaviour, such as coalition formation, support, helping, agonistic aiding, interventions, alliances, fight interference etc. These terms will be used as synonyms throughout the chapter (cf. de Waal & Harcourt 1992). While a coalition describes any support observed between two individuals, an alliance, in contrast, describes a enduring relationship with respect to support (see de Waal & Harcourt 1992).
Supporters are not altruists when they receive immediate benefits from their support of unrelated individuals (Wrangham 1982). Male chimpanzees act selfishly when supporting non-kin against certain opponents since their support can act to increase their own dominance rank (de Waal 1982). Thus co-operative (or mutualistic) behaviour may evolve among individuals with self-interests if they can reach their goals more effectively when cooperating, than acting alone (Brown 1983). Compared to a non-cooperative situation both recipient and supporter immediately benefit, although the benefit can be asymmetrically distributed among the partners (Axelrod 1984). For more details on the three theories see Widdig et al. (2000).

There is evidence for kin selection with respect to support among both male and female primates (e.g., Kurland 1977, Kaplan 1977, 1978, Massey 1977, Walters 1980, Silk 1982, Bernstein & Ehradt 1985a, Widdig et al. 2000, Silk et al. 2002), especially females support their kin at a high risk when they intervene against opponents which are higher-ranking than themselves (Datta 1983b,c, Bernstein & Ehradt 1985a, de Waal & Luttrell 1985). Recall that earlier studies only distinguished between maternal kin and maternal unrelated individuals, pooling paternal kin and non-kin. Therefore, nothing is known about the impact of paternal kinship on coalition formation.

Reciprocal altruism was first reported among pairs of maternally unrelated male baboons who alternate in enlisting each other to take over an oestrous female from a consort male (Packer 1977). Later studies questioned the extent of reciprocity involved in these coalitions (Bercovitch 1988, Noë 1989) since both partners were as likely to gain access to the consort female. Bercovitch (1988) suggested that coalitions are the outcome of co-operation between males pursuing self-interests.

De Waal (1982) showed that male chimpanzees intervene in conflicts in favour of unrelated males to increase their own dominance rank against the target of support. Additional studies have provided evidence of non-kin support in terms of co-operative interactions for both male (Noë 1992, Widdig et al. 2000) and female primates (Chapais et al. 1991, Silk et al. 2002).

While juvenile individuals benefit from support by their maternal kin in order to acquire the dominance rank predicted from birth order (reviewed in Chapais 1992), interventions among adults are more likely to stabilise the existing dominance hierarchy (ibid.), even though adults sometimes use coalitions to increase their dominance rank (e.g., Samuels et al. 1987).

In addition, Chapais (1988b) showed using an experimental study on rank reversal, that any female, regardless of age, depends on allies to maintain her rank. Coalition formation is therefore important for the acquisition and maintenance of the rank structure in a group.
Recall, that female macaques stay in their natal group with their kin throughout their life, while males migrate and thus have reduced opportunities to support kin (Kaplan 1977, 1978, Bercovitch 1988, Silk 1992a). Studies on coalition have suggested a sex difference as interest of males and females in interventions seems to be different (e.g., Bond & Vinacke 1961, Kaplan 1977, de Waal 1984, Bernstein & Ehardt 1985a). Since rank relations among male primates are more unstable than in females, the interest of male partners change over time (de Waal 1985). Therefore, coalition formation among males is more changeable and dominance-orientated than among females, who tend to support the lower-ranking but familiar opponent more often (see also Hemelrijk & Ek 1991).

Having paternity data available when investigating decision making in coalition formation, interesting questions will arise. Given that an individual is going to intervene in a conflict between its maternal cousin and its paternal sibling, who should it support? Kin selection theory (Hamilton 1964) would predict that the intervener supports the opponent with whom its shares more genes assuming all others being equal. In other words, one would expect that the individual gives support to its paternal sibling while targeting its maternal cousin. However, other factors might influence this decision. As shown in the previous chapter, affiliation (as a measure of familiarity) is less among paternal half-siblings than among maternal cousins. In addition, maternal kinship reflects rank relations which are extremely important among female rhesus macaques. In removal experiments it was shown that female Japanese macaques clearly depend upon the support by their high-ranking maternal kin or other maternally unrelated individuals of high rank in order to stay high-ranking themselves (Chapais et al. 1991). Therefore, it is likely that constraints to an individuals’ own competitive ability also play an important role.

The present study has shown that adult female rhesus macaques are capable of discriminating their paternal kin from non-kin, but whether or not they treat their paternal kin preferentially is context-dependent (chapter 4). Here, we will focus on the question of whether paternal kin discrimination is expressed in coalition formations, a behaviour which can be of enormous cost to the intervener. As outlined above, coalition formation might result from kin selection, reciprocal altruism or selfishness depending upon the cost associated to the supporter. In some conflicts, females may intervene at high costs to themselves to increase their own dominance rank which is likely to increase their own reproductive success (cf. Silk 1987, van Noordwijk & van Schaik 1999). In other conflicts, females may intervene at high costs to themselves in favour of their kin, both maternal and paternal, but if self-interests conflict with kin support females may also intervene against their kin with whom they compete over rank (cf. Chapais
The costs to intervene seem to differ depending upon the target of the support with costs defined as the risk of retaliation assuming that injuries have an effect on fitness (cf. Chapais 1992, 2001).

This chapter will focus on two issues: (i) it will re-evaluate the function of agonistic intervention by testing the three introduced functional explanations with the knowledge of paternity, i.e., when maternally unrelated individuals can be separated into paternal kin or non-kin and (ii) it will investigate whether paternal kinship has an impact on coalition formation. Recall from the Methods, that all coalitions observed over the 8 months study period, either collected ad libitum or in a focal protocol, were included in the data analyses, whenever a focal female (N=34) or an adult female (N=49) was intervening. Which sample (N=34 or 49) will be noted below. Both, female support either given to a recipient or against a target belonging to a certain kin and age category were analysed. Depending upon the question addressed, the kin and age categories were either maternal half-siblings, paternal half-siblings, non-kin or adult females in general. The third party in a coalition considered could be any other individual of group R including adult males.

Results

1. Testing variables related to support

Table 6.1 shows the correlation between individual attributes such as age, rank and number of kin and non-kin.

Table 6.1: Correlation between individual attributes

<table>
<thead>
<tr>
<th></th>
<th>N MS</th>
<th>N PS</th>
<th>N NK</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rank</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>r_s=0.113</td>
<td>r_s=-0.064</td>
<td>r_s=-0.599</td>
</tr>
<tr>
<td>P</td>
<td>0.438</td>
<td>0.660</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Rank</td>
<td>r_s=0.150</td>
<td>r_s=-0.217</td>
<td>r_s=0.257</td>
</tr>
<tr>
<td>P</td>
<td>0.303</td>
<td>0.134</td>
<td>0.075</td>
</tr>
</tbody>
</table>

Spearman's correlation coefficient (r_s) for all adult females (N=49) using age in years (Age), basic rank (Rank), and number of kin and non-kin. Abbreviations are as follows: number of maternal half-sisters (N MS), number of paternal half-sisters (N PS) and number of non-kin (N NK), pooling peer and non-peers in each kin category.

First and most important, rank and age did not correlate with each other which was expected given that daughters socially inherit the rank of their mother. Rank was neither related to the number of kin nor number of non-kin. Younger females had significantly more paternal half-
sisters than older females as older females were more likely to lose their peers (which tend to be paternal half-siblings, see chapter 3) with years due to death. In contrast, the older females had significantly more female non-kin than younger females. Additionally, these individual attributes for all 49 adult females were correlated with variables of relevance for interventions such as the number of dyadic aggression initiated and received, the number of being the target or the recipient of support and the number of support given per individual female (see Table 6.2).

Table 6.2: Testing individual attributes with variables related to support

<table>
<thead>
<tr>
<th></th>
<th>Aggressor</th>
<th>Victim</th>
<th>Target</th>
<th>Recipient</th>
<th>Support</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>$r_s=-0.360$</td>
<td>$r_s=-0.446$</td>
<td>$r_s=-0.224$</td>
<td>$r_s=-0.263$</td>
<td>$r_s=-0.015$</td>
</tr>
<tr>
<td></td>
<td>$P=0.011$</td>
<td>$P=0.001$</td>
<td>$P=0.121$</td>
<td>$P=0.068$</td>
<td>$P=0.917$</td>
</tr>
<tr>
<td>Rank</td>
<td>$r_s=-0.745$</td>
<td>$r_s=0.322$</td>
<td>$r_s=0.079$</td>
<td>$r_s=-0.537$</td>
<td>$r_s=-0.581$</td>
</tr>
<tr>
<td></td>
<td>$P&lt;0.001$</td>
<td>$P=0.024$</td>
<td>$P=0.589$</td>
<td>$P&lt;0.001$</td>
<td>$P&lt;0.001$</td>
</tr>
</tbody>
</table>

Spearman's correlation coefficient ($r_s$) for all adult females (N=49) using age in years (Age), basic rank (Rank), the number of dyadic aggression initiated (Aggressor), the number of dyadic aggression received (Victim), the number of being the target of support (Target), the number of being the recipient of support (Recipient), the number of support given (Support).

Regarding age, the older the females were, the less they initiate and receive dyadic aggression. Older females also showed a trend of receiving less support. Regarding rank, the higher in rank (highest rank is 1, lowest 49) the more aggression was initiated and the less aggression was received by the female. High-ranking females were more engaged in coalition formation, both they gave and received more support than lower-ranking females.

