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## Kin selection and the distribution of altruism in relation to degree of kinship in Japanese macaques (*Macaca fuscata*)

Received: 29 September 2000 / Revised: 22 January 2001 / Accepted: 5 February 2001 / Published online: 15 March 2001  
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**Abstract** Using kin selection theory and Hamilton's equation ( $B/C > 1/r$ ) to determine how group-living individuals should allocate altruism among their various categories of kin has proven extremely difficult. Among the factors responsible are: (1) the unclear altruistic status of many behavioral categories, (2) the difficulty of assessing the values of  $B$  and  $C$ , and hence their impact on the distribution of altruism according to relatedness, (3) the potentially confounding effect of reciprocal altruism on kin selection, and (4) the various time constraints limiting the ability of individuals to favor distant kin. We report experiments on Japanese macaques (*Macaca fuscata*) which made it possible to assess or control the effect of these factors on the distribution of altruism in relation to degree of kinship. We concentrated on a clearly altruistic behavioral category with a particularly large  $B/C$  ratio to maximize the distribution of altruism according to relatedness. The behavior was unilaterally distributed between kin, hence minimizing the confounding effect of reciprocal altruism on its distribution. Time constraints were eliminated by giving potential donors equal opportunities to behave altruistically with every kin tested. In each experiment, an adult female was given an opportunity to help at low cost one of her juvenile kin outrank its dominant peers. In previous experiments of this sort carried out on juveniles females, we had tested the impact of four categories of adult female kin. In the present experiments carried out on juvenile males, we tested new categories of adult female kin and increased our sample of kin dyads considerably. Altruism toward young males extended to  $r=0.125$  among direct kin (great-grandmother/great-grandson dyads), and to  $r=0.25$  among collateral kin (siblings), or inconsistently to  $r=0.125$  (aunt-nephew dyads). These relatedness lim-

its of nepotism may reflect the limit of the profitability of altruism as defined by the terms of Hamilton's equation and/or the limit of kin discrimination in our group.

**Keywords** Primates · Altruism · Kin selection · Kinship

### Introduction

Inclusive-fitness theory (Hamilton 1964; or kin selection: Maynard Smith 1964) defines whether kin altruism is advantageous in any specific set of circumstances defined by the equation  $B/C > 1/r$  (where  $C$  stands for the cost to the donor,  $B$  the benefit to the kin, and  $r$  their degree of relatedness). In group-living species in which individuals live with a variety of kin, the set of conditions favorable to altruism may be met repeatedly on a daily basis. Assuming that individuals have a limited amount of time and energy to devote to the care of others, how should they allocate altruism among their various categories of kin? This basic question was tackled empirically by Kurland (1977) and addressed in theoretical terms by Altmann (1979) with regard to primates. Since then, however, the role of kin selection in the distribution of nepotism within groups has received relatively little attention, more interest being paid to its explanatory value at the group level (Morin et al. 1994; Bradley 1999; Gagneux et al. 1999; Pope 2000).

Most studies on kin biases in behavior in non-primate mammals have focused on the mother-offspring and sibling kin classes (Blaustein et al. 1987; Halpin 1991; Hepper 1991). Few studies have tested kin discrimination between more distant relatives. Sherman (1980, 1981) found that in Belding's ground squirrels, *Spermophilus beldingi*, daughters and sisters were treated as kin while granddaughters, nieces, and cousins were treated as non-kin. Hepper (1987) reported that laboratory rats, *Rattus* spp., spent more time investigating cousins than non-kin.

In primate species characterized by female philopatry and male dispersal, networks of matrilineal kin are po-

Communicated by P. Kappeler

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tentially extensive. Considering only the subset of kin with a coefficient of relatedness  $r \geq 0.0625$ , an individual embedded in a four-generation matrilineal structure may be expected to meet 12 different categories of kin over its lifetime. Matrilineal kinship is known to be an important factor promoting favoritism in primates (Gouzoules 1984; Gouzoules and Gouzoules 1987; Walters 1987; Bernstein 1991). Assuming that some categories of nepotistic interactions meet the conditions defined by Hamilton's equation, how many kin and which ones should individuals favor?

Hamilton's equation determines one aspect of this question, namely the minimal degree of relatedness at which a given form of altruism is profitable, in other words its maximal distribution among kin classes. For example, for a  $B/C$  ratio of 4, altruism is profitable only between kin sharing an  $r > 0.25$ , but for a  $B/C$  ratio of 8, it is profitable at  $r > 0.125$ . Hence, the larger the  $B/C$  ratio, i.e., the larger the benefits to the recipient and/or the smaller the cost to the donor, the more extensive the distribution of altruism. Although this reasoning is straightforward, using kin selection to predict the distribution of a given form of altruism among kin classes has proven extremely complex for a number of reasons. First, as stated repeatedly in the past, the altruistic status of various categories of behaviors (e.g., allomothering, interventions in conflicts, and social grooming) is often unclear. Several contextual categories of these behaviors may represent self-beneficial, mutualistic interactions, in the course of which both partners gain similar or different benefits (Chapais 2001). Hamilton's equation does not predict the distribution of mutualistic behaviors among kin, only that of altruistic behaviors. And even in the case of altruistic behaviors, the difficulty of assessing the values of  $B$  and  $C$  makes it almost impossible to predict the distribution of altruism.

