



Patterns of coalition formation by adult female baboons in Amboseli, Kenya

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Coalitionary support in agonistic interactions is generally thought to be costly to the actor and beneficial to the recipient. Explanations for such cooperative interactions usually invoke kin selection, reciprocal altruism or mutualism. We evaluated the role of these factors and individual benefits in shaping the pattern of coalitionary activity among adult female savannah baboons, *Papio cynocephalus*, in Amboseli, Kenya. There is a broad consensus that, when ecological conditions favour collective defence of resources, selection favours investment in social relationships with those likely to provide coalitionary support. The primary features of social organization in female-bonded groups, including female philopatry, linear dominance hierarchies, acquisition of maternal rank and well-differentiated female relationships, are thought to be functionally linked to the existence of alliances between females. Female savannah baboons display these characteristics, but the frequency and function of their coalitionary aggression is disputed. In our five study groups, 4–6% of all disputes between females led to intervention by third parties. Adult females selectively supported close maternal kin. There was no evidence that females traded grooming for support or reciprocated support with nonkin. High-ranking females participated in coalitionary aggression most frequently, perhaps because they derived more benefits from group membership than other females did or could provide support at lower cost. Females typically supported the higher ranking of two contestants when they intervened in disputes between subordinates, so most coalitions reinforced the existing dominance hierarchy. Results indicate that female baboons participate in coalitionary aggression in a manner strongly influenced by nepotism and individual benefits.

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For several decades, our understanding of cooperative behaviour has been shaped by two theoretical constructs, kin selection and reciprocal altruism. In recent years, however, the explanatory power of these theories has been challenged, as researchers have suggested that individual benefits and market forces shape the deployment of cooperative behaviour in nature. For example, Clutton-Brock (2002) argued that helpers may derive direct benefits from helping to rear young in many cooperatively breeding vertebrates, and Noë (2001)

proposed that market forces may shape exchanges of services in a wide range of species. We examined the patterns of intervention by adult female baboons in agonistic disputes that occur within their social groups. Coalitions are potentially costly to actors, who expend energy and risk injury when they intervene in ongoing disputes, and are potentially beneficial to recipients, who obtain valuable support against opponents. In primate groups, support is typically nepotistic, but is not completely limited to kin (Chapais 2001; Silk 2002). Both reciprocal altruism (Packer 1977; Seyfarth & Cheney 1984; Hemelrijk 1994; Schino 2001) and individual benefits (Bercovitch 1988; Noë 1990; Chapais 2001) have been invoked to explain patterns of coalition formation in primate groups. Thus, intervention patterns present an appropriate context for investigating the explanatory power of kin selection, reciprocal altruism and individual benefits.

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Coalitionary aggression is thought to be closely linked to the evolution of social organization in primates (Wrangham 1980, 1987; van Schaik 1989; Isbell 1991; van Hooff & van Schaik 1992; Sterck et al. 1997; Isbell & Young 2002). When ecological conditions favour collective defence of resources, selection is expected to favour investment in social relations with those who are likely to provide coalitionary support. The primary features of social organization in cercopithecine primate groups, including female philopatry, linear dominance hierarchies, acquisition of maternal rank and well-differentiated female relationships, are expected to be linked to the existence of alliances between females.

Baboons, however, may constitute an exception to the proposed pattern. Although savannah baboon females are philopatric, form matrilineal dominance hierarchies and establish strong social bonds, there are several sites in southern Africa where coalitions do not occur (Barrett et al. 1999). Even where coalitions are regularly observed, we know virtually nothing about the patterning of coalitionary behaviour between adult females. For instance, do female baboons intervene nepotistically? Do they distinguish between close and distant kin? When females support nonkin, do they restrict support to reciprocating partners? Do females exchange grooming for coalitionary support? Do females derive direct benefits from participating in coalitions?

The fact that we cannot answer any of these questions about the patterning of coalitionary support between adult female baboons makes it difficult to determine the effect of coalitions in their lives, and what evolutionary forces have shaped the deployment of coalitionary support in baboon groups. We evaluated the patterning of support using data from a 26-month study of coalition formation in five wild groups of savannah baboons in Amboseli, Kenya. Evidence suggests that kin selection, reciprocity and individual benefits may all shape patterns of coalitionary activity between primates, but no studies have examined all three factors. Predictions related to these factors are outlined briefly below and summarized in Table 1.

