

Reconciliatory grunts by dominant female baboons influence victims' behaviour

DOROTHY L. CHENEY & ROBERT M. SEYFARTH
Departments of Biology and Psychology, University of Pennsylvania

(Received 14 June 1996; initial acceptance 30 August 1996;
final acceptance 3 November 1996; MS. number: A7629)

Abstract. Following aggressive interactions, dominant female baboons, *Papio cynocephalus ursinus*, occasionally grunt to their victims. To examine the effect of these apparently reconciliatory grunts on victims' subsequent behaviour, a series of playback experiments was designed to mimic reconciliation. Victims were played their opponents' grunts in the minutes immediately following a fight and then observed for half an hour. After hearing these grunts, victims approached their former opponents and also tolerated their opponents' approaches at significantly higher rates than they did under control conditions. They were also supplanted by their opponents at significantly lower rates. By contrast, playbacks of control females' grunts did not influence victims' behaviour. Playbacks of reconciliatory grunts did not increase the rate at which opponents approached or initiated friendly interactions with their former victims. Playbacks of reconciliatory grunts, therefore, appeared to influence victims', but not opponents', perception of recent events.

© 1997 The Association for the Study of Animal Behaviour

Female baboons utter low-amplitude tonal grunts during many of their social interactions. The majority of grunts occur in the context of handling other females' infants, but females may also grunt as they approach one another, as they feed near or groom one another or as they move into new areas of their range. Grunts can be given singly or in bouts, and they occur at high rates (more than 10 grunts per female per hour of observation). As is true also of many other non-human primates' calls (e.g. cotton-top tamarins, *Saguinus oedipus*: Cleveland & Snowdon 1982; squirrel monkeys, *Saimiri sciureus*: Boinski 1992; Japanese macaques, *Macaca fuscata*: Blount 1985, Masataka 1989, Sakuro 1989; stump-tailed macaques, *M. arctoides*: Bauers & de Waal 1991, Bauers 1993; vervet monkeys, *Cercopithecus aethiops*: Cheney & Seyfarth 1982; mountain gorillas, *Gorilla gorilla*: Harcourt et al. 1993; Seyfarth et al. 1994; reviewed by Hauser 1996), baboons' grunts appear to function at least in part to facilitate social interactions. Dominant females that grunt as they approach more subordinate individuals, for example, are less likely to supplant these individuals, and more likely to handle their

infants, than females that remain silent (Cheney et al. 1995b).

Female baboons also grunt to their subordinate victims following approximately 13% of all aggressive interactions. Two lines of evidence suggest that these apparently 'reconciliatory' grunts act to reduce victims' anxiety and to restore opponents' relationships to baseline tolerance levels (see Watts 1995 for similar data on gorillas). First, observations have shown that grunts are correlated with an increased frequency of friendly interactions between victims and their opponents in the minutes immediately following a fight (Silk et al. 1996). Second, playback experiments have shown that, when victims are played a tape-recording of a former opponent's scream, they attend to this potentially threatening call for a significantly shorter duration if their opponent has recently grunted to them than if she has not (Cheney et al. 1995b).

The hypothesis that baboon females' grunts serve a reconciliatory function is, however, based on several assumptions. First, in the case of the observational data, it presumes that the correlation between grunts and subsequent friendly interactions is causally related and that other signals, such as visual cues, are not essential. Second, in the case of the playback experiments, the hypothesis

Correspondence: D. Cheney, Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, U.S.A. (email: cheney@psych.upenn.edu).

presumes that a diminished response to an opponent's scream is an accurate reflection of reduced anxiety. Finally, it assumes that reconciliation is appropriately defined in terms of reduced anxiety. Using similar reasoning, it has been argued that reconciliation functions to lower stress in captive groups of macaques because it decreases victims' scratching (Aureli & van Schaik 1991) and heart rates (Smucny et al. 1996).

Most studies to date have also failed to consider whether apparently reconciliatory behaviour by dominant opponents towards lower-ranking victims has any functional significance to victims beyond a reduction in anxiety and a willingness to tolerate former opponents' approaches. Despite the proliferation of research on reconciliation in recent years, only one study of captive long-tailed macaques, *M. fascicularis*, has shown that reconciliation has an effect on victims' subsequent behaviour towards former opponents (Cords 1992; see also Cords & Thurnheer 1993). Even in this valuable study, the interactions of former opponents may have been artificially influenced by the fact that the animals were forced into proximity with one another during the post-conflict period. Similarly, although baboon grunts appear to serve a reconciliatory function, no study has considered whether vocalizations alone, in the absence of other friendly gestures or visual signals, influence victims' subsequent interactions with their opponents.

