Coalition Formation Among Male Barbary Macaques (*Macaca sylvanus*)

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A coalition is formed when one animal intervenes in an ongoing conflict between two parties to support one side. Since support of one party is also an act against the other party, coalitions are triadic interactions involving a supporter, a recipient, and a target. The purpose of this study was to test which of three possible theories explains coalition formation among male Barbary macaques: 1) Males support kin to enhance their indirect fitness (kin selection). 2) Males support nonkin to receive future reciprocal support (reciprocal altruism). 3) Males pursue self-interests and immediately benefit via nonkin support (cooperation). Coalition formation was investigated among 31 semi-free male Barbary macaques in the Salem Monkey Park, Germany during the mating season. The results show: 1) Males intervened more often in dyadic conflicts in which a related opponent was involved and supported related opponents more than unrelated opponents. Close kin supported each other more often than distant kin. 2) Some evidence for reciprocal support was found. However, reciprocity was probably a by-product of targeting the same individuals for dominance. 3) Coalition formation among nonkin is best interpreted as cooperation, based on self-interests. Male Barbary macaques seem to intervene more often to stabilize and less often to improve their rank. Although our data were limited, the results revealed that kin support, reciprocal support, and cooperative support were all involved in coalition formation among male Barbary macaques. Am. J. Primatol. 50:37–51, 2000.   © 2000 Wiley-Liss, Inc.

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INTRODUCTION

Conflicts between two animals are often interpreted as competition over limited resources. However, dyadic conflicts in which a third individual intervenes to support one of the two opponents (coalition formation) are harder to understand since selection is not expected to favor individuals who reduce their own fitness to increase the fitness of others. Darwin [1859] realized that altruistic behavior contradicted his theory of natural selection since an indi-

vidual should only help another when it is likely to benefit from the support it provides.

Considering the function of support there are two possible explanations: 1) intervention can be altruistic or 2) selfish. Altruistic behavior is associated with costs to the altruist (i.e., time, energy, risk of injury, and retaliation) and benefits to the recipient (i.e., access to a limited resource and suffering lesser injury in an attack). If coalition formation is altruistic, it is expected to be directed towards kin or reciprocal partners.

The theory of kin selection [Maynard Smith, 1964] predicts that individuals who support kin enhance their indirect fitness because they share genes with the recipient [Hamilton, 1964]. Selection is expected to favor altruism among kin, the closer individuals are related, the lower the costs to the altruist, and the greater the benefits to the recipient [Hamilton, 1964]. There is evidence of kin support among primates [e.g., *Macaca fuscata*: Kurland, 1977; *M. radiata*: Silk, 1982; *Papio cynocephalus*: Walters, 1980], even though male dispersal has reduced the availability of kin. For example, male rhesus macaques prefer to join the same group as their older brothers and form coalitions with them [Meikle & Vessey, 1981].

In reciprocal altruism, however, the altruistic act incurs costs and no immediate benefits, but the altruist receives future benefits from the recipient [Trivers, 1971; Axelrod & Hamilton, 1981]. Since the benefits to the recipient are greater than the costs to the altruist, both partners enhance their direct fitness over a longer period of time even when unrelated. Repayment by the former recipient can be given in the same (support for support) or in different (grooming for support) currencies. Packer [1977] first reported that pairs of unrelated male baboons alternate in enlisting each other to take over an oestrous female from a consort male. Later studies questioned the extent of reciprocity involved in these coalitions [Bercovitch, 1988; Noë, 1989] since both partners were as likely to gain access to the consort female.

Supporters are not altruists when they receive immediate benefits from their support of unrelated individuals [Wrangham, 1982]. Male chimpanzees act selfishly when supporting nonkin against certain opponents since their support can act to increase their own dominance rank [de Waal, 1982]. Thus cooperative behavior may evolve among individuals with self-interests, if they can reach their goals more effectively when cooperating than when they act alone [Brown, 1983]. Compared to a non-cooperative situation, both recipient and supporter immediately benefit, although the benefit can be asymmetrically distributed among the partners [Axelrod, 1984]. Here we prefer the term cooperation instead of mutualism since the latter is conventionally used for inter-specific interactions [Wilson, 1975].

All three theories ultimately result in an increase of the supporter's inclusive fitness via their direct or indirect components [Brown, 1980]. However, they have clear differences [Fig. 1; see also Rothstein & Pierotti, 1988], which have often been overlooked. First, both kin and reciprocal support involve costs. Considering nonkin support, the direct fitness of the supporter is only enhanced over the long term by future reciprocal support from the recipient. In contrast, kin support immediately increases the indirect fitness. Kin can also engage in reciprocity, but support among relatives need not be reciprocal [de Waal, 1985]. Second, in cooperation the costs of support are trivial and the supporter immediately enhances its direct fitness via nonkin support [Chapais, 1995; Dugatkin, 1997]. Furthermore, there is no probability of cheating [Connor, 1986] as in reciprocal altruism. We follow Trivers'

altruistic behaviour		selfish behaviour
kin selection	reciprocal altruism	cooperation
benefit to recipient (kin)	benefit to recipient (nonkin)	benefit to both recipient (nonkin) and supporter
cost to supporter	cost to supporter	no cost to supporter
↓	↓	↓
indirect fitness of the supporter (immediate)	direct fitness of the supporter (delayed)	direct fitness of the supporter (immediate)

Fig. 1.   Three theories to explain coalition formation (see text for distinction between the theories).

[1971, p. 36] definition of cheating as a "failure to reciprocate; no conscious intent or moral connotation is implied."

The purpose of our study was, first, to test which of the three theories are consistent with data on male Barbary macaques since most previous studies have focused only on one theory or used different methodological approaches, which makes comparison difficult [Silk, 1992b]; second, to only consider males, because of the sex difference in coalition formation [e.g., Bond & Vinacke, 1961; Kaplan, 1977; de Waal, 1978; Bernstein & Ehardt, 1985], and third, to test cooperation (i.e., self-interests) on the triadic rather than the dyadic level to avoid a loss of information about one of the participants. Few studies have examined triadic processes [e.g., Datta, 1983a; de Waal, 1984; Bernstein & Ehardt, 1986; Harcourt & Stewart, 1989; Chapais, 1992; Silk, 1993; Vasey, 1996]. We apply the triadic definition introduced by Chapais [1992].

