

The role of grunts in reconciling opponents and facilitating interactions among adult female baboons

DOROTHY L. CHENEY*, ROBERT M. SEYFARTH* & JOAN B. SILK†

*Departments of Biology and Psychology, University of Pennsylvania, Philadelphia, PA 19104, U.S.A.

†Department of Anthropology, University of California, Los Angeles, CA 90024, U.S.A.

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Abstract. Female baboons, *Papio cynocephalus ursinus*, often grunt when approaching lower-ranking females. These grunts appear to have a mollifying effect on subordinates. Observations of 19 adult females conducted over an 11-month period in the Okavango Delta, Botswana, revealed that high-ranking females were less likely to supplant more subordinate females, and more likely to engage in friendly interactions with them, when they grunted to their lower-ranking partners than when they remained silent. Grunts also functioned to reconcile opponents following fights. In a series of playback experiments, subjects were played the potentially threatening scream of a higher-ranking female that had recently attacked them. Subjects responded less strongly to these screams when the dominant opponent had apparently reconciled after the fight by grunting to them than when the opponent had not interacted with them again. Subjects' responses after a vocal 'reconciliation' were similar to their responses following a control period when the two females had not interacted at all. Even in the absence of more overt friendly behaviour, therefore, baboon grunts act to restore the relationship of opponents to baseline tolerance levels.

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In the past two decades, there has been much attention devoted to the function and information content of primate alarm calls (e.g. Seyfarth et al. 1980), distress calls (e.g. Gouzoules et al. 1984), and inter-group vocalizations (e.g. Robinson 1981; Mitani 1985). Monkeys and apes, however, spend comparatively little time fighting with other groups or alarm calling at predators. Instead, the most common calls given by many non-human primates are low amplitude grunts, coos, or trills that occur in the context of social interactions or group movement (e.g. Japanese macaques, *Macaca fuscata*: Green 1975; Blount 1985; Japanese and rhesus macaques, *M. mulatta*: Owren et al. 1993; toque macaques, *M. sinica*: Dittus 1984; vervet monkeys, *Cercopithecus aethiops*: Cheney & Seyfarth 1982; cotton-top tamarins, *Saguinus oedipus*: Cleveland & Snowdon 1982; squirrel monkeys, *Saimiri sciureus*: Boinski 1992; mountain gorillas, *Gorilla gorilla*: Seyfarth et al. 1994). Surprisingly, however, the function of these calls remains largely unexplored. While we can say with some certainty that, for example, dominant individuals often vocalize when approaching a subordinate, we still know almost nothing about the social consequences of vocalizing as opposed to remaining silent.

In a recent study of the function of intra-group calls in captive stump-tailed macaques, *Macaca arctoides*, Bauers (1993) found that individuals that grunted to mothers before attempting to handle their infants were less likely to receive aggression than when they remained silent (see also Bauers & de Waal 1991). Grunts, it appeared, acted to signal benign intent and to facilitate social interactions. Similarly, in Japanese macaques, grooming interactions are often initiated when one female grunts to a potential partner (Masataka 1989; Sakuro 1989). As yet, however, there has been no experimental test of the hypothesis that grunts and subsequent friendly interactions are causally related.

If grunts or other vocalizations do function to facilitate affiliative interactions, they might also be expected to play a role in reconciling opponents following aggression. Non-human primates are frequently aggressive towards one another, yet they live in relatively stable, cohesive social groups. Recent studies have suggested that opponents may mollify the effects of aggressive competition by reconciling soon after fighting or threatening one another (e.g. de Waal & van Roosmalen 1979; de Waal & Yoshihara 1983;

York & Rowell 1988; Aureli et al. 1989, 1993; Cheney & Seyfarth 1989; Judge 1991; Aureli 1992). Two animals are said to have reconciled if, within minutes of behaving aggressively, they interact in a friendly way by touching, hugging, grooming, or approaching one another. Only one study of captive long-tailed macaques, *Macaca fascicularis*, however, has demonstrated experimentally that apparently reconciliatory behaviour does in fact function to restore opponents to baseline tolerance levels (Cords 1992, 1993; see also Kappeler & van Schaik 1992). No study has ever considered the role that vocalizations might play in reconciling former opponents.

