

## REDIRECTED AGGRESSION AND RECONCILIATION AMONG VERVET MONKEYS, *CERCOPITHECUS AETHIOPS*

by

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### Introduction

The data gathered by human observers studying the behavior of nonhuman primates often reveal a social structure of apparently striking complexity. Social groups are composed of a number of different families of different dominance ranks, each of which both competes and cooperates with other families in the group. It is often difficult for the observer to imagine that the monkeys could function or compete effectively without some understanding of the nature of kinship and dominance rank. At the same time, however, the apparent complexity of the animals' social structure may simply be an artifact resulting from our own ability to discern their matriline and dominance hierarchies. The monkeys themselves may behave 'intelligently' while at the same time not recognizing the subtle discriminations that underlie their behavior.

Numerous studies have now documented kin recognition in animals, in the sense that kin are treated differently from unrelated individuals (see reviews by HOLMES & SHERMAN, 1983; GOUZOULES & GOUZOULES, 1987; FLETCHER & MICHENER, 1987; WALDMAN *et al.*, 1988). Furthermore, several studies of Old World monkeys have also suggested that nonhuman primates recognize the close associates of other individuals. In an earlier study of redirected aggression among vervet monkeys, for example, we found that animals were significantly more likely to threaten

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a given individual if they had previously been involved in a fight with that individual's close maternal kin. Similar suggestion of kin- or associate-biased redirected aggression has been found in pigtail macaques (JUDGE, 1982) and baboons (SMUTS, 1985).

Reconciliatory behavior can also be directed preferentially toward specific individuals. Studies of captive chimpanzees (DE WAAL & VAN ROOSMALEN, 1979), rhesus macaques (DE WAAL & YOSHIHARA, 1983), juvenile male longtailed macaques (CORDS, 1988) and female patas monkeys (YORK & ROWELL, 1988) have shown that opponents often seek affiliative contact with each other following fights. In two of these studies (DE WAAL & YOSHIHARA, 1983; YORK & ROWELL, 1988) kin reconciled more often than nonkin, while in a third (CORDS, 1988) kin reconciled less than nonkin.

It is not only the primary antagonists who reconcile, however, because monkeys will also reconcile with the kin of their former opponents. In their study of reconciliation among captive patas monkeys, YORK & ROWELL (1988) found that unrelated animals contacted the kin of their former opponents almost twice as often following a fight than during matched control periods (see also JUDGE, 1983 for similar observations on captive pigtail macaques). These observations provide additional support for the hypothesis that nonhuman primates recognize the close associates of others. Given the fact that related animals form aggressive alliances with each other at high rates (reviewed in WALTERS & SEYFARTH, 1987), such kin-biased reconciliation suggests that animals recognize the importance of resolving conflicts not just with their specific opponents but with entire matriline.

There is also evidence that nonhuman primates may be capable of a more abstract form of kin recognition, in which certain types of relationships are judged to be similar regardless of the individuals involved. Perhaps the best evidence that monkeys possess an abstract concept of a close social relationship comes from a series of experiments performed by DASSER (1988) on longtailed macaques. Using both a simultaneous discrimination procedure and a match-to-sample procedure, DASSER trained females to discriminate slides of one mother-offspring pair from unrelated group members. Following training, the females generalized easily and accurately to novel slides, correctly identifying other mother-offspring pairs despite wide variation in the age and sex of offspring.

Although it is more difficult in a purely observational study to determine whether animals compare social relationships, there is some evidence that, even in the absence of training, free-ranging monkeys rec-

ognize the similarity between their own close bonds and the close bonds of other animals. In our earlier study of vervet monkeys, for example, we found that females and juveniles were more likely to threaten a particular individual if that individual's close kin and their own close kin had previously been involved in a fight (CHENEY & SEYFARTH, 1986). Such discrimination does not necessarily mean that monkeys have a concept of 'kinship', but it does suggest that they recognize that certain types of bonds share similar characteristics. Vervets seem able to compare social relationships across different individuals, even if they do not understand the concept of genetic relatedness.

In this paper, we use new data gathered during 1985-86 to investigate in more detail what factors influence the distribution of redirected aggression and reconciliation among vervet monkeys. The paper has two aims. First, we attempt to replicate our previous findings with the more appropriate, better controlled method used by researchers studying reconciliation in captive primates (see below). Second, we attempt to determine whether patterns of redirected aggression and reconciliation differ within and between families, and examine the extent to which animals discriminate between the close bonds that exist among their own kin and the close bonds that exist among unrelated animals. This analysis was not possible in our earlier work, both because kinship among all adult females was not yet known and because none of the study groups contained known extended families.

