



# Recognition of other individuals' social relationships by female baboons

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We describe a series of playback experiments designed to test whether free-ranging baboons, *Papio cynocephalus ursinus*, recognize the calls of other group members and also associate signallers with their close genetic relatives. Pairs of unrelated females were played sequences of calls that mimicked a fight between their relatives. As controls, the same females heard sequences that involved either (1) only the more dominant female's relative or (2) neither of the females' relatives. When call sequences involved their relatives, subjects looked towards the speaker for a longer duration than when the sequences involved nonkin. When the sequences involved the other female's relative, they also looked towards that female. Subjects did not look towards one another when call sequences involved nonkin. Dominant subjects were more likely to supplant their subordinate partners following playbacks of sequences that mimicked a dispute between their relatives than following the two control trials. In contrast, both subjects were more likely to approach one another and to interact in a friendly manner following the two control trials than following the test trial. Results indicate that female baboons recognize the screams and threat grunts not only of their own close relatives but also of unrelated individuals. They also replicate previous studies in suggesting that female monkeys recognize the close associates of other individuals and adjust their interactions with others according to recent events involving individuals other than themselves.

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Individuals in many animal species recognize their kin, in the sense that they are more friendly towards individuals with whom they have mated and with whom they interact regularly than towards other group members (see reviews by Hepper 1986, 1991a, b; Fletcher & Michener 1987; Gouzoules & Gouzoules 1987; Gamboa et al. 1991). Monkeys appear to go one step further: they appear to recognize the close relationships that exist among individuals other than themselves. Perhaps the best evidence for this comes from a series of experiments performed by Dasser (1988) on captive longtailed macaques, *Macaca fascicularis*. In one test, for example, Dasser trained a female subject to choose between slides of one mother-offspring pair and slides of two unrelated individuals. Having been trained to respond to one mother-offspring pair, the subject was then tested with 14 novel slides of different mothers and offspring paired with an equal number of novel pairs of unrelated animals. In all tests, she correctly selected the mother-offspring pair. The female appeared to use an abstract category to classify

pairs of individuals that was analogous to our concept of 'mother-child affiliation' (Dasser 1988, page 229).

A number of more naturalistic studies have also suggested that monkeys recognize the close associates of other group members. For example, playback experiments using the contact calls of rhesus macaques, *Macaca mulatta*, have demonstrated that females not only distinguish the identities of different signallers but also categorize signallers according to matrilineal kinship (Rendall et al. 1996). Similarly, in a playback experiment conducted with free-ranging vervet monkeys, *Cercopithecus aethiops*, we found that when females were played the scream of an unrelated juvenile, they were more likely to look towards that juvenile's mother than towards other females (Cheney & Seyfarth 1980).

Finally, several observational studies have reported that monkeys that have recently fought with an opponent will selectively reconcile or redirect aggression towards their opponents' close relatives (vervet monkeys: Cheney & Seyfarth 1986, 1989; pigtail macaques, *Macaca nemestrina*: Judge 1982, 1983; Japanese macaques, *Macaca fuscata*: Aureli et al. 1992). Vervet monkeys even seem to change their behaviour towards others according to recent interactions between their own relatives and other

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individuals' relatives. For example, they are more likely to threaten a particular other individual if that individual's relative has recently fought with their own relative (Cheney & Seyfarth 1989).

Monkeys, therefore, appear to classify other individuals according to the relationships that those individuals have with other group members, and their behaviour appears to be affected both by their perception of recent events and their recognition of other individuals' relationships. These abilities are interesting from a cognitive perspective, because knowledge of other individuals' social relationships can only be obtained by observing the behaviour of others and attending to interactions in which oneself is not involved.

Despite support for the hypothesis that monkeys recognize the close associates of other individuals, however, the evidence is also flawed by small sample sizes and conflicting accounts from other studies. For example, although Dasser's experiments involved prodigious training of a number of different individuals, only two of these individuals ever successfully performed the task. Similarly, in our playback experiment on vervet monkeys (Cheney & Seyfarth 1980), only a small number of control females ever looked towards the signaller's mother before the mother had responded herself.