Here we consider the function of grunts in the social interactions of free-ranging female baboons, *Papio cynocephalus ursinus*. In the first part we present observational data indicating that grunts act to mollify more subordinate individuals and to facilitate social interactions, and in the second part we describe the results of a playback experiment designed to test the hypothesis that grunts function to reconcile opponents.

ROLE OF GRUNTS IN FACILITATING INTERACTIONS

Like adult females in many species of Old World monkeys, female baboons form stable, linear dominance hierarchies (Seyfarth 1976; Hausfater et al. 1982; Smuts & Nicolson 1989). Although most affiliative interactions occur among close kin, adult females also interact with unrelated females, particularly if those females have infants. Normally, if a dominant female approaches a subordinate, the subordinate is supplanted and moves away. Frequently, however, the dominant female vocalizes to the subordinate, using a low-pitched, tonal grunt (R. M. Seyfarth, D. L. Cheney & M. J. Owren, unpublished data). These grunts appear to have an appeasing function, because they seem to increase the probability of a subsequent friendly interaction, such as grooming or the handling of an infant.

Methods

Subjects were 19 adult females (aged at least 6 years) that were part of a group of approximately 70 baboons living in the Okavango Delta, Botswana. The group has been observed continu-

ously since 1977 by Hamilton and his colleagues (e.g. Bulger & Hamilton 1988; Hamilton & Bulger 1992), and all animals are fully habituated to human observers on foot. Maternal relatedness for all natal animals is known. Here we define 'close kin' as siblings and mothers and offspring. 'Unrelated' animals are defined as first cousins or less closely related individuals.

To test the hypothesis that grunts serve to mediate social interactions among females, we conducted 185 10-min focal animal samples on each of 19 adult females over an 11-month period. In this paper we are concerned only with the function of calls given by dominant females to subordinates. Subsequent analysis (unpublished data) will consider calls given by subordinates to those higher ranking than themselves.

Whenever a dominant female approached (came to within 2 m of) a subordinate female, we noted whether she grunted to the subordinate. We also recorded all subsequent behaviour by both parties. A supplant was defined as occurring whenever one female approached another individual and that individual moved away. Friendly, or affiliative, behaviour included presenting to, touching, hugging, or grooming a female, as well as handling a female's infant. Aggression was defined as occurring whenever a female head-bobbed, lunged at, chased, or bit another individual.

Results

Effect of grunts

If a dominant female grunted while approaching a subordinate, the subordinate was significantly less likely to be supplanted and the dominant female was significantly more likely to engage in friendly behaviour.

We recorded 2698 incidents in which one female approached another that ranked lower than herself; in 621 (23%) of these cases the dominant female grunted to the other female. There were 17 females that could approach at least one lower-ranking, unrelated female. For 15 of these individuals, the mean frequency of approaches to all possible partners that was followed by a friendly interaction was higher if the dominant female first grunted than if she did not (Fig. 1a; one-tailed Wilcoxon matched-pairs signed-ranks test: 1 tie, $t=1$, $P<0.001$). Similarly, for 14 of 17 individuals,

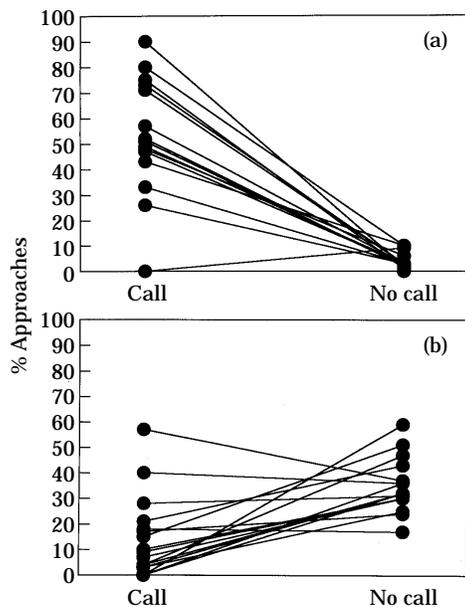


Figure 1. The mean percentage of 17 females' approaches towards subordinate partners that was followed by either (a) friendly behaviour by the dominant or (b) a supplant of the subordinate. Approaches are divided according to whether the dominant female grunted as she approached or whether she remained silent. Only interactions among unrelated females are included in the analysis. Additional analyses that considered each dyad separately revealed similar results.

the mean frequency with which a female supplanted her lower-ranking partner was higher when she did not call than when she did (Fig. 1b; $t=10$, $P<0.001$). Results were unaffected by the relative difference in rank between the two females. Grunts, therefore, appeared to mediate and facilitate social interactions among unrelated adult females.