2. Testing the effect of dyadic attributes on grooming and support

The following table presents the correlation between a behaviour (such as grooming, support given or support against) and a dyadic attribute (such as rank distance, age distance or degree of relatedness) within dyads. **Rank distance** was calculated in absolute terms ranging from 1 to 48, with the rank difference between the highest- and the lowest-ranking adult female (N=49) being 48. **Age distance** was also measured in absolute terms (ranging from peers, i.e., 0 to the maximum age difference among adult females, i.e., 16 years). **Degree of relatedness** was calculated by incorporating all degrees of maternal and paternal relatedness. As an example, the question will be addressed whether an increased frequency in grooming within dyads is correlated with the rank differences of this dyad, etc. The Mantel R-test (Hemelrijk...
1990a,b, de Vries 1993) testing reciprocity on the dyadic level was performed using 2000 permutations per test. Recall from the Methods, that this test investigates whether the sequence of preference among all dyads is correlating between the two matrices. Roughly spoken, for the tests on grooming the questions to answer would be (i) is the closest ranking dyad also grooming each other the most, while the most distant ranking dyad is also grooming each other the lowest (i) is the closest ageing dyad also grooming each other the most, while the most distant ageing dyad is also grooming each other the lowest and (iii) is the closest related dyad also grooming each other the most, while the most distant related dyad is also grooming each other the lowest (see Table 6.3).

Table 6.3: Testing the effect of dyadic attributes on grooming and support

<table>
<thead>
<tr>
<th>Matrix 1</th>
<th>Matrix 2</th>
<th>Coefficient</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rank distance</td>
<td>Groom</td>
<td>-0.45</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Rank distance</td>
<td>Support given</td>
<td>-0.33</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Rank distance</td>
<td>Support against</td>
<td>-0.12</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Age distance</td>
<td>Groom</td>
<td>-0.07</td>
<td>P=0.018</td>
</tr>
<tr>
<td>Age distance</td>
<td>Support given</td>
<td>+0.01</td>
<td>P=0.407</td>
</tr>
<tr>
<td>Age distance</td>
<td>Support against</td>
<td>+0.00</td>
<td>P=0.497</td>
</tr>
<tr>
<td>Degree of relatedness</td>
<td>Groom</td>
<td>+0.44</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Degree of relatedness</td>
<td>Support given</td>
<td>+0.44</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Degree of relatedness</td>
<td>Support against</td>
<td>+0.12</td>
<td>P&lt;0.001</td>
</tr>
</tbody>
</table>

Correlation between a dyadic attribute (such as rank distance, age distance or degree of relatedness) and a behaviour (such as grooming, support given or support against) based on a 49x49 matrix including all adult females (for details on the tests see above or Methods).

Rank distance showed a significant negative correlation with both grooming and support given, implying that females groom and support each other more, the closer they are in rank. This result was expected as close maternal kin are of adjacent rank. Testing reciprocity between rank distance and support against also revealed significant results, but we should not consider this a relevant association, because of the very low correlation coefficient (cf. large sample sizes also tend to result in significant results without a relevant correlation coefficient). Age distance showed no relevant association with grooming, support given or support against which is not contradicting the importance of age proximity found in chapter 4, instead it supports the results of chapter 5, that the closest bonds were the one between mothers and daughters which are of distant age. As predicted from kin selection theory
(Hamilton 1964), the degree of relatedness showed a significant positive correlation with both grooming and support given, implying that females groom and support each other more, the higher their degree of relatedness. No relevant association was found between degree of relatedness and support against.

From these finding one could predict that the degree of relatedness and rank distance are associated with each other, meaning that females with a small rank distance will also share a higher degree of relatedness (cf. de Waal 1991). A comparison between them revealed a significant negative correlation using the Mantel R-test with 2000 permutations (Table 6.4).

<table>
<thead>
<tr>
<th>Matrix 1</th>
<th>Matrix 2</th>
<th>Coefficient</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rank distance</td>
<td>Degree of relatedness</td>
<td>-0.43</td>
<td>P&lt;0.001</td>
</tr>
</tbody>
</table>

Correlation between rank distance and the degree of relatedness based on a 49x49 matrix including all adult females (for details see Table 6.3).

This result was expected from what we know about the social structure in macaques where daughters socially inherit their dominance rank of their mother and maternal half-siblings are of adjacent rank. As a consequence, it makes sense to control for rank distance when correlating a behaviour with the degree of relatedness. Therefore, the correlation between the degree of relatedness and a behaviour was re-done, while controlling for rank distance at the same time. The partial Kr-test (Hemelrijk 1990a,b, de Vries 1993) was performed using 2000 permutations per test. The partial Kr-test tests reciprocity on the individual level, in contrast to the Mantel R-test which tests reciprocity on the dyadic level (see Methods). So, the question is slightly different than tested above. A perfect correlation would occur if for each female the sequence of grooming preferences corresponds with the degree of relatedness among her partners even though one controls for rank distance (Table 6.5).

<table>
<thead>
<tr>
<th>Matrix 1</th>
<th>Matrix 2</th>
<th>Coefficient</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Degree of relatedness</td>
<td>Groom</td>
<td>+0.35</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Degree of relatedness</td>
<td>Support given</td>
<td>+0.39</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Degree of relatedness</td>
<td>Support against</td>
<td>+0.09</td>
<td>P&lt;0.001</td>
</tr>
</tbody>
</table>

Correlation between the degree of relatedness and a behaviour (such as grooming, support given or support against) while controlling for rank distance based on a 49x49 matrix including all adult females (for details on the tests see Methods).
When controlled for rank distance, but now tested on the individual level, the degree of relatedness was still associated with grooming and support given, while support against was of no relevant association (see above). In other words, rank distance alone was not explaining the correlation between the degree of relatedness and grooming or support, respectively.

3. Testing kin selection theory with respect to support

Data were analysed to investigate the distribution of support either given to or against a maternal, paternal half-siblings or non-kin controlling for age proximity as in chapter 4 (see Table 6.6). All coalitions where a focal female (N=34) was intervening either in favour or against a certain kin and age category were considered. As outlined in the Methods, two different procedures were used to compare whether adult females intervened more on behalf of a particular kin and age category. The number of observed interventions was either divided (i) by the number of potential partners available in a particular kin and age category (hereafter: availability) or (ii) by the number of opportunities to intervene on behalf of particular kin and age categories (hereafter: opportunities) (cf. Silk et al. 2002). The number of available partners was based on the number of individuals of a particular kin and age categories present during the study period. The number of opportunities to intervene on behalf of a potential recipient were derived from the number of non-silent dyadic conflicts (see Methods) in which this potential recipient was involved.

Table 6.6: Testing kin selection theory with respect to support

<table>
<thead>
<tr>
<th>Mean frequency</th>
<th>N</th>
<th>Support given&lt;sub&gt;ava&lt;/sub&gt;</th>
<th>Support given&lt;sub&gt;opp&lt;/sub&gt;</th>
<th>Support against&lt;sub&gt;ava&lt;/sub&gt;</th>
<th>Support against&lt;sub&gt;opp&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS-NP</td>
<td>34</td>
<td>1.578 ± 1.331</td>
<td>0.023 ± 0.029</td>
<td>0.419 ± 0.635</td>
<td>0.004 ± 0.006</td>
</tr>
<tr>
<td>PS-P</td>
<td>15</td>
<td>0.267 ± 0.704</td>
<td>0.002 ± 0.005</td>
<td>0.200 ± 0.368</td>
<td>0.002 ± 0.003</td>
</tr>
<tr>
<td>PS-NP</td>
<td>19</td>
<td>0.083 ± 0.152</td>
<td>0.000 ± 0.001</td>
<td>0.320 ± 0.570</td>
<td>0.002 ± 0.004</td>
</tr>
<tr>
<td>NK-P</td>
<td>34</td>
<td>0.212 ± 0.273</td>
<td>0.002 ± 0.002</td>
<td>0.192 ± 0.241</td>
<td>0.002 ± 0.002</td>
</tr>
<tr>
<td>NK-NP</td>
<td>34</td>
<td>0.065 ± 0.047</td>
<td>0.001 ± 0.000</td>
<td>0.156 ± 0.085</td>
<td>0.002 ± 0.001</td>
</tr>
</tbody>
</table>

Cell values are mean proportions (± SD) of the focal females who intervened either in favour of a recipient or against a target. Data analysis was restricted to interventions where the focal females (N=34) choose a maternal half-sisters, non-peer (MS-NP), a paternal half-sisters either a peer (PS-P) or a non-peer (PS-NP) or a non-kin either a peer (NK-P) or a non-peer (NK-NP) either as a target or a recipient. N is the number of individuals tested (N). Proportions were derived from two different procedures (i) observed support of a kin and age category with respect to number of available partner in this kin and age category (Support
given \text{ava} or Support against \text{ava}) and (ii) observed support of a kin and age category with respect to number of opportunities (Support given \text{opp} or Support against \text{opp}, see above).

As evident from Table 6.6, focal females intervened most often in conflicts in favour of a maternal half-sibling (being the recipient) but also against a maternal half-sibling (being the target). No clear pattern was visible for all other kin groups. All data will be tested below.

Testing age proximity controlling for kinship

In order to investigate whether patterns of coalition include a peer effect, unrelated peers were compared with unrelated non-peers (Table 6.7).

Table 6.7: Testing age proximity controlling for kinship

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Support given \text{ava} $z$</th>
<th>Support given \text{opp} $z$</th>
<th>Support against \text{ava} $z$</th>
<th>Support against \text{opp} $z$</th>
</tr>
</thead>
<tbody>
<tr>
<td>NK-P</td>
<td>34</td>
<td>-4.958</td>
<td>-2.057</td>
<td>-0.419</td>
<td>-1.086</td>
</tr>
<tr>
<td>vs. NK-NP</td>
<td>P&lt;0.001</td>
<td>P=0.040</td>
<td>P=0.675</td>
<td>P=0.278</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>P'=0.013</td>
<td>P'=0.017</td>
<td>P'=0.025</td>
<td>P'=0.017</td>
</tr>
</tbody>
</table>

Data from Table 6.6 were tested using the Wilcoxon-test because some data did not meet the assumptions of parametric tests. In order to keep results comparable all tests on the same data set (Table 6.7-6.9) were tested with non-parametric tests (see Methods). P’ represents the Dunn-Šidák correction for multiple testing including all five different tests for the same behaviour in Table 6.7-6.9 (for more details see Methods).