Barbary macaques live in multi-male, multi-female groups with males migrating from their natal group. They have a promiscuous mating system. The reproductive career of males contains three phases [see Kuester & Paul, 1992; Paul & Kuester, 1992]: Between 4 to 5 years of age, males sneak copulations or disturb matings by others (satellite males), at 6 to 7 years of age, males pursue a low risk strategy by staying at the edge of the group during the mating season (peripheral males). Typically around 7 years of age males become established group members. At first, an age-dependent hierarchy exists due to physical differences, e.g., 7-year-old males dominate 6-year-old males etc., but later older males are often subordinate to young adults in dyadic fights and therefore depend on coalition partners during conflicts [see Kuester & Paul, 1992; Paul & Kuester, 1992].

In contrast to baboons [Packer, 1977], male Barbary macaques rarely form coalitions to take over an oestrous female from a consort male [Kuester & Paul, 1992]. Therefore, males are expected to compete for mates mainly via rank relations [van Hooff & van Schaik, 1992; Chapais, 1995]. Witt et al. [1981] suggested that among male Barbary macaques coalition formation results in rank improvement and an increased access to females, but these data were limited to three adult males in captivity.

Here we present data on coalition formation among 31 semi-free male Barbary macaques during the mating season since the knowledge of male patterns in coalition formation of this species is still limited [for females see Prud'homme & Chapais, 1993].

SUBJECTS AND METHODS

The study was conducted at the Salem Monkey Park, Germany, where approximately 300 animals live in four groups in a 14.5 hectare outdoor enclosure. This population is provisioned daily [for details Paul & Kuester, 1988]. Group B was observed for two months during the mating season in 1994. Data were collected from 8 a.m. to 5 p.m. The study group consisted of 31 males (4 male infants were excluded) and 46 females. All males were individually recognized.

Analyses were based on data from "focal animal sampling" conducted on seven males for a total of 196 hr and additional coalitions via "all occurrences sampling" on all 31 males [Altmann, 1974; Martin & Bateson, 1986]. Data analyzed here included displacement behavior, dyadic conflicts and coalition formation (triadic or polyadic conflicts).

Rank acquisition of a male depended on the rank of his mother and the presence of older brothers [Kuester & Paul, 1988]. While we had limited information about the rank of the mothers, the number of male maternal kin present in the group was known. Variables considered per individual male were rank, age and number of male maternal kin. Age of males as well as number and degree of maternal kin were known from previous studies of Kuester and Paul. Rank relations within each male dyad were determined by the distribution of dominant (threaten, bite, hit, and chase) and submissive behavior (retreat after being approached and flee or scream after being the subject of aggression) [see Deag, 1977; Kuester & Paul, 1992]. The resulting dominance hierarchy was constructed as a matrix with minimal reversals (i.e., entries below the diagonal). All males were born in the group.

A coalition was formed when one animal intervened in an ongoing conflict between two parties to support one of them. Depending on the role in this interaction, one distinguishes between the supporter, who intervenes and supports one party, the recipient, who receives the support, and the target, against whom the coalition was formed. If a coalition among non-focal animals occurred during focal sampling, the sample was interrupted to record the coalition. The sample was resumed, if the interruption was less than 3 min [see Silk, 1992b]. Opponents vocalize to recruit support [Gouzoules et al., 1984] and coalitions in the study species are relatively long lasting and noisy events. Thus, together with the fact that males could be recognized over long distances, it is unlikely that a substantial number of dyadic conflicts followed by coalition formation were missed [compare Altmann, 1974]. In a coalition there are clearly three roles to distinguish: The two opponents stand face to face screaming (possibly for minutes), threatening, or attacking each other, while the supporter (or more than one) stands parallel to the recipient and threatens or attacks the target. Since screaming can trigger support "any expression of dominance is suppressed in favor of an appeal for support" even by the dominant opponent [Angst, 1987, p. 51]. Data were restricted to coalition formation among male participants.

For data analyses, coalitions with more than one supporter (polyadic conflict) were split into triads (one supporter) [see Watanabe, 1979; Chapais et al., 1994]. Datta [1983a, p. 289] suggests: "More than three individuals may often be involved but the situation remains fundamentally triadic: the two parties to the dispute and the third, interfering, element." De Waal [1984] could show that male chimpanzees intervene independently of their relationship to other supporters in the same conflict, i.e., they support a particular male and simultaneously have a negative attitude towards his closest ally. Thus males are treated on an individual basis. This was also assumed for all 31 male Barbary macaques in this study, because all pairs of supporters in the same polyadic conflicts (N=78

dyads out of all 465) were also found as target-recipient dyads (N=16) or target-supporter (N=26) dyads in other coalitions. They were also found in recipient-supporter dyads (N=38) but never exclusively there. This and the fact that participants have clear roles justifies the splitting into triads, because it suggests they intervene to support one opponent against the other, and they do not intervene to support other supporters. Therefore, they were assumed to be statistically independent. In this study a sum of 106 dyadic conflicts resulted in coalition formation (triadic or polyadic conflicts). We split the 106 conflicts into 211 triads including just one target, one recipient and one supporter. The 211 triads were separated into categories as follows: 1) the supporter was related vs. was unrelated to the recipient (N=46 kin vs. N=165 nonkin intervention) and 2) the supporter was related (N=7) vs. was unrelated (N=157) to both opponents or just related to one of the opponents (N=47).

Males were separated into three rank-classes [high-ranking (HR), middle-ranking (MR), and low-ranking (LR)] and three age-classes [sub-adults (SA) between 4 and 6 years, young adults (YA) between 7 and 9 years, and old adults (OA) of 10 or more years] [see Kuester & Paul, 1992]. Furthermore, three degrees of maternal kinship were distinguished: brothers, uncle/nephews, and cousins [Kuester et al., 1994]. Since paternity data were not available, the precise degree of relatedness was not known.