Predictions Based on Kin Selection

If inclusive fitness benefits underlie the evolution of coalitionary aggression, then coalitionary support is expected to be nepotistic. Females are expected to support close maternal kin more than distant maternal kin and to support distant maternal kin more than they support unrelated individuals. In principle, we might also expect paternal kinship to influence patterns of support. However, evidence suggests that female rhesus macaques, *Macaca mulatta*, do not preferentially support paternal half siblings (Widdig 2002), even though both female rhesus macaques and female baboons interact selectively with paternal sisters in other behavioural contexts (Widdig et al. 2001, 2002; Smith et al. 2003). Studies of coalition formation in macaques and vervets show that females direct a disproportionate share of support to maternal kin (Chapais 2001; Silk 2002), and immature baboons in Amboseli are most often supported by their own mothers

Table 1. Summary of predictions

Hypotheses	Predictions
Kin selection favours intervention	Females support close maternal kin more than distant maternal kin Females support distant maternal kin more than 'nonrelatives'
Reciprocal altruism favours intervention	Females selectively support unrelated females who support them Females selectively support unrelated females who groom them Females establish stable alliances with particular partners
Individual benefits favour intervention	High-ranking females intervene more frequently than low-ranking females Females support subordinate females more often than they support dominant females Females intervene on behalf of the higher-ranking of two contestants (conservative support) High-ranking females are more conservative in their intervention behaviour than low-ranking females

and siblings (Walters 1980; Pereira 1988). However, we do not know how maternal kinship influences patterns of support among adult female baboons.

Predictions Based on Reciprocal Altruism

If reciprocal altruism shapes the pattern of coalitionary support, then females are expected to restrict support to those who support them or those who provide them with other kinds of services, such as grooming. We would expect our data to reflect this prediction in two ways. First, we would expect to observe positive correlations between support given and received or between support given and grooming received. Second, we would expect to detect alliance partnerships, that is, pairs of unrelated females that regularly support one another or exchange grooming for support. In some cases, positive correlations exist between support given and support received (Silk 1992; Watts 2002). Grooming is sometimes correlated with support between nonrelatives in naturalistic settings (Cheney & Seyfarth 1990, pp. 67–71; Silk 1992), and experimental studies have demonstrated short-term contingencies between grooming and subsequent support of nonrelatives (Seyfarth & Cheney 1984; Hemelrijk 1994). However, there are also a number of groups in which positive correlations between grooming given and support received have not been found (Henzi & Barrett 1999; Schino 2001). Stable alliance partnerships have been documented for pairs of male (Smuts & Watanabe 1990; Noë & Sluiter 1995) and female savannah baboons (Wasser & Starling 1988).

Predictions Based on Individual Benefits

Primate females may sometimes benefit directly when they participate in coalitions (Chapais 2001). This may influence coalitionary activity in two ways. First, when

dominance hierarchies regulate access to resources and influence reproductive success, high-ranking females may benefit more from group life than low-ranking females do (van Schaik 1989). If the benefits of group membership are distributed unequally, and low-ranking individuals can leave the group, then high-ranking individuals may need to provide incentives, such as coalitionary support, for low-ranking females to stay (Altmann & Alberts 2003 and unpublished data). Baboon and macaque groups regularly split when they grow large (Dunbar 1987), so departures of subordinates present a real threat to dominants. Consequently, we would expect high-ranking females to form coalitions more often than lower-ranking females. Furthermore, we would expect most support to be directed towards subordinates.

Second, animals may sometimes derive direct benefits from participating in coalitions (Bercovitch 1988; Chapais 2001; Widdig 2002). Females may use coalitions to preserve their own position in a dominance hierarchy by preventing instability in dominance relationships between their subordinates (reviewed by Chapais 2001). Consequently, we would expect females to support dominants against subordinates when they intervene in disputes between females ranking lower than themselves. We term this 'conservative' support. Because high-ranking females have a greater stake in preserving the status quo than low-ranking females do, we would expect high-ranking females to intervene more conservatively than low-ranking females.

METHODS

This study was conducted in Amboseli, Kenya over a 26-month period. We studied five well-habituated groups that occupied overlapping home ranges in the Amboseli basin at the foot of Mt Kilimanjaro. Three of the study groups are descended from Alto's group, which has been monitored continually since 1971. The other two groups are descended from Hook's group, which has been monitored continually since 1980. Information about maternal kin relationships is available for all natal members of these groups. Paternal kin relationships are unknown for the majority of adult females in this study. This made it impossible to address the role of paternal kinship in the current analysis, although we view it as a potentially important predictor of social relationships (Widdig et al. 2001; Smith et al. 2003).

The groups ranged in size from Omo's group (18–21 members) to Nyayo's group (54–62 members). Over the course of the study, there were 72 adult females in the five study groups. Of these females, 44 were present for the entire study period, 18 matured during the study period and 10 died.