In Old World monkey species such as baboons, macaques and vervets, close kin typically share adjacent ranks and interact at high rates with one another (reviewed by Walters & Seyfarth 1987). As a result, grunts might be expected to have been relatively less important in mediating the social relationships of kin. To some extent this was true. There were 11 dyads of close kin among the 19 females. For eight dyads, the mean frequency of approaches that was followed by a friendly interaction was higher if the dominant relative first grunted than if she did not (Wilcoxon matched-

pairs signed-ranks test: 1 tie, $t=3.5$, $P<0.01$). A grunt had no significant effect, however, on the likelihood that a female would supplant a lower-ranking relative, largely because approaches towards kin seldom resulted in a supplant in any case.

Effect of infants

Infant baboons are highly attractive to other females, although their attractiveness declines with increasing infant age (Seyfarth 1976; Altmann 1980). In this group, 60% of the grunts that females gave to other females were directed towards mothers of young infants (under 3 months of age). In contrast, only 5% of all females' grunts were given to females without infants. It might be argued, therefore, that the presence or absence of an infant was more important in determining the nature of social interactions among females than the presence or absence of a grunt. It is possible, for example, that females simply grunted more and attempted to interact more with mothers carrying infants than with other kinds of females. Even when the analysis was restricted only to interactions with mothers of young infants, however, grunts still seemed to have a significant effect on social interactions.

There were 14 females that on at least one occasion approached an unrelated, lower-ranking mother with a young infant. In all 14 cases, the mean frequency of approaches that was followed by a friendly interaction was higher if the dominant female first grunted to her lower-ranking partner than if she did not (Fig. 2a; $t=0$, $P<0.001$).

Grunts had no apparent effect, however, on the frequency with which dominant females supplanted mothers with infants (Fig. 2b). This was probably because mothers with young infants often appeared to be apprehensive of approaching animals and frequently moved away from them (see also Altmann 1980).

ROLE OF GRUNTS IN RECONCILING OPPONENTS

Because the grunts given by dominant females appear to mollify lower-ranking individuals, it seems reasonable to predict that grunts might also

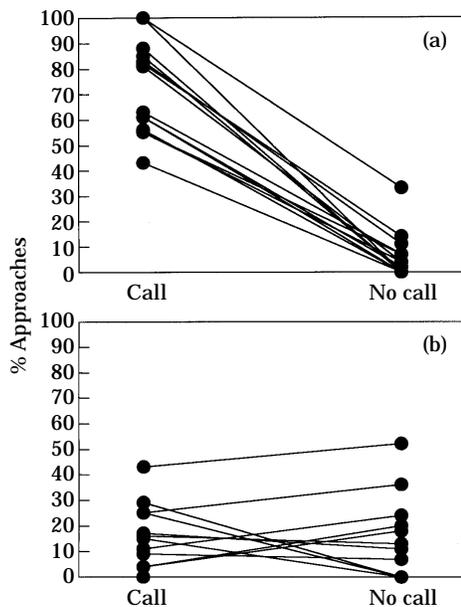


Figure 2. The mean percentage of 14 females' approaches towards subordinate mothers of young infants that was followed by either (a) friendly behaviour by the dominant or (b) a supplant of the subordinate. Legend as in Fig. 1.

serve to reconcile opponents following fights. In fact, baboons do occasionally grunt to one another after aggression. Although these calls seem to serve a reconciliatory function, their role is difficult to assess from observation alone because they often occur in conjunction with other friendly behaviour such as grooming or infant handling.

Whenever two females were involved in an aggressive interaction, we followed the aggressor for 10 min to determine whether she subsequently interacted with her victim in any way (J. B. Silk, D. L. Cheney & R. M. Seyfarth, unpublished data). In 27 (5%) of 502 such samples, the aggressor subsequently interacted in a friendly manner with her opponent by touching her, grooming her, or interacting with her infant. Eighty-five per cent of these friendly interactions also included a grunt by the aggressor. In 43 (9%) of the 502 samples, the aggressor only grunted to her victim and did not interact with her in any other way.