Statistical tests were taken from Siegel [1985] and Bortz et al. [1990]. Data were analyzed with SPSS and INSTAT, using two-tailed tests with the level of significance set at alpha 0.05. When we conducted a Bonferroni adjustment, only the significance but not a P-value for each pair-test is shown. A matrix partial correlation test was performed calculating the partial form of the Kr test according to Hemelrijk [1990a,b] who provided her program MATSQP.

RESULTS
General Results

Partial correlation coefficients (Table I) were calculated to test whether there was a relation between the frequency of being a participant in a coalition (target, recipient, or supporter) and the male rank, the age, and the number of maternal male kin, respectively. The data showed that older males were more likely to provide support than younger males (partial correlation coefficient between age and number of supports given controlled for rank and number of relatives: r=0.595, N=27, P=0.001). There was no significant difference among the three rank-classes (ANOVA, N=31 males) concerning the frequency of being target (P=0.251), re-

TABLE I. Partial Correlation Coefficients Between Rank, Age, Number of Male Relatives per Male, and His Frequency of Being a Target, Recipient, or Supporter in a Triad, Controlling for the Two Remaining Variables Out of Rank, Age, and Number of Kin (N=27 Males)

Correlation between	Rank	Age	Number of Male Relatives
Target	0.211	0.109	−0.164
	P=0.272	P=0.573	P=0.397
Recipient	0.211	0.248	−0.106
	P=0.250	P=0.195	P=0.584
Supporter	−0.245	0.595	−0.052
	P=0.220	P=0.001*	P=0.789

*Indicates significance.

cipient (P=0.613), or supporter (P=0.438). The three age-classes (ANOVA, N=31 males) differed in receiving support (P=0.003) and in giving support (P=0.002), but not in being the target (P=0.170). The subsequent multiple pair-wise comparisons (post hoc tests) revealed significant differences among all three pairs of age-classes in receiving support (mean number of support received: OA=5.1, N=17 males; YA=1.5, N=11 males; and SA=11.7, N=3 males) as well as among old adults vs. young adults and old adults vs. sub-adults in giving support (mean number of support given: OA=10.1, N=17 males; YA=2.7, N=11 males; and SA=3.3, N=3 males). No differences were found among the rank-classes for the same tests.

Kin Selection

Support was observed in 18 of 50 kin dyads (36.0%) and in 96 of 415 nonkin dyads (23.1%) (chi-square test, N=465 dyads, P=0.046). However, incorporating the number of opportunities of support should provide a clearer picture. Therefore, we based additional tests on figures per male considering these entities. At first, we tested the null hypothesis, whether males intervened equally often in dyadic conflicts in which one opponent was related to the intervener than in conflicts in which both opponents were unrelated to the intervener. Two ratios per male were calculated: first, the number of his interventions in conflicts between his kin vs. nonkin divided by the total number of conflicts between his kin vs. nonkin, and second, the number of his interventions in conflicts between two unrelated opponents divided by the total number of conflicts between nonkin. There was a significant association between kinship and intervention: males intervened in a larger proportion of conflicts that involved a kin (average proportions: interventions in conflicts between kin and nonkin=0.114; interventions in conflicts between nonkin=0.060; N=27 males; Wilcoxon test, P=0.025).

Males could choose to support related or unrelated opponents in a conflict, but if kin selection is to work they should prefer supporting related opponents. To test this, two ratios were calculated for each male: first, the number of his kin support in conflicts between his kin vs. nonkin divided by the number of conflicts between kin and nonkin, and second, the number of his nonkin support in conflicts between his kin and nonkin divided by the number of conflicts between kin and nonkin. When males had the choice they prefer to support the related opponents (average proportions: kin support=0.097; nonkin support=0.018; N=27 males; Wilcoxon test, P=0.0001).

Kin selection theory also predicts, assuming equal costs that close kin should support each other more often than distant kin. For each of the three degrees of relatedness a ratio was calculated: first, the proportion of his support of brothers in conflicts between his brothers and nonkin, and second, the proportion of his support of uncles or nephews, respectively, in conflicts between his uncles or nephews and nonkin; third, the proportion of his support of cousins in conflicts between his cousins and nonkin. We found a marginally significant relation between provision of support and the degree of relatedness (average proportions: brothers=0.16, N=24 males; uncles/nephews=0.05, N=11 males; and cousins=0.02, N=9 males; Kruskal-Wallis test, P=0.048).

Reciprocal Altruism

We tested reciprocity for the same currency (support for support) by correlating the supporter-receiver matrix with its transposed form. The (i,j)th value in the 31×31 supporter-receiver matrix denotes the number of times support given by supporter i to receiver j. To consider relatedness, a third 31×31 matrix was

constructed with zero values for maternal unrelated individuals and one values otherwise. The partial *Kr* correlation test [Hemelrijk, 1990a,b] for the supporter-receiver matrix partialling out the relatedness matrix was based on 10,000 permutations and revealed that $\tau=0.137$, $P=0.0035$; τ is the partial correlation coefficient based on the *Kr* statistic and *P* is the *P*-value assigned to τ.

In 4 of 50 kin dyads (8.0%) and 14 of 415 nonkin dyads (3.4%) bilateral support was found, but this difference was not significant (chi-square test, N=465 dyads, *P*=0.116). Furthermore, support was observed in 114 of all 465 kin and nonkin dyads, but in only 18 of them support was bilateral. Data to test reciprocity for different currencies were too limited.