A second potential weakness of the vervet study arises from the use of an orienting response as the sole dependent variable. Orientation provides an accurate assessment of the attention paid by listeners to different vocal stimuli. It does not, however, reveal much information about a call's social or ecological significance, because it does not measure the extent to which calls influence listeners' subsequent behaviour. Moreover, an orienting response can underestimate the effect that calls have on nearby listeners. Monkeys sometimes show no obvious orienting response to naturally occurring calls, even though their subsequent behaviour indicates that they have attended to the call and noted the caller's identity. For example, female baboons, *Papio cynocephalus ursinus*, often fail to orient towards the grunts produced by others (Cheney et al. 1995a; Rendall et al. 1999). Nevertheless, these grunts can strongly influence females' subsequent interactions with others, particularly when the grunts occur in a reconciliatory context following a fight (Cheney & Seyfarth 1997).

Finally, although some species of Old World monkeys may selectively target their opponents' relatives following fights, other species appear not to do so. In particular, there is no evidence for kin-biased redirected aggression in female baboons (Silk et al. 1996; unpublished data). This may be due to the fact that adult female baboons seldom form aggressive alliances with each other, although they frequently give threat grunts when they observe a close relative involved in a dispute (Seyfarth 1976; Cheney 1977; unpublished data). It may therefore be relatively unimportant to threaten opponents' kin explicitly. It is also possible, however, that kin-biased agonism is more subtle in baboons than it is in some other monkey species and more likely to take the form of avoidance or an increase in the rate of supplants. Of course, it might also be the case that

baboons simply cannot recognize other individuals' close associates.

The supposition that monkeys recognize other individuals' relationships and modify their behaviour according to recent interactions between their own relatives and other individuals' relatives is, therefore, a hypothesis that remains to be tested more thoroughly. In an effort to do so, we designed an experiment involving free-ranging baboons in which two unrelated female subjects were played sequences of calls that mimicked a fight between either both of the females' relatives, only one of the females' relatives, or neither of the females' relatives.

In the test sequence, the threat grunts of a dominant animal (e.g.  $A_1$ ) were paired with the screams of a more subordinate individual (e.g.  $B_1$ ), to mimic a dispute. This sequence of calls was then played to two adult females (e.g.  $A_2$  and  $B_2$ ) that were sitting or foraging near one another and who were close relatives of  $A_1$  and  $B_1$ . In separate playback trials, the same two subjects also heard two control call sequences. In the first control (dominant kin condition), subjects were played a sequence in which the threat grunts of the same dominant individual ( $A_1$ ) were paired with the screams of a subordinate animal unrelated to either of the two subjects (e.g.  $D_1$ ). In the second control (no kin condition), subjects heard a sequence of threat grunts and screams produced by two animals (e.g.  $C_1$  and  $D_1$ ) who were both unrelated to the subjects. We predicted that, if females recognized not only the individual identities of signallers but also their relationships with other group members, they should look both towards the speaker and towards each other upon hearing an apparent dispute between their own close relatives. Furthermore, we predicted that subjects might behave more antagonistically towards each other after hearing a dispute that apparently involved two of their relatives than after hearing a dispute involving only one or none of their relatives (see below for a more complete description of predictions).

## METHODS

### Study Area and Subjects

The study site lies in the Okavango Delta, a vast seasonal swamp created by the floodplain of the Okavango River in northwestern Botswana. The habitat consists of seasonally flooded grasslands interspersed by slightly elevated wooded patches ranging from less than 1 ha to over 100 ha (Hamilton et al. 1976; Ross 1987). The average size of a baboon group's range in this area is 450 ha (range 210–650; Hamilton et al. 1976).

At the time of this study, the group contained 79 individuals, including six adult males and 26 sexually mature females. The group was observed between 1977 and 1991 by Hamilton and colleagues (e.g. Bulger & Hamilton 1988; Hamilton & Bulger 1992; Bulger 1993) and has been the focus of detailed observation since 1992. All animals are fully habituated to human observers on foot. Maternal relatedness for all natal animals is known. 'Close kin' are defined as maternal siblings, and mothers and offspring.

Like many other species of Old World monkeys (e.g. Walters & Seyfarth 1987), female baboons in this population form linear dominance hierarchies that remain stable over long periods (Seyfarth 1976; Hausfater et al. 1982; Saunders 1988). Daughters acquire ranks similar to those of their mothers, but the dominance ranks of males are determined primarily by age and size (Hausfater 1975; Packer 1979; Bulger 1993). Males are typically dominant to females. Females remain in their natal groups throughout their lives; males usually emigrate to neighbouring groups at sexual maturity.