A reconciliatory grunt could potentially affect a victim's behaviour by increasing the probability that she approached or initiated a friendly interaction with her opponent. In principle, this hypothesis could be tested by following a subordinate female for some period after a fight and comparing her behaviour after she received a reconciliatory grunt with her behaviour after she did not. This procedure, however, suffers from the drawback that grunts often occur in association with other friendly behaviour. It is therefore difficult to determine solely through observational means whether a vocalization can, by itself, function to influence victims' behaviour.

In this paper, we describe a playback experiment designed to circumvent this confound. Specifically, we attempted to mimic vocal reconciliation by playing the grunts of former opponents to victims in the minutes immediately following a fight. The experiment's aim was to determine whether an apparently reconciliatory call not only reduced victims' anxiety but also

influenced their subsequent interactions with former opponents.

METHODS

Study Area and Subjects

The study site lies in the Okavango Delta, a vast seasonal swamp created by the flood-plain of the Okavango River in northwestern Botswana. The habitat consists of seasonally flooded grasslands interspersed by slightly elevated wooded patches ranging from less than one hectare to hundreds of hectares (Hamilton et al. 1976; Ross 1987). The average size of a group's range is 450 ha (range=210–650; Hamilton et al. 1976).

Subjects were 23 sexually mature females that were part of a group of approximately 70 baboons. The group was observed more or less continuously 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 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 neighboring groups at sexual maturity.

Throughout this paper, we use the term 'victim' to refer to the female that was the recipient of aggression and the subject of subsequent experimental and observational analysis. We use the term 'opponent' to refer to the more dominant female that originally threatened her.

Observational and Experimental Protocol

To determine whether opponents' grunts affected victims' behaviour, we conducted half-hour-long behavioural samples of females immediately after they had been threatened (lunged

at, chased or bitten) by a more dominant, unrelated female. During these samples, we noted the identities of all individuals that either approached (came to within 2 m) or were approached by the victim, as well as all subsequent social interactions.

Post-conflict samples were conducted under three conditions. In the test condition, we played a tape-recording of the opponent's grunt to the victim as soon as possible following the fight (see below), in an attempt to mimic reconciliation ('reconciliatory grunt' condition).

We compared the data obtained in the half-hour following playback of a reconciliatory grunt with post-conflict samples involving the same victim and the same opponent under two control conditions. In the first control condition, the victim was played the grunt of a female that had not been involved in the fight ('control grunt' condition) but had nevertheless been in the general vicinity (within 50 m) when the fight occurred. The female whose call was chosen for this control playback was always higher-ranking than the victim, although she might be either higher- or lower-ranking than the opponent. Data collected following playback of a control grunt allowed us to determine whether a victim might change her behaviour toward her opponent after hearing any higher-ranking female's grunt, not just specifically her opponent's.

In the second control condition, we sampled the same victim for half an hour in the absence of any playback, to determine the victim's baseline probability of approaching her opponent ('no vocalization' condition). This additional control could not specifically examine the victim's behaviour in the absence of hearing any grunts at all, because in the half-hour following a fight the victim invariably heard the naturally-occurring grunts of many individuals. The control did, however, allow us to reduce the possibility that some aspect of our experimental protocol influenced victims' behaviour.

The experimental design assumed that baboons' grunts are individually distinctive, a supposition supported by prior acoustical analysis (M. Owren, R. Seyfarth & D. Cheney, unpublished data) and playback experiments (Cheney et al. 1995a). Grunts used as playback stimuli were ones that had originally been recorded as females either reconciled with an unrelated lower-ranking opponent or handled an unrelated, lower-ranking

female's infant. All stimuli were first analysed in the field using Canary software for waveform digitization (Cornell Laboratory of Ornithology) to ensure that they were of similar acoustic structure, of similar duration and free of background noise. All grunts used as playback stimuli had been recorded within the previous 3 months. Calls from the same pool were used in both the reconciliatory grunt condition and the control grunt condition. For example, following a fight between females B and D, B's grunt would be played to D as a test call. On another occasion, following a fight between females A and D, B's call might be played to D as a control call.

Methods were similar to those used in earlier playbacks of grunts to vervet monkeys (reviewed in Cheney & Seyfarth 1990) and baboons (Cheney et al. 1995b). All experiments and subsequent post-conflict samples were conducted in wooded areas, when individuals were frequently out of sight of one another. Grunts were played from a concealed Nagra DH loudspeaker placed 3–6 m behind the subject's current orientation and direction of gaze, to mimic the imminent approach of a dominant female. Grunts were played back at the same amplitude as naturally occurring grunts (median amplitude = 64.5 dB, range = 61–68 dB SPL at 1 m).