Unrelated females preferred to support their peers more often than their non-peers, but they did not differ in targeting peers or non-peers. Targeting peers as often as non-peers, females either do not discriminate between both age categories in this specific context or data may also reflect competition among peers.
**Testing maternal vs. paternal half-siblings and non-kin controlling for age proximity**

Maternal half-siblings were compared with paternal half-siblings and non-kin, all being non-peers (Table 6.8).

Table 6.8: Testing maternal vs. paternal half-siblings and non-kin controlling for age proximity

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Support given ava</th>
<th>Support given opp</th>
<th>Support against ava</th>
<th>Support against opp</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS-NP</td>
<td>34</td>
<td>z=-5.035</td>
<td>z=-5.035</td>
<td>z=-1.744</td>
<td>z=-0.778</td>
</tr>
<tr>
<td>vs. NK-NP</td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P=0.081</td>
<td>P=0.437</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P'=0.010</td>
<td>P'=0.010</td>
<td>P'=0.010</td>
<td>P'=0.025</td>
<td></td>
</tr>
<tr>
<td>MS-NP</td>
<td>19</td>
<td>z=-3.599</td>
<td>z=-3.621</td>
<td>z=-0.786</td>
<td>z=-1.572</td>
</tr>
<tr>
<td>vs. PS-NP</td>
<td>P&lt;0.001</td>
<td>P&lt;0.001</td>
<td>P=0.432</td>
<td>P=0.116</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P'=0.017</td>
<td>P'=0.013</td>
<td>P'=0.013</td>
<td>P'=0.013</td>
<td></td>
</tr>
</tbody>
</table>

Data from Table 6.6 were tested using the Wilcoxon-test. See Table 6.7 for more details.

Maternal half-siblings supported each other more often than either paternal half-siblings or non-kin, but maternal half-siblings were also targeting each other equally often than either paternal half-siblings or non-kin. In other words, females preferred to help their maternal half-siblings, but they also directed support against their maternal half-siblings.

**Testing paternal half-siblings vs. non-kin controlling for age proximity**

Table 6.9 shows the comparison between paternal half-siblings and non-kin being either peers or non-peers.

Table 6.9: Testing paternal half-siblings vs. non-kin controlling for age proximity

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Support given ava</th>
<th>Support given opp</th>
<th>Support against ava</th>
<th>Support against opp</th>
</tr>
</thead>
<tbody>
<tr>
<td>PS-P</td>
<td>15</td>
<td>z=-0.730</td>
<td>z=-3.621</td>
<td>z=-0.497</td>
<td>z=-1.572</td>
</tr>
<tr>
<td>vs. NK-P</td>
<td>P_e=0.625</td>
<td>P_e=0.875</td>
<td>P_e=0.656</td>
<td>P_e=0.773</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P'=0.025</td>
<td>P'=0.050</td>
<td>P'=0.017</td>
<td>P'=0.050</td>
<td></td>
</tr>
<tr>
<td>PS-NP</td>
<td>19</td>
<td>z=-0.402</td>
<td>z=-1.730</td>
<td>z=-0.402</td>
<td>z=-1.932</td>
</tr>
<tr>
<td>vs. NK-NP</td>
<td>P=0.687</td>
<td>P=0.084</td>
<td>P=0.687</td>
<td>P=0.053</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P'=0.050</td>
<td>P'=0.025</td>
<td>P'=0.050</td>
<td>P'=0.010</td>
<td></td>
</tr>
</tbody>
</table>

Data from Table 6.6 were tested using the Wilcoxon-test. $P_e$ refers to the exact P-value as this test has a sample size of only $N=15$ (see Mundry & Fischer 1998 or Methods). See Table 6.7 for more details.
Testing peers, females did not support their paternal half-siblings more often than unrelated females and they also did not differ in targeting paternal half-siblings and non-kin. In other words, no evidence of paternal kin discrimination emerged among peers with respect to coalition formation. Testing non-peers, there seems an indirect indication for paternal kin discrimination as paternal half-siblings tended to targeting each other less often than non-kin.

4. Testing reciprocal altruism with respect to support

Reciprocity can arise among both kin and non-kin (Trivers 1971). However, reciprocity among kin is expected to be evolved through kin selection, not reciprocal altruism, and reciprocity among non-kin might be evolved through reciprocal altruism if associated with a cost to the supporter. The tests below will use the matrix correlation method (Hemelrijk 1990a,b, de Vries 1993) as outlined in the Methods.

The following two question will be analysed: (i) is there reciprocity for the same behaviour on the individual level, i.e., a perfect correlation would be if female A grooms female B most often, female C second most often and female D third most often and if female A then also receives grooming in this sequence (most often from female B, second most often from female C, third most often from female C) and (ii) is there interchange for different behaviour on the individual level, i.e., a perfect correlation would be if female A grooms female B most often, female C second most often and female D third most often and if female A then also receives support in this sequence (most often from female B, second most often from female C, third most often from female C). The goal of this section is to analyse the extent of reciprocity or interchange on two levels: (i) on all adult females (N=49) and (ii) on all adult females when controlling for maternal half-siblings, paternal half-siblings or non-kin (N=49).

Reciprocity for the same behaviour among all adult females

Reciprocity for the same behaviour (grooming for grooming, support given for support given and support against for support against) was analysed using all ad libitum data involving an adult female (N=49) as supporter by correlating the initiator-receiver matrix with its transposed form (Table 6.10). In other words, the matrix was diagonally split and correlated with the mirror image taken around the diagonal so called transposed matrix. The K_r-test was performed to investigates reciprocity on the individual level (see Methods) and the number of permutations per test was 2000 (Hemelrijk 1990a,b). The question we ask here is therefore: assume that female A gave most of her grooming to female B and second most to female C, a
perfect correlation would mean that female A would also receive most of her grooming from female B, and second most from female C (more details in Methods).

<table>
<thead>
<tr>
<th>Matrix 1</th>
<th>Matrix 2</th>
<th>Coefficient</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Groom</td>
<td>Groom(_{\text{transposed}})</td>
<td>+0.56</td>
<td>(P&lt;0.001)</td>
</tr>
<tr>
<td>Support given</td>
<td>Support given(_{\text{transposed}})</td>
<td>+0.37</td>
<td>(P&lt;0.001)</td>
</tr>
<tr>
<td>Support against</td>
<td>Support against(_{\text{transposed}})</td>
<td>+0.01</td>
<td>(P=0.425)</td>
</tr>
</tbody>
</table>

Tests for reciprocity are based on a 49x49 matrix including all adult females (for details on the tests see Methods).

As evident from this table, grooming and support given were based on reciprocity, implying that the sequence of preferred grooming partners of female A corresponds with the sequence of grooming received by female A. However, no such correlation was found for support against, but this result was expected as a low-ranking female will hardly ever intervene against high-ranking females, even though high-ranking females often intervene against them.

Reciprocity for the same behaviour among half-siblings and non-kin
As maternal and paternal half-siblings share on average the same degree of relatedness assuming costs and benefits being equal we would expect the same extent of reciprocity among them. Reciprocity for the same behaviour was separately analysed for maternal half-siblings, paternal half-siblings or non-kin by correlating the 1\(^{st}\) with the transposed of the 2\(^{nd}\) matrix. The number of permutations per test was 2000 and the partial \(K_r\)-test (Hemelrijk 1990a,b) was used to test reciprocity on the individual level while controlling for one of the three kinship categories (Table 6.11).
Table 6.11: Reciprocity for the same behaviour among half-siblings and non-kin

<table>
<thead>
<tr>
<th>Kin category</th>
<th>Matrix 1</th>
<th>Matrix 2</th>
<th>Coefficient</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS Groom</td>
<td>Groom</td>
<td>Groom</td>
<td>+0.52</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>MS Support given</td>
<td>Support given</td>
<td>Support given</td>
<td>+0.32</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>MS Support against</td>
<td>Support against</td>
<td>Support against</td>
<td>+0.00</td>
<td>P=0.480</td>
</tr>
<tr>
<td>PS Groom</td>
<td>Groom</td>
<td>Groom</td>
<td>+0.56</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>PS Support given</td>
<td>Support given</td>
<td>Support given</td>
<td>+0.37</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>PS Support against</td>
<td>Support against</td>
<td>Support against</td>
<td>+0.00</td>
<td>P=0.406</td>
</tr>
<tr>
<td>NK Groom</td>
<td>Groom</td>
<td>Groom</td>
<td>+0.46</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>NK Support given</td>
<td>Support given</td>
<td>Support given</td>
<td>+0.23</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>NK Support against</td>
<td>Support against</td>
<td>Support against</td>
<td>-0.01</td>
<td>P=0.336</td>
</tr>
</tbody>
</table>

Tests for reciprocity among maternal half-siblings (MS), paternal half-siblings (PS) and non-kin (NK) based on a 49x49 matrix including only adult females who have at least one maternal half-sister, paternal half-sister or non-kin (for details on the tests see Methods).

Repeating the analyses from Table 6.10, but controlling for the three kin categories, the results reveal the same trend. Independent of whether we test kin or non-kin, grooming and support given was based on reciprocity. Among non-kin, the effect of reciprocity in grooming was strong, but reciprocity in support given should only be interpreted as a trend, as the correlation coefficient (+0.23) is quite small (see text below Table 6.3). As maternal half-siblings are always of adjacent rank, but paternal half-siblings and non-kin can vary in their rank distance, the fact, that reciprocity was found in all three groups may imply that reciprocity is not due to differences in rank.