### Experimental Design and Protocol

In designing these experiments, we made the assumption that both threat grunts and screams were individually recognizable by other baboons, including individuals unrelated to the signallers. Threat grunts are tonal calls that are typically given in bouts. They are roughly similar in spectral structure to grunts used in affiliative social contexts. Unlike other grunt types (Owren et al. 1997), however, threat grunts are composed of several rapid pulses, the first pulse being of lower frequency than subsequent pulses. Because both acoustical analysis and playback experiments have shown other grunt types to be individually distinctive and recognizable (Cheney et al. 1995b; Cheney & Seyfarth 1997; Owren et al. 1997; Rendall et al. 1999), it seemed probable that threat grunts are recognizable as well.

The evidence for individual recognition of screams is more equivocal. Although several experiments on different species have suggested that monkeys recognize the identity of screaming animals (vervet monkeys: Cheney & Seyfarth 1980; rhesus macaques: Gouzoules et al. 1984; baboons: Cheney et al. 1995b; Palombit et al. 1997), one playback study of rhesus macaques has suggested that subjects have some difficulty in assigning screams to specific signallers (Rendall et al. 1998). In this latter study, however, playback stimuli consisted only of a single, short scream. Playbacks of longer scream sequences, which include a number of acoustical elements and preserve the bout's temporal structure, are more likely to be individually distinctive. Acoustical analysis of the individual distinctiveness of baboon threat grunts and screams is currently underway (D. Rendall, R. Seyfarth & D. Cheney, unpublished data).

For 3 months prior to the initiation of playback trials, we tape-recorded threat grunts and screams from adult females and juveniles aged at least 2 years. We then created sequences of calls in which a dominant individual's threat grunts were combined with a more subordinate individual's screams. This combination of calls was designed to mimic a natural aggressive interaction: dominant animals that are threatening subordinates often give threat grunts while doing so, and subordinate individuals often respond by screaming.

In creating sequences for playback, we attempted both to maintain the natural characteristics of a typical bout of threat grunting and screaming and to hold the characteristics of a bout constant while systematically varying the calls used to make up that bout. For example, to create a

test sequence involving individual A's threat grunts and individual B's screams, we first used Canary software (version 1.2; Charif et al. 1995) to extract threat grunts by A and screams by B from digitized tapes of social interactions involving A with another individual and B with another individual. A's threat grunts and B's screams were then stored on disc, preserving their natural within-call bout structure. Next, we reassembled these stored vocalizations into a sequence that preserved, to the best of our abilities, the typical structure of a naturally occurring scream and threat grunt bout. This was the playback stimulus for the test condition. Finally, to create playback stimuli for the dominant kin (DK) and no kin (NK) conditions, we held this overall structure constant but inserted either different screams for the DK condition or different screams and different threat grunts for the NK condition.

The resulting stimuli consisted of 25 different sequences composed of eight individuals' threat grunts (six adult females and two juvenile males) and 10 individuals' screams (three adult females, four juvenile females and three juvenile males). Sequences that served as test stimuli for some dyads served as control stimuli for other dyads. Sequences contained five to seven threat grunts interspersed with two to six scream bouts. The average duration of the entire call sequence was 5.4 s (range 3.5–8.6).

Subjects were adult females who were close relatives (mothers, daughters, or sisters) of the signallers. The eventual sample consisted of 26 pairs of females. Eight females served as dominant subjects, appearing in one to five different trial sequences. Nine females served as subordinate subjects, and also appeared in one to five trials sequences. Four females appeared as both a subordinate and a dominant subject in different trials. Each dyad heard three different call sequences in separate trials, for a total of 78 trials. Sample size was constrained by the availability of appropriate vocal stimuli and by the fact that several potential dyads were seldom seen in proximity when their relatives were also out of sight.

Before each trial, we first ensured that the individuals whose calls were to be played were not in the immediate vicinity (within 50 m). We then waited until both subjects were seated or foraging within 1–7 m of each other but not interacting. Next, we hid the speaker at a distance of 5–10 m from the subjects, at such an orientation that each female could look in the direction of the speaker without also looking directly at her partner. Although no trial was ever conducted when a subject's partner was positioned in the same direction as the speaker, it is impossible to state with absolute certainty that subjects could never see each other when they looked towards the speaker.