These observations suggested that vocalizations alone, even in the absence of other affiliative interactions, might function to reconcile opponents.

To test this hypothesis, we carried out the following playback experiment. First, we waited until a higher-ranking female, A, had threatened or chased an unrelated subordinate female, B. We then followed female A for 10 min to determine whether she interacted affiliatively with her opponent, and, if so, what form this affiliative interaction took. After this 10-min period, but within the next 30 min, we played a tape-recording of individual A's distress scream to B and videotaped B's response. Screams were played back to subjects under three conditions: (1) after A had been aggressive to B and did not interact with her again; (2) after A had been aggressive to B and then grunted to B without interacting with her in any other way; and (3) as a control, after a period of at least 90 min in which A and B had not interacted.

We hypothesized that subordinate females that heard the scream of a more dominant, unrelated female would interpret this call as a potential threat to themselves (see below). We predicted that B would react strongly to the sound of A's scream if A had recently threatened B but had not reconciled with her. B's response in this context should be stronger than it was following a control period when the two females had not interacted. If, however, A had grunted to B following the fight, B's anxiety should be diminished. We predicted that B's response after vocal reconciliation would be similar to her response following the control period of no interaction.

Methods

Choice of stimuli

Screams were chosen as playback stimuli because they mimicked a context in which subordinate females are sometimes attacked. When a female baboon receives aggression from an even higher-ranking female or male, she typically screams; occasionally, she then 'redirects' aggression by threatening a more subordinate animal (see also Hall & DeVore 1965). During the 11 months in which behavioural sampling took place, adult females were the victims of 5589 episodes of aggression. In 266 cases (5%), the victim threatened a third, previously uninvolved individual within the next 60 s.

It seemed unlikely that subjects would regard the screams of higher-ranking, unrelated females as solicitations for aid. Female baboons, vervets

and macaques form most of their alliances against opponents that already rank lower than themselves (Watanabe 1979; Walters 1980; Cheney 1983; Datta 1983; Chapais et al. 1991). When forming alliances against lower-ranking opponents, females give threat grunts rather than screams (Green 1975; Seyfarth & Cheney 1984, unpublished data; Machida 1990). Equally important, adult female baboons in this group almost never formed alliances with each other. Female-female alliances appear to be generally less common in baboons than in vervet monkeys and macaques (Seyfarth 1976; Datta 1983). In this group, they occurred in only 2% of aggressive interactions between adult females (compared, for example, with 22% for female vervets; Cheney & Seyfarth 1987). Of the 27 alliances that we observed in this study of baboons, all were formed against opponents that ranked lower than the two allies, and in no case did either of the allies scream. For all these reasons, therefore, we predicted that subjects would interpret scream playbacks as signalling potential attack.

Experimental procedure

Our observations of baboons' responses to naturally occurring screams had indicated that females typically respond to the screams of unrelated, higher-ranking females by either ignoring the call entirely or by looking briefly (usually <5 s) in the direction of the call (D. L. Cheney & R. M. Seyfarth, unpublished data; R. Palombit, unpublished data). We therefore used as our response measure the duration that subjects looked towards the speaker following the onset of the scream compared with the length of time that they looked towards the speaker in the seconds before the scream was played. We predicted that subjects would look longer towards the source of the scream when their opponents had not reconciled with them than when they had.

All trials were videotaped. To facilitate the scoring of 'looks' towards the speaker, filming did not begin until the subject was either facing away from the speaker or oriented at right angles to it. Filming commenced 10 s before the onset of the call and continued for another 10 s following the end of the scream.

Nine different females' screams were used as stimuli. All screams had originally been recorded

while the calling female was being supplanted or threatened by an adult male, a subadult male, or a higher-ranking, unrelated female. All subjects were lower ranking to the screaming female and unrelated to her. In all other respects, the pairing of subjects and screams was determined opportunistically, depending upon the occurrence of fights and the presence or absence of a 'reconciliatory' grunt. Although external circumstances dictated the timing of playbacks following fights, the order of control trials relative to the other two trials was systematically varied for each subject.

