

# Kinship, competence and cooperation in primates

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### 3.1 Introduction

In primate groups composed of several individuals varying in their degrees of relatedness to each other, cooperative activities, defined as interactions providing participants with direct benefits, are often expected, either implicitly or explicitly, to take place preferentially among closest kin (e.g. Silk, this volume). In contrast to this view, I will argue here that the role of kinship in the patterning of cooperation has probably been overestimated, that cooperation is expected to be kin-biased only under certain specific conditions, and that competence, rather than kinship, should drive the selection of partners for many cooperative activities. The widespread expectation that cooperative activities should be consistently kin-biased is based on solid empirical evidence, but on evidence which apparently underwent some important shifts in meaning. The expectation derives from two categories of observations: (1) some types of cooperative activities are indeed kin-biased, and (2) some types of non-cooperative social activities, namely altruistic ones, for which Hamilton (1964) proposed kin selection theory, may be extremely kin-biased, if not entirely restricted to kin when altruism is directed unilaterally.

When a mother protects her newborn against an aggressor or a predator, she does not gain any direct, personal benefits, whether immediate or delayed. She is altruistic, and unilaterally so. Unilateral altruism is not restricted to mother-offspring relationships in primate groups; it may be performed by other categories of kin, for example by grandmothers and sisters in the form of aiding in conflicts (Chapais et al. 2001). Inclusive fitness theory (Hamilton 1964), which posits that donors obtain indirect fitness benefits by contributing to the fitness of their kin, has proven especially useful to account for unilateral altruism, for which the theory of reciprocal altruism (Trivers 1971) is of no use, by definition. Accordingly, unilateral altruism is expected to be highly kin-biased, and kin selection has been consistently invoked to account for altruism in primate groups (Kurland 1977, Chapais & Schulman 1980, Silk 1982, 1987, 2002a, this volume, Walters 1987, Dunbar 1992, Maestripieri 1993, Schaub 1996, Chapais 2001, Chapais et al. 2001, Combes & Altmann 2001, Chapais & Bélisle 2004).

But the situation is different with cooperation. As mentioned above, the term cooperation subsumes various types of interactions that provide participants with direct, personal benefits (Pusey & Packer 1997). As a first possibility, referred to as mutualism, the benefits may be obtained concurrently by the

participants in the course of the interaction itself. Examples include coalitions, group-hunting and food-sharing. In theory, the benefits could also be obtained through the reciprocation of altruistic acts that are immediately costly to the donor, but provide mutual benefits in the long run (reciprocal altruism, Trivers 1971). However, interactions that unambiguously meet the criteria of reciprocal altruism have barely been documented in non-human primates. Although the “donor” may incur a slight cost in terms of time and energy, the possibility of its simultaneously obtaining significant benefits cannot be eliminated (Dunbar & Sharman 1984, Bercovitch 1988, Chapais et al. 1991, Hemelrijk et al. 1992, Noë 1992, Chapais et al. 1994, Prud’homme & Chapais 1996, Widdig 2000, Chapais 2001). Rather, cooperation through reciprocation appears to involve actions which simultaneously provide both partners with a net benefit, but which are initiated or performed alternatively by each of them. Possible examples include reciprocal aiding against third parties, reciprocal grooming, and exchange of grooming for tolerance, access to food, or aiding (see below). Such interactions have much in common with mutualism, but differ in that partners take turns in initiating or performing the same or different behaviors.

Importantly, because partners in cooperative activities obtain direct (personal) benefits whether they are related or not, cooperation can take place between non-kin just as well as between kin. Nevertheless, kin selection theory may be used to predict that cooperation should be performed preferentially among kin because when kin cooperate together they benefit both directly, through the cooperative act itself, and indirectly, through the fitness benefits accrued via kin selection (Wrangham 1982; see below). Partly on this basis, it has become common to explain nepotism in general, whether altruistic or cooperative, in terms of kin selection (e.g. Gouzoules 1984, Walters 1987, Morin et al. 1994, Kapsalis & Berman 1996, Silk 2002a), as if kinship should have a similar impact on the two functional categories of interactions.

In this chapter, I argue that the impact of kinship on the patterning of cooperation should be much less extensive than its impact on unilateral altruism, and that in many circumstances, cooperation should not take place between closest kin in primate groups. I first describe two theoretical arguments for the existence of kin biases in cooperation. I then define the conditions under which one expects cooperation to be kin-biased, and those under which cooperation should not necessarily be kin-biased. I conclude that cooperative activities whose payoff is significantly affected by the partners’ relevant qualifications, that is, by their competence, should not be consistently kin-biased. In reviewing the relevant empirical evidence, I focus on the striking difference in the degree of kin bias between male philopatric species, such as chimpanzees (*Pan troglodytes*), which exhibit relatively low levels of nepotism among matrilineal kin, and female philopatric species such as macaques, characterized by comparatively much higher levels of matrilineal nepotism. I argue that this comparison is deceptive, that a number of factors help considerably reduce the discrepancy, and that the role of kinship in shaping cooperation in primates has probably been overestimated.

Given the paucity of studies on the influence of patrilineal kinship on behavior in primates (reviewed by Strier 2004), let alone on the effect of patrilineal

kinship on the patterning of cooperative activities, I test the present ideas on matrilineal kinship only. Nonetheless, I assess the possibility that patrilineal kinship might affect my interpretations.