No post-conflict samples or experiments were initiated unless the victim and her opponent had separated by at least 4 m immediately following the fight and (to the best of our knowledge) moved out of visual contact of one another. Observational data had suggested that over 50% of the reconciliatory grunts given by dominant females under natural conditions occurred within 90 s of the original fight (Silk et al. 1996). By playing grunts to victims soon after the aggressive interaction, therefore, we hoped to mimic the context in which most reconciliatory grunts occur. All playback experiments were conducted within 5 min of the original fight, and over 85% occurred within the first 2 min.

Playback trials and post-conflict samples were conducted opportunistically, depending upon the occurrence of a fight involving a particular victim and a particular opponent. Trials involving a given victim and any opponent were, however, always separated by at least 24 h. Because females grunt at a mean rate of over 10 calls per hour (D. Cheney & R. Seyfarth, unpublished data), this schedule ensured that playbacks occurred at a far

lower rate than did naturally-occurring grunts. Trial order for each of the three conditions was systematically varied for each dyad.

Baboon females are highly attracted to mothers with infants, and they approach and interact with mothers at high rates. To guard against the possibility that female reproductive state might influence interaction rates, we ensured that all post-conflict samples involving a particular victim and a particular opponent were conducted when the victim was in the same reproductive state. Thus, for example, if a control sample was conducted on a given victim when she was pregnant, any playback of a 'reconciliatory' grunt was also conducted while she was still pregnant.

We attempted to obtain post-conflict samples on as many dyads as possible in all three post-conflict conditions. This required, however, that we observe the same opponent threaten the same victim in the same general context on at least three occasions. Over a 6-month period, we obtained post-conflict samples in all three conditions from 35 different dyads (involving 17 different victims). From an additional 33 dyads (17 different victims) we obtained samples of victims in the 'reconciliatory' grunt condition and in one of the two control conditions. Finally, there were numerous other dyads from which we were able to obtain a sample of the victim's post-conflict behaviour in only one of the three conditions (reconciliatory grunt condition only: 22 dyads, 11 different victims; control grunt only: 12 dyads, 9 victims; no vocalization control only: 27 dyads, 11 victims). All but the highest-ranking female appeared as subjects at least once in each condition.

On a number of occasions, dominant opponents uttered grunts of their own after their victims had begun to move away from the immediate vicinity but before any experiment had been conducted. If the victim was facing her opponent when the grunt occurred, we initiated no post-conflict sample. In some cases, however, the victim was already at a distance of 4–8 m, with her vision occluded by vegetation or a termite mound, when her opponent grunted. We decided to conduct post-conflict samples of victims following 26 of these naturally-occurring 'reconciliatory' grunts to determine whether a victim's behaviour following playback of her opponent's grunt was similar to her behaviour following a naturally-occurring grunt.

Victims' behaviour following a grunt playback did not differ statistically from their behaviour following a naturally occurring grunt. Victims were not more likely to approach their former opponents after hearing a naturally occurring grunt as opposed to a grunt playback ($\chi^2_1=1.63$, $P>0.20$). Similarly, opponents were not more likely to approach their former victims after grunting to them than after they remained silent and the victim heard only a grunt playback ($\chi^2_1=0.35$, $P>0.80$).

In eight cases when we sampled victims following a naturally occurring grunt, we were also able on another occasion to conduct a matching playback experiment. In these cases, the sample obtained with the naturally occurring grunt was not used in subsequent analysis, except as a check for our playback experiments. In 18 other cases, however, we were subsequently unable to mimic reconciliation through a playback experiment, and we included the naturally occurring call as a sample in the 'reconciliatory' grunt condition. As a result, of the 90 post-conflict samples that were conducted in the 'reconciliatory' grunt condition, 72 (80%) involved a playback experiment and 18 (20%) involved naturally occurring grunts.

Analysis

Post-conflict samples were subjected to two sorts of analysis. In the first analysis, for each of the three post-conflict conditions, we noted whether the victim subsequently came near her opponent and interacted with her at all, and, if so, which of the two individuals was the first to initiate contact with the other. By focusing only on the initial contact between the two females, the effects of a 'reconciliatory' grunt on the victim's behaviour could be examined in the absence of any confounding effects of subsequent interactions.

In the second analysis, we compared each victim's rate of interaction with a particular opponent during the entire (half-hour) post-conflict period with her rate of interaction with the same female under baseline conditions, in the absence of a recent fight. Baseline data were obtained from the set of half-hour post-conflict samples ($N=252$), in which we recorded not just the interactions that occurred between the subject and her former opponent but also all interactions that occurred between the subject and any other group

member. For any given victim, therefore, there was a variable number of half-hour samples (range=4–26) from which we could calculate baseline rates of interactions with females in the absence of a fight. The sample for this analysis ($N=20$) included all but the second- and third-ranking females, who were excluded for lack of sufficient baseline data.