Observation Protocol

The data were collected by three experienced observers, Raphael Mututua, Serah Sayialel and Kinyua Warutere. The observers were able to recognize all group members quickly and accurately, and were trained to collect a range

of demographic, developmental and behavioural data. Throughout the observation day, observers collected 10-min focal samples, using a random permutation schedule, on all adult females in the study group and were therefore moving throughout the group. Observers recorded all grooming interactions and all agonistic interactions and coalitions on an ad libitum basis. For each instance of grooming, observers recorded the identity of the participants and the role of participants as groomer or recipient. In each case of agonism, observers recorded the identity of individuals involved in the encounter and the outcome of the aggressive encounter. Disputes were considered to be decided if (1) one individual displayed only submissive signals while the other displayed only aggressive signals, or (2) if one individual displayed submissive signals while the other displayed no aggression or submission. All other disputes were considered to be 'undecided'.

When third parties intervened in ongoing disputes, observers recorded the identities of the individual who intervened (ally), the individual that received support (beneficiary) and the individual against whom support was directed (opponent), as well as the type of support that was provided. In some cases, allies directed overt aggression to one of the original participants or their allies. In other cases, allies directed threat vocalizations at the opponent, or established close proximity or nonaggressive physical contact with the beneficiary. Preliminary analyses revealed no substantive differences in the distribution or pattern of these kinds of support, so we pooled them in the analyses presented below. Multiple acts of support directed against the same opponent within the same dispute were considered to be part of the same event and were recorded only once.

Ad libitum data are subject to certain biases: for example, loud and conspicuous events are more likely to be noticed and recorded than are inconspicuous events, and activities that take place near the centre of the group are more likely to be observed than activities that take place at the periphery. We have some reason to be confident that our data set is not systematically biased. First, coalitions are fairly noisy events (Walters 1980), because victims often scream to broadcast their predicament. Although grooming is not noisy, grooming bouts often last for several minutes or more, thereby increasing the likelihood that they will be observed. Second, the observers' sampling schedule required them to move through the group on a regular basis. Third, the observers were able to recognize all group members quickly and accurately, and were well accustomed to recording behavioural interactions involving any group members.

Analysis

For the purposes of our analyses, we extracted the following information from the behavioural records: the date of the event, identity of the participants and the role of each participant in the interaction. For each interaction of interest, we extracted the birth date, maturation date and sex of the participants from demographic records. We used age and maturational data to assign individuals to

age–sex classes. Males and females were categorized as infants until they were 1.5 years of age, and then as juveniles. When females began oestrous cycles, marked by visible perineal swellings, they were classified as adults. For males, subadulthood was marked by testicular enlargement, and adulthood was marked by the attainment of adult dominance rank (Alberts & Altmann 1995).

We extracted information about the current dominance rank of the ally, beneficiary and opponent from the long-term records. Monthly dominance ranks for adult males and adult females were computed based on the outcome of dyadic agonistic encounters. Adult females maintained stable, matrilineal dominance hierarchies in which maternal kin occupied adjacent ranks. Using females' dominance ranks at the beginning of the study period, and placing maturing females immediately below their mothers and older sisters, we could predict the outcome of 98% of the 5859 decided agonistic interactions between adult females over the next 26 months. Only one rank change occurred in the five study groups, when one female rose in rank over her sister and niece.

Although there were almost no changes in relative rank between adult females, normal demographic events (maturations, deaths) produced small changes in females' ordinal ranks over the study period. Therefore, we used females' monthly dominance ranks to compute their average rank over the study period. We used these average ranks to assess the relation between female dominance rank and participation in coalitions.

Individual ranks of subadult males, juveniles and infants were not assessed. For infants and juveniles whose mothers were present, we used current maternal ranks. In some cases, we were unable to assign ranks to immatures because their mothers were dead. All adult and subadult males outranked all adult females, juveniles and infants. Analyses that rely on information about dominance rank are based on the subset of the original data set for which our rank information was complete.

We used demographic records to evaluate maternal kinship relationships between the ally and beneficiary, ally and opponent, and beneficiary and opponent. We place quotes around the terms 'nonkin' and 'nonrelatives' to emphasize that paternal kinship is unknown and that it may influence behaviour (Widdig et al. 2001; Smith et al. 2003). We used maternal kinship ties to estimate degrees of relatedness (r), and we assumed that maternal siblings have different fathers ($r = 0.25$). We defined close maternal kin as those individuals related by 0.25 or 0.5, distant maternal kin as those related by 0.125 or 0.0625 and others as 'nonkin'. Other work on cercopithecine primates suggests that 0.25 is the threshold for nepotism (Chapais 2001).

To determine whether patterns of support were consistent across adult females it is necessary to account for variation in the number of potential partners in particular categories (e.g. close kin, distant kin, 'nonkin') and the number of opportunities that females had to support these individuals. To compute the number of interventions per potential partner for each female, we tabulated the number of possible partners in a particular category that were present on the first day of each month of the study. For females who matured or died during the study

period, we included only the months that they were included in the study. We used these values to compute the average number of partners that were available to each female. Then we divided the number of interventions on behalf of particular categories of beneficiaries by the average number of potential beneficiaries present.