Second, the distribution of altruism among kin does not necessarily reflect the sole operation of kin selection. Suppose that some forms of kin altruism have evolved through reciprocal altruism (Trivers 1971). In this situation, relatives exchanging altruistic behaviors would benefit personally when they are payed back by their kin. In an evolutionary perspective, any inclusive-fitness benefits would be incidental and secondary in importance. Thus, it would be misleading to draw conclusions about the role of kin selection in the allocation of altruism from an analysis of altruistic interactions that are distributed bilaterally among kin. One way out of this problem would be to focus on altruistic behaviors that are distributed unilaterally among kin, because such behaviors would be attributable to kin selection only.

Third, the distribution curve of altruism among kin could reflect various time constraints, in addition to the three variables of Hamilton's equation. For example, long-duration behaviors, such as grooming, might not be allocated to distant kin if individuals use all the grooming time they have available to satisfy the needs of their very closest kin, as may be predicted on theoretical grounds (Altmann 1979; Weigel 1981; Reiss 1984).

Thus, all else being equal, the limit of the distribution of lengthy behaviors among kin classes should be less likely to reflect the limit of the profitability of altruism, compared to brief behaviors (e.g., interventions in conflicts). Another type of time constraint is the size of kin classes. An individual living with a large number of close kin in extended genealogies (e.g., in expanding groups) should have less time and energy left to satisfy the needs of its more distant kin, compared to an individual living with a small number of close kin. The smaller the average size of kin classes, the larger the potential distribution of altruism in relation to degree of kinship (Chapais 2001).

In sum, to assess the range of operation of kin selection in terms of degrees of kinship, at least four conditions must be satisfied. The behavior must be (1) contextually homogeneous and clearly altruistic, (2) characterized by a particularly high  $B/C$  ratio, (3) unilaterally distributed between kin, and (4) minimally time constrained. A number of observational studies have presented data on the distribution of various behaviors according to degree of kinship in primates (Kurland 1977; Massey 1977; Kaplan 1978; Berman 1982; Glick et al. 1986; Singh et al. 1992; Kapsalis and Berman 1996; Rendall et al. 1996). However, most of these were not designed to test kin selection theory and those that were could not address simultaneously all the conditions mentioned above. Hence, the extent to which the frequency distributions of behaviors in relation to degree of kinship reflect the operation of kin selection is not at all clear.

The present paper is a follow-up of a previous study (Chapais et al. 1997) in which we analyzed the distribution of nepotism according to degree of kinship in a group of Japanese macaques (*Macaca fuscata*). In this species, females establish matrilineal dominance orders by socially inheriting the rank of their mother (Chapais 1992; Pereira 1992). In our prior experiments, an adult female was isolated with a group of juvenile females, the lowest-ranking of which was a relative of the adult female. Due to her larger size, the adult female was dominant to all juveniles and had the opportunity of acting nepotistically by performing low-cost interventions in favor of her kin against dominant peers. We tested the impact of four categories of adult female kin. Mothers, grandmothers, and sisters intervened promptly in conflicts involving their young female kin, which outranked their peers as a result. In contrast, aunts appeared unconcerned by peer conflicts and no rank reversals occurred. We concluded that nieces were beyond the relatedness limit of nepotism in this context.

The present paper presents the results of similar experiments, but differs in a number of respects from our previous study. First, in that study (Chapais et al. 1997), we were mostly concerned with kin discrimination and we did not explore the implications of our experimental design for testing kin selection theory, as we do here. Our experiments indeed satisfy the four conditions stated above which are required to assess the range of degrees of kinship at which kin selection may operate: the inter-

ventions of adult females were contextually homogeneous and altruistic; they were characterized by a particularly large *B/C* ratio that maximized their expected distribution; they were unilaterally directed between kin, hence minimizing the potential confounding effect of reciprocal altruism on their distribution, and the effect of time constraints on the allocation of altruism was eliminated by giving potential donors equal opportunities to help each kin tested.

Second, the present experiments allowed us to increase the number of kinship categories tested, hence to extend our investigation of the distribution of altruism at, and beyond, the degree of relatedness at which nepotism appeared to drop markedly in our prior experiments ( $r=0.125$ ). Indeed, in addition to the four categories of kin mentioned above, we tested great-grandmother/great-grandson dyads, grandaunt-grandnephew dyads, and a few dyads of cousins. Third, the experiments reported here increased considerably the sample size of the kin categories that had already been tested, e.g., to the sample of 5 aunt-niece dyads tested (Chapais et al. 1997) we added 16 aunt-nephew dyads. Finally, the present experiments were conducted on peer groups composed, this time, of juvenile males. In several species of macaques and baboons, males are part of their natal group's matrilineal hierarchy early in their lives prior to transferring into other groups (Koyama 1967; Sade 1967; Lee and Oliver 1979; Johnson 1987; Kuester and Paul 1988; Pereira 1988) and behave like females in this respect (Chapais and Gauthier 1993).