Cooperation

Since support of one party is always directed against the other party [de Waal, 1992], all three participants of a triad of males (target (x) vs. recipient (y) plus supporter (z)) were simultaneously analyzed. If A is the highest-ranking, B the middle-ranking, and C the lowest-ranking male within a triad, one of six possible rank patterns can be observed in each triad (Fig. 2). In the notation of a rank pattern (e.g., A vs. B plus C), the first letter is assigned to the target x, the second to the recipient y, and the third to the supporter z. The expected proportion for a triadic rank pattern can be calculated assuming that each combination of three interacting males has the same probability to occur as a triad [see de Waal, 1984 for similar approach for age- and sex-classes]. For example, the expected proportion for A vs. B plus C is the number of all triads (x, y, z) with rank(x) > rank(y) > rank(z) divided by the number of all possible triads. To investigate support among nonkin, this calculation was restricted to triads in which y (recipient) was not related to z (supporter) and then performed for each of the six rank patterns. To compare the observed and expected proportions for each rank pattern, the Binomial test was used. Since we have done six tests on the data set, an alpha adjustment (Bonferroni) was undertaken [Bortz et al., 1990]. The units in these tests were the triads of males (x, y, z).

A vs. B plus C	B vs. C plus A
A vs. C plus B	C vs. A plus B
B vs. A plus C	C vs. B plus A

Fig. 2. Six rank pattern with A as the highest-ranking, B as the middle-ranking and C as the lowest-ranking male *within* a triad (A>B>C, reading: target vs. recipient plus supporter). On the left side supporter are said to risk retaliation [Ehardt & Bernstein, 1992], when they intervene against a higher-ranking target.

Two out of six rank patterns (C vs. B plus A and B vs. C plus A) were observed more often than expected among nonkin (Fig. 3). In both patterns the supporter (A) was higher-ranking than both opponents. Two out of six rank patterns (A vs. B plus C and A vs. C plus B) were observed less often than expected among nonkin (Fig. 3). In both patterns the target (A) was the highest-ranking male within the triad. The observed frequency of the two remaining rank patterns (B vs. A plus C and C vs. A plus B) did not differ from what we expected.
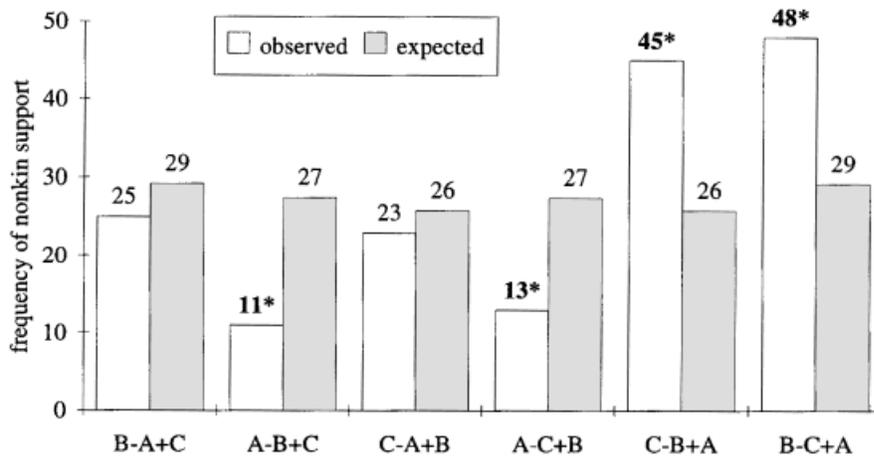
Fig. 3. Observed and expected frequency of rank patterns among nonkin triads (Binomial test, N=165). Note: the expected values for kin and nonkin support for the six rank patterns are equal over all 31 males. This figure includes only the expected values of nonkin support which are multiplied here by the number of observations.

Intervention can occur in three kinds of dyadic conflicts: 1) when both opponents are lower-ranking than the intervener, 2) when both opponents are higher-ranking than the intervener, and 3) when one opponent is lower-ranking and one opponent is higher-ranking than the intervener. Males could be expected to differ in their likelihood of intervening in conflicts, based on their rank- and age-classes, since the risk of retaliation by the target varies accordingly.

We investigated whether individuals belonging to different rank- and age-classes, respectively, differed in their frequency of intervention when both opponents were lower-ranking than the intervener. The ratio between the observed and possible supports per male were calculated. There was a marginally significant difference between the probability of intervention among the three rank-classes (average proportions: HR=0.069, N=8 males; MR=0.079, N=12 males; and LR=0.019, N=8 males; Kruskal-Wallis test, P=0.046). High- and middle-ranking males were more likely to intervene when both opponents were lower-ranking. Data on conflicts of this type were only available for old and young adults. We also found a difference between the probability of intervention among these two age-classes (average proportions: OA=0.086, N=17 males and YA=0.016, N=11 males; Mann-Whitney test, P=0.0041). Old adults were more likely to intervene when both opponents were lower-ranking.

Furthermore, we considered whether individuals from different rank- or age-classes, respectively, differed in their frequency of intervening in conflicts when both opponents were higher-ranking than the intervener. No significant differences were found among rank-classes (average proportions: HR=0.00, N=2 males; MR=0.045, N=11 males; and LR=0.044, N=11 males; Kruskal-Wallis test, P=0.247), or age-classes (average proportions: OA=0.060, N=13 males; YA=0.019, N=8 males; and SA=0.017, N=3 males; Kruskal-Wallis test, P=0.97).

When a male intervenes in the third kind of conflict, he can either support the opponent that is higher-ranking or lower-ranking than himself. Did males prefer to support one type of opponent? For each male, the proportion of support for the lower-ranking and the proportion of support for the higher-ranking opponent were calculated. When males intervened, they significantly biased their support towards the higher-ranking opponent (average proportions: higher-ranking

opponent=0.042 and lower-ranking opponent=0.017; N=24; Wilcoxon test, *P*=0.037). Further tests indicated that this preference was independent from the rank- or age-class that the male belongs to.

DISCUSSION

The data indicate that kin support, reciprocal support, and cooperative support were involved in coalition formation among male Barbary macaques of the study group, although it appears that they differ in the extent. It is problematic to compare our results with those in the literature since studies on coalition formation often differ in their methods [see Silk, 1992b].