Having placed the speaker, we then positioned the video camera so that both subjects could be filmed and their orientation towards the speaker and towards each other could be distinguished. We filmed subjects for 20 s after the onset of each call playback to allow sufficient time to measure subjects' orienting responses towards both the speaker and each other. However, trials yielded similar results when we analysed subjects' responses only

**Table 1.** Predicted responses of dominant and subordinate subjects in each type of playback trial

Playback type	Look towards speaker	Look towards partner	Behaviour towards partner
Dominant subject			
Test	Yes	Yes	More agonistic than DK and NK
DK	Yes	No	Less agonistic than test
NK	No	No	Less agonistic than test
Subordinate subject			
Test	Yes	Yes	More submissive than DK and NK
DK	Yes, although less	Yes, although less	Less submissive than test
NK	No	No	Less submissive than test

Test condition: Both subjects' relatives were included in the call sequence; DK (dominant kin) condition: only the dominant subject's relative was included in the call sequence; NK (no kin) condition: neither subject's relatives were included in the call sequence.

during the first 10 s. Finally, following each trial, we conducted a focal animal sample (Altmann 1974) of both subjects for 15 min to determine the nature of each female's subsequent social interactions with others.

Two dependent variables, then, were used in analysis. The first, the orienting response, was used in part to permit comparison with other work (e.g. Cheney & Seyfarth 1980; Holekamp et al., *in press*). The second, the focal animal sample, served both to provide information about the effects of different call sequences on subjects' behaviour and to validate the usefulness of the orienting response.

Playback trials were conducted over a 4-month period. On most days we conducted only one or two trials, and no more than three trials were ever carried out on any given day. Successive trials always involved subjects that had not been in the vicinity (within 50 m) during a previous trial. All trials were separated by at least 1 h, a rate that was considerably lower than the rate of naturally occurring screams. Under natural conditions, scream bouts by adult females occur at a rate of 3.6/h, while those by juveniles occur at a rate of 6.4/h (J. Fischer, personal communication).

Below, we term the female paired with a given subject as that subject's 'partner'. For ease of discussion, we use the term 'recognition of another individual's relative' as a synonym for the 'recognition of another individual's close associate'. As we discuss later, these experiments do not purport to distinguish between the ability to recognize genetic relatives as opposed to close associates.

## Predictions

Predicted responses were based on the assumption that females recognized the calls of other group members and also associated other individuals with their close genetic relatives (Table 1). First, we predicted that dominant and subordinate subjects would look towards both the speaker and each other in the test trial, when the calls of their close relatives were played. We also predicted that the dominant subject would be more likely to behave antagonistically towards her subordinate partner and that the

subordinate subject would be more likely to avoid her dominant partner in the test trial than in either of the two control conditions.

In the dominant kin (DK) condition, when the call sequence included only the dominant subject's relative, we predicted that the dominant subject would look towards the speaker but not towards her subordinate partner. We predicted that the subordinate subject would look towards both the speaker and towards her dominant partner in the DK condition, although perhaps for a shorter duration than in the test trial, because the call sequence mimicked an aggressive interaction in which the nearby dominant subject might potentially become involved.

Finally, in the no kin (NK) condition, we predicted that both subjects' responses would be weak, with neither female likely to orient towards the speaker or her partner.

## RESULTS

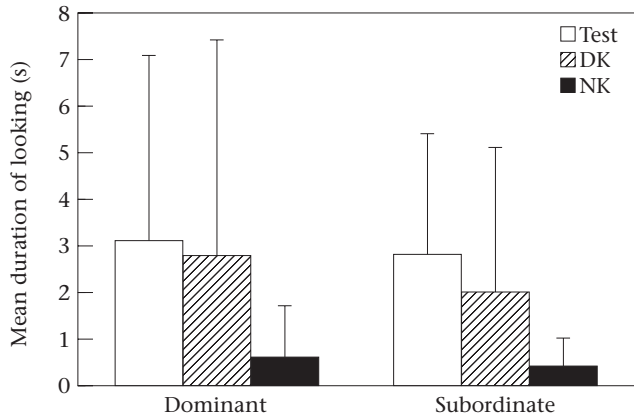
### Orienting Responses

There was considerable variation in subjects' orienting responses to playback trials. When the calls of their own relatives were played, dominant subjects oriented towards the speaker in 73% of trials, while subordinate subjects oriented towards the speaker in 88% of trials. When the playback sequence involved neither of the two females' relatives, however, only 35% of dominant subjects and 29% of subordinate subjects oriented towards the speaker.

These orienting frequencies mirrored females' responses to natural screams. Observations of a small sample of females' orienting responses to the natural screams of unrelated animals indicated that females oriented towards other females' screams in 42% of 55 scream bouts and towards juveniles' screams in only 10% of 119 scream bouts (J. Fischer, personal communication).

When subjects did respond to the playback sequences, they behaved as if they recognized not only their own relatives' calls but also the calls of nonkin. Furthermore, they apparently associated signallers with their close relatives.