Screams were played to females from a concealed Nagra DH loudspeaker at a mean distance of approximately 9 m. Because the group was often dispersed through thick brush over distances of up to 1 km, it was relatively easy to ensure that trials were conducted only when subjects were out of sight of their former opponent. The speaker was placed in the same direction relative to the subject as the individual whose scream was being played. Trials involving the same subject were always separated by at least 24 h.

This experiment assumed that baboons could recognize other group members' screams. There is independent evidence, from studies of both baboons and other species of Old World monkeys, to support this assumption (reviewed in Cheney & Seyfarth 1990; R. Palombit, unpublished data).

Results

Subjects' responses

There were 15 dyads that met all three test conditions. Ten different females appeared as subjects. Two of these females were used as subjects three times and one twice. In each case, these subjects heard the screams of different females in different sets of trials. For the sample of fights on which the experiments were based, the mean (\pm SD) period of time elapsed between a fight and a 'reconciling' grunt by the dominant aggressor was 3.0 (\pm 3.8) min. The modal time was less than 1 min.

If a dominant female had grunted to her subordinate opponent following a fight, the opponent responded for a significantly shorter period to that female's scream than she did following a fight when no further interaction had taken place (Fig. 3; one-tailed Wilcoxon matched-pairs

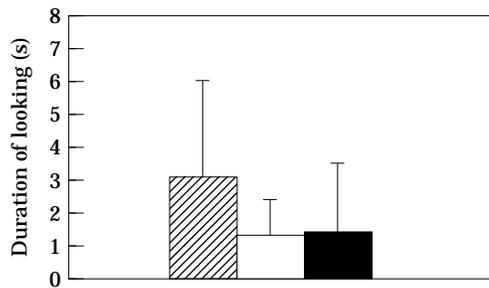


Figure 3. The duration of subjects' responses to the screams of dominant opponents after the dominant threatened the subject and did not interact with her again (▨); the two females had not interacted for at least 90 min (□); and the dominant threatened the subject and then reconciled by grunting to her (■). Shown are $\bar{X} \pm SD$ values for 15 dyads in each of the three conditions. Subjects' responses were scored as looking in the direction of the speaker.

signed-ranks test: 1 tie, $t=17.5$, $N=15$, $P<0.025$). Subordinate subjects also responded less strongly to dominant females' screams after a control period of no interaction than after a fight with no reconciliation (Fig. 3; 1 tie, $t=24$, $N=15$, $P<0.05$). In contrast, subordinates' responses to dominants' screams after a fight with a vocal 'reconciliation' were statistically indistinguishable from their responses following a control period of no interaction (Fig. 3; 2 ties, $t=47.5$, $N=15$, NS).

There were 14 other dyads that met two of the conditions described above. For seven dyads, 'fight with no reconciliation' could be compared with the 'no prior interaction' control. For seven other dyads, 'fight with vocal reconciliation' could be compared with the 'no prior interaction' control. For the first set of seven paired trials, subjects were five females, with two females appearing as subjects twice. For the second set of seven paired trials, subjects were six females, with one female appearing twice.

Results from these trials further supported the hypothesis that grunts functioned to restore opponents' relationship to baseline levels of tolerance. A significant number of subjects responded more strongly to their opponent's scream after a fight when they had not reconciled than after the control period (Fig. 4; $t=1$, $N=7$, $P<0.01$). If, however, the dominant female had grunted to her opponent, the opponent's response was the same as after the control period (Fig. 4; 1 tie, $t=3.5$, $N=7$, NS).

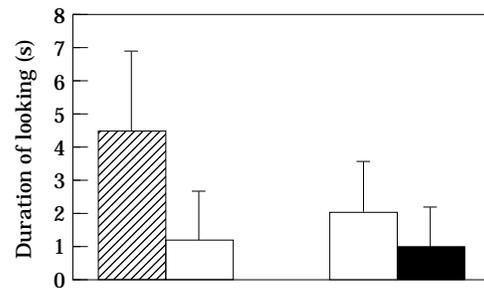


Figure 4. Comparison of the 'no prior interaction' control (□) with the 'fight with no reconciliation' condition (▨) for seven dyads and the 'no prior interaction' control with 'fight with vocal reconciliation' (■) for another seven dyads. Legend as in Fig. 3.