### 3.2

#### Why should cooperation be kin-biased?

At least two different forces may generate kin biases in cooperation. The first requires kin selection and was proposed most explicitly by Wrangham (1982). When a female cooperates with a relative, she benefits in two ways. She obtains the direct (personal) benefits of the cooperative act  $B$ , and she also derives indirect fitness benefits that amount to a fraction  $r$  (degree of relatedness) of the direct benefits accruing to her kin  $Br$ . If the same female cooperates with a non-relative instead, she derives only the direct fitness benefits  $B$  of the cooperative act. Because  $B + Br > B$ , and considering only these factors, cooperation between kin pays more than cooperation between non-kin, hence cooperation should be kin-biased. In sum, when individuals have equal access to kin and non-kin (Wrangham 1982), those who choose kin as partners obtain a fitness bonus  $Br$ . Because the fitness bonus is obtained reciprocally between kin, kin partners are mutually dependent on two accounts: (i) to obtain the direct benefits of cooperation and (ii) to obtain its indirect benefits, which dictates their cooperating together. By comparison, non-kin are mutually dependent only to obtain  $B$ ; they would not lose any fitness bonus by defecting. For this reason, kin would constitute more reliable partners compared to non-kin, and kin partnerships would be more stable as a result.

An alternative explanation for the occurrence of kin biases in cooperation is based essentially on the direct benefits of cooperation, and thus does not require kin selection (Chapais 2001). In group-living primates, maternal investment often extends throughout the lifespan, mothers maintaining long-term supportive and affiliative relationships with their daughters in female philopatric species (Fairbanks 2000), and with their sons in male philopatric species (Goodall 1986, Furuichi 1997). The very existence of lifelong bonds between mothers and offspring entails that siblings meet around the same mother on a regular basis and become disproportionately available and familiar to each other compared to non-kin. This bias is independent of any intrinsic attraction between the siblings themselves; it is a consequence of the siblings' common attraction to the same mother. Then, if siblings are suitable social partners, and if disproportionate availability and familiarity *per se* increase the chances of forming partnerships, it follows that siblings should cooperate preferentially with each other.

The two explanations differ fundamentally in that the second one does not require kin selection. It states that kin cooperate together for the same reason non-kin cooperate together, namely for the direct fitness benefits of cooperation, but that kin may cooperate more often than non-kin because they are more readily available as partners. While the indirect fitness bonus of kin cooperation is a central component in the first explanation, it is ancillary in the second (Chapais 2001). The two explanations should prove extremely difficult to differ-

entiate because even if kin-biased cooperation was driven by the greater availability of kin, rather than by indirect fitness benefits, the fact is that kin obtain the indirect fitness bonus in any case. Fortunately, this problem does not matter for the present discussion.

### 3.3 The effect of competence

Whatever their relative merits, the two explanations have a central aspect in common; they do not take into account the qualifications and relative competences of partners as a criterion in the formation of cooperative partnerships. Not all types of activities call for competence. For example, suppose that two animals cooperate to keep warm in the context of huddling or co-sleeping (Anderson 1984, Takahashi, 1997). In this situation, the main qualification required from each partner is the ability to produce heat, which requires a minimal body size. Because kin easily meet this qualification, the two explanations for kin biases in cooperation should apply. First, the equation  $B + Br > B$  is always satisfied; cooperation provides the same direct benefits  $B$  whether one cooperates with kin or with non-kin, but by cooperating with kin, individuals obtain additional indirect fitness benefits. Second, because close kin are no less valuable than non-kin for the task, but close kin are disproportionately available and familiar, they could be chosen as partners if only for this reason. I refer to cooperative activities such as social thermoregulation, whose payoff is little affected by variation in the partner's qualifications, as low-competence cooperation. The expression "attribute-independent cooperation" was used in a previous paper; Chapais & Bélisle 2004. Low-competence cooperation should be markedly and consistently kin-biased.

In contrast, competence differentials may be crucial in other situations. For example, suppose that an individual's goal is to gain access to resources monopolized by a high-ranking individual, and that this relationship translates into a grooming-for-tolerance cooperative partnership. The dominant partner's main qualification is its absolute power, determined to a large extent by its absolute rank. In this situation, kin are not necessarily the best partners. Which partner, then, should ego cooperate with? Let  $B$  represent the direct benefits of cooperation with a given kin, and  $q$  the ratio of competence between a potential non-kin partner and that kin, so that cooperating with the non-kin yields  $qB$ . For cooperation to be more advantageous with the non-kin,  $qB > B + Br$ , which reduces to  $q > 1 + r$ ; that is, the ratio of competence between the non-kin and kin partners must be greater than one plus the degree of relatedness between ego and its kin. For example, a female having a choice between cooperating with a half-sibling ( $r = 0.25$ ) or a non-kin, should choose the non-kin if its competence for the task is more than 1.25 times (or 25%) higher than the kin's competence. This condition may be easily satisfied considering that kin of the wrong age or rank may be considerably less competent than non-kin. I refer to such cooperative activities, whose payoff is markedly affected by variation in the partners' qualifications, as competence-dependent cooperation. The expression "attribute-dependent

cooperation” was used in Chapais & Bélisle 2004. Competence-dependent cooperation should not be strongly and consistently kin-biased.

### 3.3.1

#### Low-competence cooperation

Table 3.1 classifies a sample of cooperative activities according to whether they belong to the low-competence category or to the competence-dependent category, specifying for each the nature of the partnership, the qualifications required, whether kin may meet these qualifications, and whether one expects kin biases as a result. Besides social thermoregulation, another possible form of low-competence cooperation is reciprocal grooming, assuming that grooming is performed for hygienic or comfort-related reasons (Hutchins & Barash 1976, Barton 1985, Schino et al. 1988, Boccia et al. 1989, Keverne et al. 1989, Tanaka & Takefushi 1993, Aureli et al. 1999). In this situation, a partner’s qualification is its ability to reciprocate grooming, which only requires a minimal age. Because an individual’s kin are likely to include such suitable grooming partners, one expects grooming to be kin-biased for the same reasons given in the case of social thermoregulation; that is, both because kin are readily available and because cooperating with them yields additional indirect fitness benefits. If, on the other hand, grooming is performed to obtain social benefits such as increased tolerance levels (Hemelrijk et al. 1992, Muroyama 1994, Henzi & Barrett 1999), access to food (de Waal 1997a), or coalitionary support (Seyfarth 1977, Seyfarth & Cheney 1984, Hemelrijk 1994), kin are not necessarily the most competent partners and grooming should not necessarily be kin-biased.