In both analyses, we focused on a number of behavioural measures. First, we noted whether the victim grunted to her former opponent. Second, we noted whether the victim approached her former opponent to within 2 m. We interpreted both behaviours as a measure of the victim's willingness either to initiate a friendly interaction with her former opponent or to risk feeding or resting in close proximity to her. Third, we noted whether the victim was approached by her opponent without being supplanted beyond 2 m from her (termed, for purposes of brevity, a 'tolerated' approach). Again, we interpreted this behaviour as a measure of the victim's willingness to permit her opponent's close proximity. Fourth, we noted whether the victim was approached and supplanted beyond 2 m by her former opponent. We interpreted this behaviour as a measure of the victim's disinclination to risk an interaction with her opponent. Finally, we recorded whether either the victim or her opponent initiated any form of friendly interaction with the other. Friendly interactions were defined as occurring whenever one female touched, embraced, or groomed another or handled the other's infant.

RESULTS

Responses to Playbacks

Subjects responded to all playback trials either by orienting in the direction of the speaker or by apparently ignoring the call entirely. However, victims responded to playbacks of their opponents' grunts more strongly than to playbacks of higher-ranking control females' grunts. The mean \pm SD duration of victims' orientation to playbacks of control females' grunts was 0.3 ± 0.5 s. This response was similar in duration to females' responses to naturally occurring grunts (Cheney et al. 1995a). By contrast, victims responded for a significantly longer mean duration to playbacks of their opponents' grunts

(1.1 ± 1.8 s; two-tailed Mann–Whitney U -test: $z=3.04$, $P<0.01$).

First Contact

In the initial analysis we noted whether the victim and her opponent subsequently came into close proximity of one another, and, if so, which female was responsible for initiating contact. Matched-pair statistical comparisons were possible only for those dyads from which we obtained post-conflict samples either in all three conditions or in the reconciliatory grunt plus one of the two control conditions. Results were similar, however, for those dyads from which there were post-conflict samples in only one condition (Table I).

Because these experiments were conducted on free-ranging animals, there were many post-conflict samples when the victim and her opponent simply moved out of each other's vicinity and never interacted at all. In other cases, however, the victim and her opponent did subsequently come into proximity of one another. There were 35 dyads with post-conflict samples in each of the three conditions. In 26 of these dyads, the victim and her opponent came into close proximity of one another at least once in the half-hour following a 'reconciliatory' grunt. For 15 dyads, the first contact occurred either when the victim grunted to her opponent from a distance of 2–5 m or approached her opponent to within 2 m. In no case did these same victims approach or grunt to their opponents in the half-hour following playback of a control vocalization (two-tailed binomial test, corrected for ties: $x=0$, $N=15$, $P<0.001$) or in the period following no playback at all ($x=0$, $N=15$, $P<0.001$). For another 11 dyads, the first contact occurred when the opponent approached to within 2 m of the victim but did not supplant her from the immediate vicinity (a 'tolerated' approach). Again, these same victims did not permit tolerated approaches following playback of a control vocalization ($x=1$, $N=12$, $P<0.01$) or following no vocalization at all ($x=0$, $N=11$, $P<0.001$). In five of the tolerated approaches, the opponent also grunted to her victim as she approached, and in one additional instance the victim grunted to her opponent as she was approached.

In contrast, when victims had been played either a control vocalization from another female or no vocalization at all, they did not approach

Table I. A summary of the first interaction between victims and opponents in each of the three post-conflict conditions

	Dyads with samples in how many conditions?	Reconciliatory grunt	Control grunt	No grunt
Victim approaches or grunts to opponent	3	15/35	0.43	0/35
	2*	14/33	0.42	0/9
	1	9/22	0.41	1/12
	Overall	38/90	0.42	1/56
Victim 'tolerates' opponent's approach	3	11/35	0.31	1/35
	2*	9/33	0.27	0/9
	1	5/22	0.23	0/12
	Overall	25/90	0.28	1/56
Opponent approaches and supplants victim	3	0/35	0	4/35
	2*	0/33	0	3/9
	1	0/22	0	1/12
	Overall	0/90	0	8/56

*In all cases, the sample consisted of the reconciliatory grunt condition and one of the two control conditions.

their former opponents, nor did they allow their opponents to approach them. Indeed, when opponents did approach their victims in the absence of a prior reconciliatory grunt, they typically supplanted them from the immediate vicinity (control vocalization versus reconciliatory grunt condition: $x=0$, $N=4$, NS; no vocalization versus 'reconciliatory' grunt condition: $x=0$, $N=10$, $P<0.01$). There were no significant differences in victims' behaviour following either playback of a control female's vocalization or no playback at all (Table I).