Interchange for different behaviours among all adult females

Interchange for the different behaviours (grooming for support given, grooming for support against, support given for support against) was analysed for all adult females by correlating the 1st with the transposed of the 2nd matrix (Table 6.12). The number of permutations per test was 2000 and the K-r-test (Hemelrijk 1990a,b) was used to test reciprocity on the individual level described above.
Table 6.12: Interchange for different behaviours among all adult females

<table>
<thead>
<tr>
<th>Matrix 1</th>
<th>Matrix 2</th>
<th>Coefficient</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Groom</td>
<td>Support given</td>
<td>+0.34</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Support against</td>
<td>+0.13</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Support given</td>
<td>Support against</td>
<td>+0.08</td>
<td>P&lt;0.001</td>
</tr>
</tbody>
</table>

Correlation between behaviours based on a 49x49 matrix including all adult females (for details on the tests see Methods).

Although, all tests reveal significant results, we should only consider the first one as a relevant association (see text below Table 6.3). However, testing grooming for support, the results showed that while female A groomed female B more than female C, female A also received more support from female B than female C.

Interchange for different behaviour among half-siblings and non-kin

Interchange for different behaviours was analysed separately for maternal half-siblings, paternal half-siblings or non-kin by correlating the 1st with the transposed of the 2nd matrix (Table 6.13). The number of permutations per test was 2000 and the partial Kₚ-test (Hemelrijk 1990a,b) was used to test reciprocity on the individual level.

Table 6.13: Interchange for different behaviour among half-siblings and non-kin

<table>
<thead>
<tr>
<th>Kin</th>
<th>Matrix 1</th>
<th>Matrix 2</th>
<th>Coefficient</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS</td>
<td>Groom</td>
<td>Support given</td>
<td>+0.29</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Support against</td>
<td>+0.12</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Support given</td>
<td>Support against</td>
<td>+0.07</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>PS</td>
<td>Groom</td>
<td>Support given</td>
<td>+0.34</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Support against</td>
<td>+0.13</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Support given</td>
<td>Support against</td>
<td>+0.08</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>NK</td>
<td>Groom</td>
<td>Support given</td>
<td>+0.20</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Support against</td>
<td>+0.09</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Support given</td>
<td>Support against</td>
<td>+0.03</td>
<td>P=0.055</td>
</tr>
</tbody>
</table>

Tests for interchange among maternal half-siblings (MS), paternal half-siblings (PS) and non-kin (NK) based on a 49x49 matrix including only adult females who have at least one maternal half-sister, paternal half-sister or non-kin (for details on the tests see Methods).

The trend stays the same when kin categories were tested separately for interchange. Only grooming was clearly associated with support given among maternal and paternal half-
siblings. This trend was less pronounced among non-kin given the smaller correlation coefficient (cf. again Text below Table 6.3). However, independent of whether we test kin or non-kin, there seemed to be (at least) a trend of interchanging grooming for support which is unlikely to be influenced by rank distance given the rank difference among maternal half-siblings, paternal half-siblings and non-kin as explained above.

5. Testing co-operation with respect to support

Intervening is one of the best examples that a behaviour can be costly to the actor, as the supporter invests at least time and energy, but also risks injuries and retaliation, especially by intervening against higher-ranking targets. Since support of one party is always directed against the other party (de Waal 1992), a coalition is a triadic interaction involving a target, a recipient and a supporter. Here an attempt was made to simultaneously analyse all three participants with respect to the cost of interventions, measured as the risk of retaliation when the supporter intervenes either against a higher-ranking or lower-ranking individual (cf. Widdig et al. 2000).

If female A is the highest-ranking, female B the middle-ranking and female C the lowest-ranking individual within a triad, one of six possible rank patterns can be observed in each triad. In the notation of a rank pattern (e.g., A vs. B + C, hereafter: ABC), the first letter is assigned to the target, the second to the recipient and the third to the supporter (Box 6.1).

**Box 6.1: The six rank pattern and their risk of retaliation**

<table>
<thead>
<tr>
<th>High risk</th>
<th>Low risk</th>
</tr>
</thead>
<tbody>
<tr>
<td>A vs. B + C</td>
<td>B vs. C + A</td>
</tr>
<tr>
<td>A vs. C + B</td>
<td>C vs. A + B</td>
</tr>
<tr>
<td>B vs. A + C</td>
<td>C vs. B + A</td>
</tr>
</tbody>
</table>

Six rank patterns with A as the highest-ranking, B as the middle-ranking and C as the lowest-ranking male within a triad (A>B>C, reading: target vs. recipient + supporter). The rank patterns are distinguished in terms of potential risk of retaliation. High risk of retaliation is assumed by intervening against a higher-ranking target. Low risk (if any) of retaliation is assumed by intervening against a lower-ranking target.

These six rank patterns are assumed to be associated with a different risk to the intervener (Bernstein & Ehardt 1985a). In Box 6.1 the rank patterns on the left side are likely to include a high risk of retaliation (Ehardt & Bernstein 1992) as the supporter intervenes against a higher-ranking target. These rank patterns are interpreted to destabilise the existing hierarchy.
Rank patterns on the right side are likely to include a low (if any) risk of retaliation as the supporter intervenes against a higher-ranking target. In contrast, these rank patterns are thought to stabilise the existing hierarchy either the supporters’ or the recipients’ rank (cf. Chapais 1992). The following analysis aims to investigate whether all six rank patterns are equally likely to occur. In other words, if the risk of retaliation by a higher-ranking target is minimum (or close to zero) all rank patterns are expected with equal frequencies.

If the risk of retaliation by a higher-ranking target is minimum or close to zero, no risk should be involved in intervening and all rank patterns may be predicted with equal frequency. However, if some rank patterns involve a higher risk of retaliation than other rank patterns, kin selection theory would predict that individuals should risk more when helping their kin than non-kin (Hamilton 1964).

All coalitions in which an adult female (N=49) was intervening in favour of a maternal half-sibling, a paternal half-sibling or a non-kin were presented (see Fig. 6.1-6.3). The third party in this coalition could be any other individual of group R including adult males.

Fig. 6.1: Support given to maternal half-siblings. The distribution of the six rank patterns of support given by adult females (N=49) to their maternal half-siblings (MS). The white bars are the observed distribution, the blue bars are the expected distribution.

The risky rank patterns are the first three starting from the left side, because the intervener is lower-ranking than the target. In contrast, the three rank patterns of the right are of low cost to the intervener (see above). Support given to maternal half-siblings was observed more often than expected when the target was the highest-ranking individual within the triad (rank pattern ABC and ACB). Both rank patterns are risky, they are mainly used against adult males.
Fig. 6.2: Support given to paternal half-siblings. The distribution of the six rank patterns of support given by adult females (N=49) to their paternal half-siblings (PS). Details in Fig. 6.1.

Similar to maternal half-siblings, but with a very limited amount of data, the risky rank pattern ABC also tended to be observed more often than expected in support given to paternal half-siblings. In addition, two rank patterns involving no risk (CAB and CBA) tended to be observed more often than expected. Note, that the total number of dyads for paternal half-siblings is much smaller, therefore the likelihood of being involved in a conflict is smaller than the number of opportunities to receive support by a paternal half-siblings.

Fig. 6.3: Support given to non-kin. The distribution of the six rank patterns of support given by adult females (N=49) to non-kin (NK). Details in Fig. 6.1.

The rank patterns found for support given to non-kin were similar as found among paternal half-siblings, that is, two rank patterns without risk (CAB and CBA) were more often observed than expected. One exception should be noted here in comparison to paternal half-siblings. Support given to non-kin was not more at risk than expected.

In sum, support given to non-kin was less associated with a risk of retaliation, but support given to maternal half-siblings is more often associated with a risk of retaliation. However,
support given to paternal half-siblings seems to include a combination of rank patterns found among maternal half-siblings (risky pattern) and non-kin (no risky pattern). The results of this analysis suggest that supporters pursue self-interests when intervening in conflicts, as competition over rank with the recipient of support seems to be present both in kin and non-kin support.

**Discussion**

The data indicate that kin support, reciprocal support and co-operative support were involved in coalition formation among adult female rhesus macaques, although it appears that the extent differs depending upon the costs involved in intervening. All three theories will be discussed in more detail now.

**Kin selection**

Maternal half-siblings supported each other more often than either paternal half-siblings or non-kin, but maternal half-siblings were targeting each other equally often than paternal half-siblings and non-kin. In other words, females preferred to help their maternal half-siblings, but they also directed support against their maternal half-siblings which may be a result of competition amongst them. Chapais (1995) pointed out that kin can be both associate and competitor which may lead to conflicts of interests (cf. Chapais *et al.* 1994). Competition may also explain, why unrelated peers preferred to support each other more than unrelated non-peers, while both groups did not differ in targeting each other. Recall that the present study found evidence for paternal kin discrimination in affiliation, but not aggression (chapter 4). With respect to coalition formation, paternal half-siblings did not support each other more often than non-kin neither among peer nor among non-peers. However, an indirect indication of paternal kin discrimination might be that testing non-peers, paternal half-siblings were targeting each other less often than non-kin (see below).

It should be noted, that the number of paternal half-siblings available per adult female was much smaller than the number of non-kin per adult female, resulting in fewer conflicts involving paternal half-siblings and therefore less opportunities given to support them. Infants born in close age proximity have a large number of paternal half-siblings as shown in chapter 3, but the number of paternal half-siblings will be reduced as older individuals will die or be trapped. Therefore, the number of paternal half-siblings available as adults is much smaller. Coalition formation is a behaviour not as frequently to observe as affiliation or dyadic aggression and it also requires a preceding dyadic aggression in order to have an opportunity
to intervene. This, in addition to the small number of paternal half-siblings available, might have resulted in the small number of observed support in favour of a paternal half-sibling.