To test the present hypothesis about the differential impact of kinship on grooming distribution, one needs to differentiate and analyze separately the grooming episodes that individuals perform to obtain social benefits (competence-dependent cooperation), and those they perform to obtain grooming in return (low-competence cooperation). The difficulty of this task is commensurate to that of establishing clear causal relationships between behavioral categories, as exemplified by the relationship between grooming given and aiding received, first proposed by Seyfartyh (1977) and still debated 25 years later; e.g. contrast Schino (2001) with Henzi & Barrett (1999) and Henzi et al. (2003). But another way of testing the present hypothesis would be to compare whole grooming distributions in two situations: (i) when grooming is performed to obtain social benefits and (ii) when it is performed for its own value; only in the latter situation should grooming be reciprocal within dyads and markedly kin-biased.

Data on grooming among female chacma baboons (*Papio ursinus*) lend themselves to such a test. Henzi et al. (2003) compared the distribution of grooming in the same group between two periods, when ecological conditions favored contest competition for food, and later when this was not the case. When food competition was profitable, females had more diverse grooming partners in terms of rank distance, presumably because they sought to exchange grooming for tolerance at food sites with higher-ranking females. In contrast, when food competition was lower, females had a smaller number of partners, who ranked closer to themselves on average, presumably because they exchanged grooming only for

**Table 3.1.** Non-exhaustive classification of cooperative activities in primates according to whether the activity's payoff is affected by the partners' qualifications (competence-dependent cooperation) or not (low-competence cooperation). See text for references.

Goal of cooperation	Nature of partnership	Qualifications required	Determinants of qualifications	Do kin meet qualifications?	Kin bias expected?
<b>Low-competence cooperation</b>					
Thermo-regulation	Huddling/co-sleeping	Minimal heat produced	Minimal size	Yes	Yes
Receive grooming	Reciprocal grooming	Ability to groom	Minimal age	Yes	Yes
Gain maternal experience	Allomothering	Caring for an infant	Minimal age	Yes	Yes
<b>Competence-dependent cooperation</b>					
Gain access to resources <sup>a</sup>	Grooming for tolerance	Absolute power	High rank	Not necessarily	No
Obtain aid/rise in rank <sup>b</sup>	Grooming for aiding	Absolute power	High rank	Not necessarily	No
Rise in rank <sup>c</sup>	Mutual aiding	Relative power	Rank similarity	Not necessarily	No
Maintain one's rank <sup>d</sup>	Mutual aiding and grooming	Relative power	Rank similarity	Yes (matrilineal hierarchies)	Yes but amplified <sup>e</sup>
Gain access to resources	Mutual sharing	Relative power	Rank/age similarity	Not necessarily	No
Practice motor/social skills	Social play	Size similarity	Age similarity	Not necessarily	No
Catch preys/obtain meat	Group hunting/meat-sharing	Hunting experience	Absolute age	Not necessarily	No

<sup>a</sup> In exchange for grooming.

<sup>b</sup> Bridging alliance (Chapais 1995) formed between A and C in a  $A > B > C$  rank order.

<sup>c</sup> Revolutionary alliance (Chapais 1995) formed between B and C in a  $A > B > C$  rank order.

<sup>d</sup> In exchange for grooming and/or aiding

<sup>e</sup> In matrilineal hierarchies, kin rank close to each other, which may amplify nepotism. See text.

its own value (Henzi et al. 2003). Given that in baboons females close in rank are usually kin (Lee & Oliver 1979, Walters 1980, Hausfater et al. 1982, Johnson 1987, Silk et al. 1999), the data suggest that grooming was more kin-biased when food competition was lower and social benefits were less at stake. In a previous study, Barrett et al. (1999) also reported that when competition was lower grooming was exchanged reciprocally, presumably because females needed not exchange it for social benefits with high-ranking females. In sum, these data support the hypothesis that when grooming is performed in the context of a low-competence cooperative activity, it is more kin-biased, as predicted.

A third possible example of low-competence cooperation is the care of infants by individuals other than the mother, or allomothering. For allomothering to qualify as a low-competence cooperative activity, it must in the first place qualify as a cooperative one. Although not all allomothering is cooperative (Hrdy 1976, Nicolson 1987), Fairbanks (1990a) reported the existence of a system of mutualistic cooperation between helpers and mothers in vervet monkeys (*Cercopithecus aethiops*). Females who spent more time allomothering were more successful in keeping their first-born infant alive, presumably due to their greater maternal experience, and mothers using allomothers had shortened inter-birth intervals. Thus, both the helpers and the recipient mothers derived direct fitness benefits from allomothering. Second, for allomothering to qualify as a low competence activity, it should require few qualifications on the part of both the allomother and the infant and its mother. From the perspective of a helper seeking to gain maternal experience, the infant's qualifications and competence are probably irrelevant; any infant will do. But infant kin (e.g. sisters) are more available and familiar, and taking care of them provides additional inclusive fitness benefits (Fairbanks 1990a). From the infant's and mother's viewpoint, the same reasoning applies; older sisters are readily available to allomother their younger siblings, and allowing them to allomother provides the infant and the mother with inclusive fitness benefits (Fairbanks 1990a). Kin allomothers may also be less likely to harm the infant (Nicolson 1987).