Results were similar for the dyads with post-conflict samples in the 'reconciliatory' grunt plus one of the two control conditions (Fig. 1). After hearing their opponent's reconciliatory grunt, victims in this group were more likely to approach or grunt to their opponents than they were under control conditions ($x=0$, $N=14$, $P<0.001$). Victims were also more likely to tolerate their opponent's approach ($x=0$, $N=9$, $P<0.01$) and less likely to be supplanted ($x=0$, $N=8$, $P<0.01$).

Although playbacks of reconciliatory grunts appeared to influence victims' propensity both to approach their opponents and to tolerate their opponents' approaches, this increase in proximity did not necessarily lead to subsequent friendly interactions. On only 8% (3/38) of the occasions that a victim approached her former opponent following a reconciliatory grunt did either the victim or her opponent initiate a friendly inter-

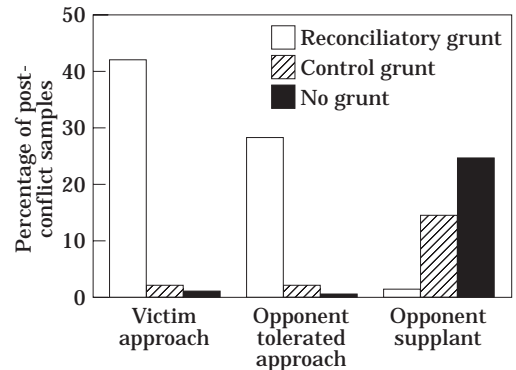


Figure 1. The proportion of first interactions between victims and their opponents that took various forms in each of the post-conflict conditions. Histograms show means for all dyads taken together. □: Victims' behaviour following playback of a 'reconciliatory' grunt; ▨: victims' behaviour following playback of a control female's grunt; ■: victims' behaviour in the absence of a playback trial. First interactions were defined as follows: Victim approach=the victim grunted to or approached her opponent to within 2 m; Opponent tolerated approach=the victim allowed her opponent to approach her without moving more than 2 m away; Opponent supplant=the opponent approached the victim and the victim moved more than 2 m away. Reconciliatory grunt='reconciliatory' grunt condition.

action within the next minute. In contrast, a friendly interaction occurred on 48% of the

occasions that an opponent made a tolerated approach of her former victim following a reconciliatory grunt.

Although reconciliatory grunts appeared to increase victims' willingness to approach their opponents, playbacks of control females' vocalizations appeared to have little effect on victims' inclination to approach these individuals. Victims approached their opponents at least once in 47% of the 90 post-conflict samples that followed a reconciliatory grunt. In contrast, they approached control females in only 11% of the 56 samples following playback of a control vocalization. This difference may have occurred in part because control females were not always in as close proximity to victims as opponents were. Nevertheless, because we tried to ensure that females whose grunts were chosen as control stimuli were in the same general vicinity as the victim when the playback was conducted, it seems unlikely that this explanation accounts entirely for the difference.

Comparison of Post-conflict Periods with Baseline Rates of Interaction

Analysis of victims' rates of interactions with former opponents during the entire half-hour post-conflict period also suggested that 'reconciliatory' grunts increased victims' propensities to attempt to interact with their former opponents. The mean rate that each victim approached or grunted to her former opponents in the half-hour after hearing their reconciliatory grunts was higher than the mean rate that she approached the same females under baseline conditions, in the absence of a fight (two-tailed Wilcoxon matched-pairs test: 3 ties, $T=4$, $N=20$, $P<0.001$; Fig. 2). By contrast, such grunts had no effect on opponents' tendencies to approach their victims. This was probably because most 'reconciliatory' grunts were not produced by the opponents themselves, but were instead mimicked through artificial playbacks.

When opponents did approach their victims during post-conflict periods, however, victims were more likely to tolerate these approaches if they had recently heard an apparently 'reconciliatory' grunt than if they had not (Fig. 3). Victims tolerated their opponents' approaches at higher rates following a reconciliatory grunt than under baseline conditions (no ties, $T=34$, $N=20$,

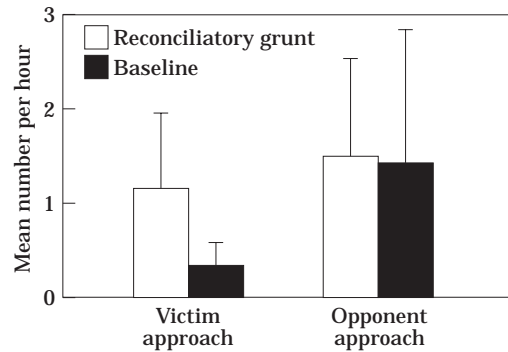


Figure 2. The mean hourly rate at which victims and opponents approached each other in the reconciliatory grunt condition compared with the rate that they approached the same individuals under baseline conditions. Histograms show means and standard deviations for all victims and their opponents. □: Rate of behaviour following playback of a 'reconciliatory' grunt; ■: baseline rate of behaviour. Legend as in Fig. 1.