Role of proximity

Some studies of macaques have suggested that proximity alone may serve a reconciliatory function (de Waal 1989; Cords 1993). Because baboons typically grunt when in relatively close proximity to one another, it might be argued that proximity alone, rather than the vocalization, was the reconciliatory mechanism.

In 23% of the 'no reconciliation' fights, dominant opponents approached their victims within the next 10 min without vocalizing or interacting with them in any other way. Had proximity alone acted to reconcile opponents, subjects' responses in this subset of trials should have been relatively weak. Conversely, their responses should have been relatively strong in those trials that were conducted after opponents had not come near each other again. If anything, however, the opposite was true. The mean duration of subjects' responses to an opponent's scream after the opponent had recently approached was 5.3 s, compared with 2.9 s after the opponent had not approached (Mann-Whitney U -test: $U=25.5$, $N_1=5$, $N_2=17$, NS).

Similarly, if proximity alone had functioned to reconcile opponents, subjects that were simply approached by their opponents following a fight should have responded as weakly to the playbacks as did subjects that received a grunt. Again, however, this was not true. Subjects that had only been approached responded significantly more strongly than did subjects that were both approached and grunted to (Fig. 5; Mann-Whitney U -test: $U=22.5$, $N_1=5$, $N_2=22$, $P<0.05$).

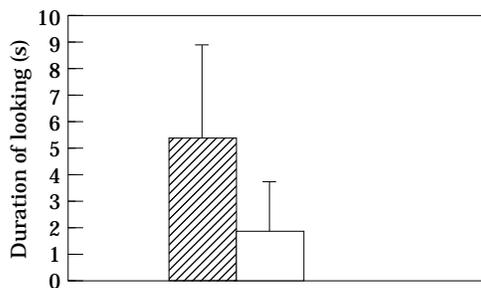


Figure 5. The duration of subjects' responses to the screams of dominant opponents after the opponent had either only approached the subject (▨) or both approached and grunted to her (□). Legend as in Fig. 3.

Finally, subjects' strong responses to playbacks following a fight with no reconciliation did not occur because a recent interaction primed females to respond to one another. Playbacks after a reconciliatory grunt were preceded by two interactions rather than one, yet these trials evoked responses as weak as those that occurred after control periods when females had not interacted at all.

DISCUSSION

The results reported here suggest that vocalizations comprise a major component of reconciliatory behaviour in female baboons. Even in the absence of more overt friendly behaviour, baboon grunts act to restore the relationship of opponents to baseline tolerance levels. Grunts serve to mediate and repair social relationships. They also function to initiate and facilitate affiliative contact between individuals of disparate ranks that might not otherwise interact.

The observational results reported here are not exactly comparable to those described by Bauers (1993). Although Bauers did not discuss the relative ranks of her subjects, her study seems to have dealt with the mollifying effects of grunts given by more subordinate individuals to potentially aggressive mothers (see also Blount 1985 for similar data). In the present study, in contrast, we focused on the mollifying effects of grunts given by dominant females to more subordinate partners. Taken together, the two studies reinforce the hypothesis that vocalizations act to appease

potential partners and to facilitate friendly interactions generally.

The experimental results provide further support for this hypothesis. The experiment made no attempt to test the general question of reconciliation or to examine the rate at which dominant females reconciled with their victims. Rather, it was explicitly designed to exclude all friendly behaviour except grunts in order to determine whether a vocalization alone could act to restore opponents to baseline levels of tolerance. Having shown that grunts do function to reconcile opponents, we can now suggest that vocalizations be included, along with grooming and more conventionally accepted friendly behaviour, in operational definitions of reconciliation. This, in turn, may permit more accurate estimation of reconciliation rates.

In contrast to what has been reported for some species of macaques, proximity alone was not sufficient to reconcile female baboons. Previous studies, however, have not reported whether former opponents also vocalized to each other when they came into proximity. The baboons' responses raise the strong possibility that it is not proximity but rather the presence or absence of a vocalization that serves to reconcile opponents.

In conclusion, there is now evidence from a number of different species that many of the most common vocalizations given by non-human primates function to initiate and facilitate social interactions. The experiment described here suggests that vocalizations also serve to repair social relationships. It is to be hoped that future investigations of reconciliation will take note of the occurrence of vocalizations to test this hypothesis in species other than baboons.

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