Thus, even though allomothering may require some competence (e.g. experience), it is open to a large array of individuals, kin and non-kin, because specific qualifications which are often found among non-kin, such as a high rank or age similarity, are not required. In this sense, cooperative allomothering would be a low-competence activity, which could explain why it is often kin-biased (Nicolson 1987, Chism 2000).

### 3.3.2 Competence-dependent cooperation

Table 3.1 also lists possible examples of competence-dependent cooperative activities. In these examples, the partners' qualifications vary between absolute power (a correlate of high rank), relative power (a correlate of closeness in rank), experience (determined by absolute age) and size similarity (a correlate of age similarity among immatures). Because kin do not necessarily meet these criteria, the corresponding partnerships should not be consistently kin-biased. For example, as mentioned above, individuals might use grooming as a currency to

obtain aid (Seyfarth 1977, Schino 2001) or tolerance at food sites (Henzi & Barrett 2003), from high-ranking individuals. Hence, such cooperative partnerships should not be markedly kin-biased. However, they could be among members of high-ranking matriline because in this situation, the targeted partners are both related and high-ranking. Interestingly, rates of affiliative relationships were reported to be higher within high-ranking matriline than within lower-ranking ones in baboons (Silk et al. 1999).

Social play provides another illustration of competence-dependent cooperation. Social play is hypothesized to provide mutual benefits to partners through its role in the development of motor and social skills (Fagen 1993). Thus, although social play is rarely viewed as a cooperative activity, it satisfies the criteria for mutualistic cooperation; partners gain direct benefits and they do so in the course of the interaction itself. When individuals have a choice between partners, age similarity proves to be a major determinant in the formation of play partnerships, presumably because age similarity correlates positively with peer familiarity and similarity in size and strength (Fagen 1981). Similar-age partners are often not available among close kin (e.g. siblings), even though older or younger close kin are often available. Thus, similar-age unrelated partners seem to be favored over dissimilar-age kin. In this sense, social play is a competence-dependent activity whose major qualification is age similarity. Accordingly, play is slightly or not kin-biased (Walters 1987, Janus 1989, Berman 2004).

Primates may also form partnerships on the basis of rank similarity. For example, among the chimpanzees (*Pan troglodytes*) of the Ngogo community (Uganda), Mitani et al. (2000) found that matrilineally-related males did not associate or cooperate preferentially. Cooperation was measured by mutual participation in alliances, meat sharing and boundary patrols. In a subsequent study, Mitani et al. (2002b) reported that males selected their partners on the basis of age similarity (same age class) and rank similarity (same rank class), and reasoned that the absence of nepotism reflected the non-availability of kin partners of the right age and rank due to the long birth interval of chimpanzees (5-6 years). Stated differently, chimpanzees gave priority to age and rank rather than to kinship; they were non-nepotistic because they engaged in competence-dependent cooperation. Chimpanzees are male-philopatric and live with several patrilineal relatives. I consider the possibility of patrilineal nepotism in a later section.

The effect of the rank similarity criterion on cooperation also operates among females, but then it may be confounded by kinship in situations where close-ranking females are also kin, as commonly happens in matrilineal dominance hierarchies. The observed high levels of attraction between female kin in matrilineal societies are commonly attributed to the effect of kinship *per se* because the respective effect of its correlate, rank similarity, is most often not assessed. But two studies that analyzed the separate influences of kinship and rank similarity revealed that both factors contributed to attraction and tolerance among close-ranking female kin. De Waal (1991b) found that closeness in rank significantly increased levels of proximity and co-drinking in two groups of rhesus monkeys (*Macaca mulatta*) independently of kinship, and, similarly, Kapsalis & Berman (1996) reported that rank similarity significantly increased



levels of affiliation (approaches, proximity, contact and grooming) among free-ranging rhesus monkeys, independently of kinship. Both sets of results indicate that competence-dependent cooperative activities driven by rank similarity were probably underestimated in groups characterized by matrilineal dominance systems (see below). Both studies also found that kinship increased rates of behaviors independently of closeness in rank. Thus, in these studies and in others (e.g. Silk et al. 1999), the effect of kinship is real; it is not an artifact of the rank similarity correlate (see Silk, this volume).

### 3.3.3

#### The relationship between kinship and competence

The foregoing argument about the relative role of kinship and competence in patterning cooperation was framed in dichotomous terms. I argued that cooperative activities whose outcomes are minimally affected for competence differentials should be kin-biased, whereas cooperative activities whose outcomes vary substantially in relation with the partners' qualifications should not be kin-biased. At first sight, this dual classification may appear justified because any given cooperative activity can either require some well-defined qualifications (e.g. rank-based power and the capacity to offer help), or not (e.g. the capacity to provide heat). Although heuristically useful, the dichotomy is nonetheless somewhat simplistic because competence is a continuous variable.

As stated previously, ego should prefer a more competent non-kin over a less competent kin when  $q > 1 + r$ , where  $q$  reflects the competence ratio between the non-relative and the relative. When the competence ratio is higher than 1.5, ego should always choose the non-kin partner over all potential kin partners, even its closest kin because the maximal degree of kinship (in outbred populations) is 0.5. But when  $q$  is lower than 1.5, some kin could be advantageously chosen over the non-kin partner. For example, half-siblings ( $r = 0.25$ ) should be chosen over non-kin when  $q < 1.25$ . Thus, competence-dependent cooperation could be kin-biased provided  $q$  is relatively low. In the previous discussion of competence-dependent cooperation, I assumed that high levels of competence were required for the activities considered (Table 3.1), and that there were no reasons to believe that kin partners were better qualified than non-kin. This assumption appears generally reasonable in light of the examples reviewed.

