

Vocal alliances in Chacma baboons (*Papio hamadryas ursinus*)

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Abstract Theory predicts that females in species with matrilineal dominance hierarchies should use nepotistic support systems to maintain their family's rank. Female Old World monkeys, however, form alliances against other females at surprisingly low rates. Nonetheless, in many species, females utter threat vocalizations when observing others' disputes, suggesting that these vocalizations may function as 'vocal alliances'. We describe a playback experiment testing the efficacy of vocal alliances in free-ranging female baboons. Subjects were played the same female's threat-grunts under three separate conditions: after being threatened by the signaller's close relative to mimic kin support, after being threatened by a female maternally unrelated to the signaller to mimic non-kin support, and after a friendly interaction with the signaller's close relative as a control. Subjects responded more strongly to the playback and avoided the signaller and her matrilineal relatives for a longer period of time in kin support trials than in either non-kin support or no aggression trials. In contrast, there was no difference in subjects' behaviour between non-kin support and no aggression trials. These results corroborate observational data showing that vocal support occurs at a higher rate than physical support in female baboons, and that kin are more likely to provide

vocal support than non-kin. We conclude that vocal support plays a similar role as physical support in the alliances of female baboons.

Keywords Vocal support · Alliance · Relationship · Female dominance · Old World monkeys · Baboons · Socio-ecological model

Introduction

Socio-ecological models hypothesize that coalitionary support is closely linked to the evolution of social organization in female primates (Wrangham 1980; van Schaik 1989; Sterck et al. 1997; Koenig 2002). These models predict that, when ecological conditions favour the collective defence of resources, selection will favour investment in social relationships with those individuals who are likely to provide such support. Thus, the primary features of 'despotic' female-bonded primate societies, including female philopatry, a matrilineal dominance hierarchy, inheritance of maternal rank, and well-differentiated female relationships, are thought to be functionally linked to the existence of alliances among female members of the same group. Alliances occur when two or more females jointly threaten, chase, or attack another individual. Alliances permit females to defend resources against other females in both their own and other groups, and they act to reinforce the matrilineal dominance hierarchy.

When females in such Old World monkey species as baboons (*Papio hamadryas* spp.), macaques (*Macaca* sp.), and vervet monkeys (*Cercopithecus aethiops*) form alliances against other females, they almost always target

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lower-ranking individuals (Cheney and Seyfarth 1990; Chapais et al. 1991; Silk et al. 2004). Kin support each other at significantly higher rates than non-kin, and when forming alliances with non-kin, females tend to support the higher-ranking of the two opponents (reviewed by Cheney and Seyfarth 1990; Chapais 2001; Silk 2002a). These non-kin alliances may be as effective as kin support in reinforcing and stabilizing the current female dominance hierarchy (Chapais 1988, Chapais et al. 1991).

Given the predominant role played by female alliances in socio-ecological models, it is surprising that female Old World monkeys actually form alliances against other females at strikingly low rates. Although female baboons, macaques, and vervet monkeys support their immature offspring in a high proportion of their disputes, fewer than 5% of females' disputes with other females result in physical alliances (*P. h. cynocephalus*: 2%, Silk et al. 2004; *C. aethiops*: 3%, Cheney and Seyfarth, unpublished data; *M. fuscata*: 5%, Vasey 1996). In some groups of baboons in South Africa, alliances seem to be entirely absent (Barrett et al. 1999). In the literature, alliance rates among female Old World monkeys have usually been perceived as being much higher. However, this perception may be due in part to the relatively high rate at which female macaques and vervet monkeys form alliances against males (see Walters and Seyfarth 1987).

Individuals in many primate species utter aggressive vocalizations when observing other animals' disputes. In baboons, such bystanders are usually either close kin of the dominant aggressor or dominant to at least one of the opponents (Silk et al. 2004). In some cases, these bystanders subsequently also intervene in the dispute. Because these threat vocalizations follow the same pattern and direction as physical alliances, they may function as 'vocal alliances'.

In order for vocal alliances to be effective, a female must be able to infer whether or not a vocalization is being directed at herself or at some other individual. Experimental studies have shown that baboons are able to make these inferences, and that they take into account such information as signaller identity and the nature of recent interactions when attempting to deduce who is the target of a signaller's attention (Cheney and Seyfarth 1997; Engh et al. 2006a; Wittig et al. in review). For example, although females respond strongly to another female's threat vocalization if they have recently been threatened by that female, they ignore the same call if they recently engaged in a friendly interaction with her (Engh et al. 2006a). Thus, it seems probable that the aggressive vocalizations uttered by bystanders do serve as vocal alliances, and that they are interpreted as such by the combatants. Because the signaller is typically looking at both combatants when she utters her vocalization, however, this

hypothesis is difficult to test by observational methods alone.