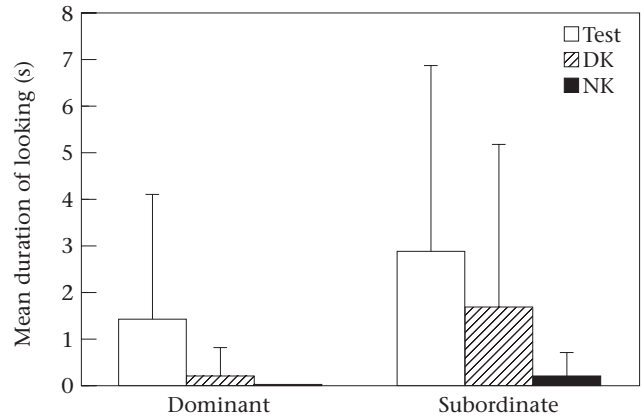
**Figure 1.** The mean duration that dominant and subordinate subjects looked towards the speaker following playback of sequences that included the calls of both of their close relatives (test condition) only the dominant subject's relative (DK condition), or neither of the subjects' relatives (NK condition). Histograms show means+SD for 26 dominant and subordinate subjects in each of the three conditions.

If dominant subjects recognized their relatives' threat grunts, they should have looked towards the speaker for an equally long duration in the test and DK conditions. Moreover, the duration of their orienting response in these two conditions should have been significantly longer than in the NK condition (Table 1). This was the case (Fig. 1; one-tailed Wilcoxon signed-ranks test, corrected for ties: test versus DK:  $T=151.5$ ,  $N=25$ , NS; test versus NK:  $T=36.5$ ,  $N=24$ ,  $P<0.001$ ; DK versus NK:  $T=55$ ,  $N=24$ ,  $P<0.01$ ).

Also as predicted (Table 1), in a significant number of trials, subordinate subjects looked towards the speaker for a longer duration in the test condition than in the NK condition (Fig. 1;  $T=16$ ,  $N=21$ ,  $P<0.001$ ). There was no difference, however, in the duration that subjects looked towards the speaker in the test and DK condition ( $T=110$ ,  $N=24$ , NS). This may have been because in each case the call sequences included the threat grunts of the nearby dominant female's relative. Perhaps for the same reason, subordinate subjects also looked towards the speaker for a longer duration in the DK condition than in the NK condition ( $T=13$ ,  $N=17$ ,  $P<0.001$ ).

Subjects' orientation towards each other suggested that they also associated unrelated signallers with their kin. As predicted (Table 1), dominant subjects looked towards their subordinate partners for a significantly longer duration in the test condition than in either of the two control conditions (Fig. 2; test versus DK:  $T=13.5$ ,  $N=14$ ,  $P<0.01$ ; test versus NK:  $T=0$ ,  $N=14$ ,  $P<0.001$ ). Most dominant subjects failed to look towards their partners at all in the two control conditions. Those that did, however, did so more in the DK than in the NK condition ( $T=0$ ,  $N=5$ , NS).

Similarly, we predicted that subordinate subjects would orient towards their dominant partners for roughly equal durations in both the test and DK condition, because in both trials the threat grunts of their dominant partner's relative were played. This was the case (Fig. 2;  $T=84$ ,



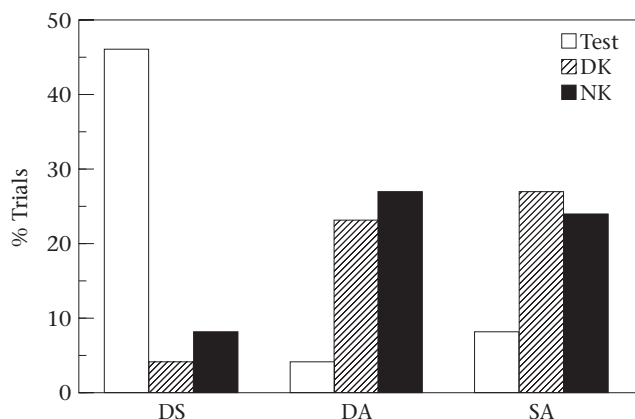
**Figure 2.** The mean duration that dominant and subordinate subjects looked towards each other following playback of sequences that included the calls of both of their close relatives (test condition), only the dominant subject's relative (DK condition), or neither of the subjects' relatives (NK condition).

$N=22$ , NS). Subordinate subjects looked towards their dominant partners for a significantly shorter duration in the NK condition, when neither of the two females' relatives were involved (test versus NK:  $T=12$ ,  $N=20$ ,  $P<0.001$ ; DK versus NK:  $T=15$ ,  $N=14$ ,  $P<0.01$ ).