However, even when  $q$  is higher than 1.5, cooperation might be performed among kin for two reasons. First, kin might be the most competent partners. Two examples have already been mentioned. Assuming that the main qualification for a given cooperative activity is rank similarity, that criterion coincides with kinship in matrilineal hierarchies; hence, cooperation among females would be kin-biased because female kin have similar ranks. The other example concerned the high-rank qualification in matrilineal hierarchies. For members of the highest-ranking matriline, high-ranking partners are also close-ranking individuals so that cooperation among highest-ranking individuals could be kin-biased because it is rank-biased.

Second, competence-dependent cooperation could be kin-biased because competent non-kin are not available, even though they are present in the group.

In such a situation, individuals would have no choice but to cooperate with kin. For example, low-ranking individuals might be unable to interact with high-ranking non-kin if they are prevented from doing so by mid-ranking individuals, as in Seyfarth's (1977) grooming model. Such a situation would favor cooperation among kin.

I have hitherto discussed situations where competence-dependent cooperation could be kin-biased contrary to the main argument presented here. The reciprocal may also be true. Low-competence cooperation, which is expected to be kin-biased, could take place both among kin and non-kin if not enough kin are available. This is expected when matrilineal groups are small as in decreasing populations (Dunbar 1988), or due to random demographic fluctuations.

I conclude that, in general, kinship should have little effect on the selection of partners for cooperative activities: (i) when the competence ratio ( $q$ ) is high, or more specifically, higher than 1.5, and (ii) provided individuals have equal access to both kin and non-kin. Cooperation should be kin-biased when  $q$  is low and kin are available.

### 3.4

#### **Matrilineal kinship and competence: the contrast between male and female philopatric societies**

In this section, I pursue the investigation of the relative role of competence and kinship in the patterning of cooperation by examining an apparent contradiction between the importance of matrilineal kinship in male and female philopatric species. In female philopatric species, such as macaques and baboons, matrilineal kinship has a strong impact on the behavior of the philopatric sex (reviewed by Gouzoules 1984, Walters 1987, Bernstein 1991, Chapais 2001, Silk 2002a, Berman 2004, Kapsalis 2004). In contrast, available data on male philopatric species indicate that matrilineal kinship has little effect on the behavior of the philopatric sex (males). The male philopatric species for which we have the best data both on kinship and social interactions is the chimpanzee. Three studies carried out in three different populations of chimpanzees found that affiliation and cooperation among males were not biased towards matrilineal kin as assessed by mitochondrial DNA (mtDNA) haplotype sharing (Goldberg & Wrangham 1997, Mitani et al. 2000, 2002b, Boesch et al., this volume, see also Strier 2004). Similar results, but on smaller samples, were obtained for other male philopatric species: bonobos, *Pan paniscus* (Hashimoto et al. 1996) and muriquis, *Brachyteles arachnoïdes* (Strier et al. 2002). In light of these studies, the instances of cooperation between maternal brothers observed among the Gombe chimpanzees by Goodall (1986) would constitute the exception rather than the rule.

Why would matrilineal kinship promote cooperation among philopatric females, but much less so among philopatric males? One might think that this question is biased, or even irrelevant, because it does not take into account the other half of genetic relatedness, patrilineal kinship. Future studies might indeed reveal that male chimpanzees are nepotistic with their male patrilineal kin even though they are not with their matrilineal kin. I consider the issue of patrilineal

kinship in a separate section (see below). However, treating matrilineal kinship separately in male philopatric societies, as was done by Hashimoto et al. (1996), Goldberg & Wrangham (1997) and Mitani et al. (2001, 2002b), is no less relevant than treating it separately in female philopatric societies, as was done in almost all studies on kinship in these species. If philopatric females are nepotistic with their matrilineal relatives, philopatric males should be as well. So, why do the available data apparently fail to support this prediction? I will examine three different reasons, dwelling on the last two.

First, the discrepancy might reflect a sex difference in the role of competence in the formation of cooperative partnerships. If cooperation in chimpanzees is not kin-biased because it is mostly competence-dependent, as argued above, conversely the high levels of nepotism of philopatric females might reflect a female bias for low-competence cooperative activities. For example, allomothering is practiced essentially by females and is markedly kin-biased (see above). Whether other cooperative activities display such a sex bias – for example whether grooming between males more often aims at obtaining social benefits, and grooming between females more often at obtaining further grooming – remains to be explored.

Two other factors help account for the greater importance of kin biases in female philopatric societies: (i) kin compositions and (ii) the confounding effect of rank similarity on kinship. I examine these factors in the next two sections.

### 3.4.1

#### **Philopatry patterns and differences in kin compositions**

Networks of matrilineal kin differ fundamentally between male and female philopatric societies. In female philopatric groups, females co-reside with several categories of matrilineal kin and discriminate some of them. For example, experiments on Japanese macaques (*Macaca fuscata*) revealed that the degree of kinship beyond which females treated their kin as non-kin was the same for three different categories of behavior: (i) aiding in conflicts (Chapais et al. 1997, 2001), (ii) tolerance at a monopolizable food source (Bélisle & Chapais 2001) and (iii) homosexual inhibition among females (Chapais & Mignault 1991, Chapais et al. 1997). Kin discrimination was manifest between mothers and daughters, grandmothers and grandoffspring, great-grandmothers/great-grandoffspring (tested for only one behavioral category: aiding), and between sisters. Kin discrimination was not manifest between aunts and nieces, and only inconsistently so between aunts and nephews. Using a different methodology, Kapsalis & Berman (1996) reported very similar results for free-ranging rhesus monkeys. Generalizing from these studies, philopatric females would discriminate a minimum of four or five categories of matrilineal kin among all those present.