To compute the number of opportunities to intervene, we tabulated the number of agonistic disputes in which each female's close maternal kin, distant maternal kin and 'nonkin' were involved (excluding those in which the focal subject herself was the aggressor or victim). Because females rarely intervened in interactions that involved only spontaneous submission, we limited the analysis to interactions that involved overt acts of aggression by one or both parties. For females who were not present for the entire study period, we included only disputes that occurred during the months that they were included in the study. Then we divided the number of interventions by the number of opportunities to obtain the number of supports per opportunity.

To determine whether patterns of support were consistent across females, we used Wilcoxon matched-pairs signed-ranks tests. We computed nonparametric Spearman rank correlations to assess the relation between dominance rank and participation in coalitions. Because not all females were present for the entire study period, and this would affect the total frequency of support given, we divided the number of interventions by the number of months present to obtain the number of interventions per month.

To assess the extent of reciprocity and interchange between adult females, we used matrix correlation methods, which test the null hypothesis of no correspondence between support given and received or support given and grooming received. We computed the partial rowwise matrix correlation test (de Vries 1993) while controlling for the effects of maternal kinship. We used MATMAN 1.0 software (Noldus Information Technologies, Wageningen, The Netherlands) to run these analyses.

To determine whether patterns were consistent across groups, we performed separate analyses for each study group. The power of group-level analyses is low because sample sizes are reduced. Therefore, we report statistics for individual groups as well as for the combined sample. In some cases, data from only a subsample of females within each group were available. In these cases, it was not practical to compute separate statistics for each group, so we present the results of analyses based on the combined sample.

RESULTS

Size, Composition and Frequency of Coalitions

Approximately 6–9% of all dyadic aggressive encounters led to intervention by third parties (Table 2). Most coalitions were small. In all five groups, the modal number of allies per nondyadic dispute was one. The mean number of allies per coalition ranged from 1.64 (Linda's group) to 1.78 (Weaver's group).

When coalitions were formed, adult females were involved about as often as expected based on their prevalence in their study groups (Table 3). Adult females

Table 2. Frequency of dyadic aggression, coalitions and numbers of allies pooled across individuals

Group	Dyadic agonisms	Coalitions	Allies	Coalitions/agonism	Allies/coalition
Linda's	2495	183	301	0.0733	1.64
Nyayo's	3270	280	494	0.0856	1.76
Omo's	1641	94	159	0.0573	1.69
Viola's	2220	185	313	0.0833	1.69
Weaver's	2583	232	412	0.0898	1.78
Total	12 209	974	1679	0.0798	1.72

constituted 27–35% of the membership of the study groups and performed 24–40% of all interventions in the five study groups. Adult females were the beneficiaries of 26–42% of all interventions and were the targets of 17–46% of all interventions.

Although adult females often participated in coalitions, interventions in disputes between adult females were relatively uncommon. Adult females received support from other group members in only 4–6% of their agonistic disputes with other adult females (Table 4). Adult females received support from other adult females in even fewer disputes with other adult females (1–4%). However, when adult females did receive support in disputes with other females, their allies were other adult females in 23–75% of these instances (Table 4).

Maternal Kinship

Females in all five groups supported close maternal kin ($r \geq 0.25$) much more often than they supported distant maternal kin or 'nonkin' (Fig. 1). Nearly all adult females supported close maternal kin at higher rates than they supported distant maternal kin (Table 5). The mean rate of support for distant maternal kin was higher than that for 'nonkin' in four study groups, and in the fifth group the rate of support for distant maternal kin and 'nonkin' was nearly the same (Fig. 1). Although rates of support for distant maternal kin did not differ consistently from rates of support for 'nonkin' in any of the groups, a significant difference emerged when females in all groups were combined (Table 5). Results based on the number of interventions per opportunity showed virtually the same patterns (Table 5). Thus, females showed strong and

consistent biases in favour of close maternal kin, and smaller and less consistent biases in favour of distant maternal kin.

Reciprocity and Interchange

Females were expected either to trade support in kind with reciprocating partners or to exchange it for grooming or other services (interchange). We examined the correlation between support given and support received for each of the five groups, holding the degree of maternal kinship constant. The partial rowwise correlation was significantly positive for only one of the five study groups (partial rowwise matrix correlation tests; Linda's: $Kr = 0.0949$, $P = 0.118$; Nyayo's: $Kr = 0.0852$, $P = 0.055$; Omo's: $Kr = 0.1315$, $P = 0.142$; Viola's: $Kr = 0.1062$, $P = 0.165$; Weaver's: $Kr = 0.2324$, $P = 0.004$). We also examined the relation between grooming given and support received. Again, the partial rowwise correlation between support given and grooming received was significant for only one of the five study groups (Linda's: $Kr = 0.0203$, $P = 0.382$; Nyayo's: $Kr = 0.0491$, $P = 0.142$; Omo's: $Kr = -0.0216$, $P = 0.580$; Viola's: $Kr = 0.3339$, $P = 0.001$; Weaver's: $Kr = 0.0609$, $P = 0.181$).