Evidence that maternal kin support each other more than non-kin is available for both male and female primates (e.g., Kurland 1977, Kaplan 1977, 1978, Massey 1977, Walters 1980, Silk 1982, Bernstein & Ehardt 1985a, reviewed by Chapais 1992). In addition it was shown, that close kin support each other more than distant kin (e.g., Massey 1977, Kaplan 1978, Petit & Thierry 1994, Widdig et al. 2000, Silk et al. 2002). What not has been studied in much details is, that even maternal half-siblings do both: they give support towards each other, but, on the other hand, they also direct support against each other which might be a by-product of sharing continuously close spatial proximity (cf. Silk et al. 2002). Another explanation for this finding is suggested for Japanese macaques, where females act nepotistically more often towards those maternal kin with whom they do not compete for dominance (Chapais et al. 1994). Nepotism seems to prevail when it does not conflict with the supporter’s self-interest. Therefore, kin bias does not necessarily imply kin selection (i.e., altruistic act), when it cannot be excluded that the supporter benefits from kin support (see co-operation below).

To date, no data are available investigating the impact of paternal kinship on coalition formation. Silk et al. (2002) used peerage as a proxy to test paternal kin discrimination among female baboons, but they did not found evidence for a peer-effect with respect to support. In order to asses whether females discriminate their paternal kin from non-kin in the context of coalition formation, the present study tested support given to paternal half-siblings in comparison to both maternal half-siblings and non-kin. Consistent with measurements of affiliation and aggression there appears a bias of supporting maternal half-siblings more often than paternal half-siblings which again needs to be discussed as possible by-product of the attraction to similar ranking females (Waal 1991, Kapsalis & Berman 1996a,b, Chapais et al. 1991, 1994). Paternal kin discrimination found for affiliation could not be explained by rank difference as paternal half-siblings did not differ in mean rank from non-kin both among peers and non-peers (chapter 4). In contrast, the mean rank difference among maternal half-siblings should be much smaller than among both paternal half-siblings and non-kin (unpubl. data), as maternal half-siblings are of adjacent rank, while the two others can vary from being close in rank upon to the maximum rank difference possible (i.e., one individual can be high-, the other can be low-ranking). As a general rule, there seems a higher risk involved by supporting a paternal half-sibling or a non-kin than supporting a maternal half-sibling assuming that rank distance within a coalition is relevant. It would therefore make sense that no paternal kin
discrimination emerged in support given, but indirect evidence for paternal kin discrimination emerged from avoiding to intervene against paternal half-siblings more often against non-kin. It should also be pointed out, that the effect of paternal half-siblings targeting each other less often than non-kin was restricted when non-peers (including multiple ages) were compared. In contrast, paternal kin discrimination was stronger among peers (same age) investigating affiliation and no evidence for paternal kin discrimination emerged for both peers and non-peers investigating aggression (chapter 4).

To sum, in contrast to other behaviours measured, coalition formation seems to give no clear evidence in favour of paternal kin discrimination as paternal half-siblings do not give more support towards each other than non-kin. This suggests that earlier studies which lacked paternity data did probably not bias their data by combining paternal and non-kin with respect to coalition formation. On the other hand, paternal half-siblings were targeting each other less often than non-kin indicating that avoidance to intervene against a paternal half-sibling may also reflect the ability to discriminate them from non-kin. Absence of an effect does not mean it does not exist, and as we saw before, paternal kin discrimination seems to be context-dependent. More detailed data would be required than just the 8-month study period to clarify indeed the impact of paternal kinship on coalition formation.

**Reciprocal altruism**

If reciprocity is the basis for coalition formation, females should support those from whom they received support in the past and refuse to support those who have failed to return support (Trivers 1971). The data of the present study revealed that grooming and support given was based on reciprocity, but reciprocity was not found for support against. The latter result was expected as low-ranking females will hardly ever intervene against high-ranking females, even though high-ranking females often target low-ranking females which is probably due to the risk of retaliation by higher-ranking females. Interestingly, the same trend was found when testing maternal half-sibling, paternal half-sibling or non-kin separately, implying that reciprocity cannot be restricted to kin, even though the trend was less pronounced for non-kin. As maternal half-siblings are always of adjacent rank, but paternal half-siblings and non-kin can vary in their rank distance, the fact, that reciprocity was found in all three groups suggests that reciprocity is not due to differences in rank. Interchange was found in grooming for support given and this trend was still evident when maternal half-sibling, paternal half-sibling and non-kin were tested separately. Again, interchange is suggested for both kin and non-kin, but the trend was less pronounced among non-kin. In addition, rank distance is unlikely to influence the findings (see above).
When dyadic attributes were tested with the behaviours measured, females groomed and supported each other more, the less their absolute rank difference and the higher their degree of relatedness was. From these finding one could expect that the degree of relatedness and rank distance are associated with each other, meaning that females with a small rank distance will also share a higher degree of relatedness. However, even when controlled for rank distance, females still groom and support each other more, the higher their degree of relatedness.

Direct evidence for reciprocal altruism is difficult to assess as many proposed examples involve questionable assumptions concerning costs and benefits of the partners (reviewed in Koenig 1988, Wilkinson 1988, Ligon 1991). For example, there must be a direct fitness cost to the donor that is less than the fitness benefit received when the act is reciprocated (Koenig 1988). The only convincing evidence (cf. Ligon 1991) comes from vampire bats, *Desmodus rotundus*, which share food by regurgitation of blood on the basis of reciprocity with both close kin and familiar non-kin (Wilkinson 1984). While the donor’s cost is the loss of weight and time by regurgitating some blood, this will save the recipients from starvation (ibid).

The classical example for reciprocal altruism in primates was reported among unrelated male baboons who alternate in enlisting each other to take over an oestrous female from a consort male (Packer 1977), but later studies questioned the extent of reciprocity involved in these coalitions (Bercovitch 1988, Noë 1989) since both partners were as likely to gain access to the consort female. Ever since several studies reported reciprocal support in several primate species (e.g., Hunte & Horrocks 1987, de Waal & Luttrell 1988, Watts 1997, Hemelrijk & Ek 1991) and others, in addition, suggested interchange between grooming for support (e.g., Seyfarth & Cheney 1984, Silk 1992b, Hemelrijk 1994, Vervaecke et al. 2000). Interchange seems only to occur in groups with a linear hierarchy (Henzi & Barrett 1999) and reciprocity was reported only to be evident when the hierarchy is stable (de Waal 1978). Chapais et al. (1995) tested the affiliation-for-support hypothesis via experimentally induced rank reversals among Japanese macaques. However, mutual selfishness rather than reciprocal altruism provided a better explanation as groomer and supporter seem both to immediately benefit (see co-operation below).

A problem, related to studies of reciprocity and interchange was pointed out by Hemelrijk (1990a,b), is that an association between grooming given for the support received may in fact be a by-product of the correlation with other variables. Testing Seyfarth’s data (1976, 1980) on vervet monkeys and baboons with the use of the matrix partial correlation test, Hemelrijk (1990b) found that the correlation in vervet monkeys, but not in baboons, was indeed a by-
product of rank as high-ranking female gave more grooming and support than low-ranking females. Hemelrijk (1990a) concluded that in order to detect a genuine relationship between two variables, other variables should be kept constant. This problem may have influence the present data, too, but by analysing maternal half-sibling, paternal half-sibling or non-kin separately, it was controlled for rank distance (see above).

Following the theory of reciprocal altruism, a reciprocal relationship should be immune against cheating (Trivers 1971). However, refusal to reciprocate need not end reciprocal relationships (see Noë 1990). Reciprocal relationships among male baboons did not break off when one partner refused to join a coalition against a consort male (Bercovitch 1988). This suggested to Bercovitch that coalitions are the outcome of co-operation between males pursuing self-interests. Females in the present study did not show a trend of cheating as (i) they reciprocate support given within dyads, i.e., when female A supported female B, female B also supported female A and (ii) there was no interchange between support given and against, i.e., when female A supported female B, female B did not targeting female A.

Reciprocity was found for both kin and non-kin, although reciprocity constraints might also be more relaxed among kin than among non-kin (Chapais 2001). However, it seems difficult to distinguish between bilateral altruism among kin produced by kin selection or produced by reciprocal altruism, as the former does not require to be exchanged bilaterally. In other words, reciprocity among kin may simply be a by-product of the symmetry in relatedness within a kin dyad (cf. Chapais 2001). Ideally, unilaterally altruistic behaviour should be investigated which is testable on adult-immature dyads as immature primates still receive more support than they are able to provide (ibid.). However, the present study was focused on adult females. Bilateral support might also evolve as a by-product when both partners target the same individual for dominance and should therefore be interpreted in terms of self-interest even when observed among kin (Prud’homme & Chapais 1996, see below).

Co-operation
Testing whether the concept of co-operation can also explain coalition formation, data were analysed with respect to interventions being associated with a risk of retaliation when intervening against higher-ranking targets or without (or low) risk when the supporter was higher-ranking than the target which is likely to stabilise the existing hierarchy. The results suggest that a supporter sometimes also seems to benefit from intervening depending upon the kin relationship between the supporter and the recipient of support. Support given to maternal half-siblings was found to be most often associated with a risk of retaliation, targeting higher-ranking individuals, most often adult males. Non-kin support, in contrast, was most often
found without risk as females seem to stabilise the existing hierarchy through non-kin support. Support given to paternal half-siblings seemed to be a combination of rank patterns most often found among maternal half-siblings (risky patterns) and non-kin (non-risky patterns). Therefore, the present study suggests that supporters pursue self-interests in some interventions both kin and non-kin support.