Kin Selection

Males in this study intervened nearly twice as often in conflicts in which a maternal kin was involved than in conflicts involving only nonkin. When there was a choice between related and unrelated opponents, males preferred to support their kin. Our results suggest that male Barbary macaques distinguished between maternal kin and nonkin, even though nonkin males were familiar, due to a lack of migration. Kin may be more reliable coalition partners than nonkin because support by relatives is more likely [Harcourt, 1989]. That males support their kin on a higher proportion than nonkin was also shown in bonnet macaques [Silk, 1992a].

As in other macaque species, the degree of relatedness seems also to be relevant for Barbary macaques. Data on female Japanese macaques suggest that there is a relatedness threshold for effective kin support above the aunt-niece level of relatedness [Chapais et al., 1997]. Close kin support each other more than distant kin in *M. nemestrina* [Massey, 1977], *M. mulatta* [Kaplan, 1978], and *M. tonkeana* [Petit & Thierry, 1994]. However, these studies do not differentiate between males and females being recipients or supporters, although there are functional differences in coalition formation between the sexes [see above]. Juvenile baboons already differ in agonistic support and rank acquisition between the sexes [Pereira, 1989]. Since rank relations among male primates are more unstable than in females, the interest of male partners change over time [de Waal, 1985]. Therefore, coalition formation among males is more changeable and dominance-orientated than among females, who tend to support the lower-ranking but familiar opponent more often [see also Hemelrijk & Ek, 1991]. Furthermore, female macaques stay in their natal group with their kin, while males migrate and thus have reduced opportunities to support kin [Kaplan, 1977, 1978; Bercovitch, 1988; Silk, 1992a].

Female Japanese macaques act nepotistically more often towards those kin with whom they do not compete for dominance [Chapais et al., 1994]. Nepotism seems to prevail when it does not conflict with the supporter's self-interest. Therefore, nepotism does not necessarily imply kin selection (i.e., altruistic act) when it cannot be excluded that the supporter benefits from kin support [Chapais et al., 1994, 1997].

However, male Barbary macaques do not restrict their support to kin, thus coalition formation cannot be explained entirely by kin selection.

Reciprocal Altruism

If reciprocal altruism is the basis for coalition formation, males should support those from whom they received support in the past and refuse to support those who have failed to return support [Packer, 1977].

Our data indicate that males gave support to those males from whom they received support in return. This statement, however, should be treated with caution since the partial correlation coefficient is very small, indicating at most a weak correlation. Its significance might be due to the large matrices considered. Reciprocal support was only evident in a few dyads, but this may be due to our relatively short period of observation rather than a lack of reciprocity.

Previous studies have reported that reciprocal support occurs in several primate species [e.g., *Pan troglodytes*, *Macaca mulatta*, and *M. arctoides*: de Waal & Luttrell, 1988; *Gorilla gorilla*: Watts, 1997; *Papio anubis*: Packer, 1977; *Cercopithecus aethiops*: Hunte & Horrocks, 1987; *M. radiata*: Silk, 1992b]. Male bonnet macaques are also known to exchange grooming for support [Silk, 1992b]. Seyfarth & Cheney [1984] used play-back experiments to show that support was more likely after grooming in unrelated vervet monkeys. A similar experiment on long-tailed macaques revealed that after being groomed individuals supported their groomer [Hemelrijk, 1994]. Among adult male Barbary macaques grooming has rarely been observed and never outside a male-infant interaction [Paul et al., 1996]. However, Chapais et al. [1995] tested the affiliation-for-support hypothesis via experimentally induced rank reversals among Japanese macaques. Mutual selfishness rather than reciprocal altruism provided a better explanation as both groomer and supporter immediately benefited.

Male Barbary macaques intervened against their reciprocal partner in 9 of 14 nonkin dyads. Following the theory of reciprocal altruism, a reciprocal relationship should be immune to cheating (i.e., refusal to reciprocate) [Trivers, 1971]. However, refusal need not end reciprocal relationships [see Noë, 1990]. Reciprocal relationships among male baboons did not break off when one partner refused to join a coalition against a consort male [Bercovitch, 1988]. This suggested to Bercovitch that coalitions are the outcome of cooperation between males pursuing self-interests.

Barbary macaques seem not to limit nonkin support to reciprocal partners. Males who intervened chose their reciprocal partner sometimes as recipient and sometimes as target. Bilateral support might evolve as a by-product when both partners target the same individual for dominance and should therefore be interpreted in terms of self-interest [Prud'homme & Chapais, 1996]. However, since our sample size is limited, additional data are needed.

Cooperation

Our analysis of cooperation among nonkin triads showed that males intervened more often than expected when they were higher-ranking than both opponents, suggesting that the supporter was avoiding possible retaliation from a higher-ranking target [Kaplan, 1978; Bernstein & Ehardt, 1985]. Both rank patterns were most frequent observed among male bonnet macaques as well [Silk, 1993, Table 8]. Our data also indicated that if the supporter outranks both opponents, he was equally likely to support the lower- and the higher-ranking opponent. If he supports the lower-ranking one (B vs. C plus A), a bridge coalition results [Chapais, 1992]. Chapais suggested that A supports C to prevent a rank challenge by B. This should be most likely when the rank difference between A and B is small. Support of the higher-ranking opponent (C vs. B plus A) is called conservative support [Chapais et al., 1991], and is expected when A clearly dominates B, and A seeks to prevent a coalition between B and C that might threaten A's rank. From the supporter's point of view, in both triads he benefits by stabilizing his own rank via nonkin support [Chapais et al., 1991].

If A intervenes in a conflict between B vs. C, both alternatives of support (of

B or C) prevent revolutionary coalitions against A (see below) [Chapais, 1992]. Using removal experiments, Chapais et al. [1991] have shown that unrelated female Japanese macaques from two dominant matrilines were dependent on each other to maintain their dominance of females from the third-ranking matriline. Owing to the selfish interests of the supporters, Chapais et al. [1991, p. 490] concluded that "cooperation provides a more satisfactory explanation of non-kin interventions, compared to reciprocal altruism."