In nine (35%) of the 26 test trials, one of the subjects scratched herself upon hearing the playback sequence (three dominant and six subordinate females). In contrast, subjects scratched themselves in only five (10%) of the two control trials (chi-square test:  $\chi^2_1=7.2$ ,  $P<0.01$ ). If scratching is a manifestation of anxiety and tension, as has been argued by Aureli & van Schaik (1991; see also Aureli 1997), these observations suggest that subjects may have become anxious when seated near females whose relatives were apparently fighting with their own kin.

It might be argued that subjects looked towards one another not because they recognized each other's relatives but simply because they were responding to changes in their partners' behaviour. If, for example, females recognized only their own relatives' calls and not the calls of nonkin, they might have oriented towards the speaker whenever one of their relatives' calls was played, which in turn might have caused nearby females to orient towards them. This, however, seems unlikely. In the test condition, subordinate subjects looked towards their dominant partner in 77% of 26 trials. In 40% of these trials, they looked towards their partner before that female had begun to look towards the speaker, while in 60% of cases they did so afterwards (sign test, corrected for ties:  $x=8$ ,  $N=20$ , NS). Conversely, dominant subjects looked towards their subordinate partner in 50% of test trials. In 31% of these trials, they looked towards their partner before she had begun to look towards the speaker ( $x=4$ ,  $N=13$ , NS).

There was no indication that subjects were more likely to ignore their relatives' screams than their relatives' threat grunts, or that the screams of some individuals were ignored more than others. The screams of juvenile males or adult sisters, for example, were not more likely



**Figure 3.** The proportion of subjects' first interactions with their partners that took various forms following each trial condition. Histograms show means for 26 dyads in the test, DK and NK conditions. DS: Dominant subject supplanted her subordinate partner; DA: dominant subject approached her subordinate partner without supplanting her or approached and interacted in a friendly manner with her subordinate partner; SA: subordinate subject approached her dominant partner or approached and interacted in a friendly manner with her dominant partner.

to be ignored than the screams of juvenile females or offspring.

### Behavioural Responses

As described earlier, all subjects were followed for 15 min after each of the three trials to determine whether their behaviour was influenced by the type of playback sequence they had just heard. In the following analysis, we focus only on the first interaction between the two subjects, noting whether either of the two females approached (came within 2 m of) her partner, and, if so, what the nature of their interaction was. By concentrating only on the initial contact between the two females, the effects of the playback sequence on subjects' behaviour can be examined in the absence of any confounding effects of other interactions.

Because these experiments were conducted on free-ranging animals, there were many postplayback periods when the two subjects simply separated and never interacted at all. In 53% of cases, however, the two females did come into proximity. The likelihood that subjects would interact with each other following playback trials was unrelated to the frequency with which they looked towards each other during the trial. For example, following 12 (46%) test trials, the first interaction between the two females occurred when the dominant subject supplanted her subordinate partner. In six cases, the dominant subject had looked at her partner at the time of the call playback, and in six other cases she had not.

Following test trials, when the playback sequence had included both females' relatives, dominant subjects were more likely to supplant their lower-ranking partners than following either of the two control trials (Fig. 3; one-tailed sign test, corrected for ties: test versus DK:  $x=0$ ,  $N=11$ ,  $P<0.001$ ; test versus NK:  $x=2$ ,  $N=14$ ,  $P<0.01$ ).

Dominant subjects seldom supplanted their subordinate partners following playback of either of the control sequences.

In contrast, dominant subjects were more likely to approach their subordinate partners without supplanting them, or to approach and interact with them in a friendly manner (usually by handling their infants), following the two control trials than following the test trial (Fig. 3; test versus DK:  $x=0$ ,  $N=5$ ,  $P<0.05$ ; test versus NK:  $x=1$ ,  $N=8$ ,  $P<0.05$ ). The two control trials did not differ from one another in this respect ( $x=5$ ,  $N=11$ , NS).

Subordinate subjects were also more likely either to approach their dominant partners or to approach and interact with them in a friendly manner following the two control trials than following the test trial (Fig. 3; test versus DK:  $x=0$ ,  $N=5$ ,  $P<0.05$ ; test versus NK:  $x=2$ ,  $N=6$ , NS).

It was not possible to determine whether the increase in frequency of supplants following test trials was due to subtle changes in the dominant subject's behaviour, an increase in submission on the part of the subordinate subject, or both. In any case, subjects' behaviour following test trials was qualitatively different than following either of the two control trials, when there was a greater tendency for both dominant and subordinate subjects to approach each other and interact in a friendly manner.