## Methods

### Study group and husbandry

The founding members of the study group came from the Arashiyama colony of Japanese macaques translocated to Texas in 1972 (Fedigan 1991) and were established at the Université de Montréal in 1984. The initial group consisted of 15 animals belonging to three distantly related and structurally similar matrilines named A, B, and C. The present experiments were carried out over five research seasons, in 1986, 1993, 1994, 1995, and 1997. In 1997, the group numbered 51 individuals: 17 adult females ( $\geq 5$  years), 10 younger females, four adult males ( $\geq 6$  years), and 20 younger males. Prior to 1992, the colony lived in five indoor rooms and one outdoor pen covering 120 m<sup>2</sup>. In 1992, the colony was moved into a larger but similarly structured facility (five rooms and two pens; 230 m<sup>2</sup>). The monkeys had access to all rooms and pens through sliding doors. All areas were equipped with climbing devices. The animals received daily monkey chow, fruits, vegetables, and various grains distributed in the woodchip litter. Water was available at will. Subgroups of individuals were formed in a few minutes by first directing the whole group into a small central room. By manipulating the sliding doors, we let one monkey at a time go into an adjacent room from which the animal joined its subgroup.

### Definitions

The definitions used here are similar to those described in Chapais et al. (1997). Dominance was established on the basis of the direction of submissive behaviors. Dominance relationships were considered stable when submission was unidirectional from the subor-

dinate animal and aggression unidirectional from the dominant one. Ever since the formation of the group, rank relations followed the typical matrilineal pattern, with the adult females of the A matriline dominant to those of the B matriline and both of these dominant to the females of the C matriline. Aggressive interventions occurred when an individual entered a conflict and sided with one opponent against the other. The intensity of the intervener's aggression determined the intensity of interventions (level 1: threats; level 2: lunging at; level 3: chasing; level 4: contact aggression; level 5: bites). The mean intensity level of a subset of interventions was calculated by weighting each intervention by its corresponding level of intensity, summing up these values and dividing the sum by the number of interventions, yielding values between 1 and 5. Solicitations for support include head-flagging, approaching, and making contact with a potential protector while threatening or being threatened by an opponent, and high-pitched distress calls uttered in association with aggressive behaviors toward an opponent.

Siblings are assumed to be maternal half-siblings ( $r=0.25$ ), this assumption defining the other degrees of matrilineal kinship. The assumption of no patrilineal relatedness is probably simplistic but appears nonetheless acceptable because what is specifically assumed here is the absence of significant differences in the degree of patrilineal relatedness between the various categories of kin dyads tested, e.g., a juvenile male is not more patrilineally related to a sister than to an aunt. In any case, patrilineal kinship does not appear to translate into detectable favoritism in macaques and baboons, i.e., to be recognized (Fredrikson and Sackett 1984; Kuester et al. 1994; Erhart et al. 1997). Because some kinship classes share the same matrilineal  $r$  (e.g.,  $r=0.125$  for great-grandmother/great-grandson dyads and aunt-nephew dyads), we distinguish between direct relatedness ( $r_d$ ) and collateral relatedness ( $r_c$ ).

### Experimental protocols and statistical analysis

Each experiment began with the formation of a subgroup of juveniles, composed of one or two juveniles per matriline, hence three or six per subgroup. The subgroup was maintained for 2–3 days (depending on the experiment) during which time rank relations were assessed. We then introduced an adult female kin of the juvenile(s) that ranked lowest in the peer subgroup. The adult female remained with the juveniles over 3–4 days during which time her presence could either have no effect on the rank of her juvenile kin, or induce rank reversals. In a third step, we removed the adult and assessed the rank relations between the juveniles over 2–3 days. We pursued the series by returning to step 1, introducing an adult female kin of the lowest-ranking juvenile, and so on. In each experimental series, the phase during which the peers were by themselves (step 3) served as the baseline period for the following phase in which a new adult female was introduced.

Here we present results on the impact of seven categories of adult females: mothers ( $r_d=0.50$ ), grandmothers ( $r_d=0.25$ ), older sisters ( $r_c=0.25$ ), great-grandmothers ( $r_d=0.125$ ), aunts ( $r_c=0.125$ ), grandaunts ( $r_c=0.0625$ ), and cousins ( $r_c=0.0625$ ). Experiments were carried out separately on 1- and 2-year-old males, called young juveniles and older juveniles, respectively. The experiments on young juvenile males were carried out over two seasons using 13 different adult females and 9 different males. The experiments on older juvenile males extended over three seasons and involved 12 different adult females and 9 different males. The introductions of the 13 adult females in the peer subgroups composed of 3 or 6 young juveniles produced 27 different kin dyads (adult female-young juvenile male). Similarly, the introductions of the 12 adult females in the peer subgroups composed of 3 or 6 older juveniles produced 18 different kin dyads (adult female-older juvenile male). The two sets of dyads were analyzed separately. In each set, the dyads were treated as independent points, although in some cases, the same individual could appear in more than one dyad, e.g., as a son in one subgroup and as a nephew in another (Tables 1, 2). This was unavoidable given the constraints imposed