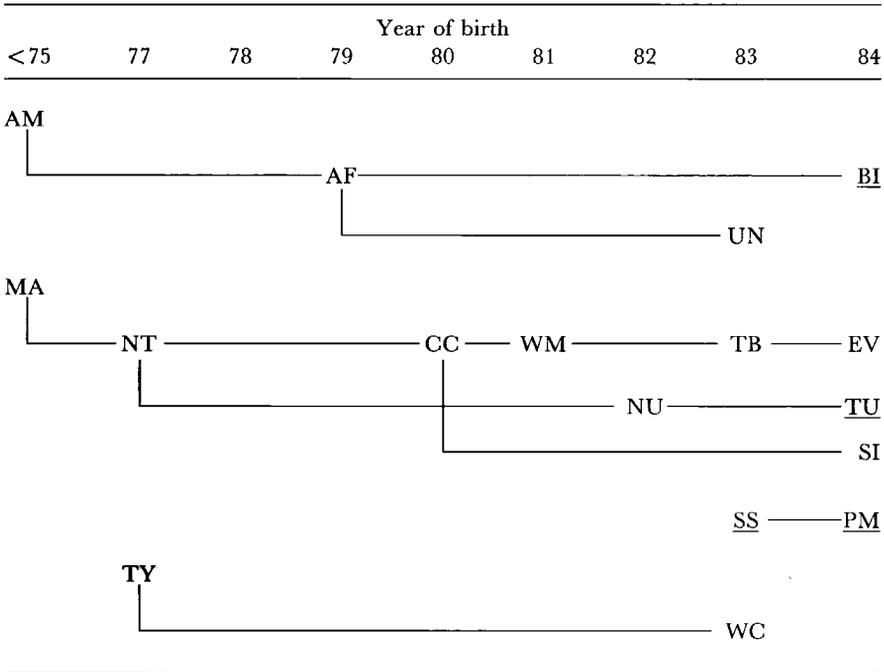
### Methods

The data described here were obtained during an eight month period in 1985-86 on one social group (B) in Amboseli National Park, Kenya. This group is part of a larger population that has been observed continuously since 1977, and is one of the groups described in our earlier paper. Because of an overall decline in population size over the past ten years (CHENEY *et al.*, 1988), Group B was the only group in the study population that contained more than one large (>2 individuals) matriline during 1985-86. The composition of the group is shown in Table 1.

Vervet monkeys in Amboseli live in stable social groups composed of one to seven adult males and two to eight adult females. Females remain in their natal groups throughout their lives, while males emigrate to neighboring groups at around sexual maturity. Females are considered to be adult at four, and males at five, years of age. Like many other cercopithecines, adult female vervets can be ranked in linear dominance hierarchies based on the direction of approach-retreat interactions (SEYFARTH, 1980). Offspring assume ranks similar to their mothers', with the result that matrilineal kin occupy adjacent ranks (CHENEY, 1983; LEE, 1983; see also HORROCKS & HUNTE, 1983; FAIRBANKS & MCGUIRE, 1986).

The analysis that follows concerns aggressive and affiliative interactions among adult females and juveniles. Aggressive interactions or threats included head bobs, eye flashes, lunges, chases and bites. Redirected aggression was said to occur whenever an animal threatened another individual following a previous fight. Affiliative interactions occurred

TABLE 1. The composition of Group B during the 1985-86 period of observation



Mothers and offspring are connected by vertical lines, siblings by horizontal lines. Males are underlined. Only animals who were alive during the period of observation are shown. Infants born in the 1985 birth season have also been excluded.

whenever an animal groomed, touched, hugged, or handled the infant of another individual. Reconciliation was said to occur whenever an individual initiated an affiliative interaction following a fight. In contrast to previous studies of reconciliation (CORDS, 1988; YORK & ROWELL, 1988), proximity was not used as a measure of affinity or of reconciliation in this study, hence making the criteria for reconciliation more stringent. Interactions involving adult males or infants (animals less than one year of age) were excluded from analysis.