The number of discriminated categories of matrilineal kin is substantially smaller in male philopatric species, such as chimpanzees, due to the dispersal pattern. Assuming that all males are resident and that most females disperse (Vigilant et al. 2001, Doran et al. 2002), male matrilineal kin reduce to a single category, maternal brothers, because female transfer entails that sons do not co-

reside with their mother's kin. Even assuming that some females reproduce in their natal group so that these females' sons co-reside with their maternal uncles, given that kin discrimination is inconsistent between aunts and nieces in female philopatric societies (see above), the same may apply between uncles and nephews. Matrilineal kin also include mother-son dyads but I focus here on dyads of male matrilineal kin. Hence, to compare adequately the relative importance of matrilineal nepotism between male philopatric societies and female philopatric ones, one should focus on siblings, the only kin that are both available and discriminated on a regular basis in the two types of societies. The question then becomes: does the discrepancy in matrilineal nepotism remain, i.e. do maternal sisters in female philopatric societies cooperate more than maternal brothers in male philopatric societies?

It is not easy to answer this question because very few studies on female relationships partitioned data according to degree of kinship, and further differentiated between cooperative interactions and altruistic ones. But three sets of factors appear to reduce the discrepancy. First, sisters in matrilineal hierarchies have similar ranks and their cooperation may be rank-driven. In other words, if sisters ranked independently of each other, as do maternal brothers in chimpanzees, they might be less kin-biased (see below). Second, much of the cooperation between sisters may be of the low-competence type (e.g. reciprocal grooming, allomothering), which could account for a further portion of the kin bias. Third, it is noteworthy that levels of nepotism between sisters are much lower than between mothers and daughters (Kaplan 1977, Kurland 1977, Massey 1977, Glick et al. 1986, Kapsalis & Berman 1996, Chapais et al. 1997, Chapais & Bélisle 2004), and may even be lower than between grandmothers and granddaughters (Chapais et al. 1997) despite these two categories of kin sharing the same degree of kinship ( $r = 0.25$ ), and sisters being even more closely related on average, if some sisters are full-siblings. Relatively low levels of nepotism between sisters probably reflect the intense and long-lasting dominance competition between them (Datta 1988, Chapais et al. 1994), whereas it is weak between grandmothers and granddaughters. Dominance competition was indeed found to act as a significant constraint on sister nepotism in Japanese macaques (Chapais et al. 1994).

The point here is that by limiting the comparison of the nepotistic tendencies of philopatric males and philopatric females to siblings, the discrepancy in the overall extent of kin biases between the two categories of species is reduced.

### **3.4.2 The amplifying effect of rank similarity on female nepotism**

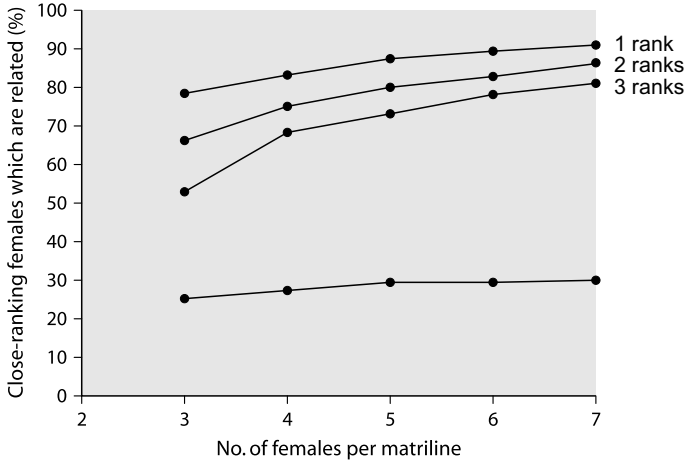
All female-philopatric societies for which we have good data on both kinship and behavior exhibit matrilineal hierarchies in which, by definition, kin rank close to each other. As mentioned above, both kinship and rank similarity contribute, independently, to increase attraction between individuals (de Waal 1991b, Kapsalis & Berman 1996). Thus, observed levels of nepotism in female-philopatric species are consistently amplified to a variable extent and this factor artificially

increases the discrepancy in nepotism between these species and male-philopatric ones.

To better understand how rank similarity amplifies kin biases in cooperation, I have modeled the effect of rank similarity as if females chose their partners on that basis alone; that is, independently of kinship. Consider a matrilineal hierarchy composed of three matrilines (a, b and c) of four females each ( $a_1$ ,  $a_2$ , and so on, in decreasing rank order). Suppose that any female cooperates preferentially with the two females ranking immediately below her, and the two ranking immediately above her. The female's four partners may be kin or non-kin. For example, of the four females that rank closer to  $b_1$ , two are kin ( $b_2$ , and  $b_3$ ), and two are non-kin ( $a_3$  and  $a_4$ ); thus, 50% are kin. I calculated this percentage for each of the 12 females composing the hierarchy; the average is 75%. In other words, assuming that females in a nepotistic hierarchy choose their partners solely on the basis of closeness in rank, 75% of the partners nonetheless happen to be kin. If the rank order were not matrilineal (i.e. if female kin ranked independently of kinship in relation to each other), the average percentage of kin among a female's close ranking partners would be 27% (the proportion of kin dyads out of all dyads). The difference between the two percentages represents the maximal amplification of nepotism due to rank similarity *per se* in this particular hierarchy.