by the age-sex composition and genealogical structure of the group at the beginning of any research season. However, we consider our data to be weakly dependent for three reasons: (1) the absolute number of juvenile males and adult females tested was relatively important, (2) the experiments extended over five research seasons so that an individual appearing in more than one dyad most often did so over different years, and (3) in primates, the behavior of an individual changes as a function of the dyad in which it participates, as shown by the bulk of evidence on the differential effect of degree of kinship on social interactions (Kurland 1977; Massey 1977; Berman 1982; Gouzoules 1984; Glick et al. 1986; Walters 1987; Bernstein 1991; Singh et al. 1992; Kapsalis and Berman 1996; Rendall et al. 1996; Bélisle and Chapais, in press), hence dyads sharing one individual are nonetheless independent to some extent.

All statistical tests are two-tailed.

#### Data collection

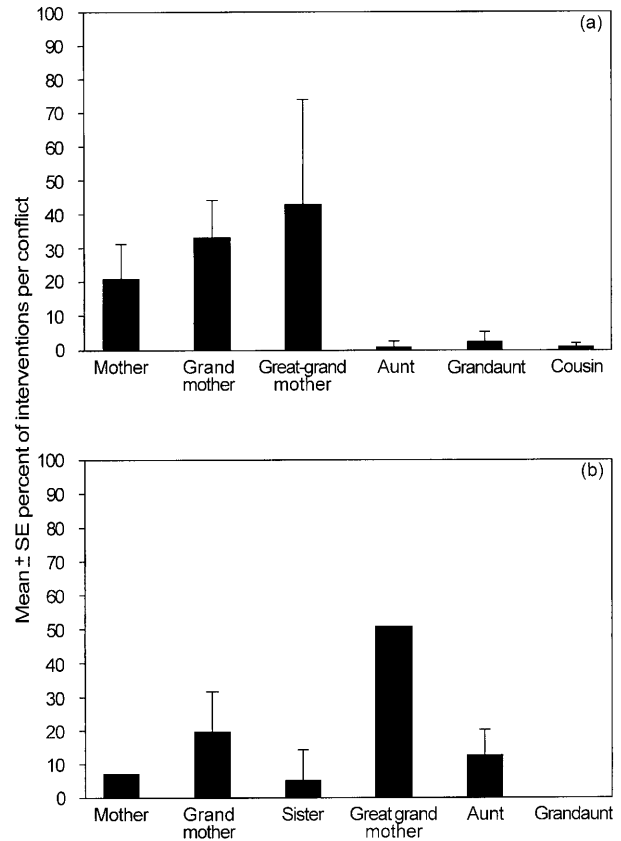
Observations were made from a central observation area, behind windows. Data collection began as soon as a subgroup was formed. We observed the subgroup continuously until rank relations stabilized and then conducted 60-min observation periods every 1 or 2 h until 1700 hours. We recorded all agonistic interactions of all group members. Data were coded on paper in a temporal sequence marked by 1-min intervals. The experiments with 1-year-old males totaled 204 observation h (daily mean=3.6 h) during test periods (adult kin present) and 105 observation hours (daily mean=2.8 h) during baseline periods (adult kin absent). The experiments with 2-year-old males totaled 280 observation hours (daily mean=4.1 h) during test periods (adult kin present) and 189 observation hours (daily mean=3.3 h) during baseline periods (adult kin absent).

## Results

### Young males

Table 1 summarizes data on the dominance relations of young (1-year-old) males before and after the introduction of an adult female kin. We tested 27 different adult female-young male kin dyads. In 11 of the 27 dyads, the male kin outranked its dominant peers. Only the males that were related to the adult female outranked their peers, pointing to the effect of kinship on the rank relations of males. The effect of kinship varied according to degree of relatedness. The mean degree of relatedness between the adult female and her male kin was significantly higher when rank reversals occurred [ $0.38 \pm 0.2$  (SE)] than when none took place ( $0.13 \pm 0.01$ ; Mann-Whitney test:  $n_{1,2}=11,16$ ,  $Z=3.5$ ,  $P=0.005$ ). Young males could outrank dominant peers in the presence of their mother, grandmother, and great-grandmother, but did not do so in the presence of their aunt, grandaunt, and cousin.

The adult females performed a total of 61 interventions in conflicts between their young male kin and dominant peers while their kin was subordinate to its peers (i.e., prior to the rank reversals if they occurred, or over the whole experimental period if none took place). Adult females sided 100% of the time with their male kin. Thus, they consistently acted nepotistically, but the rates at which they did so varied according to their degree of



**Fig. 1** Mean rates of intervention by each category of adult female on behalf of male juvenile kin: young (1-year-old) males (a), older (2-year-old) males (b). Rates of intervention were calculated for the period during which the male kin was behaving submissively toward its peers

kinship with the young male. Figure 1a shows a marked drop in the rates of intervention of adult females, which coincides with the categories of females (aunts, grandaunts, and cousins) whose presence did not induce rank reversals.