In our study, two other rank patterns, in which the recipient and the supporter were lower-ranking than the target, were rare. Both these patterns were also least often observed in male bonnet macaques [Silk, 1993, Table 8]. Chapais [1992] called both triads revolutionary coalitions because the supporter challenges the rank of the higher-ranking target. Such interventions involve a risk of retaliation by the target and may cause rank instability. Studies on wild and captive chimpanzees have shown that supporters used such triads to challenge higher-ranking targets [Riss & Goodall, 1977; de Waal, 1982]. The same was found by Witt et al. [1981], but their results were limited to three adult captive male Barbary macaques.

Why are revolutionary coalitions formed so rarely? First, at least for macaques they are associated with a high risk of retaliation [Datta, 1983a; Bernstein & Ehardt, 1985; Kaplan, 1978]. In contrast, chimpanzees frequently intervene against higher-ranking targets to improve their rank [de Waal & Luttrell, 1988]. Second, Noë [1992, p. 308] has pointed out that "a coalition will be successful when the combined fighting ability of two males exceeds the fighting ability of their opponent." However, for chimpanzees [Goodall, 1986] and baboons [Noë & Sluijter, 1995], it has been shown that two partners do not always exceed the fighting ability of the target male. Therefore, conflicts between higher-ranking opponents may stay dyadic because lower-ranking individuals are inhibited from interfering [Colvin, 1983]. Third, high-ranking animals may recruit more support than low-ranking animals [Cheney, 1983] because they may provide more efficient support in return [Cheney, 1977; Seyfarth & Cheney, 1988].

As mentioned above, triadic patterns in Barbary macaques (Fig. 3) have a lot in common with bonnet macaques [Silk, 1993, Table 8]. Males in both species are most likely to intervene when they outrank both opponents and least likely to intervene against a target that is the highest-ranking male in the triad. Data from both species suggest that males rarely form coalitions that put them at risk of retaliation [see Bernstein & Ehardt, 1985]. Silk [1993] concluded that male bonnet macaques do not use coalitions to increase in rank as do chimpanzees [de Waal, 1982]. In Barbary macaques, nonkin interventions seem to stabilize the existing rank of the supporter. This is in line with an increase in helping as male bonnet macaques rise in rank [Silk, 1993].

Our data also suggest that high- and middle-ranking males tend to intervene more often when they outrank both opponents. Although these types of interventions are generally associated with low risk of retaliation for the supporter, low-ranking males rarely use them. Among baboons low-ranking males rarely form coalitions with each other since they are not effective [Noë & Sluijter, 1995], whereas coalitions between middle- and low-ranking males increase their mating success [Noë & Sluijter, 1990]. Among different age-classes old adult males intervened more often than young adults in conflicts where they outrank both opponents. Old adult males seemed to use interventions of low risk to stabilize their rank because at a certain age, older males are subordinate to young adults unless they have coalition partners [Paul & Kuester, 1992]. Young adults may lack the social experiences to initiate successful coalitions. However, for baboons the relative fighting ability of the partners rather than experience, familiarity,

or affinitive bonds is most important to form successful coalitions [Noë & Sluijter, 1995]. Our data suggest that among male Barbary macaques who provide support, age is more important than rank; thus coalition formation is chiefly the domain of old adult males in this species.

Individuals who cooperate can temporarily increase their competitive ability [Harcourt, 1989]. Therefore, competitive ability should not be restricted to features like size, power, and health because social skills are also important [Bernstein, 1976; Bercovitch, 1991]. However, paternity analyses of the study population have shown that male rank was correlated with reproductive success in three out of four birth seasons [Paul et al., 1993]. If genes of high-ranking males are likely to be represented much more in the next generation, males should be selected to attain their highest possible rank [Datta, 1983b]. Yet less is known about the long-term advantage of being high-ranking because life-time reproductive success is a function of differential reproduction, longevity, and offspring survivorship [Cheney & Seyfarth, 1990]. Males may occupy their highest individual rank only for a short period; thus they may also use alternative tactics, such as coalition formation, to maximize their reproductive success [Bercovitch, 1991; Berard et al., 1994].

CONCLUSIONS

We tested three theories to explain coalition formation among male Barbary macaques during the mating season. While support of related individuals can be accounted by kin selection, support of unrelated individuals appears to be of selfish (cooperation) rather than of altruistic origin (reciprocal altruism). Reciprocal support is discussed as a by-product when individuals target the same individual for dominance. Nonkin interventions are interpreted in terms of self-interest. The interests of an intervener depended on the rank relations among the participants in a coalition. Male Barbary macaques seem to intervene more often to stabilize (instead of improve) their rank via nonkin support. This may be due to the risk of retaliation when they intervene against higher-ranking targets.

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REFERENCES

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Angst W. 1980. Aggression bei affen und menschen. Berlin: Springer.

Angst W. 1987. Some basic biological terms and concepts of primate aggression, with a focus on aggressive alliances. In: Mc-Guinness D, editor. Dominance, aggression, and war. New York: Paragon House Publishers. p 42–63.

Axelrod R. 1984. The evolution of cooperation. New York: Basic Books.

Axelrod R, Hamilton WD. 1981. The evolution of cooperation. Science 211:1390–1396.

Berard JD, Nuernberg P, Epplen JT, Sch-

midtke J. 1994. Alternative reproductive tactics and reproductive success in male rhesus macaques. Behaviour 129:177–201.

Bercovitch FB. 1988. Coalitions, cooperation and reproductive tactics among adult male baboons. Anim Behav 36:1198–1209.

Bercovitch FB. 1991. Social stratification, social strategies, and reproductive success in primates. Ethol Sociobiol 12:315–333.

Bernstein IS. 1976. Dominance, aggression and reproduction in primate societies. J Theoret Biol 60:459–472.

Bernstein IS, Ehardt CL. 1985. Agonistic aiding: kinship, rank, age and sex influences. Am J Primatol 8:37–52.

Bernstein IS, Ehardt CL. 1986. Selective interference in rhesus monkey (*Macaca mulatta*) intragroup agonistic episodes by age-sex class. J Comp Psychol 100:380–384.