I calculated the percentages of close-ranking females that are kin for various matriline sizes, from three females per matriline (hierarchy of nine females) to seven females per matriline (hierarchy of 21 females), and for various definitions of closeness in rank, from one rank on each side of ego (two close-ranking partners) to three ranks on each side of ego (six close-ranking partners). The results are summarized in Fig. 3.1. The top curve defines closeness in rank as one rank on each side of ego and shows how the percentages of close-ranking females that are kin vary according to matriline size. The second and third curves define closeness in rank as two and three females on each side of ego, respectively. The bottom curve gives the percentage of close-ranking females that are kin when kinship and closeness in rank are decoupled in non-matrilineal hierarchies. The three curves are well above the baseline, indicating that nepotism is amplified for all three definitions of closeness in rank.

All three curves are ascending, indicating that for all three definitions of closeness in rank, the amplification of nepotism increases with matriline size. This is because in hierarchies composed of very small matrilines, close-ranking females are more likely to belong to different kin groups. But the larger the matrilines, the more likely close-ranking females are kin. The most detailed data on matrilineal kinship structures in primates come from provisioned populations of only two species, the rhesus macaques of Cayo Santiago (Rawlins & Kessler 1986) and various populations of Japanese macaques (Fedigan & Asquith 1991). Provisioned populations are often growing, and therefore have particularly extensive kinship structures (Dunbar 1988), which easily extend over four generations in macaques. Thus, given that our best data on the effect of matrilineal kinship on behavior come from provisioned groups composed of especially large matrilines, the amplification of the role of kinship in female cooperation, and our expectations of kin biases have been maximized.



**Fig. 3.1.** Maximal amplification of nepotism due to kin ranking close to each other in matrilineal dominance hierarchies. The model assumes that females form cooperative partnerships solely on the basis of closeness in rank, which is defined in three ways: 1 rank: any female cooperates only with the female ranking immediately below her and the one ranking immediately above her; 2 ranks: the female cooperates with the two females immediately below her and the two above her; 3 ranks: the female cooperates with the three females immediately below her and the three above her. For any matriline size, the percentage of close-ranking females which happen to be kin increases the narrower the definition of closeness in rank. For any definition of closeness in rank, the percentage increases the larger the size of matrilines. The bottom curve (baseline) gives the percentage of close-ranking females that are kin when kinship and closeness in rank are decoupled in non-matrilineal hierarchies.

Fig. 3.1 also shows that for any matriline size, the amplification of nepotism increases as the definition of closeness in rank becomes narrower, being maximal for adjacent-ranking females (one rank position). In this situation, the closest-ranking female is almost always a relative, whereas in the case of larger rank distances, partners may belong to different matrilines. How close in rank to ego a female must be to be treated preferentially can only be determined through empirical studies. For example, data in de Waal (1991b, Fig. 3) show that a rank distance of one stands out from all other rank distances as having the maximal effect on attraction. If this result is representative of other groups and species, the one-rank curve in Fig. 3.1, nepotism maximally amplified, would be closer to reality than the other two curves.

In sum, both historical biases in the selection of populations for which we have the best data on kinship, and the meaning of closeness in rank from the animals' perspective, may have contributed in amplifying our perception of the importance of nepotism in female relationships. It follows that in order to assess the effect of kinship *per se* on female relationships, one needs data on female philopatric species that do not exhibit matrilineal hierarchies. Examples include Hanuman langurs, *Presbytis entellus* (Hrdy & Hrdy 1976, Borries 1993, Koenig 2000) and captive sooty mangabeys, *Cercocebus torquatus atys* (Gust & Gordon 1994), wherein females establish well-defined dominance relationships,

but do not rank close to their kin. Kin biases in behavior should be weaker in such societies if only because nepotism is not amplified by closeness in rank. Unfortunately, detailed data on kinship are not yet available for these species. Even if they were, however, testing the prediction should prove difficult because non-matrilineal societies could exhibit lower levels of nepotism for another, confounding, reason. If female kin do not form alliances to transmit, acquire and maintain their birth rank, as they do in matrilineal hierarchies, levels of altruism and cooperation among female kin should be significantly lower. Thus, levels of nepotism in non-matrilineal societies could be lower both because they are not amplified by rank similarity and because females are socially less dependent on their kin. This is not to say that kin biases should be absent altogether. Kin biases should be clearly manifest in the females' low-competence cooperative activities.

In any case, when data on kinship and behavior become available for female-philopatric societies lacking matrilineal hierarchies, the discrepancy in levels of nepotism between maternal sisters in these groups, and maternal brothers in male-philopatric groups, should be much reduced, if still significant.

### 3.4.3

#### **What about patrilineal kinship?**

Although male chimpanzees do not cooperate preferentially with their matrilineal kin, they might do so with some of their patrilineal kin. One possible process of patrilineal kin discrimination derives from male reproductive skew. The fact that single males may fertilize several females over a limited period of time generates paternal sibships among the resulting offspring. The more pronounced male reproductive skew, the larger the resulting paternal sibships within a given birth cohort. Hence, age similarity might reflect paternal relatedness to some extent (Altmann & Altmann 1979, van Hooff & van Schaik 1994, Strier 2004). Interestingly, as mentioned above, age similarity was found to pattern cooperation among male chimpanzees, along with rank similarity (Mitani et al. 2002b). If age similarity does reflect patrilineal kinship, males might in fact be cooperating with their paternal half-brothers, a possibility evoked by Mitani et al. (2002b), Silk (2002a) and Strier (2004). To understand the implications of this idea, however, it is useful to distinguish clearly between two possibilities.