Recall from the Introduction that female and male primates differ in their distribution of support. Male rank is likely to change over time, which may change their interests (de Waal 1985). Coalition formation among males was therefore suggested to be more dominance-orientated than among females, who tend to support their lower-ranking kin at high risk to themselves. Comparing non-kin support among male bonnet (Silk 1993, Table 8), male Barbary macaques (Widdig et al. 2000, Fig. 3) with the present data on female rhesus macaques (Fig. 6.3, this chapter) gives additional evidence that males tend to be (even) more conservative than females. Fig. 6.4 summarises three studies.

![Fig. 6.4: Percentage of support given to non-kin (NK) across the three studies of macaques](image)

Note the six rank patterns are arranged as introduced in Box 6.1, with the first three on the left side representing risky interventions in terms of retaliation and the three remaining rank patterns representing low (if any) risk interventions. As evident from this figure, the distribution of interventions comparing both male studies are very similar, but differ from the female’s pattern. Female rhesus show higher percentage of risky intervention even in favour of non-kin than both male bonnet and Barbary macaques, but as pointed out before, rhesus females tend to support their non-kin using no-risk interventions, while supporting kin using more often risky interventions. However, even in no-risk interventions male and female macaques differ. Males mainly gave support when they were themselves the highest-ranking individual within the triad (CBA and BCA), while females mainly gave support when ranking between the recipient and the target (CAB). How to explain the last pattern just mentioned for
females? Using removal experiments Chapais et al. (1991) showed for Japanese macaques that unrelated females from two dominant matrilines dependent upon supporting each other in order to maintain their dominance over females from low-ranking matrilines, which is exactly the pattern (CAB) just described. Due to the selfish interests of the supporters, Chapais et al. (1991) concluded that co-operation provides a better explanation of non-kin interventions than reciprocal altruism.

Male chimpanzees frequently intervene against higher-ranking targets to improve their rank (de Waal 1982). Male macaques, in contrast, rarely form coalitions that put them at risk of retaliation. Silk (1993) concluded from her study that male bonnet macaques do not use coalitions to increase in rank, because only after rising in rank they intervene more often in conflicts. Colvin (1983) suggested that conflicts between higher-ranking opponents may stay dyadic, because lower-ranking individuals are inhibited from interfering. This seems especially likely for female macaques as dominance hierarchy can be predicted nearly 100% by the birth order (this study) and is very stable over time.

One of the most significant predictions testing kin altruism is that females should intervene on behalf of kin against higher-ranking targets at higher rates than supporting distant kin or non-kin. Females intervene on behalf of their kin, but rarely on behalf of non-kin, against adult males and females ranking higher than themselves (Kurland 1977, Kaplan 1977, Silk 1982, Datta 1983b, Lee 1983, de Waal & Luttrell 1985, this study). However, it cannot be concluded that supporting kin is always associated with a net cost which is the assumption of an altruistic act (cf. Silk 2002), therefore I agree with Chapais (2001) that distinguishing between altruistic nepotism evolved via kin selection and mutualistic nepotism evolved via natural selection is difficult at least for interventions with a questionable cost. In other words, assuming that kin are as competent as non-kin to provide support, the greater availability and familiarity due to close proximity of kin might generate nepotism by natural selection, regardless of the fact that they are genetically related. A female that faces a choice between co-operating with kin or non-kin, gains the same direct fitness, but in co-operating with a kin, she additionally gains indirect fitness, too. Therefore, it pays more to co-operate with kin. Kin bias in coalition formation may therefore be expressed as a joint operation of natural and kin selection.

**Summary**
Female rhesus macaques gave support most often to maternal half-siblings. In addition, unrelated peers supported each other more often than unrelated non-peers. Females did not support their paternal half-siblings more often than non-kin, but results may indicate indirect
evidence for paternal kin discrimination as females were targeting their paternal half-siblings less often than non-kin. This finding might be due to the fact, that paternal half-siblings can be very different in rank, while maternal half-sibling are of adjacent rank, implying that a low-ranking female cannot provide actual help to its paternal half-siblings, but may risk a higher probability of retaliation. As a compromise, females may instead selectively avoid to target their paternal half-siblings, suggesting that constraints to an individuals’ own competitive ability play an important role in coalition formation. Females also supported their maternal half-siblings at risk against adult males which are higher-ranking than themselves, while females supported non-kin without (or low) risk, mainly to stabilise the existing hierarchy. Paternal half-siblings tended to show an intermediate pattern. The results of this chapter also suggest that non-kin showed at least a trend in reciprocity and interchange, but also a high proportion of low (if any) cost interventions which can be explained by mutualism. Kin, on the other hand, showed a stronger trend in reciprocity and interchange and also provided a higher proportion of costly interventions towards each other than non-kin. However, at least low cost interventions by kin can also be explained by mutualism, as the cost to the intervener seems to be neglectable. It should also be concluded that patterns of coalition formation using paternity data can still be explained to a similar extent by kin selection, reciprocal altruism and co-operation compared to studies where paternity is unknown. In order words, lacking paternity data might not have such an important influence investigating coalition formation than shown for affiliation or dyadic aggression, but this assertion has be to proven by future studies.
7. Conclusions

1. Summary of findings
The impact of maternal kinship on social behaviour has been studied in detail for many primate species, but it is difficult to assess the importance of kin selection in shaping the evolution of social behaviour when studies are limited to maternal kin, completely ignoring paternal kinship. This thesis aimed to investigate the extent of paternal kinship and its impact on the social relationships among adult females in one group of free-ranging rhesus macaques (Macaca mulatta) living on the island of Cayo Santiago. The main findings can be summarised as follows:

Firstly, in order to access the extent of paternal kinship, paternity has been analysed for all infants of the study group born between 1993 and 1998. Results revealed that male reproduction was highly skewed over the study period as few males have sired a high number of offspring, but the majority of potential sires have sired no or few offspring. This created a kinship structure in which nearly all animals born during the study period had at least one paternal half-sibling in close age proximity, i.e., either of the same age (74%) or within a two-year age difference of themselves (15%). Assuming that male reproductive success is also skewed in other primate species, then the importance of paternal kinship in primate societies should be re-emphasised. One of the most important consequences of male reproductive skew is that many individuals will have more paternal than maternal half-siblings during their lifetime.

Secondly, in order to access the impact of paternal kinship on the social relationships among adult females, focal data on affiliation and aggression have been collected on 34 adult females with respect to their social partners who were either their maternal half-sisters, paternal half-sisters or unrelated females. The present study confirmed that the closest affiliative relationships characterise maternal half-sisters. Probably the most important result of this study was the finding that adult females were significantly more affiliative with their paternal half-sisters than with their non-kin. The recognition of paternal sisters was more pronounced among females of the same age than among females of different age, with a decrease in affiliation as the exact age difference (measured in years) increased among paternal half-sisters. This indicates that age proximity had an additional regulatory effect upon affiliative behaviour. However, evidence for paternal kin discrimination was only found with respect to
affiliation, but not with respect to dyadic aggression suggesting context-dependent kin discrimination.

Thirdly, when more kin categories were included in the analysis, adult females showed a strong bias towards maternal kin in comparison to paternal kin. This bias towards maternal kin when the degree of relatedness was held constantly suggests, that maternal kinship had a larger impact on the social relationships among adult female rhesus macaques than paternal kinship at least in the study group. Both affiliation and aggression declined with decreasing degrees of relatedness, but distant kin still differentiated each other from non-kin contradicting the existence of a relatedness threshold.

Fourthly, paternal kinship was finally investigated with respect to coalition formation. A coalition is formed when an individual intervenes in an ongoing conflict between two opponents in order to support one party against the other. Female rhesus macaques intervened most often on behalf of their maternal half-sisters. In addition, unrelated female peers supported each other more often than unrelated female non-peers. Females did not support their paternal half-sisters more often than non-kin, but data may indicate indirect evidence for paternal kin discrimination as females tended to target their paternal half-sisters less often than non-kin. This finding might be due to the fact, that paternal half-sisters can be very different in rank, while maternal half-sisters are of adjacent rank, implying that a low-ranking female cannot provide actual help to her paternal half-sisters, as she may risk a higher probability of retaliation when intervening in a conflict between two higher-ranking opponents. As a compromise, females may instead avoid to target their paternal half-sisters, suggesting that constraints to an individuals’ own competitive ability play an important role in coalition formation. Moreover, maternal and paternal half-sisters showed a stronger trend in reciprocity and interchange than non-kin and also provided a higher proportion of costly interventions towards each other.

Finally, the results of the present study strongly suggest that familiarity among individuals can arise through association in early development by at least two alternatives: (i) mothers mediating familiarity among their offspring (which are maternal half-siblings) caused by the close mother-offspring relationship during lactation and (ii) age proximity is mediating familiarity among age mates (including both paternal related and unrelated peers) who go through important life history stages such as infancy, menarche, pregnancy or motherhood at similar times while females of different age do not. In any case, paternal half-siblings additionally need a mechanism such as phenotype matching to discriminate paternal half-siblings from non-kin even within their peer group.
2. Importance of findings

Historically seen, this study is one of the first on free-ranging primates focusing on paternal kinship, because lacking paternity data most studies on kinship were limited to maternally related individuals. Why do we still lack studies investigating paternal kinship in primates? Firstly, technical difficulties to establish paternity from blood, hairs or even faeces samples had to be overcome (see Launhardt 1998, Gerloff et al. 1999, Smith et al. 2000). Secondly, for species with a long life span as primates it takes a considerable amount of time (after accumulate demographic data to reconstruct maternal kinship) to establish paternity for a whole group taking into account that males from outside the group are also likely to sire offspring (Berard et al. 1993, Soltis et al. 2001, this study). Thirdly, when paternally related individuals were combined with non-kin into “maternally unrelated individuals” in studies lacking paternity data, there was consistently reported a strong bias towards maternal kin in a number of species which seems to imply that paternal kinship is not likely to be important. As this study showed this might be true when comparing maternal half-siblings with paternal half-siblings, but there is still a difference when comparing paternal half-siblings with non-kin.