Females were also expected to establish stable alliances with reciprocating partners. If such partnerships exist, we would expect to observe multiple instances of support within pairs of adult females. Adult females were involved in 82 ally–beneficiary dyads across all five study groups. The mean \pm SE number of interventions per dyad was 1.73 ± 0.19 (range 1–11). The modal number of interventions per dyad was 1, and nearly all the dyads with multiple interventions were composed of close kin (Fig. 2). Bilateral support occurred in 13 of 82 (16%) of the adult female dyads. That is, in most dyads one female supported the other, but was not observed being supported by her partner. Nearly all of the dyads with bilateral support were maternal kin (11/13 = 85%). Bilateral support was observed in 26% of the maternal kin dyads and 5% of the 'nonkin' dyads.

Individual Benefits

High-ranking females, who derive more benefits from group membership than do low-ranking females, were expected to be more active in coalitionary aggression. High-ranking females intervened in ongoing disputes

Table 3. Adult females' participation in coalitions pooled across individuals

Group	Adult females in group		Allies		Beneficiaries		Opponents	
	N	Proportion	N	Proportion	N	Proportion	N	Proportion
Linda's	10.65	0.29	80	0.27	89	0.30	66	0.22
Nyayo's	16.54	0.29	169	0.34	127	0.26	144	0.29
Omo's	6.88	0.35	64	0.40	61	0.38	73	0.46
Viola's	9.58	0.27	96	0.31	133	0.42	104	0.33
Weaver's	14.38	0.29	97	0.24	117	0.28	71	0.17
Total	11.61	0.30	506	0.30	527	0.31	458	0.27

Table 4. Intervention in disputes between adult females

Group	Dyadic disputes between adult females N	Support from all group members in disputes between adult females		Support from adult females in disputes between adult females		Proportion of support provided by adult females*
		N	N/dispute	N	N/dispute	
Linda's	339	16	0.0472	12	0.0354	0.75
Nyayo's	378	15	0.0397	5	0.0132	0.33
Omo's	316	16	0.0506	9	0.0285	0.56
Viola's	270	17	0.0630	7	0.0259	0.41
Weaver's	279	13	0.0466	3	0.0108	0.23
Total	1582	77	0.0487	36	0.0228	0.47

*Aid from adult females/all aid.

more often than did lower-ranking females. This pattern held in all five study groups (Spearman's r : Linda's: $r_s = -0.897$, $N = 14$, $P < 0.001$; Nyayo's: $r_s = -0.898$, $N = 22$, $P < 0.001$; Omo's: $r_s = -0.840$, $N = 9$; $P = 0.005$; Viola's: $r_s = -0.720$, $N = 10$, $P = 0.019$; Weaver's: $r_s = -0.872$, $N = 17$, $P < 0.012$; all groups: $r_s = -0.790$, $N = 72$, $P < 0.001$; Fig. 3a). The relation between female rank and frequency of intervention might be an artefact if high-ranking females had more maternal kin in their groups or if high-ranking females had more opportunities to support maternal kin. If this were the case, then the correlation should disappear when we limit the analysis to interventions on behalf of 'nonrelatives'. In all five groups, high-ranking females tended to support 'nonkin' more often than lower-ranking females did, but not always significantly so (Linda's: $r_s = -0.482$, $P < 0.081$; Nyayo's: $r_s = -0.723$, $P < 0.001$; Omo's: $r_s = -0.468$, $P = 0.408$; Viola's: $r_s = -0.519$, $P = 0.248$; Weaver's: $r_s = -0.416$, $P = 0.097$; all groups: $r_s = -0.426$, $P < 0.001$; sample sizes as above; Fig. 3b). Thus, female dominance rank explained roughly 50–80% of the variance in total support and 18–50% of the variance in support for 'nonkin'.