Data were obtained over an eight month period in 1985-86. In order to increase the sample of interactions, the data described below combine observations from focal and *ad libitum* sampling methods. Strictly speaking, these two methods should not be combined, since the latter does not always accurately reflect rates of interaction. However, since group size was small (Table 1), and because the group was observed simultaneously by at least two, and usually three, observers, we feel confident that almost all interactions were observed, and that no particular individual was either over- or underrepresented (see also CHENEY & SEYFARTH, 1986).

Kinship was defined through the maternal line, since paternity could not be determined. Interactions between kin and nonkin were considered separately. Kin included mothers, offspring, siblings, aunts, nieces, nephews, grandmothers, grandchildren, and first cousins. Kin therefore included all the members of the same matriline.

As in our previous study, we distinguished between 'simple' and 'complex' redirected aggression and reconciliation. Cases in which an animal redirected aggression or reconciled with its opponents' kin were termed 'simple' redirected aggression or reconciliation. Cases in which a previously uninvolved animal threatened or behaved affiliatively toward the kin of its *relative's* prior opponent were termed 'complex' redirected aggression or reconciliation. In the case of reconciliation, we also measured the likelihood that animals would groom or initiate friendly interactions with their opponents themselves. We call reconciliation between the two original opponents 'direct' reconciliation.

In calculating the frequency of kin-biased (either simple or complex) redirected aggression and reconciliation, we considered only interactions involving the opponents' *close* kin, defined as mothers, maternal siblings, or offspring. Close kin were chosen as the potential targets of kin-biased behavior both to increase the rigor of the analysis and to accord with the methods employed in our previous study.

In our previously analysis (CHENEY & SEYFARTH, 1986) we examined the frequency with which individuals threatened each other following a fight with their opponents' kin, compared with their behavior in the absence of such a fight. This method has several advantages, particularly when applied to free-ranging groups that are not observed for equal amounts of time each day. Nevertheless, the method differs from that employed by other studies of reconciliation among captive primates, and does not permit a direct comparison with results obtained in other populations. In this paper, therefore, we follow as closely as possible the methods of analysis employed by DE WAAL & YOSHIHARA (1983), CORDS (1988), and YORK & ROWELL (1988).

Following every aggressive interaction, we observed both the opponents and their kin for a period of half an hour, noting all of their aggressive and affiliative interactions. Although all interactions among relevant individuals were noted, each interaction with a given individual was counted only once. Next, using the half hour preceding the conflict as a control period, we compared the behavior of individuals during the post-conflict period with their behavior during the matched-control pre-conflict period. If an individual interacted even once with its opponent or its opponent's kin during the control period, this interaction negated any subsequent reconciliatory or retaliatory behavior during the post-conflict period. This procedure is more stringent than that employed in previous studies, and biased against finding kin-biased reconciliation or redirected aggression in the post-conflict period.

Our choice of a control period differed slightly from other studies, in which matched-control observations were usually made at the same period of time on subsequent days. We followed this slightly different procedure for two reasons. First, since our behavioral study involved a total of six groups we rarely observed the same group during the same time period on two successive days, and there was frequently a gap of several days before a given group was observed twice during the same period of time. Second, some days were more socially active than others. By taking our control period from the same observation session as our post-conflict period, we assured that both post-conflict and matched-control periods occurred on days in which there were fights and affiliative interactions. This procedure again biased against finding reconciliation or redirected aggression, since it increased the likelihood of affiliative and aggressive interactions during the control period.

In order to ensure that no instances of redirected aggression and reconciliation were missed, we eliminated from our sample all threats and affiliative interactions that occurred in the half hours immediately following or preceding the start or end of the observation session. Since most observation sessions lasted for approximately three hours, this procedure considerably reduced in the sample of aggressive and affiliative interactions. After removing the first and last half hours of each observation session, there was a total of 113 hours of observation on Group B.

The study group included a total of 44 kin dyads and 92 nonkin dyads. Since reconciliation and redirected aggression occurred at very low frequencies, most dyads did not contribute to the analysis, while a few dyads were represented more than once. The analysis is not, therefore, truly independent, a problem that is difficult to avoid in any study of spontaneous aggression (see discussion by CORDS, 1988). In all statistical tests, however, we correct for the number of individuals involved, such that each individual only contributes once to the pooled results.

Since the study aimed to test previous findings, all statistical tests are one-tailed unless otherwise stated. Probability levels are only reported for tests that approached  $P < 0.05$ .