In this paper, we describe a playback experiment designed to examine the function and efficacy of vocal alliances in free-ranging female baboons (*P. hamadryas ursinus*). Each subject heard the same female's threat-grunts under three separate conditions. In the 'kin support' condition, the subject heard the threat-grunts of a dominant female (e.g. female A) within minutes after being threatened by that female's close relative (e.g. A₁) to mimic a vocal alliance between kin. In the 'non-kin support' condition, the same subject heard the same female's (A's) threat-grunts, but this time, after the subject had been threatened by a high-ranking female from a different matriline (e.g. B) to mimic a vocal alliance between non-kin. Finally, in the 'no aggression' control condition, subjects heard the threat-grunts of the same female (A) minutes after a friendly interaction between the subject and the signaller's close relative (A₁).

On the assumption that bystanders' threat-grunts function as vocal alliances, we predicted that, after an aggressive interaction, subjects would infer that the threat-grunts were directed at themselves and directly related to the recent dispute. In contrast, in the absence of a recent dispute, we predicted that they would infer that the threat-grunts were directed at someone else (Engh et al. 2006a). We therefore predicted that subjects would respond more strongly to the call playbacks and avoid the aggressor and the signaller for a longer period of time in the kin and non-kin support conditions than in the control condition. If kin and non-kin vocal alliances are equally effective, subjects' responses in these two conditions should have been similar. If, however, kin support is more often effective than non-kin support, subjects should have responded more strongly to the same female's threat-grunts after being threatened by that female's close relative than after being threatened by a female unrelated to the signaller.

Materials and methods

Study area and subjects

The study was conducted in the Moremi Game Reserve, in the Okavango Delta of Botswana, on a troop of free-ranging chacma baboons (*P. hamadryas ursinus*). The study group's habitat consists of seasonal flood plain interspersed with small 'islands' (Bulger and Hamilton 1987; Cheney et al. 2004). The group has been observed since 1978, and all animals are fully habituated to human observers on foot. At the time of these experiments (Jan–Dec 2005), the group contained approximately 70 individuals, including between 21–26 adult females and 5–10 adult males, 4–5 adolescent

males, 2–9 adolescent females, and 21–40 juveniles and infants. Experimental subjects were 13 adult females (>7 years). We conducted 16 matched-pair within-subjects playback experiments including 13 different subjects.

As in other species of Old World monkey, female baboons form stable, linear dominance hierarchies based on the direction of approach-retreat interactions and aggression. Females assume ranks similar to their mothers', so that matrilineal relatives typically occupy adjacent ranks (Silk et al. 1999).

We defined close relatives as maternally related females that share at least 25% of their genes ($r \geq 0.25$: pairs of mother–daughters, sisters, or grandmother–granddaughters; see Cheney and Seyfarth 2007) and matrilines as clusters of closely related females. For ease of discussion, we use the term 'non-kin' when describing maternal non-kin. Although individuals from different matrilines may share paternal kinship (Alberts 1999; Widdig et al. 2001, 2002; Smith et al. 2003), paternal kin in baboons tend to be very close in age (Silk et al. 2006a). This is because the alpha male monopolizes most matings (Bulger 1993; Altmann et al. 1996), and in this population of baboons, male tenure in the alpha position rarely exceeds 1 year (Kitchen et al. 2003; Cheney et al. 2004). As a result, a similarity in age of less than 1 year seems to be a reasonable proxy for paternal sisters. Females in only one of the 16 dyads used in these experiments had an age difference of less than 1 year.

Behavioural observations

In addition to the playback experiments, we conducted regular focal animal sampling of each adult female and ad libitum sampling of aggression and support (Altmann 1974). Focal animal observations lasted 10 min, and each female was sampled on average twice a week for a period of 15 months. We used focal and ad libitum data to estimate natural frequencies of possible instances of vocal and physical support.

We defined a female as forming a vocal alliance, or providing vocal support, when she gave threat-grunts while observing another female threaten (head bob or ground slap), lunge at, chase, or bite another female. We distinguished vocal alliances from physical alliances, which occurred when a female actively intervened in a dispute on behalf of another female, by threatening, lunging at, chasing, or biting the target of that female's aggression. Physical alliances might or might not also include threat-grunts.

Playback stimuli

Calls used as playback stimuli were recorded opportunistically from known individuals using Sennheiser

ME88 microphones and Nomad digital recorders. Digital sound files were saved in '.wav' format and used within 9 months from the time of the recording. After transferring the calls from the Nomad to a laptop, we used CoolEdit software (Syntrillium, Phoenix, AZ) to ensure that the natural call sequences used as playback stimuli were high quality, without vocalizations from other baboons or masking background noise. All sequences were selected to be similar in call and bout length, rate, and amplitude and to match the amplitude of naturally occurring calls. Calls were broadcast from a Bose Roommate II loudspeaker.

Threat-grunts are tonal calls that are given during aggressive interactions and are almost always directed by higher-ranking individuals towards lower-ranking opponents. They are typically given in bouts and are roughly similar in spectral structure to grunts used in friendly social contexts. Unlike other grunts (Owren et al. 1997), however, threat-grunts are composed of several rapid pulses, the first pulse being of lower frequency than subsequent pulses. Previous playback experiments have demonstrated that threat-grunts are individually distinctive (e.g. Cheney and Seyfarth 1999; Bergman et al. 2003; Engh et al. 2006a).