There was (and probably still is) an additional problem. The first evidence in favour of paternal kin recognition among primates (Wu et al. 1980) was contradicted by all subsequent studies (Fredrickson & Sackett 1984, Sackett & Fredrickson 1987, Welker et al. 1987, Erhart et al. 1997). Unfortunately, it was rarely questioned (but see Walters 1987), whether individuals isolated from their mothers soon after birth, reared in peer groups, tested with strangers rather than group members may have lacked important developmental stages, which might be necessary to recognise paternal half-siblings. Ever since most primatologist seemed to be convinced that nepotism among primates is a consequence of familiarity and therefore paternal kin cannot recognise each other (e.g., Gouzoules & Gouzoules 1987, Walters 1987, Bernstein 1991, Chapais et al. 2001), even though there is evidence from non-primate species that they can recognise paternal kin (e.g., Kareem & Barnard 1982, Holmes 1986b, Todrank et al. 1998, Petrie et al. 1999). However, kin discrimination should be expected when individuals live with their kin and non-kin together, exhibiting behaviours costly to the actor (cf. Silk 2002). Recent studies on free-living baboons and macaques have resurrected the interest in the prospect of paternal kin recognition (Alberts 1999, Smith 2000, Widdig et al. 2001, 2002), but more studies are still needed.
3. Confounding variables for maternal and paternal kinship

It is difficult to assess the influence of kinship when similarity in relatedness is associated with a high level of familiarity (measured as spatial proximity) as well as similarity in rank. These are variables which maternal kin commonly share and which are likely to be confounded. For example, it has been suggested that female primates are attracted to others most resemble in rank, age and kinship (de Waal & Luttrell 1986, de Waal 1991), but Kapsalis & Berman (1996b) could demonstrate using the matrix correlation method that maternal kinship is the primary factor influencing female social relationship, not similarity in rank.

What are likely confounding factors among paternal half-siblings? As most paternal half-sibling tend to be members of the same birth cohort or at least similar in age, age may be a confounding factor with respect to paternal kinship. However, one can separate this by controlling either for age or kinship resulting in four test groups: paternal half-siblings being either peers or non-peers and non-kin being either peers or non-peers which the present study was able to do. In addition, the mean rank difference between paternal half-siblings and non-kin did not differ, but is likely to be larger than among maternal half-siblings which are always of adjacent rank (Widdig et al. 2001, chapter 4).

Smith (2000) discussed that kin bias among paternal half-siblings should be even stronger than among maternal half-siblings due to a higher degree of relatedness, a closer similarity in age proximity and the larger difference in rank with the latter reflecting the attraction for higher-ranking females. I agree with the first two points, but not with the third point she made for the following reason. Assumed, a pair of paternal half-sisters which is very distant in rank, one high-ranking in the centre of the group, one low-ranking in the periphery of the group. First, they need to overcome the problem of spatial distance in order to interact. Following Smith (2000) we would only expect the lower-ranking paternal half-sister to approach and groom her higher-ranking paternal half-sister, not vice versa. With respect to coalition formation it seems even more unlikely that the lower-ranking paternal half-sister will intervene in favour of her higher-ranking paternal half-sister. In case that the higher-ranking paternal half-sister outranks her opponent, she does not require the support of her lower-ranking paternal half-sister, while in case the higher-ranking paternal half-sister does not outrank her opponent, her lower-ranking paternal half-sister may not intervene as she risks retaliation. In fact, the variation in affiliation among dyads of paternal half-siblings in the present study was probably due to large rank distance within some dyads (unpubl. data) an effect which can even be more pronounced with increasing group size as on Cayo Santiago.
4. Future studies

What should future work focus on? Firstly, data from other populations and other species than the one studied are needed as variation is already seen when comparing the baboon and the rhesus studies probably reflecting differences in population. Secondly, it would be worth investigating whether paternal kin discrimination also works among males. When a male grows up in his natal group he is as likely as a females to be paternally related with his peers. Assuming that a mechanism for paternal kin recognition develops in early development, males are expected to learn this, too, even though they leave their group around puberty to migrate elsewhere. But even then, studies on long-tailed macaques reported that males tend to migrate with their peers which are like to be their paternal half-siblings (de Ruiter & Geffen 1998). Dispersal is associated with a higher probability of mortality (increased predation risk) while losing chances to mate (Alberts & Altmann 1995). Are paternal half-brothers who leave their natal group together more successful in entering and reproducing in the new social group than unrelated males migrating together? Or if males migrate alone, do they join the group that they have paternal half-brothers in as reported for maternal half-brothers (Meikle & Vessey 1981)? Likewise, do males avoid to immigrate into groups that consist of a large proportion of paternal half-sisters as inbreeding via the paternal line is likely to be costly, too. And when reproducing successfully, do males recognise their offspring to avoid infanticide or mating with their daughters? Some studies suggested that fathers preferentially interact with their offspring (e.g., Stein 1984, Taub 1984), but studies using paternity data do not support this hypothesis (Paul et al. 1996). In species with infanticide as the Hanuman langurs, only genetic fathers or resident males at the time of the infants conception were likely to protect infants, but never males who immigrated after the infants conception suggesting that males count copulations with fertile females as clues for paternity (Borries et al. 1999). Alberts (1999) reported that pairs of paternal half-siblings exhibited less sexual behaviour than unrelated pairs. In contrast, Barbary macaques showed no mating avoidance among paternal kin (father-daughter and brother-sisters), but only 2 out of 62 potential inbred infants were found via the paternal line (Kuester et al. 1994).

Thirdly, more evidence is required for females. For adult baboons and macaques who showed evidence for paternal kin recognition it would be worth investigating when they start learning to distinguish between paternally related and unrelated individuals. In addition, which cue do they use, is it smell, vision, or maybe personality matching as hypothesised by the present study. The extent of context-dependent kin discrimination as well as the asymmetry in
behaviour found between maternal half-siblings and paternal half-siblings should be compared across populations.

Fourthly, it would be worth studying paternal kinship effects related to group fission in more detail as it was reported that female baboons are more likely to end up in the same fission group with their paternal half-sibling peer than with their maternal kin (Smith 2000) suggesting that groups not only split along matriline (Chepko-Sade & Stone Sade 1979, de Ruiter & Geffen 1998). Studies on baboons also found that social groups will be genetically structured by age as age cohorts tend to be paternal half-siblings (Altmann et al. 1996).

And finally, in species where males stay in their natal group with their kin, e.g., as in chimpanzees, is the picture of paternal kin bias reverse as in species, like the rhesus macaque, where females stay in their natal group together with their kin?
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I wished human beings would watch more carefully our close relatives in order to learn things we have forgotten.
11. Publications

1996


1997


1998


(5) **Widdig, A.**: Competition and cooperation among female rhesus macaques. What means kinship: familiarity or relatedness? (Abstract 16\textsuperscript{th} Conference of Ethology, Halle).

1999


2000


(2) **Widdig, A.**: What does "Kinship" mean among Female Rhesus Macaques: Familiarity or Degree of Relatedness? Folia Primatologica 71: 215 (Abstract 6\textsuperscript{th} Conference of the Society for Primatology, Utrecht, Netherlands).


(4) **Widdig, A.** & Nürnberg, P.: The meaning of “kinship” among female rhesus macaques: familiarity or degree of relatedness? (Abstract 8\textsuperscript{th} International Behavioral Ecology Congress, Zürich, Switzerland).

2001

(1) **Widdig, A.** & Nürnberg, P.: Paternal kin discrimination in adult female rhesus macaques at Cayo Santiago. (Abstract 18\textsuperscript{th} Conference of the International Primatological Society, Adelaide, Australia).


2002


## Appendix 1: Study group

### Table A.1.1: Study group R during the behavioural study in 1997

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<td></td>
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</tbody>
</table>

*Note: Details of each entry are not provided in the table.*

145
During the behavioural observation period in 1997, group R had a total of 126 core members i.e., 91 natal females and 35 natal males (not involving adult males which are non-natal), but the behavioural analyses were restricted to interactions among adult females and their female descendants (N=91). The table contains the 3 matrilines (named D07, CS, 262) which are ranged depending upon their dominance rank. Note that family 897 ranked lowest from all families despite they belonged to the matriline CS. The table gives also name of the families (N=11) with their number of females (Nf) and males (Nm). The name given in the family column is considered as the family founder female. Note that not all family founder females from matriline 262 are direct descendants of the matrilineal founder female 262, i.e., only some of them are maternal half-sisters. Group subjects are sorted by birth cohort, adult females born in 1987 or before are summarised. Focal females (N=34, marked in bold) were born between 1988 and 1994. Identities of males are replaces by the small letter m. Infants born in 1997 did not yet have their official tattoo, therefore they had their mother’s tattoo in addition with the capital letter I. The last column contains the mother of all individuals in this row. † indicates individuals not alive during the behavioural study.
Appendix 2: Ethogram

This ethogram was developed during a pilot study on Cayo Santiago in the summer of 1996 and owes much to previously published ethograms by Altmann (1962), Hinde & Rowell (1962) and Bernstein & Ehardt (1985b) for affiliative and agonistic behaviour, Dixson (1998) for sexual behaviour and van Hooff (1962) and de Waal & Luttrell (1985) for descriptions of facial and gestural signals.