To assess more precisely the role of adult females in the ability of their young male kin to outrank peers, we compared their intervention behavior in the situations in which rank reversals took place ( $n=11$  dyads) and when none occurred ( $n=16$  dyads). The adult females were notably more nepotistic in the first category of situations. Their hourly rates of intervention on behalf of their male kin were higher when rank reversals occurred than when none took place (Mann-Whitney test:  $n_{1,2}=11,16$ ,  $Z=2.1$ ,  $P=0.04$ ), although they intervened with similar intensity in both situations ( $n_{1,2}=6,8$ ,  $U=21$ ,  $P=0.70$ ). Their rates of intervention per conflict ( $n=567$ ) tended to be higher when rank reversals occurred ( $n_{1,2}=11,16$ ,  $Z=1.7$ ,  $P=0.08$ ) and they answered a higher proportion of their male kin's solicitations for aid in these situations ( $n_{1,2}=3,11$ ,  $Z=2.5$ ,  $P=0.01$ ). In sum, the ability of young males to outrank dominant peers required the presence of certain categories of close adult female kin and matched the greater involvement of the latter in these circumstances.

**Table 1** Effect of the presence of an adult female on the rank relations between her 1-year-old male kin and dominant peers

Kin dyad	Number of peers outranked by juvenile kin	Percentage of submissive acts ( <i>n</i> ) <sup>a</sup>	
		Before introduction of adult kin	After introduction of adult kin <sup>b</sup>
<b>Mother/son</b>			
C31/C311	4/4	0.0 (7)	100 (69)
A7/A73	4/4	0.0 (29)	100 (70)
A32/A321	4/4	0.0 (7)	100 (12)
B5/B55	4/4	0.0 (2)	100 (29)
B9/B92	4/4	0.0 (70)	97.8 (46)
C31/C313	4/4	0.0 (29)	100 (140)
C32/C322	3/3	0.0 (67)	100 (184)
<b>Grandmother/grandson</b>			
B/B71	4/4	0.0 (37)	100 (54)
B/B92	0/4	0.0 (30)	0.0 (44)
B/B55	0/4	0.0 (8)	0.0 (23)
<b>Great-grandmother/great-grandson</b>			
C/C311	4/4	0.0 (6)	100 (27)
C/C322	4/4	5.0 (20)	100 (142)
C/C313	3/3	0.0 (42)	100 (76)
<b>Aunt/nephew</b>			
A7/A33	0/2	0.0 (8)	3.6 (28)
B9/B71	0/4	0.0 (20)	0.0 (103)
A2/A73	0/4	0.0 (6)	0.0 (56)
A31/A321	0/4	0.0 (7)	0.0 (25)
B2/B92	0/4	0.0 (74)	0.0 (122)
B2/B55	0/4	0.0 (22)	0.0 (53)
B3/B92	0/4	0.0 (54)	1.4 (71)
B3/B55	0/4	0.0 (29)	2.7 (37)
B5/B92	0/4	0.0 (9)	0.0 (46)
C31/C322	0/3	0.0 (9)	0.0 (17)
<b>Grandaunt/grandnephew</b>			
A2/A321	0/4	0.0 (7)	0.0 (64)
A7/A321	0/4	–	0.0 (47)
<b>Cousins</b>			
A31/A73	0/4	0.0 (6)	0.0 (39)
A32/A73	0/4	0.0 (6)	2.0 (50)

<sup>a</sup> Percentage of submissive acts received by juvenile male kin from its peers out of all submissive acts between them

<sup>b</sup> Following the initial rank reversal by the juvenile male kin

## Older males

Table 2 summarizes data on the dominance relations between older (2-year-old) males before and after the introduction of an adult female kin. We tested 18 different adult female-older male kin dyads. The male kin outranked dominant peers in 13 of these. As was the case with younger males, only the males that were related to the adult female outranked their peers. However, the effect of kinship in this case was not clearly related to degree of relatedness. The mean *r* between adult females and older male kin was not higher when rank reversals took place [ $0.25 \pm 0.04$  (SE)] than when none occurred ( $0.16 \pm 0.08$ ; Mann-Whitney test:  $n_{1,2}=5,13$ ,  $Z=1.7$ ,  $P=0.09$ ). Older males could outrank dominant peers in the presence of their mother, grandmother, older sister, great-grandmother, aunt, and grandaunt. Table 3 summarizes the results of Tables 1 and 2.

Also in contrast with the results for young males was the role of adult female kin in the rank reversals. The

following analyses exclude the three mother-son dyads observed in 1986 for which comparable data were not available. Adult females performed a total of 38 interventions in conflicts between their older male kin and dominant peers while the juvenile kin was subordinate to its peers. They favored their kin 97.4% of the time, hence consistently behaving nepotistically, as with younger male kin. However, the rates at which they did so was not clearly related to their degree of kinship with the male (Fig. 1b) and the ability of older males to outrank dominant peers was not related to the greater involvement of their adult kin. The hourly rates of intervention of adult females on behalf of their male kin were not higher when rank reversals took place than when none occurred ( $n_{1,2}=5,10$ ,  $U=22$ ,  $P=0.71$ ), nor were their rates of intervention per conflict ( $n=455$ ) ( $n_{1,2}=5,10$ ,  $U=26.5$ ,  $P=0.85$ ), the intensity of their interventions ( $n_{1,2}=4,6$ ,  $U=5.5$ ,  $P=0.15$ ) and the frequency with which they answered their male kin's solicitations for aid ( $n_{1,2}=3, 7$ ,  $U=10$ ,  $P=0.90$ ). In sum, older males needed