Females were expected to selectively support females that ranked lower than themselves, but they did not

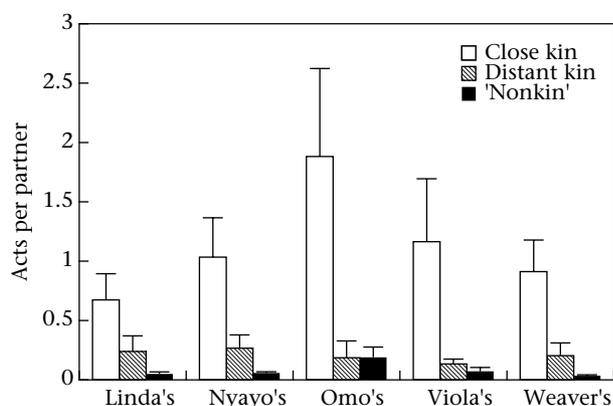


Figure 1. Effect of maternal kinship on coalitionary support by adult females. We computed the rate of intervention by each adult female on behalf of close maternal kin, distant maternal kin and 'nonkin'. Mean + SE rates are shown for females in the five study groups.

consistently do so. In the majority of cases, allies outranked the beneficiaries of support (83/122 = 68%). However, this pattern was not consistent across females. Forty-five females in the five study groups supported 'unrelated' adult females or immatures with known rank; the remaining females never supported 'nonkin' ($N = 25$) or supported 'nonkin' whose rank was not known ($N = 2$). Twenty-two of the 45 females supported 'unrelated' females ranking lower than themselves more often than they supported females ranking higher than themselves, 20 females did the reverse, and three provided support equally to those ranking lower and higher than themselves.

Females were also expected to intervene conservatively (i.e. on behalf of the higher-ranking party), and they did so. Overall, 76% of adult females' interventions in disputes involving 'unrelated' adult females or juveniles were conservative. We were able to compare the frequency of conservative and nonconservative support for 39 females in the five study groups. The remaining females never supported 'nonkin' ($N = 25$), or did not intervene in disputes between 'nonkin' in which ranks of both the beneficiary and opponent were known ($N = 8$). Twenty-eight females intervened conservatively more often than they intervened nonconservatively, four females showed the opposite pattern and seven females intervened conservatively as often as they intervened nonconservatively.

Females might intervene conservatively because they risk receiving retaliatory aggression when they intervene against females who outrank themselves. If so, the preponderance of conservative interventions should disappear when females intervene in contests between contestants ranking lower than themselves. We were able to compare the frequency of conservative and nonconservative support in disputes between 'unrelated' lower-ranking animals for only 23 females. The remaining females did not intervene in such disputes ($N = 24$) or did not support 'unrelated' adult females or immatures ($N = 25$). Among these 23 females, 12 intervened conservatively more often than they intervened nonconservatively, two females showed the opposite pattern, and nine females showed no difference.

High-ranking females, who benefit more from the status quo than do low-ranking females, were expected to be more conservative in their support than low-ranking

Table 5. Effect of maternal kinship on intervention behaviour

	N	Close kin versus distant kin			Distant kin versus 'nonkin'		
		T/Z*	P	Ties	T/Z*	P	Ties
Linda's							
Per partner	10	5	>0.050	3	10	>0.050	3
Per opportunity	10	9	>0.050	3	10	>0.050	3
Nyayo's							
Per partner	19	7	0.020	8	-1.603	0.109	3
Per opportunity	19	10	0.050	8	-1.138	0.255	3
Omo's							
Per partner	7	0	0.050	1	11	>0.050	0
Per opportunity	7	0	0.050	0	11	>0.050	0
Viola's							
Per partner	8	2	0.020	0	4	>0.050	1
Per opportunity	8	2	0.020	0	3	>0.050	1
Weaver's							
Per partner	11	1	0.010	1	8	>0.050	3
Per opportunity	11	2	0.010	2	7	>0.050	3
All groups							
Per partner	55	-4.944	0.001	14	-2.489	0.013	10
Per opportunity	55	-4.890	0.001	13	-1.947	0.052	10

*Wilcoxon matched-pairs signed-ranks test statistic; *T* is reported when *N*-ties ≤ 15; *Z* is reported when *N*-ties > 15.

females. However, there was no consistent association between female dominance rank and the proportion of conservative support across groups (Spearman's r : $r_s = 0.278$, $N = 39$, $P = 0.086$). The correlation remained the same when we limited the analysis to intervention in disputes between two contestants ranking lower than the focal animals ($r_s = -0.063$, $N = 23$, $P = 0.774$).

Females rarely intervened in contests between adult females or immatures when both ranked higher than themselves ($N = 5$ interventions). However, when they did intervene in disputes between their superiors, they were equally likely to support the higher ranking ($N = 2$) and the lower ranking ($N = 3$) of the two contestants.