### Subjects' Mean Scores

Because analysis by dyad could not control for the possibility that some subjects might have contributed disproportionately to the results, in a second analysis we calculated each subject's mean response score for each trial type, so that each subject contributed equally to the statistical tests. Although this analysis reduced the sample size considerably, it revealed similar results.

As predicted, there was no difference between the test and DK conditions in the mean duration that each dominant subject looked towards the speaker (one-tailed Wilcoxon test:  $T=13$ ,  $N=8$ , NS). Also as predicted, the mean duration of dominant subjects' orienting response in the test and DK conditions was significantly longer than in the NK condition (test versus NK:  $T=5$ ,  $N=8$ ,  $P<0.05$ ; DK versus NK:  $T=5$ ,  $N=8$ ,  $P<0.05$ ).

Subordinate subjects looked towards the speaker for a longer mean duration in the test condition than in either the DK or NK condition (test versus DK:  $T=11$ ,  $N=9$ , NS; test versus NK:  $T=0$ ,  $N=9$ ,  $P<0.01$ ). The mean duration of their orienting response was also stronger in the DK than in the NK condition ( $T=1$ ,  $N=9$ ,  $P<0.01$ ).

As in the analysis by dyad, the mean duration that dominant subjects looked towards their subordinate partners was significantly longer in the test condition than in either the DK or NK condition ( $T=0$ ,  $N=8$ ,  $P<0.01$  for both comparisons). There was no significant difference in this response between the DK and NK conditions (corrected for ties,  $T=0$ ,  $N=4$ ).

Also as predicted, subordinate subjects looked towards their partners for a longer mean duration in the test and DK conditions than in the NK condition (test versus

DK:  $T=9.5$ ,  $N=8$ , NS; test versus NK:  $T=1$ ,  $N=8$ ,  $P<0.01$ ; DK versus NK:  $T=1$ ,  $N=8$ ,  $P<0.01$ ).

Because subjects did not always interact with their partners following playbacks, it was not possible to assign a score to the 'mean' first interaction. We therefore measured the mean rate at which subjects approached and/or supplanted their partners in the 15 min following playback in the three different conditions.

As in the analysis by dyad, the mean number of times that each dominant subject supplanted her subordinate partner was significantly higher following test trials than following either DK or NK trials (one-tailed sign test, corrected for ties: test versus DK:  $x=0$ ,  $N=6$ ,  $P<0.05$ ; test versus NK:  $x=0$ ,  $N=5$ ,  $P<0.05$ ). There was no difference between DK and NK conditions in the rate that dominant subjects supplanted subordinate partners ( $x=1$ ,  $N=3$ ).

Similarly, dominant subjects approached their subordinate partners without supplanting them at a higher mean rate following DK and NK trials than following test trials. Because some subjects never approached their subordinate partners at all, however, this difference was not significant (test versus DK:  $x=1$ ,  $N=5$ ; test versus NK:  $x=0$ ,  $N=4$ ). As expected, there was no difference in the rate of supplants between DK and NK conditions ( $x=2$ ,  $N=6$ ). Subordinate subjects also approached their dominant partners at a higher mean rate following DK and NK trials than following test trials, although again these differences were not always significant (test versus DK:  $x=1$ ,  $N=6$ ,  $P<0.05$ ; test versus DK:  $x=1$ ,  $N=4$ , NS; DK versus NK:  $x=3$ ,  $N=7$ , NS).

### Subjects' Behaviour Towards Signallers' Other Relatives

Although postplayback behavioural samples focused on each subject's interactions with her partner, many subjects also interacted with additional relatives of the signaller. Analysis of subjects' interactions with these individuals was by necessity more opportunistic and less well controlled than that with their designated partner. Nevertheless, this analysis, too, suggested that subjects selectively altered their behaviour towards the relatives of their own kin's opponents.

Following test trials, dominant subjects supplanted a relative of the signaller that had apparently screamed in a dispute with their own kin on 80% of the 30 occasions that they approached them. Following control trials, in contrast, they supplanted these individuals on only 31% of 29 approaches (chi-square:  $\chi^2_1=14.27$ ,  $P<0.001$ ). This result did not occur simply because dominant subjects supplanted all females at a higher frequency after hearing their own relatives' threat grunts, although there was a slight trend in that direction. Following test and DK trials, dominant subjects supplanted lower-ranking females unrelated to the screaming individual on 51% of the 94 occasions that they approached them. By contrast, following NK trials they supplanted lower-ranking females on 38% of 74 approaches ( $\chi^2=2.97$ , NS).