**Table 2** Effect of the presence of an adult female on the rank relations between her 2-year-old male kin and dominant peers

Kin dyad	Number of peers outranked by juvenile kin	Percentage of submissive acts ( <i>n</i> ) <sup>a</sup>	
		Before introduction of adult kin	After introduction of adult kin <sup>b</sup>
Mother/son			
A/A4	2/2	0.0 (88)	100 (2)
B/B4	1/1	0.0 (78)	100 (64)
C/C4	2/2	0.0 (42)	100 (161)
C3/C31	0/1	0.0 (13)	31.8 (22)
Grandmother/grandson			
A/A23	3/3	2.5 (119)	98.8 (80)
B/B22	3/3	0.0 (199)	99.2 (126)
B/B23	0/1	33.3 (3)	9.1 (11)
C3/C311	2/2	0.9 (40)	97.7 (86)
Older sister/brother			
A31/A33	2/2	0.0 (81)	100 (15)
B21/B23	2/2	0.0 (42)	100 (96)
Great-grandmother/great-grandson			
C/C311	1/2	0.0 (5)	98.1 (52)
Aunt/nephew			
A2/A33	2/2	0.0 (82)	100 (50)
A7/A33	2/2	2.1 (48)	100 (44)
B7/B22	0/2	1.5 (69)	2.4 (82)
B7/B23	0/1	23.5 (34)	5.9 (17)
B9/B23	0/2	0.0 (46)	3.2 (31)
C32/C311	2/2	0.0 (29)	94.4 (18)
Grandaunt/grandnephew			
C7/C311	1/2	0.0 (14)	100 (85)

<sup>a</sup> Percentage of submissive acts received by juvenile male kin from its peers out of all submissive acts between them

<sup>b</sup> Following the initial rank reversal by the juvenile male kin

**Table 3** Summary of the effect of the presence of adult females on the rank relations between their male kin and dominant peers. For example, in the presence of their mother, 2-year-old males outranked dominant peers in three of the four mother-son dyads tested

Category of adult female kin	One-year-old males	Two-year-old males	Total
Mother	7/7	3/4	10/11
Grandmother	1/3	3/4	4/7
Sister	–	2/2	2/2
Great-grandmother	3/3	1/1	4/4
Aunt	0/10	3/6	3/16
Grandaunt	0/2	1/1	1/3
Cousin	0/2	–	0/2

the presence of an adult female kin to outrank dominant peers, but not necessarily her active participation in the process.

Given this, why were the older males sometimes unable to outrank peers? We tested whether the agonistic dimension of the relationship between the male and its adult female kin might affect the male's ability to benefit from her presence. More specifically, we checked whether agonism between them was more pronounced in situations in which the male did not outrank peers compared to when he did. The rates of aggression directed by the adult female to her male kin were higher in situations where the males did not outrank peers (Mann-Whitney test:  $n_{1,2}=5,10$ ,  $U=8$ ,  $P=0.04$ ), although the intensity of that aggression was similar in both situations ( $n_{1,2}=5,8$ ,  $U=18$ ,  $P=0.77$ ). Thus, older males had a more negative relationship with those adult female kin whose presence

did not induce rank reversals. Interestingly, this was not the case with younger males (rates of aggression:  $P=0.43$ ; intensity of aggression:  $P=0.23$ ), whose ability to outrank peers depended more on the active involvement of their adult kin, as seen above.

## Discussion

The interventions of adult females in the present experiments were assumed to be altruistic, i.e., to impose a net cost to the performers. This implies that when intervening, the adult females did not derive personal benefits that outweighed the costs of their interventions. This could indeed be the case in situations where two individuals jointly defeat a higher-ranking target (revolutionary alliance), or when they combine forces against a lower-

ranking but strong individual to reinforce their dominance position over the latter (conservative alliance). In both situations, the alliance partners are likely to derive immediate, personal benefits that outweigh the costs incurred; consequently, such alliances are best viewed as instances of mutualism (Bercovitch 1988; Chapais et al. 1991; Noë 1992; Chapais 1995; Widdig 2000). In the experiments described here, in contrast, the male targets were very young and clearly subordinate to the adult females, hence the interventions did not apparently provide adult females with obvious personal benefits. On the other hand, the costs of intervening appeared to be small and limited to the expenditure of time and energy because the adult females incurred no risk of retaliation from the juvenile males.

The interventions of adult females were also assumed to provide important benefits to the male recipients in terms of rank increments. This assumption rests on the argument that primate males establish well-defined dominance orders and are prone to compete for higher ranks (Walters and Seyfarth 1987), notably through alliances (Chapais 1995), and that dominance rank, in conjunction with several other factors, explains a variable but often significant portion of the variance in male reproductive activity and success (e.g., Cowlishaw and Dunbar 1991; Paul et al. 1993; de Ruiter and van Hooff 1993; Berard 1999; Takahata et al. 1999).