DISCUSSION

In Amboseli, coalitionary aggression by adult females is highly nepotistic. This comes as no surprise, because

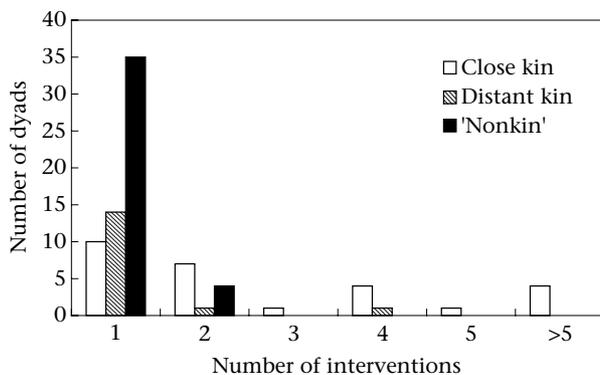


Figure 2. Number of interventions per dyad. At least one act of support was observed in 82 adult female dyads. For each of these dyads the number of interventions per dyad is plotted for close maternal kin, distant maternal kin and 'nonkin'.

similar patterns have been documented in many other cercopithecine populations (reviewed by Chapais 2001; Silk 2002), and previous analyses of intervention on behalf of immatures in Amboseli identified strong biases in favour of maternal kin (Walters 1980, 1981; Pereira 1988, 1989). Amboseli females consistently distinguished between close kin and distant kin, but less consistently between distant kin and 'nonkin'.

We found no evidence that females reciprocated support in kind with 'nonrelatives', exchanged support for grooming with 'nonrelatives' or established stable alliance partnerships with 'nonrelatives'. These negative results can be interpreted in two ways. Reciprocal altruism may have little effect on the evolution of coalitionary support between unrelated female baboons. This interpretation is consistent with the fact that very few examples of reciprocal altruism have been documented in animals (Clutton-Brock 2002). Even the best-documented cases involve short-term exchanges of relatively low-cost commodities (Barrett & Henzi 2002). However, it is also possible that reciprocal altruism is operating, but coalitions between nonrelatives are not common enough to detect underlying associations between coalitionary support given and received, or interchanges between coalitionary support and grooming (Schino 2001) or to identify long-term alliance partnerships. If this is the case, then baboons would have to monitor and balance infrequent behavioural exchanges over long periods. Some researchers are sceptical that monkeys can do this (Barrett & Henzi 2001; Brosnan & de Waal 2002).

High-ranking females intervened at higher rates than lower-ranking females did. This result is not simply an artefact of the fact that high-ranking females have more relatives in the group, because high-ranking females were more active in supporting both kin and 'nonkin'. High-ranking females may be more active participants in

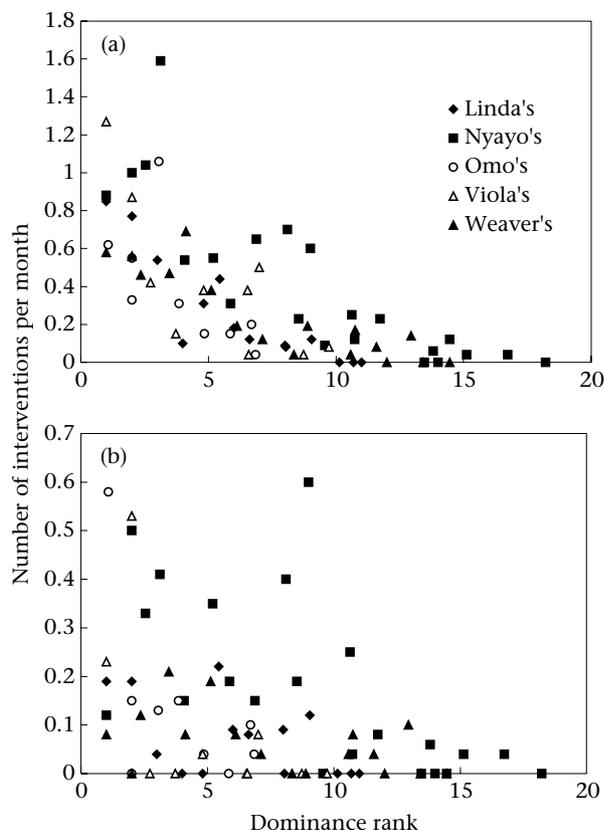


Figure 3. Effects of rank on intervention behaviour. Each data point represents a single adult female. (a) Effect of female dominance rank on total frequency of interventions. (b) Effect of dominance rank on frequency of interventions on behalf of 'nonkin'.

coalitionary aggression because they gain more benefits from group life than lower-ranking females do, because the costs of intervention for high-ranking females are lower than the costs of intervention for lower-ranking females, or both.

Females were usually conservative when they intervened in disputes between other adult females and immatures. In most cases, females supported higher-ranking individuals against lower-ranking individuals, even when they outranked both contestants. There was no support for our prediction that high-ranking females, who derived more benefits from the status quo, would be more conservative in their support than lower-ranking females. It is not clear what factors contribute to the high degree of conservatism among females. It is possible that females would receive aggression from other group members if they supported subordinate females in conflicts with more dominant females. It is also possible that all females have an interest in preserving the status quo, perhaps because frequent rank reversals between pairs of females cause disruptions of social life and foraging that are harmful to all females.