## Results

### 1. The frequency of redirected aggression and reconciliation.

Vervet monkeys redirected aggression and reconciled with each other at very low frequencies. Following 18 (14%) of the 129 fights observed among kin, an individual subsequently threatened its opponent's relative (simple redirected aggression). Among nonkin, only 8 of 160 fights (5%) were followed by simple redirected aggression.

Reconciliation also occurred infrequently. Only 14% of fights among kin were followed by reconciliation among the primary opponents (direct reconciliation), while unrelated opponents reconciled after only 2% of all fights (Table 2). The frequency of direct reconciliation, though low, was comparable to that reported by DE WAAL & YOSHIHARA (1983) for captive rhesus macaques. In that study, approximately 9% of all fights were fol-

TABLE 2. The frequency of different forms of redirected aggression and reconciliation following fights between related and unrelated opponents

	Nonkin	Kin
Redirected aggression		
Direct	3%	7%
Simple	5%	14%
Complex	7%	12%
Reconciliation		
Direct	2%	14%
Simple	11%	18%
Complex	6%	24%

There were 160 fights among nonkin, 129 fights among kin. Data are taken from post-conflict periods only. 'Direct' redirected aggression refers to sequential fights between the same two opponents.

lowed by affiliative interactions between the two opponents (see also SCUCCHI *et al.*, 1988). Individuals reconciled with their opponents' *kin* (simple reconciliation) in 18% of the fights involving kin and 11% of the fights involving nonkin. No other studies have reported the frequency of simple reconciliation.

Similarly, only a small proportion of all possible related and unrelated dyads ever engaged in kin-biased redirected aggression or reconciliation, although such behavior was more common among kin than among nonkin (Table 3). Direct reconciliation was observed among 16 (36%) of the 44 kin dyads and 3 (3%) of the 92 nonkin dyads. Reconciliation among primary opponents, therefore, occurred among considerably fewer dyads than in either CORDS' (1988) study of juvenile male longtailed macaques or YORK & ROWELL's (1988) study of adult female patas monkeys. This difference seems to have been due primarily to the fact that proximity was used as a measure of reconciliation in both of the other studies, whereas in our study reconciliation was said to have occurred only after the initiation of an affiliative interaction. It is also possible that the low frequency of reconciliation in our study reflected a genuine difference between vervet monkeys (at least in Amboseli) and other species, or between free-ranging monkeys and captive ones. It is possible, for example, that reconciliation may be more important for the avoidance of subsequent conflict in captivity, where opponents cannot easily escape each other, and are less easily able to avoid each other than in the wild.

TABLE 3. The proportion of all possible related and unrelated dyads that showed different forms of redirected aggression and reconciliation

	Nonkin	Kin	Total
Redirected aggression			
Direct	3%	16%	<b>8%</b>
Simple	8%	23%	<b>13%</b>
Complex	12%	27%	<b>17%</b>
Reconciliation			
Direct	3%	36%	<b>14%</b>
Simple	16%	32%	<b>21%</b>
Complex	9%	41%	<b>19%</b>

There was a total of 92 unrelated and 44 related dyads. Legend as in Table 2.

## 2. The relative frequency of direct and kin-biased interactions.

Simply because some individuals had more than one close relative, kin-biased reconciliation might have been predicted to occur more frequently than direct reconciliation between primary opponents. In this study, for example, a vervet could reconcile directly only with its prior opponent. When reconciling with its opponent's kin, however, it could choose among as many as five other individuals. In order to compare the frequency of direct reconciliation with the frequency of kin-biased (or simple) reconciliation, therefore, it was first necessary to control for the number of possible recipients in each case.

When aggressive and affiliative interactions were corrected for the number of possible recipients, kin and nonkin were as likely to redirect aggression to their opponents as to their opponents' kin (Table 4). There was a difference, however, between kin and nonkin in the likelihood that individuals would reconcile with their opponents' kin as opposed to their

TABLE 4. A comparison of the frequency of direct and simple redirected aggression among related and unrelated opponents

Actor	Nonkin			Actor	Kin		
	Recipient	Direct	Simple		Recipient	Direct	Simple
AM	WM		+	MA	TU	+	
AM	SS	+		WM	NT	+	
UN	CC	+		TB	CC		+
UN	NU		+	TB	SI		+
WM	SS	+		TB	NT	+	
WM	PM		+	CC	NT	+	
CC	WC		+	CC	NU		+
NT	TY	+		CC	TU	+	
NT	WC		+	SI	EV		+
SS	NT		+	SI	TU		+
SS	TU		+	NU	MA	+	
				NU	WM		+
				NU	TB		+
				NU	EV	+	
				NU	CC		+

Nonkin: N = 11; direct more: 4; simple more: 7. Kin: N = 15; direct more: 7; simple more: 8. If each individual is counted only once: Nonkin: N = 6; ties = 4; direct more: 0; simple more: 2. Kin: N = 6; direct more: 3; simple more: 3.