On the basis of this dual assumption, the central question addressed here concerns the domain of altruism of adult females: what kin were they ready to favor in a situation in which (1) the *B/C* ratio was particularly high; (2) the help was unilateral so that the adult female derived no obvious benefits through short-term reciprocity, and (3) the adult female was not limited in the range of kin she could help because she had a single one to take care of in each situation and a few interventions were sufficient to do so. In brief, how extensive is the distribution of unilateral altruism when it is minimally constrained both by time and by the *B/C* ratio?

The results for young (1-year-old) males provide a relatively clear answer. Only mothers ( $r_d=0.5$ ), grandmothers ( $r_d=0.25$ ), and great-grandmothers ( $r_d=0.125$ ) provided help to their male kin; aunts ( $r_c=0.125$ ), grandaunts ( $r_c=0.0625$ ), and cousins ( $r_c=0.0625$ ) abstained from doing so. Furthermore, the nepotism of adult females was efficient: young males outranked dominant peers only in the presence of the adult female kin that helped them. These results indicate that altruism towards young males extended to  $r_d=0.125$ , which would correspond to the relatedness threshold for altruism (or RTA; Chapais 2001) in this particular situation.

In the course of similar experiments in which the peer subgroups were composed of juvenile females (Chapais 1988; Chapais et al. 1997), we reported that the juveniles could outrank peers in the presence of their mothers, grandmothers, and sisters, but never in the presence of their aunts. We could not test the impact of great-grandmothers, hence we were unable to assess whether altruism extended to that level of direct descent. The combi-

nation of these previous results with the present ones point to an RTA at  $r_d=0.125$  among direct kin and  $r_c=0.25$  (siblings) among collateral kin.

The results for the older males accord globally with those for the young males, but with some significant differences. As was the case with young males (and with juvenile females tested in previous experiments), adult females intervened on behalf of an older male kin when the latter was an offspring, a grandoffspring, a great-grandoffspring, or a sibling (Fig. 1b). But they could also intervene (though at low rates) on behalf of a nephew. This suggests that the aunt-nephew dyad ( $r_c=0.125$ ) could be within the RTA for this particular behavioral context. However, only half of the six aunt-nephew dyads resulted in rank reversals, which suggests that this kinship class might represent a gray area as far as the domain of altruism is concerned. This would not be surprising given that degrees of kinship can hardly be expected to be assessed precisely by the animals.

Of more importance, our results for the 2-year-old males indicate that the level of help provided by the adult females stood in no direct relation with the ability of their male kin to outrank peers. Although older males outranked peers conditionally upon the presence of an adult female, the latter's active involvement was not a necessary condition for the occurrence of rank reversals. Older males could apparently benefit from an adult female kin's presence provided they did not have a negative relationship with her. These results probably reflect the greater assertiveness of older compared to younger males (and same-aged females), a well-documented fact in primates (Lee and Johnson 1992). The mere presence of the adult kin appears to increase the older males' level of assertiveness. Whether this kinship effect reflects the fact that the adult females had favored their male kin at a younger age, or whether it relates only to the older males' growing assertiveness per se remains to be investigated. In any case, the fact that adult females might have a positive impact on their kin without acting nepotistically toward them entails that their level of nepotism is better measured on the basis of their interactions with younger and more passive males, and with juvenile females.

Our results suggest that the domain of altruism should be characterized both in terms of degree of relatedness ( $r$ ) and type of relatedness (direct or collateral). At  $r_d=0.125$  (great-grandmother/great-grandson) rank reversals always took place (4/4), but at  $r_c=0.125$  (aunt-nephew) they most often did not (3/16). A possible explanation is that the proximate correlates of direct and collateral relatedness differ in some respects. For example, juveniles might have higher levels of familiarity with their great-grandmothers than with their aunts. But more fundamental aspects of their relationships may also differ. In matrilineal dominance systems, the levels of dominance competition differ between "vertical" and collateral kin. Competition for dominance is intense and long-lasting among sisters (Datta 1988), acting as a significant constraint on nepotism between them (Chapais et al. 1994).

In contrast, competition for dominance between mothers and daughters is infrequent, maternal dominance being the rule. Thus, from a female's viewpoint, grandoffspring and great-grandoffspring are the offspring of non-competitive kin, but nieces and nephews are the offspring of competitive kin (sisters). It follows that dominance competition might constrain nepotism more strongly among collateral kin than among vertical kin in species characterized by matrilineal dominance.

Most of the available evidence for kin selection in primates comes from comparisons between kin and non-kin dyads, e.g., testing whether a given form of altruism is more frequent among kin than non-kin (for reviews, see Silk 1987; Walters 1987; Chapais 2001). Very few primate studies have tested kin selection in relation to specific degrees of relatedness (e.g., Kurland 1977) and more recent studies focused on close kin: mother-offspring and sibling dyads (Maestriperi 1993; Schaub 1996). Altruism and kin selection are particularly well documented for mother-offspring dyads in various areas of behavior including protection and food-sharing. Among siblings and grandmother-grandoffspring dyads, evidence for kin selection exists (Kurland 1977; Silk 1982, 1987; Walters 1987; Chapais 2001), but is much less abundant and sometimes equivocal (Schaub 1996). Beyond  $r=0.25$ , non-equivocal evidence for kin-selected altruism drops markedly. Our results provide evidence for kin-selected altruism up to  $r=0.125$  among direct kin, and  $r=0.25$  among collateral kin (inconsistently,  $r=0.125$ ).