Subordinate subjects approached a close relative of the signaller whose threat grunts had been paired with their own kin's screams following only 8% of test trials. By

contrast, they approached a relative of the threat-grunting signaller following 27% of control trials ( $\chi^2=4.08$ ,  $P<0.05$ ). This effect was not due to a general reluctance on the part of subordinate subjects to approach all dominant females after hearing a relative scream, because there was no difference between test and control trials in the frequency that subordinate subjects approached dominant females unrelated to the threat-grunting signaller. Subordinate subjects approached such dominant females following 46% of test trials, compared with 35% of control trials ( $\chi^2=0.81$ , NS).

Finally, although subordinate subjects were significantly more likely to be supplanted by their dominant partners following test trials than following control trials (Fig. 3), they were not more likely to be supplanted by all dominant females (although, again, there was a slight trend in that direction). Following test trials, subordinate subjects were supplanted on 71% of the 28 occasions that they were approached by dominant females unrelated to the signaller. Following the two control trials, they were supplanted by such females on 58% of 57 approaches ( $\chi^2=1.46$ , NS).

Hearing their relatives involved in a dispute, therefore, slightly increased the frequency with which dominant females supplanted all other subordinate females, and also slightly increased the frequency with which subordinate females avoided all other dominant females. This trend was negligible, however, when compared with the significant tendency of subjects selectively to supplant or avoid the close relatives of their own kin's opponents.

### DISCUSSION

Results indicate that female baboons recognize the screams and threat grunts not only of their own close relatives but also of unrelated individuals. These results also replicate previous studies on other Old World monkey species in suggesting that females recognize the close associates of other individuals and adjust their interactions with others according to recent events involving individuals other than themselves. Following an apparent dispute involving one of their own relatives, females are less friendly, and more agonistic, towards the kin of their relative's opponent than under control conditions. These latter observations are particularly interesting because they suggest that females' interactions with others can be influenced by disputes in which they are not explicitly involved and which they have not seen but only heard. They suggest, too, that subtle forms of kin-biased redirected aggression may occur even in a species in which females typically form alliances at low rates.

Although several studies have now suggested that monkeys recognize kinship relations among other group members, we still know little about the mechanisms that mediate such recognition. It seems unlikely that monkeys have a concept of genetic relatedness; instead, they seem simply to recognize the close associates of other group members. Because close associates will typically be kin, this rule of thumb seems to be the primary mechanism underlying kin recognition in nonhuman primates (Frederickson & Sackett 1984; Gouzoules & Gouzoules

1987; Welker et al. 1987; Waldman et al. 1988; Grafen 1990; Rendall et al. 1996). There is at present little evidence that monkeys discriminate kin from unrelated dyads that interact at high rates.

It is also possible that the recognition of other individuals' kin is based on rather simple conditioned responses instead of any conceptual understanding of a close social relationship. For example, Dasser (1985) has suggested that female vervet monkeys might simply orient towards signallers' mothers because they have memorized that particular screams evoke strong responses from particular females. Indeed, it has been argued that even Dasser's experiments do not necessarily imply that monkeys have a concept of kinship or even of 'closely bonded'. Instead, monkeys may simply associate individuals that share a 'history of similar functional associations' (Thompson 1995, page 206).

The experiments described here cannot rule out either of these two explanations. In fact, it seems unlikely that a monkey could form a concept such as 'closely bonded' without attending to social interactions and forming associations between one individual and another. To some extent, learning about other individuals' social relationships is by definition dependent on some form of conditioning. In the case of baboons, however, these associations are formed despite the lack of active interference in many disputes, and they concern more than just the mother-offspring relationship. Moreover, baboons' reactions to playback sequences involve more than just a conditioned orienting response. After hearing particular call sequences, females change their behaviour towards particular other individuals in a variety of subtle ways. An apparent dispute between a female's relative and a particular opponent influences that female's subsequent interactions with the members of the opponent's immediate family, but not the members of other families.

These changes in behaviour do not imply that females consciously seek revenge against families whose members have recently fought with their own relatives, merely that hearing a particular combination of calls in some way changes their attitude and behaviour towards certain other group members. Baboon females appear to view their social groups not just in terms of the individuals that comprise them but also in terms of a web of social relationships in which certain individuals are linked with several others. The behaviour of female baboons is influenced not only by their own recent interactions with others but also by the interactions of their close associates with other individuals' close associates.

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