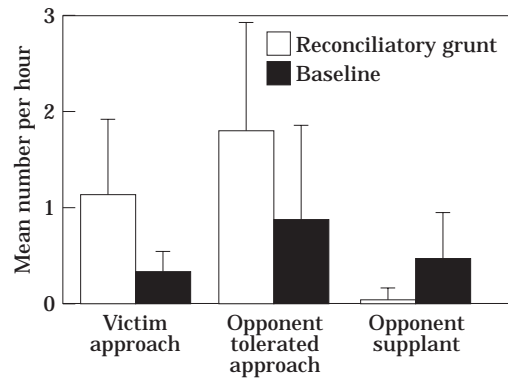


Figure 3. The mean hourly rate at which victims approached their opponent, tolerated their opponent's approach, or were supplanted by their opponent in the reconciliatory grunt condition compared with baseline conditions. Histograms show means and standard deviations for all victims. Legend as in Fig. 1.

$P<0.005$). Similarly, victims were approached and supplanted by opponents at lower rates in the reconciliatory grunt condition than under baseline conditions (3 ties, $T=1$, $N=20$, $P<0.001$; Fig. 3). Opponents threatened or chased their former victims on less than 4% of the occasions that they approached them.

In contrast, when victims were played either no vocalization at all or the vocalization of a dominant, uninvolved female, they behaved as if no

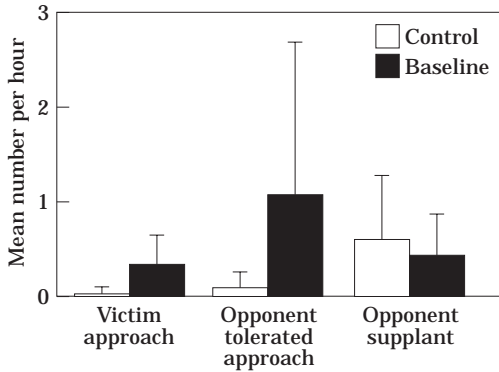


Figure 4. The mean hourly rate at which victims approached their opponent, tolerated their opponent's approach or were supplanted by their opponent in the two control conditions compared with baseline conditions. Histograms show means and standard deviations for all victims. Legend as in Fig. 1.

reconciliatory act had occurred. They approached their opponents at a significantly lower rate than they did under baseline conditions (2 ties, $T=1$, $N=20$, $P<0.001$; Fig. 4). Similarly, they permitted tolerated approaches at a significantly lower rate (1 tie, $T=1$, $N=20$, $P<0.001$) and were supplanted by them at a higher rate (5 ties, $T=18$, $N=20$, $P<0.01$; Fig. 4).

As in the previous analysis, however, reconciliatory grunts did not increase the frequency of subsequent friendly interactions over baseline conditions. Of the 16 victims that approached their opponents at all following a reconciliatory grunt, only three subsequently interacted with their opponents in the next minute at a higher frequency than they did under baseline conditions, whereas eight interacted at a lower frequency. When all females were considered together, 10% of victims' approaches to their dominant opponents after a reconciliatory grunt were followed by a friendly interaction within the next minute, compared with 21% of their approaches to the same females in the absence of a recent fight. The frequency of friendly interactions following tolerated approaches, however, was roughly the same as it was under baseline conditions. Of the 16 females that were approached by a dominant opponent at least once following a reconciliatory grunt, seven subsequently interacted with their opponents at a higher frequency than they did under baseline conditions, while five interacted

less. Taken together, 28% of tolerated approaches following a reconciliatory grunt were followed by a friendly interaction within the next minute. This frequency was the same as it was under baseline conditions.

DISCUSSION

When played the 'reconciliatory' grunt of a recent opponent, victims responded more strongly than they did to playbacks of control females' grunts, suggesting that they distinguished among different females' grunts and remembered recent aggressive interactions. Moreover, after hearing their opponents' grunts, victims approached their opponents and tolerated their opponents' approaches at a significantly higher rate than they did in either of the two control conditions. Similarly, following reconciliatory grunts, victims were significantly less likely to be supplanted by their former opponents than they were in either control condition. These experiments indicate that apparently reconciliatory grunts have a strong causal influence on the behaviour of their audience. Although they may not alter individuals' social relationships in the days following the original fight (Silk et al. 1996), over the short term, grunts appear not only to reduce victims' anxiety but also to facilitate interactions between recent adversaries.