A plus sign (+) in a given column indicates which form of redirected aggression occurred most, after correcting for the number of a given opponent's relatives. 'Direct' redirected aggression refers to a sequential fight between two individuals. Data are taken from post-conflict periods only.

opponents themselves (Table 5). When kin fought, they reconciled more often with their opponents than with their opponents' (and their own) kin. In contrast, when unrelated animals fought, they reconciled more often with their opponents' kin than with their opponents themselves. This difference between related and unrelated opponents was significant (two-tailed Fisher exact probability test,  $P < 0.01$ ).

TABLE 5. A comparison of the frequency of direct and simple reconciliation among related and unrelated opponents

Actor	Nonkin			Actor	Kin		
	Recipient	Direct	Simple		Recipient	Direct	Simple
AM	NT		+	AM	AF	+	
BI	PM		+	UN	BI	+	
AF	NT		+	MA	WM	+	
UN	MA		+	MA	NT		+
UN	WM		+	WM	MA		+
UN	NT		+	WM	NU	+	
UN	TU	+		TB	WM		+
CC	AF		+	EV	MA		+
NT	AM		+	EV	TB		+
NU	AF		+	EV	CC	+	
NU	BI	+		EV	SI	+	
SS	MA		+	EV	NT		+
WC	AM		+	EV	NU	+	
WC	MA		+	CC	MA		+
WC	TB	+		CC	WM		+
WC	EV		+	CC	NT	+	
WC	SI		+	CC	NU	+	
				SI	MA	+	
				NT	WM	+	
				NT	TB	+	
				NU	MA		+
				NU	WM	+	
				NU	TB		+
				NU	EV		+
				NU	CC	+	
				NU	SI	+	
				NU	NT	+	

Nonkin:  $N = 17$ ; direct more: 3; simple more: 14;  $P = 0.012$ . Kin:  $N = 27$ ; direct more: 16; simple more: 11. If each individual is counted only once: Nonkin:  $N = 9$ ; ties = 1; direct more: 0; simple more: 8;  $P = 0.008$ . Kin:  $N = 10$ ; ties = 4; direct more: 5; simple more: 1.

Legend as in Table 4. P-values give two-tailed probabilities for sign test.

3. Aggression and affinitive behavior in control and post-conflict periods.

Even though kin showed absolutely more reconciliatory behavior than nonkin following fights, this result appeared to be due to the overall high rates of affinitive behavior among kin. When post-conflict periods were compared with matched-control periods, kin did not interact affinitively with their opponents more following a fight than during the period preceding it (direct reconciliation). In contrast, while there were only three unrelated individuals who ever reconciled directly with their opponents, all three interacted affinitively more following a fight than during matched-control periods (Table 6).

Nonkin also reconciled with their opponents' relatives more than did kin (Table 7). Unrelated individuals were significantly more likely to interact with their opponents' kin following a fight than during matched-control periods. Kin, in contrast, were as likely to interact with their opponents' kin during control periods as during the period following a fight.

TABLE 6. The number of times that individuals reconciled with related and unrelated opponents (direct reconciliation)

Nonkin				Kin							
Actor	Recipient	PC>MC	PC=MC	Actor	Recipient	PC>MC	PC=MC				
NU	TU	1		AM	AF		1				
NU	BI	1		UN	BI	1					
WC	TB	1		MA	WM	1					
N = 3; PC>MC: 3; PC=MC: 0.				WM	NU	1					
				EV	CC	1					
				EV	NU	1					
				EV	SI	1					
				CC	NT	2					
				CC	NU	2					
				SI	MA		1				
				NT	WM		1				
				NT	TB	1					
				NU	WM		2				
				NU	CC	1					
				NU	SI	1					
				NU	NT		1				
								N = 16; PC>MC: 11; PC=MC: 5.			
								If each individual is counted only once:			
								N = 9; ties = 1; PC>MC: 3; PC=MC: 5.			