In Amboseli, adult females intervened in one to four of every 100 agonistic disputes between adult females. Comparison of the frequency of coalition formation in Amboseli with the frequency at other sites where baboons have been studied is difficult because comparable data are not available; different studies have measured

interventions in different ways. In Laikipia, Kenya, Barton et al. (1996) found that adult females intervened in disputes between adult females once in every 14 h, but the authors did not report the number of interventions per dispute. In Mikumi, Tanzania, females were reported to intervene in disputes 'regularly' and to attack other females jointly (Wasser & Starling 1988), but the number and rate of interventions was not provided. Barrett et al. (1999) reported that female baboons in southern Africa never form coalitions, but this is not completely accurate. No coalitions by adult females were observed in more than 1000 h of observation in the Drakensberg Mountains (Barton et al. 1996; Barrett et al. 1999) or in De Hoop (Barrett et al. 1999), but coalitions have been observed at other sites in southern Africa. Adult females intervened in 32 disputes between adult females over a 15-month period at Mount Zebra National Park in South Africa (Seyfarth 1976), females formed three coalitions in 800 h of observation at Mzuke, South Africa (Ron et al. 1996), and in Moremi, Botswana, coalitions between adult females were rare, but not absent altogether (Silk et al. 1999).

Given the quality of data available, it is impossible to determine whether female baboons in Amboseli intervened more or less often than did females at other sites in East Africa or even whether females in East Africa intervene more often than females in southern Africa. To make progress on this question, researchers must adopt standardized measures to evaluate rates of coalitionary support. We suggest that the number of interventions per dispute is a particularly useful measure for this purpose.

What implications do our data have for understanding the function of coalitionary support for adult females? Because challenges to higher-ranking females are rare in Amboseli, females might need little help to maintain their ranks. The rates of intervention that we observed, although apparently low, may be sufficient to provide females with the little support that they need to maintain their ranks. The presence of potential allies may be sufficient to deter challenges from lower-ranking females and reinforce the existing hierarchy (Cords 2002). For example, infants and juveniles are more likely to win disputes with larger animals when their mothers are nearby than when their mothers are out of proximity, even when their mothers do not intervene on their behalf (Walters 1980; Datta 1983a, b, c; Horrocks & Hunte 1983). Perhaps high rates of affiliative contact, such as grooming, signal the existence of alliances to other group members, and these signals provide effective deterrents to challenges by subordinates. Perhaps coalitionary support between adult females is infrequent but is particularly valuable when it does occur. Coalitionary aggression was important in the reorganization of the female dominance hierarchy in Alto's group, the ancestral group of three of our study groups, in the early 1980s (Samuels et al. 1987). Over several months, a number of subordinate females challenged higher-ranking females and succeeded in defeating them. Revolutionary alliances were common during this period.

However, our results are also compatible with the hypothesis that coalitionary support by adult female baboons is primarily linked to maternal rank acquisition by immatures and the formation of matrilineal

dominance hierarchies. Support by adult females may have little influence on the maintenance of dominance hierarchies and may not be closely linked to the development of close ties between females (Barrett & Henzi 2001). Females' social relationships may be based mainly on the benefits of having dependable grooming partners or tolerant associates at feeding sites, not on having reliable allies in intragroup encounters.

Our results raise questions about the influence of coalitions and the nature of dominance relationships between females in cercopithecine groups. First, what maintains the remarkable stability of dominance hierarchies among adult females? Experimental studies of Japanese macaques, *Macaca fuscata*, indicate that alliances between both kin and 'nonkin' are important in this process (Chapais et al. 1991; Chapais 1992), but the low frequency of coalitions between baboons in Amboseli and at other sites suggests that it takes very few alliances to stabilize dominance hierarchies. Second, what is the functional link between coalitionary aggression and the formation of social bonds between females? Socioecological models hypothesize that females form close bonds with prospective alliance partners, and some evidence indicates that female macaques and vervets selectively support former grooming partners (Seyfarth & Cheney 1984; Hemelrijk 1994). However, female baboons do not seem to establish stable alliance partnerships except with their own close maternal kin. If females derive direct benefits from conservative interventions in disputes between subordinates, then decisions to intervene may be largely independent of the quality of their relationship to potential beneficiaries. Third, what limits the development of reciprocal relationships between female baboons? Are females constrained by the difficulty of monitoring costs and benefits in different currencies over long periods, or do the economics of cooperation make such relationships unprofitable? By combining naturalistic observations in social groups with carefully designed experiments, we may eventually be able to unravel the answers to these questions.

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