Increased rates of approaches by victims following reconciliatory grunts did not occur simply because victims and opponents were more likely to be in close proximity following a recent fight than under baseline conditions, because playbacks of reconciliatory grunts had no effect on the rate that opponents approached victims. Moreover, victims of aggression were not simply motivated to approach any female whose grunt they heard. A reconciliatory grunt by a former opponent significantly increased the likelihood that the victim would approach that opponent, whereas an acoustically similar grunt by a control female had no effect on the likelihood that the victim would approach that individual.

The fact that playbacks of opponents' grunts significantly increased the rate at which victims approached them suggests that victims might even actively have sought out former opponents that had apparently reconciled with them, perhaps in an effort to restore or ameliorate their relationship. Although this explanation is plausible, it is

also possible that victims were simply attempting to return to the food or resting site from which they had been driven. These alternative explanations could be compared by playing an opponent's reconciliatory grunt to a victim from a direction different from the one where the fight had originally occurred, and then noting where the victim subsequently moved. This was not done in the present study because, in an effort to make our experiments as naturalistic as possible, we played calls only from the direction where the victim had last observed her opponent.

Because these experiments deliberately mimicked reconciliation, they created an inevitable mismatch between victims' and opponents' perceptions of recent events. The majority of post-conflict samples (80%) were conducted on victims who (speaking anthropomorphically) apparently believed that their opponent had reconciled with them when in fact she had not. Perhaps as a result, playbacks of reconciliatory grunts influenced victims' propensities to approach their opponents but not vice versa. Similarly, although the experiments may have caused victims to seek out their former opponents, once an approach had occurred they did not produce a concomitant increase in the frequency of friendly interactions relative to baseline rates. From the perspective of the victim, reconciliation apparently had occurred, but from the perspective of her opponent it had not. Although dominant females may have tolerated their former victims' more frequent approaches, therefore, they were not necessarily inclined either to initiate a friendly interaction or to signal in some way their willingness to accept such an interaction.

In contrast, when opponents rather than their victims initiated approaches following a reconciliatory grunt, a higher proportion of approaches was followed by a friendly interaction. In this case, it seems, dominant females were motivated to interact in a friendly manner with their former victims (usually because the victims had infants). The victims, in turn, tolerated their approaches more than they did in the two control conditions, perhaps because they were under the impression that their opponents had recently reconciled with them.

These experiments address the function of grunts and not the mechanisms underlying their production. They indicate that reconciliatory grunts act not only to modify the victim's affective

state (Cheney et al. 1995b), but also to alter her behaviour, at least within the half-hour following a fight. The experiments do not consider whether opponents are capable of recognizing that grunts given during the post-conflict period function to alleviate victims' anxiety. We have argued elsewhere (Cheney & Seyfarth 1996) that this interpretation seems unlikely given the probable inability of monkeys to attribute mental states different from their own to others (Cheney & Seyfarth 1990; Byrne 1995). It seems more likely that dominant females give 'reconciliatory' grunts not to reassure their victims, but simply because grunts increase the probability that they will be able to interact with their victims or their infants. Victims, in turn, learn through experience and perhaps also by observing the interactions of others that grunts honestly signal a low probability of aggression. Although a 'reconciliatory' grunt may have the effect of changing the victim's mental state, it is probably not intended to do so.

ACKNOWLEDGMENTS

We thank the Office of the President and the Department of Wildlife and National Parks of the Republic of Botswana for permission to conduct research in the Moremi Reserve. We are grateful to W. J. Hamilton III for logistical support and access to background data. M. Mokopi, C. Seyfarth and L. Seyfarth provided invaluable assistance in the field by locating and identifying aggressive interactions. We also thank J. Gros-Louis, S. Harcourt, R. Palombit, G. Ramos-Fernandez, K. Zuberbühler and especially J. Silk for suggestions concerning experimental protocol and data analysis. This research was supported by grants from the National Geographic Society, the Research Foundation of the University of Pennsylvania, and NIH grant HD-29433.

REFERENCES

- Aureli, F. & van Schaik, C. P. 1991. Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*): II. Coping with uncertainty. *Ethology*, **89**, 101–114.
- Bauers, K. A. 1993. A functional analysis of staccato grunt vocalizations in the stump-tailed macaque (*Macaca arctoides*). *Ethology*, **94**, 147–161.
- Bauers, K. A. & de Waal, F. 1991. 'Coo' vocalizations in stump-tailed macaques: a controlled functional analysis. *Behaviour*, **119**, 143–160.