PC: post-conflict; MC: matched-control period. If PC>MC, reconciliation occurred; if PC = MC, no reconciliation occurred.

TABLE 7. The number of times that individuals reconciled with the kin of related and unrelated opponents (simple reconciliation)

Nonkin				Kin			
Actor	Recipient	PC>MC	PC=MC	Actor	Recipient	PC>MC	PC=MC
AM	NT	1		MA	NT	1	
BI	PM	1		WM	MA		1
AF	NT	1		TB	WM		1
UN	MA	1		EV	MA		1
UN	WM	2		EV	TB	1	
UN	NT	1		EV	SI	1	
CC	AF	1		EV	NT	1	
NT	AM	1		CC	MA	1	
NU	AF		1	CC	WM	1	1
SS	MA	2		CC	NT	3	1
WC	AM	1		NT	WM		2
WC	MA	1		NU	MA	1	2
WC	EV	1		NU	WM		3
WC	SI	1		NU	TB		1
				NU	EV		1
				NU	CC	1	1

N = 14; ties = 0; PC>MC: 13; PC=MC: 1; P=0.001. If each individual is counted only once, N = 9, ties = 0, PC>MC: 8; PC=MC: 1; P=0.020.

N = 16; ties = 2; PC>MC: 6; PC=MC: 6. If each individual is counted only once: N = 7; ties = 0; PC>MC: 3; PC=MC: 4.

Legend as in Table 6. P-values give one-tailed probabilities for sign test.

There was less difference between kin and nonkin in the case of complex reconciliation (Table 8). For both groups, the kin of prior opponents interacted affinitively significantly more after a fight than in the period before the fight.

Similarly, there was little difference between kin and nonkin in the case of kin-biased redirected aggression. Both related and unrelated individuals were significantly more likely to threaten their opponents' kin following a fight than during control periods (simple redirected aggression) (Table 9). Furthermore, regardless of whether or not they were related, the *kin* of two opponents were more likely to threaten each other following a fight (complex redirected aggression) (Table 10). For unrelated opponents, this difference between post-conflict and matched-control periods was significant.

#### 4. Summary.

Reconciliation among related and unrelated opponents differed in the following respects. When kin fought, a much higher proportion of fights

TABLE 8. The number of times that individuals reconciled with the kin of their own relatives' opponents (complex reconciliation)

Nonkin				Kin			
Actor	Recipient	PC>MC	PC=MC	Actor	Recipient	PC>MC	PC=MC
AF	MA	1		MA	NT	2	
AF	NT	1	1	WM	NT	3	2
AF	NU	1		WM	NU		1
UN	NT	1		TB	WM		2
WM	AF	1		TB	CC		1
NU	AM	1	1	TB	NT	1	1
TY	NT	1		TB	TU	1	
				EV	MA	1	1
				EV	NT	2	
				CC	MA	2	
				CC	NT	1	
				CC	TU	1	
				NT	MA	1	1
				NT	WM		1
				NT	TB	1	
				NT	CC	1	
				NU	MA	3	2
				NU	WM	2	1
				SI	WM	1	
				SI	TB		1
				SI	NT	2	

N = 7; ties = 2; PC>MC: 5; PC=MC: 0; P=0.031. If each individual is counted only once: N = 5; ties = 1; PC>MC: 4; PC=MC: 0.

N=21; ties=3; PC>MC: 13; PC=MC: 5; P=0.048. If each individual is counted only once: N = 8; ties = 1; PC>MC: 6; PC=MC: 1; P=0.062.

Legend as in Tables 6 and 7.

was followed by affiliative behavior, either between the opponents themselves (direct reconciliation) or between one opponent and the kin of another (simple reconciliation). Relatively high frequencies of reconciliation among kin, however, were apparently just a consequence of frequent overall affiliative interactions: when behavior during post-conflict periods was compared with behavior during matched-control periods, direct and simple reconciliation were more common among nonkin than among kin. Nonkin also differed from kin in whom they reconciled *with*. Kin were equally likely to reconcile with their opponents and their opponents' kin. In contrast, nonkin reconciled more often with their opponents' kin than with their opponents themselves.