1. Affiliative activities or interactions

Affiliation has been observed in different behavioural contexts, but only the first three listed below have been systematically analysed.

(i) Activities

Sharing spatial proximity: All neighbours within the 5m radius were identified with their exact distance (in m) towards the focal female including their activities at a time. These data, in contrast to all others, are based upon point samples (see Methods).

(ii) Interactions

Grooming: Picking through fur or over the skin of another individual, using hands and/or mouth. This behaviour was not scored unless a minimum duration of 5 seconds was achieved.

Friendly approach: Approach of an individual ranging from body contact up to 2.0m, the approaching individual had to remain within the 2.0m range for at least 5 seconds. This approach was followed either by an affiliative interaction or by sitting close to each other (sharing spatial proximity).

Co-feeding: Sharing a high quality food resource by tolerating each other in body contact while feeding chow on a chow container.

Co-drinking: Sharing a limited resource by tolerating each other in body contact while drinking from a water tank.

Lipsmack: Facial expression produced by protruding and rapidly moving the lips up and down, without opening the mouth. Most often given during initiation or maintenance of peaceful contact.

Girney: Soft, low-pitched, quavering and rather nasal vocalisation during the initiation and maintenance of affiliative interactions.

Low grunt: Low amplitude, pulsed, hoarse and breathy call, typically given when one individual approached or is approached by another.
2. Agonistic interactions

This section summarises different agonistic interactions, such as agonistic approaches, non-physical or physical aggression and submissive agonistic interactions. Patterns of aggressive behaviour are presented in the order of increasing intensity, acts with higher intensity were often used in conjunction with less severe gestures. Thus, in prolonged bouts only the kind of aggression with the highest intensity was used for the analyses. Aggression is distinguished as non-physical (lacking body contact between opponents) and physical events (with body contact between opponents). If physical as well as non-physical aggression was exhibited in the same bout only the physical aggression was counted. The term fight was used to describe prolonged incidents involving bidirectional grabbing and/or biting.

(i) Agonistic approaches

Approach-avoid: Approaches directed towards a recipient, who left when the approaching individual reaching a distance between 1 and 2 m. This response was interpreted as a choice to leave in order to avoid a conflict.

Approach-displace: Approaches directed towards a recipient, who had been displaced by the approaching individual reaching a distance closer than 1 m. This response was interpreted as the leaving animal was forced to leave.

(ii) Non-physical aggression

Stare: fixed staring towards a recipient combined with brow-raising and ears flattened back.

Head-bobbing: includes stare while the head is moving forward.

Open mouth threat: open mouth without seeing the teeth usually combined with stare and head-bobbing.

Slapping on the ground: slapping the ground with one hand, accompanied with one type of aggression mentioned before.

Vocal threat: hoarse, low-pitched pulsed call, produced with rounded and protruded lips, often directed several times in quick succession, accompanied with stare and open mouth threat, intensity varies from grunts to barks, sometimes as an aggressive scream.

Lunge: rapid aggressive movement toward another individual at a close distance, usually accompanied by a vocal threat.

Charge: pursuit of an individual for less than 5 metres, recipient may avoid, fear grin or flee.

Chase: running pursuit of an individual for more than 5 metres, assumes that the recipient flees.
(iii) **Physical aggression**

*Push:* manual contact aimed to remove the recipient out of way, including pushing the recipient or pulling its tail.

*Hit:* slapping the recipient.

*Grab:* aggressive manual contact, likely to cause discomfort without injury to the victim.

*Bite:* single bite, with or without holding down of recipient.

*Attack:* sustained and/or repeated bites lasting for more than 5 seconds, often involving head-shaking or slashing with the canines and typically performed whilst pinning down the victim.

(iv) **Agonistic interactions (submissive response)**

*Fear grin:* Facial display in which the lips are retracted so that clenched teeth are exposed, given in response to another animal.

*Scream:* Loud, highly pitched, often harsh sounding calls of prolonged duration or less intense as a squeal.

*Flee:* Rapid withdrawal from another individual.

### 3. Interventions in conflicts (Coalition formation)

A *coalition* is formed when an animal intervened in an ongoing dyadic conflict between two parties in order to support one of them. Depending on the role in this interaction, one distinguishes between the *supporter*, who intervenes and supports one party, the *recipient*, who receives the support, and the *target*, against whom the coalition was formed. Since support in favour of one party is simultaneously targeting the other party, coalitions are triadic interactions involving a supporter, a recipient and a target. This behaviour pattern will separately analysed, as it simultaneously contains a co-operative interaction (support in favour of a recipient) and a competitive interaction (support against a target). Instances where two individuals simultaneously and jointly commence aggression against a third were not considered (more details in Methods).
4. Other activities or interactions

All behavioural pattern listed below are rather neutral activities or interactions with respect to
the topic of interest.

(i) Activities

Locomotion: Travelling over longer distances e.g., as a consequence of group movement.
Rest: Stationary and clearly relaxed, with eyes open.
Sleep: Stationary with eyes closed, slow and regular breathing.
Forage: Preparing or ingesting any naturally occurring food item, including vegetation,
digging and eating soil from habitually used dips in the ground, searching for and consuming
small invertebrates. The type and part of the matter ingested would additionally be specified.
Drink: Drinking water from a fountain or pool, or licking rainwater from leaves or small
crevices. The source was specified.
Self-scratching: A usually repeated movement of hand or foot, during which the digital tips
are rapidly raked across the individual's hair or skin. This behaviour may indicate insecurity.
Yawn: Performed in a variety of contexts, including when resting or falling asleep, in tense
situations.
Self-grooming: Picking through the own hair or skin. This behaviour was not scored unless a
minimum duration of at least 5 seconds was achieved.

(ii) Interactions

Muzzle up: Puckering facial expression made by males when approaching and soliciting
copulation from females.
Genital inspect: Olfactory, oral or manual examination of another individual's genital area.
Sexual present: A display in which a standing female presents her hindquarters to a male.
Sexual mount: Alignment of the male's hindquarters with the haunches of the female, and with
the actor's feet either grasping the recipient's calves or remaining on the ground.
Present: Orienting the hindquarters toward another individual. Recipient can often be used to
distinguish submissive and affinitive versions from sexual presents, together with the context
in which the act is performed.
Ignore: To fail to respond to another's affiliative or agonistic overtures in situations where the
actor appeared fully aware of the latter.
Social play: Interaction as chasing games, chase or fight, but during relaxed circumstances,
lack of ritualised agonistic signals, often involving a play face.
Appendix 3: Paternity results

This Appendix does neither give identity of sires nor identities of the offspring they produced as these are protected and unpublished data. Instead, the number of solved paternity is presented.


The first data set contains all solved paternities using 15 DNA markers for all infants born between 1993 and 1998. From all 263 infants born between 1993 to 1998 in group R, or its sister group BB, the paternity could be solved for 242 of them via 15 DNA markers and for 5 more cases via DNA-fingerprinting which results in total paternity solved of 247 cases (Table A.3.1). The range of solved paternity varied within cohorts between 87.50 and 98.00% with a mean of 94.28% (SD ± 3.70%).

Table A.3.1: Solved paternity in group R or BB for all individuals born between 1993 to 1998

<table>
<thead>
<tr>
<th>Birth cohort</th>
<th>N offspring born</th>
<th>N offspring with solved paternity</th>
<th>% of solved paternity</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>32</td>
<td>31</td>
<td>96.88 %</td>
</tr>
<tr>
<td>1994</td>
<td>38</td>
<td>32(+4)</td>
<td>94.74 %</td>
</tr>
<tr>
<td>1995</td>
<td>45</td>
<td>42</td>
<td>93.33 %</td>
</tr>
<tr>
<td>1996</td>
<td>42</td>
<td>40</td>
<td>95.24 %</td>
</tr>
<tr>
<td>1997</td>
<td>56</td>
<td>48(+1)</td>
<td>87.50 %</td>
</tr>
<tr>
<td>1998</td>
<td>50</td>
<td>49</td>
<td>98.00 %</td>
</tr>
<tr>
<td>Sum 263</td>
<td>Sum 242 (+5)</td>
<td>Mean 94.28 %</td>
<td></td>
</tr>
</tbody>
</table>

Note numbers in brackets are cases solved with DNA-fingerprinting.

2. Solved paternity of group R present in 1997 which was used for the behavioural study

In the second data set, paternity has been assigned via 15 DNA markers for 76 out of 91 females studied (84%). For 15 females in the behavioural study (3 of them were focal females) paternity could not be established via microsatellites using the two criterions described above. Their actual sire was probably not genotyped for unknown reason (e.g., dead before sample taking etc.) However, for each of these 15 females the presence of any patern sibling in group R could be ruled out since (i) none of their putative sires with the highest LR
ratio (which was always below two, see Methods) had sired any other female in the group R studied in 1997 and (ii) all confirmed sires of females present in 1997 could be excluded as sires for all of these 15 female with respect to DNA fingerprinting (see focal females above). The results of the paternity analyses per birth cohorts are shown in Table A.3.2.

Table A.3.2: Solved paternity in group R during the behavioural study in 1997

<table>
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<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>N females present</td>
<td>25</td>
<td>13</td>
<td>4</td>
<td>6</td>
<td>6</td>
<td>4</td>
<td>6</td>
<td>5</td>
<td>4</td>
<td>3</td>
<td>15</td>
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<tr>
<td>N focal females</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>6</td>
<td>4</td>
<td>6</td>
<td>5</td>
<td>4</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>N solved paternity</td>
<td>24</td>
<td>12</td>
<td>4</td>
<td>6</td>
<td>6</td>
<td>4</td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>4</td>
</tr>
</tbody>
</table>

Note females born between 1993 and 1998 were already presented in Table A.3.1.
Erklärung

Berlin, den 17.6. 2002