- Blount, B. 1985. 'Girney' vocalizations among Japanese macaque females: context and function. *Primates*, **26**, 424-435.
- Boinski, S. 1992. Ecological and social factors affecting the vocal behavior of adult female squirrel monkeys. *Ethology*, **92**, 316-330.
- Bulger, J. 1993. Dominance rank and access to estrous females in male savanna baboons. *Behaviour*, **124**, 89-122.
- Bulger, J. & Hamilton, W. J. 1988. Inbreeding and reproductive success in a natural chacma baboon, *Papio cynocephalus ursinus*, population. *Anim. Behav.*, **36**, 574-578.
- Byrne, R. W. 1995. *The Thinking Ape: Evolutionary Origins of Intelligence*. Oxford: Oxford University Press.
- Cheney, D. L. & Seyfarth, R. M. 1982. How vervet monkeys perceive their grunts: field playback experiments. *Anim. Behav.*, **30**, 739-751.
- Cheney, D. L. & Seyfarth, R. M. 1990. *How Monkeys See the World: Inside the Mind of Another Species*. Chicago: The University of Chicago Press.
- Cheney, D. L. & Seyfarth, R. M. 1996. Function and intention in the calls of nonhuman primates. *Proc. Br. Acad.*, **88**, 59-76.
- Cheney, D. L., Seyfarth, R. M. & Silk, J. B. 1995a. The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: evidence for causal reasoning? *J. comp. Psychol.*, **109**, 134-141.
- Cheney, D. L., Seyfarth, R. M. & Silk, J. B. 1995b. The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Anim. Behav.*, **50**, 249-257.
- Cleveland, J. & Snowdon, C. T. 1982. The complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). *Z. Tierpsychol.*, **58**, 231-270.
- Cords, M. 1992. Post-conflict reunions and reconciliation in long-tailed macaques. *Anim. Behav.*, **44**, 57-61.
- Cords, M. & Thurnheer, S. 1993. Reconciliation with valuable partners by long-tailed macaques. *Ethology*, **93**, 315-325.
- Hamilton, W. J. & Bulger, J. 1992. Facultative expression of behavioral differences between one-male and multimale savanna baboon groups. *Am. J. Primatol.*, **28**, 61-71.
- Hamilton, W. J., Buskirk, R. E. & Buskirk, W. H. 1976. Defense of space and resources by chacma (*Papio ursinus*) baboon troops in an African desert and swamp. *Ecology*, **57**, 1264-1272.
- Harcourt, A. H., Stewart, K. J. & Hauser, M. D. 1993. Functions of wild gorilla 'close' calls: I. Repertoires, context, and interspecific comparison. *Behaviour*, **124**, 89-122.
- Hauser, M. D. 1996. *The Evolution of Communication*. Cambridge, Massachusetts: MIT Bradford Books.
- Hausfater, G. 1975. Dominance and reproduction in baboons (*Papio cynocephalus*). *Contributions to Primatology, Vol. 7*. Basel: S. Karger.
- Hausfater, G., Altmann, J. & Altmann, S. 1982. Long-term consistency of dominance relations in baboons. *Science*, **217**, 752-755.
- Masataka, N. 1989. Motivational referents of contact calls in Japanese macaques. *Ethology*, **80**, 265-273.
- Packer, C. 1979. Male dominance and reproductive activity in *Papio anubis*. *Anim. Behav.*, **27**, 37-45.
- Ross, K. 1987. *Okavango: Jewel of the Kalahari*. New York: Macmillan.
- Sakuro, O. 1989. Variability in contact calls between troops of Japanese macaques: a possible case of neutral evolution of animal culture. *Anim. Behav.*, **38**, 900-902.
- Saunders, C. D. 1988. Ecological, social, and evolutionary aspects of baboon (*Papio cynocephalus*) grooming behavior. Ph.D. thesis, Cornell University.
- Seyfarth, R. M. 1976. Social relationships among adult female baboons. *Anim. Behav.*, **24**, 917-938.
- Seyfarth, R. M., Cheney, D. L., Harcourt, A. H. & Stewart, K. J. 1994. The acoustic features of gorilla double grunts and their relation to behavior. *Am. J. Primatol.*, **33**, 31-50.
- Silk, J. B., Cheney, D. L. & Seyfarth, R. M. 1996. The form and function of post-conflict interactions between female baboons. *Anim. Behav.*, **52**, 259-268.
- Smucny, D., Price, C. S. & Byrne, E. A. 1996. Heart rate correlates of reconciliation in captive adult female rhesus macaques (*Macaca mulatta*). Paper presented at the meeting of the International Primatological Society, Madison, Wisconsin, U.S.A.
- Walters, J. R. & Seyfarth, R. M. 1987. Conflict and cooperation. In: *Primate Societies* (Ed. by B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham & T. Struhsaker), pp. 306-317. Chicago: The University of Chicago Press.
- Watts, D. P. 1995. Post-conflict social events in wild mountain gorillas. I. Social interactions between opponents. *Ethology*, **100**, 139-157.