The first possibility is that males discriminate their paternal brothers among all their age mates, and cooperate preferentially with them through the operation of kin selection. No data on patrilineal kin recognition are available for male philopatric groups, but some data are available for female philopatric groups. Although a number of studies failed to find kin discrimination between paternal sisters (Fredrikson & Sackett 1984, Kuester et al. 1994, Ehardt et al. 1997), other studies reported kin discrimination between paternal sisters close in age in rhesus macaques (Widdig et al. 2001) and savanna baboons (Smith et al. 2003). On this basis, suppose that male chimpanzees do discriminate their paternal brothers among their age mates. Because males are expected to be equally familiar with all age mates, regardless of their degree of relatedness with them, patrilineal kin recognition could not be based on familiarity differentials. An-

other mechanism would be involved, for example phenotype matching, as suggested by Widdig et al. (2001) and Smith et al. (2003) for macaques and baboons. In male-philopatric societies, males co-reside with several categories of male patrilineal kin besides same-aged brothers, including their younger and older paternal brothers, their fathers, sons and uncles. Thus, if males use phenotype matching to recognize their similar-age paternal brothers, they should be able to use it to recognize their younger and older brothers as well as other categories of patrilineal kin, and they should cooperate preferentially with kin of various ages and ranks. This prediction is not easily reconcilable with the observation that male chimpanzees cooperate preferentially with males close in age and rank (Mitani et al. 2002b).

The second possibility is that males do not discriminate their paternal brothers among their age mates. Nonetheless, they would have been selected to cooperate preferentially with age mates because these are often paternal brothers. Thus, by cooperating with age mates in general, males would increase their inclusive fitness. In other words, males would use the age similarity criterion as a marker of potential patrilineal kinship, the age bias would be in fact a kin bias, and cooperation would be driven by kin selection. There are four problems with this hypothesis. First, only a fraction of same-age males are paternal brothers if male reproductive skew is weak. For example, in chimpanzees, Constable et al. (2001) reported that only 36% of paternities in the Kasakala community of Gombe could be attributed to the males that were in the alpha position at the time of conception (see also Strier 2004). Second, age similarity between males is a poor marker of patrilineal kinship in a male-philopatric society, as mentioned above. Only a fraction of all patrilineal kin would correctly identify each other through age similarity. Paternal brothers belonging to different age cohorts would not, nor would fathers and sons, for example. Note that age similarity is a much better marker of patrilineal kinship between females in a female-philopatric society because most patrilineal kin are paternal sisters. Third, if males use age similarity essentially as a marker of kinship, they should cooperate with all the kin that they can recognize, for example their maternal brothers. But this is apparently not the case, as mentioned above. Fourth, males also choose their partners on the basis of rank similarity. They do so independently of age similarity (Mitani et al. 2002b), and there is no reason to believe that rank similarity correlates with kinship. Thus, if the rank similarity qualification is used for its own sake, the age similarity criterion could be as well. The four arguments suggest that age similarity is not used as a marker of kinship.

Based on the available evidence, I conclude that it is unlikely that cooperation between age mates reflects patrilineal kinship in a male philopatric society. As argued above, if the cooperative activities of males are mostly competence-dependent, and age similarity a criterion of competence, partner selection may be driven by the direct benefits of cooperation, not by kin selection.



### 3.5

#### Summary and conclusions

The expectation that individuals should consistently cooperate with their kin implicitly assumes that kin and non-kin make equally valuable partners, or that individuals are unable to assess competence and its determinants, such as relative age and rank. Both assumptions are amply contradicted by empirical evidence, supporting the hypothesis that low-competence cooperation should be markedly kin-biased, but high-competence cooperation should not be, except when kin are more competent, or when competent non-kin are not accessible. Although much remains to be done to test this hypothesis, the evidence reviewed here provides preliminary support for it.

The expectation that cooperation should be kin-biased derives essentially from the role attributed to kin selection in its evolution. One important correlate of the preponderant role attributed to kin selection in the evolution of behavior in general is the idea that any kin-biased behavior is the likely product of kin selection. This correlate has also been re-examined recently. In a previous paper (Chapais 2001), I questioned the assumption that a number of kin-correlated behaviors, including certain forms of grooming, allomothering and aiding, were altruistic and the product of kin selection. Several such behaviors seem to have been forced into an altruism framework, with the emphasis being put on the costs to their performers rather than their benefits. If kin-correlated behaviors provide performers with direct benefits, they might evolve through mechanisms other than kin selection (see above), or kin selection might be involved, but secondarily (Chapais 2001; but see Silk, this volume). A similar line of argument has been made for cooperative breeding in vertebrates. Kin selection is widely invoked to explain why non-breeding individuals help others raise their young while apparently incurring a net cost, but a growing body of evidence reviewed by Clutton-Brock (2002) points to an underestimation of the direct benefits to helpers and the overestimation of the indirect benefits of helping. The role of mutualism in the evolution of cooperative breeding in vertebrates appears to have been relatively neglected (Clutton-Brock, this volume).

Due to its powerful logic and to its position as the unique evolutionary theory specifically devoted to kinship, inclusive fitness theory has had a deep impact on our view of kin-biased behavior. Perhaps as a consequence, we tend to attribute all forms of interactions between kin to the operation of kin selection, even though empirical tests of kin selection and alternative mechanisms are badly needed (Chapais 2001, Clutton-Brock 2002). By consistently equating nepotism with kin selection, we have come to view kinship as such a powerful determinant of behavior that we expect genetic relatedness to explain the distribution of cooperation as much as it explains the distribution of altruism. Such a view probably owes much to the fact that our knowledge about kinship in primates is predominantly derived from a few species and populations in which nepotism is particularly important, if not paramount (Chapais & Berman 2004). In particular, we should obtain a more balanced view of the explanatory value of kinship in female relationships when we obtain data on female-philopatric societies lacking matrilineal hierarchies.

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