Bond JR, Vinacke WE. 1961. Coalitions in mixed-sex triads. Sociometry 24:61–75.

Bortz J, Lienert GA, Boehnke K. 1990. Verteilungsfreie methoden in der biostatistik. Berlin: Springer.

Brown JL. 1980. Fitness in complex avian social systems. In: Markl H., editor. Evolution of social behaviour. Weinheim: Verlag Chemie. p 115–128.

Brown JL. 1983.Cooperation: a biologist's dilemma. Adv Study Behav 13:1–37.

Chapais B. 1992. The role of alliances in social inheritance of rank among female primates. In: Coalitions and alliances in humans and other animals. Harcourt AH, De Waal FBM, editors. Oxford: Oxford University Press. p 29– 59.

Chapais B. 1995. Alliances as a means of competition in primates: evolutionary, developmental, and cognitive aspects. Ybk Phys Anthropol 38:115–136.

Chapais B, Girad M, Primi G. 1991. Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. Anim Behav 41:481–491.

Chapais B, Prud'homme J, Teijeiro S. 1994. Dominance competition among siblings in Japanese macaques: constraints on nepotism. Anim Behav 48:1335–1347.

Chapais B, Gauthier C, Prud'homme J. 1995. Dominance competition through affiliation and support in Japanese macaques: an experimental study. Int J Primatol 16: 521–536.

Chapais B, Gauthier C, Prud'homme J, Vasey P. 1997. Relatedness threshold for nepotism in Japanese macaques. Anim Behav 53:1089–1101.

Cheney DL. 1977. The acquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. Behav Ecol Sociobiol 2:303– 318.

Cheney DL. 1983. Extrafamilial alliances among vervet monkeys. In: Hinde RA, editor. Primate social relationship, an integrated approach. Oxford: Blackwell. p 278–286.

Cheney DL, Seyfarth RM. 1990. How monkeys see the world: inside the mind of another species. Chicago: University of Chicago Press.

Colvin, J. 1983. Rank influences rhesus male peer relationship. In: Hinde RA, editor. Primate social relationship, an integrated approach Oxford: Blackwell. p 57–64.

Connor RC. 1986. Pseudo-reciprocity: investing in mutualism. Anim Behav 34:1562–1566.

Darwin C. 1859. On the origin of species. London: Murray.

Datta SB. 1983a. Patterns of agonistic interference. In: Hinde RA, editor. Primate social relationship, an integrated approach. Oxford: Blackwell. p 289–297.

Datta SB. 1983b. Relative power and acquisition of rank. In: Hinde RA, editor. Primate social relationship, an integrated approach. Oxford: Blackwell. p 93–103.

Deag JM. 1977. Aggression and submission in monkey societies. Anim Behav 25:465–474.

Dugatkin LA. 1997. Cooperation among animals. An evolutionary perspective. Oxford: Oxford University Press.

Ehardt CL, Bernstein IS. 1992. Conflict intervention behaviour by adult male macaques: structural and functional aspects. In: Harcourt AH, De Waal FBM, editors. Coalitions and alliances in humans and other animals. Oxford: Oxford University Press. p 83–111.

Goodall J. 1986. The chimpanzees of gombe: patterns of behavior. Cambridge: Belknap Press of Harvard University.

Gouzoules S, Gouzoules H, Marler P. 1984. Rhesus monkey (*Macaca mulatta*) screams: representational signalling in the recruitment of agonistic aid. Anim Behav 32:182–193.

Hamilton WD. 1964. The genetical evolution of social behaviour i/ii. J Theoret Biol 7:1–52.

Harcourt AH. 1989. Social influences on competitive ability: alliances and their consequences. In: Standen V, Foley RA, editors. Comparative socioecology: the behavioural ecology of humans and other mammals. Oxford: Blackwell Scientific Publication. p 223–242.

Harcourt AH, Stewart KJ. 1989. Functions of alliances in contests within wild gorilla groups. Behaviour 109:176–189.

Hemelrijk CK. 1990a. A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. J Theoret Biol 143:405–420.

Hemelrijk CK. 1990b. Models of, and tests for, reciprocity, unidirectionality and other

social interaction patterns at a group level. Anim Behav 39:1013–1029.

Hemelrijk CK. 1994. Support for being groomed in long-tailed macaques, *Macaca fascicularis*. Anim Behav 48:479–481.

Hemelrijk CK, Ek A.1991. Reciprocity and interchange of grooming and 'support' in captive chimpanzees. Anim Behav 41:923–935.

Van Hooff JARAM, van Schaik CP. 1992. Cooperation in competition: the ecology of primate bonds. In: Harcourt AH, De Waal FBM, editors. Coalitions and alliances in humans and other animals. Oxford: Oxford University Press. p 357–389.

Hunte W, Horrocks JA. 1987. Kin and non-kin interventions in the aggressive disputes of vervet monkeys. Behav Ecol Sociobiol 20:257–263.

Kaplan JR. 1977. Patterns of fight interference in free-ranging rhesus monkeys. Am J Phys Anthropol 47:279–288.

Kaplan JR. 1978. Fight interference and altruism in rhesus monkeys. Am J Phys Anthropol 49:241–250.

Kuester J, Paul A. 1988. Rank relations of juvenile and subadult natal males of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. Folia Primatol 51:33–44.

Kuester, J, Paul A. 1992. Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca sylvanus*). Behaviour 120:192–217.

Kuester J, Paul A, Arnemann J. 1994. Kinship, familiarity and mating avoidance in Barbary macaques (*Macaca sylvanus*). Anim Behav 48:1183–1194.

Kurland, JA. 1977. Kin selection in Japanese monkeys. Contributions to primatology 12. Basel: Karger.

Martin P, Bateson P. 1986. Measuring behaviour. 2nd ed. Cambridge: Cambridge University Press.

Massey A. 1977. Agonistic aids and kinship in a group of pigtail macaques. Behav Ecol Sociobiol 2:31–40.