#### Limit of profitability of altruism, or limit of kin discrimination?

Because the experimental protocol ensured that the decision to favor a given kin was unconstrained by time and minimally constrained by the  $B/C$  ratio, the observed relatedness limits of altruism might indicate the degrees of relatedness beyond which altruism is no longer profitable. Obviously, however, behavioral contexts characterized by higher  $B/C$  ratios could push back these limits even further. But situations such as the present experiments, in which the costs to the donor are low while the benefits to the recipient are high may be infrequent. Although several categories of interaction provide recipients with benefits substantially higher than the present ones, e.g., protection against predators or adult males, these interactions most often entail significant costs to the donors, so that their  $B/C$  ratios are probably much lower. The rarity of interactions characterized by low costs and high benefits may explain why altruism is most often limited to close kin classes. If this reasoning is correct, the RTA reported here would be close to the limit of the profitability of altruism in these species.

But there is another possibility. The absence of altruism beyond a certain degree of relatedness might also reflect the limits of kin discrimination. Adult females might be unable to recognize kin beyond a certain degree

of kinship even though nepotism toward these kin might be profitable based on the terms of Hamilton's equation. Distinguishing between these two hypotheses is not an easy task. However, the fact that the RTA for any given behavior is defined by the  $B/C$  ratio of that behavior entails that behaviors differing in their  $B/C$  ratios should vary in their RTAs. Thus, if different behaviors nevertheless showed similar RTAs, this would support the hypothesis that the relatedness limits of altruism reflects not the limit of the profitability of altruism but that of kin discrimination.

In accordance with this possibility, Sherman (1980, 1981) found that the relatedness threshold for nepotism ( $r \geq 0.25$ ) in ground squirrels held across various types of behaviors, including warning calls, cooperative defense of territory or young, and competition to defend a nest. Similarly, we found that the distribution of three categories of behaviors differing in their  $B/C$  ratios dropped significantly beyond  $r_c=0.25$ : interventions in conflicts (present experiments; Chapais et al. 1997), sexual inhibition among females (Chapais and Mignault 1991; Chapais et al. 1997), and co-feeding at a monopolizable food source (Bélisle and Chapais, in press), and beyond  $r_d=0.125$  in the present experiments. If such convergent evidence for a cutoff in nepotism past  $r_c=0.25$  and  $r_d=0.125$  indicates the limit of kin discrimination in Japanese macaques, the RTAs reported here would reflect the limit of kin discrimination, not the limit of the profitability of altruism, and the domain of kin recognition would define the range of operation of kin selection. However, more research is needed on the distribution curves of a larger range of behavioral categories before this conclusion can be drawn.

The limits of nepotism in Japanese macaques and ground squirrels are similar but only superficially so. In ground squirrels, the domain of kinship includes two generations of individuals, grandmother-grandoffspring dyads behaving as non-kin, whereas in Japanese macaques, the domain of kinship covers four generations of direct descendants. Sherman (1980, 1981) suggested that group composition and demography impose limits on the distribution of nepotism, determining the limit of kin recognition in animals: individuals would recognize as kin those relatives they live with on a regular basis, and would treat all others as non-kin. If this principle sets the maximal domain of kin discrimination in animals, it does not appear sufficient to account for the limit of nepotism in primates. In macaques, individuals do not act nepotistically toward certain kin categories, namely collateral relatives other than siblings, although they live with them on a regular basis (Gouzoules 1984; Kapsalis and Berman 1996; Chapais et al. 1997). Thus, the subset of kin categories that are treated preferentially (recognized) appears to be smaller than the total number of kin categories available. Factors other than demography, relating perhaps to the sheer number of kin classes present in a three- to four-generation social group and the difficulties of keeping track of the distinctive characteristics of all of these, might restrict the domain of kin discrimination in

macaques. Due to the remarkable paucity of studies on kin discrimination beyond the mother-offspring bond in primates, there is ample room here for future research.

We conclude that the relatedness limits in the distribution of altruism reported here could reflect either the limit of the profitability of altruism as defined by the terms of Hamilton's equation, or the limit of the kin discrimination ability of the animals, or both.

**Acknowledgements** We thank Hugues Jean, Shona Teijeiro, and Paul Vasey for technical assistance, and Patrick Bélisle, Jean Prud'homme, and three anonymous reviewers for helpful comments on an earlier version of this manuscript. The present experiments are part of a research program described in Animal Utilization Proposal No. 93094 which complies with the regulations of the Canadian Council on Animal Care and has been approved by the Université de Montréal Animal Care Committee. This work was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the Fonds FCAR of the Province of Québec.

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