Among both kin and nonkin, opponents were significantly more likely to threaten their opponents' relatives following a fight than during

TABLE 9. The number of times that individuals redirected aggression against the kin of related and unrelated opponents (simple redirected aggression)

Nonkin			Kin				
Actor	Recipient	PC>MC	PC=MC	Actor	Recipient	PC>MC	PC=MC
AM	WM	1		MA	TU	1	
UN	NU	2		WM	NT	2	
WM	PM	1		TB	CC	1	
CC	WC	1		TB	SI	1	
NT	WC	1		TB	NT	1	
SS	NT	1		CC	NU	1	
SS	TU	1		SI	EV	1	
				SI	TU	1	
				NU	MA	4	
				NU	WM	1	2
				NU	TB	1	3
				NU	EV	2	
				NU	CC	1	

N = 7; ties = 0; PC>MC: 7; PC=MC: 0; P=0.008. If each individual is counted only once: N = 6; ties = 0; PC>MC: 6; PC=MC: 0; P=0.016.

N = 13; ties = 0; PC>MC: 11; PC=MC: 2; P=0.011. If each individual is counted only once: N = 6; ties = 0; PC>MC: 6; PC=MC: 0; P=0.016.

Legend as in Tables 6 and 7.

matched-control periods (simple redirected aggression). Similarly, the relatives of two opponents were more likely to threaten each other following a fight than during matched-control periods (complex redirected aggression). Finally, the relatives of two opponents were more likely to interact affinitively following a fight than in the period preceding it (complex reconciliation).

### Discussion

Only a small proportion of all threats and affinitive interactions occurred in the context of redirected aggression and reconciliation. As a result, when all possible dyads were included in the analysis, there was no overall tendency for vervets to show kin-biased redirected aggression or reconciliation, regardless of whether or not their original opponent was a relative. In this respect, the vervets behaved like the rhesus macaques studied by DE WAAL & YOSHIHARA (1983), who also reconciled with their opponents at low rates.

TABLE 10. The number of times that individuals redirected aggression against the kin of their own relatives' opponents (complex redirected aggression)

Nonkin				Kin			
Actor	Recipient	PC>MC	PC=MC	Actor	Recipient	PC>MC	PC=MC
AM	NT	1		MA	NT	1	
BI	NU		1	MA	NU		1
AF	MA	1		MA	TU	1	
AF	TU	1		WM	NT	2	
UN	MA	1		WM	TU	1	
UN	TU	1		TB	CC	1	
MA	WC	1		TB	NT	1	1
WM	WC	1		SI	EV	1	
TB	TY	1		NT	CC	1	
EV	TY	1		NU	MA		2
SI	PM	1		NU	WM		1
NT	TY		1	NU	TB		1
NU	WC	1		NU	EV	1	
				NU	CC	1	

N = 13; ties = 0; PC>MC: 11; PC=MC: 2; P=0.011. If each individual is counted only once: N = 11; ties = 0; PC>MC: 9; PC=MC: 2; P=0.033.

N = 14; ties = 1; PC>MC: 9; PC=MC: 4. If each individual is counted only once: N = 6; ties = 0; PC>MC: 5; PC=MC: 1; P=0.109.

Legend as in Tables 6 and 7.

Despite its overall low frequency, however, redirected aggression among vervet monkeys followed a predictable pattern. First, individuals were more likely to threaten their opponents' relatives following a fight than during control periods. Moreover, the *relatives* of opponents were more likely to threaten each other following a fight than during control periods. In other words, a fight between a member of family A and a member of family B increased the likelihood that other members of families A and B would threaten each other. The monkeys behaved as if they recognized the similarity between their own close relationships and the close relationships of other individuals. Though derived from a different method of analysis, therefore, these results replicate those obtained in our earlier study (CHENEY & SEYFARTH, 1986).

While patterns of redirected aggression were similar among both kin and nonkin, reconciliation among nonkin differed in two respects from reconciliation among kin. First, when post-conflict periods were considered alone, nonkin were more likely to initiate affiliative interactions with their opponents' kin than with their opponents themselves. Kin,

however, were more likely to initiate affiliative interactions directly with their opponents.