Maynard Smith J. 1964. Group selection and kin selection. Nature 201:1145–1147.

Meikle DB, Vessey SH. 1981. Nepotism among rhesus monkey brothers. Nature 4:160– 161.

Noë R. 1989. Coalition forming among male baboons. Ph.D. thesis. University of Utrecht.

Noë R. 1990. A veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. Anim Behav 39:78–90.

Noë, R. 1992. Alliance formation among male baboons: shopping for profitable partners. In: Harcourt AH, De Waal FBM, editors. Coalitions and alliances in humans and other animals. Oxford: Oxford University Press. p 285– 321.

Noë R, Sluijter AA. 1990. Reproductive tactics of male savanna baboons. Behaviour 113:117–170.

Noë R, Sluijter AA. 1995. Which adult male savanna baboons form coalitions? Int J Primatol 16:77–105.

Packer C. 1977. Reciprocal altruism in *Papio anubis*. Nature 265:441–443,

Paul A, Kuester J. 1988. Life-history patterns of semifree-ranging Barbary macaques (*Macaca sylvanus*) at Affenberg Salem (FRG). In: Fa JE, Southwick CH, editors. Ecology and behavior of food-enhanced primate groups. New York: Alan R. Liss, Inc. p 199–228.

Paul A, Kuester J. 1992. Fortpflanzungs-strategien maennlicher und weiblicher Berberaffen (*Macaca sylvanus*). In: Voland E, editor. Fortpflanzung: natur und kultur im wechselspiel. Frankfurt am Main: Suhrkampf. p 123–144.

Paul A, Kuester J, Timme A, Arnemann J. 1993. The association between rank, mating effort and reproductive success in male Barbary macaques (*Macaca sylvanus*). Primates 34:491–502.

Paul A, Kuester J, Arnemann J. 1996. The sociobiology of male-infant interactions in Barbary macaques, *Macaca sylvanus*. Anim Behav 51:155–170.

Pereira ME. 1989. Agonistic interactions of juvenile savanna baboons. II. Agonistic support and rank acquisition. Ethology 80:152–171.

Petit O, Thierry B. 1994. Aggressive and peaceful interventions in conflicts in tonkean macaques. Anim Behav 48:1427–1436.

Prud'homme J, Chapais B. 1993. Aggressive interventions and matrilineal dominance relations in semifree-ranging Barbary macaques (*Macaca sylvanus*). Primates 34:271–283.

Prud'homme J, Chapais B. 1996. Development of intervention behavior in Japanese macaques: testing the targeting hypothesis. Int J Primatol 17:429–443.

Riss D, Goodall J. 1977. The recent rise to the alpha-rank in a population of free-living chimpanzees. Folia Primatol 27:134–151.

Rothstein SI, Pierotti R. 1988. Distinctions among reciprocal altruism, kin selection, and cooperation and a model for the initial evolution of beneficent behavior. Ethol Sociobiol 9:189–209.

Seyfarth RM, Cheney DL. 1984. Grooming, alliances, and reciprocal altruism in vervet monkeys. Nature 308:541–543.

Seyfarth RM, Cheney DL. 1988. Empirical tests of reciprocity theory: problems in assessment. Ethol Sociobiol 9:181–187.

Siegel S. 1985. Nichtparametrische statistische methoden. Frankfurt am Main: Fachbuchhandlung für Psychologie.

Silk J.B. 1982. Altruism among female

Macaca radiata: explanations and analysis of patterns of grooming and coalition formation. Behaviour 79:162–188.

Silk JB. 1992a. Patterns of intervention in agonistic contests among male bonnet macaques. In: Harcourt AH, De Waal FBM, editors. Coalitions and alliances in humans and other animals. Oxford: Oxford University Press. p 215–232.

Silk JB. 1992b. The patterning of intervention among male bonnet macaques: reciprocity, revenge, and loyalty. Curr Anthropol 33:318–325.

Silk JB. 1993. Does participation in coalitions influence dominance relationships among male bonnet macaques? Behaviour 126: 171–189.

Trivers RL. 1971. The evolution of reciprocal altruism. Quart Rev Biol 46:35–57.

Vasey PL. 1996. Interventions and alliance formation between female Japanese macaques, *Macaca fuscata*, during homosexual consortships. Anim Behav 52:539–551.

De Waal FBM. 1978. Exploitative and familiarity-dependent support strategies in a colony of semi-free living chimpanzees. Behaviour 66:268–312.

De Waal FBM. 1982. Chimpanzee politics. New York: Harper and Row.

De Waal FBM. 1984. Sex differences in the formation of coalitions among chimpanzees. Ethol Sociobiol 5:239–255.

De Waal FBM. 1985. Coalitions in monkeys and apes. In: Wilke HAM, editor. Coalition formation. Amsterdam: Elsevier Science Publishers. p 1–27.

De Waal FBM. 1992. Coalitions as part of reciprocal relations in the Arnhem chimpanzee colony. In: Harcourt; AH, De Waal FBM, editors. Coalitions and alliances in humans and other animals. Oxford: Oxford University Press. p 233–257.

De Waal FBM, Luttrell LM. 1988. Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? Ethol Sociobiol 9:101–118.

Walters J. 1980. Interventions and the development of dominance relationships in female baboons. Folia Primatol 34:61–89.

Watanabe K. 1979. Alliance formation in a free-ranging troop of Japanese macaques. Primates 20:459–474.

Watts DP. 1997. Agonistic interventions in wild mountain gorilla groups. Behaviour 134:23– 57.

Wilson EO. 1975. Sociobiology: the new synthesis. Cambridge: Belknap Press.

Witt R, Schmidt C, Schmitt J. 1981. Social rank and Darwinian fitness in a multimale group of Barbary macaques (*Macaca sylvana* linnaeus, 1758). Folia Primatol 36:201– 211.

Wrangham RW. 1982. Mutualism, kinship and social evolution. In: King's College Sociobiology Group, editor. Current problems in sociobiology. Cambridge: Cambridge University Press. p 269–289.