Second, reconciliation appeared to be a more important context for affiliative interactions among nonkin than among kin. Nonkin were significantly more likely to initiate friendly interactions with their opponents' kin following a fight than during control periods. In this respect, reconciliation among unrelated vervet monkeys was similar to reconciliation among unrelated patas monkeys (YORK & ROWELL, 1988), who also interacted more with the relatives of their opponents following a fight than during control periods. In contrast, related vervet monkeys were as likely to interact with their opponents' (and their own) kin during control periods as they were following a fight. Apparently, the generally high rates of grooming and friendly interactions among kin swamped the effect of affiliative interactions in the context of reconciliation. This result is similar to the one reported by CORDS (1988), who found that juvenile male longtailed macaques also reconciled at higher rates with nonkin than with kin. Relationships among unrelated animals are typically less predictable and stable than those among relatives, and CORDS has suggested that post-conflict affiliative interactions may function as a repair mechanism for relationships among nonkin. Such reconciliatory interactions may be less important for kin, who interact at high rates in any case.

The fact that unrelated vervets reconciled with their opponents' kin as well as (indeed, more than) with their opponents themselves suggests that conflict resolution extends beyond individual opponents to their entire families. Approximately 22% of all aggressive interactions among female vervets involve alliances by two individuals against a third, and vervets form the majority (65%) of their alliances with family members (CHENEY & SEYFARTH, 1987). Since an antagonistic interaction is likely to expand to include other members of the opponent's matriline, it may be as important to reconcile with the opponent's family as with the opponent herself (JUDGE, 1983). Kin-biased reconciliation may have the added advantage of establishing affiliative contact with an important, yet uninvolved, individual while nevertheless avoiding the opponent.

There is no evidence that vervets or any other monkey species recognize kinship in any sense other than a close association between two individuals. However, association rates do not entirely explain differential treatment of kin and nonkin, because kin do not always interact at higher rates than nonkin. Moreover, evidence from a number of studies suggests that no single behavioral or physical criterion is sufficient to

explain the ability of nonhuman primates to distinguish other animals' close bonds. In DASSER's (1988) study of mother-offspring recognition in longtailed macaques, for example, subjects generalized to a diverse array of mother-offspring pairs of different age and sex even though they had been trained with only one example from this social category. Similarly, male and female baboon 'friends' do not resemble each other, and yet other baboons nevertheless recognize that certain pairs of individuals associate at high rates (BACHMANN & KUMMER, 1980; SMUTS, 1985).

In sum, monkeys seem to use a metric to classify social relationships that cannot be explained simply in terms of physical features or the number and type of interactions. Instead, their criteria for classification seem to be based on an abstraction that includes all of these. These observations raise the possibility that monkeys recognize a distinction between members of their own matriline and members of other, unrelated families that cannot be explained entirely in terms of close bonds.

In closing, it is important to reemphasize the preliminary nature of the data presented here. Redirected aggression and reconciliation may indeed serve as a valuable tool for examining animals' understanding of other individuals' social relationships, but, both in vervet monkeys and in other primate species, spontaneous manifestations of either pattern of behavior are infrequent enough to raise questions about the significance of the results obtained. Moreover, the fact that much of the within-matriline data in this study was derived from one large extended family raises doubts about the generality of the within- and between-family differences. The data obtained from vervet monkeys are similar to those reported in previous studies, and they support the hypothesis that nonhuman primates recognize their own and other animals' close associates. However, they also highlight the liabilities of purely observational investigations. It seems clear that only experimental studies (*e.g.* CORDS, 1988; DASSER, 1988) will provide the necessary controls and conditions to allow us to explore thoroughly the ways in which animals perceive their own and other animals' social relationships.

### Summary

Among both kin and nonkin, opponents were significantly more likely to threaten their opponents' relatives following a fight than during matched-control periods (simple redirected aggression). Similarly, the relatives of two opponents were more likely to threaten each other following a fight than during matched-control periods (complex redirected aggression). Finally, the relatives of two opponents were more likely to interact affinitively following a fight than in the period preceding it (complex reconciliation).

Reconciliation among related and unrelated opponents differed in the following respects. When kin fought, a much higher proportion of fights was followed by affinitive

behavior, either between the opponents themselves (direct reconciliation) or between one opponent and the kin of another (simple reconciliation). Relatively high frequencies of reconciliation among kin, however, were apparently just a consequence of frequent overall affiliative interactions: when behavior during post-conflict periods was compared with behavior during matched-control periods, direct and simple reconciliation was more common among nonkin than among kin. Nonkin also differed from kin in whom they reconciled *with*. Kin were equally likely to reconcile with their opponents and their opponents' kin. In contrast, nonkin reconciled more often with their opponents' kin than with their opponents themselves.

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