All playback sequences consisted of four threat-grunts and were similar in duration and amplitude. To avoid the possibility that some calls might have been more salient than others, each subject heard the same threat-grunts in all three conditions. Different subjects heard different female threat-grunts (two different playback sequences from each of five females and one playback sequence from each of six females). The mean duration of the playback threat-grunt sequence was 2.29 ± 0.27 s.

Experimental protocol

The experiment followed a within-subject design, with each subject being exposed to the same call playback in three separate trials. Playback experiments were carried out after subjects had either been threatened (lunged at or chased) by or engaged in friendly behaviour (e.g. groomed with or embraced) with a more dominant female. Playbacks were conducted within 5 min of the dyadic aggressive or friendly interaction, as soon as the subject and the more dominant female had separated without interacting or vocalizing again, and the subject was out of sight of the female and all members of her matriline. The loudspeaker was hidden in vegetation at a distance of 5–8 m from the subject, at roughly 90° orientation from the subject and in the same direction from which the signaller was last seen. In all cases, the female whose call was played was also out of sight and earshot of the playback.

Playback design

- (1) In the kin support trial, the subject heard the threat-grunts of a more dominant female (e.g. female A) after being threatened by that female's close relative (A_1). This sequence suggested that the signaller was vocally supporting her close relative against the subject.
- (2) In the non-kin support trial, the subject heard the same female's (A's) threat-grunt, but this time, after a fight with another high-ranking female belonging to a different matriline (e.g. B). This sequence suggested that the signaller was providing vocal support to a non-relative against the subject.
- (3) In the no aggression control trial, the subject again heard the same female's (A's) threat-grunts after a friendly interaction with the signaller's close relative (A_1). This sequence again suggested that the signaller was threatening a female. However, if subjects' responses were guided by the nature of their recent interactions, we predicted that they would infer that they were not the target of the signaller's vocalization. Trials were conducted with the same female triads as the kin support trials to permit direct comparisons. The order of presentation of the three trials was alternated.

The average duration between the aggressive (or friendly) interaction and the playback experiment was similar for all three trial types (kin support trials = 3.9 ± 1.1 min; non-kin support trials = 3.8 ± 0.9 min; no aggression trials = 3.9 ± 0.9 min). The average distance in rank between subjects and their aggressor in kin support trials was 13.9 ± 7.6 ranks, and 6.5 ± 4.2 ranks in non-kin support trials.

We used a Sony DCR-TRV25 digital video camera to record any changes in head position relative to the speaker in the 10 s before and 1 min after playback. We then followed the subject for 60 min to determine whether she came to within 2 m of her aggressor or any of her aggressor's relatives. If she did, we noted both the time and the nature of their first interaction. The subject was defined as 'tolerating' her aggressor if she either approached her aggressor or her aggressor's matrilineal relatives to within 2 m or did not move away when they approached to within 2 m. Alternatively, the subject was considered to behave 'submissively' if she avoided her aggressor or any of her aggressor's matrilineal relatives by moving away if they approached to within 2 m or by turning away or crouching when they passed within 2 m. The subject was also considered to behave 'submissively' if the aggressor (or one of her matrilineal relatives) directly approached to within 5 m when there was no other animal in the path between them and the subject moved rapidly

away after looking at her. In case of non-kin support trials, we analysed the subject's interactions with both the signaller's matriline and the aggressor's matriline.

On the assumption that subjects would regard a threat-grunt from the kin supporter after aggression as a threat against themselves, we predicted that subjects would look for longer and, more often, towards the speaker and be more likely to move away from the speaker in kin support than in no aggression trials. We also predicted that, in the following hour, subjects would show a longer latency to tolerate the proximity of their aggressor, and that their first interaction would be more likely to be submissive. On the assumption that subjects would also treat a threat-grunt from a non-kin supporter after aggression as a threat against themselves, we predicted that subjects would show the same behavioural differences as predicted for kin support trials. If subjects treated both types of support as equally effective, we predicted no differences in subjects' behaviour between kin support and non-kin support trials.

To minimize the possibility that the baboons would habituate to the playback stimuli, a maximum of two playback experiments was conducted daily. Playback experiments were never conducted within 2 h of each other, and the same subject never appeared in more than one playback experiment on the same day. Female baboons produce threat-grunts at a mean rate of one per hour (Engh et al. 2006a), so females heard playbacks of threat-grunts at much lower rates than they heard naturally occurring threat-grunts.

Data analysis

Video films were analysed using Adobe Premier software. In coding experiments, we measured three different responses: the duration of looking and number of looks towards the speaker in the first minute after playback, as well as whether or not the subject moved away from the speaker. A 'look' was defined as a head orientation directly towards the speaker. Movement was only recorded as moving away when it was in the direction opposite to that of the speaker and when it was the first move in any direction after the playback.

To analyse continuous measures of behavioural responses, we calculated average values for each of the subjects that were tested twice ($N=13$). However, categorical bivariate measures had to be analysed per dyad ($N=16$).

To determine the legitimacy of testing three measures of behavioural response to the speaker after playback, we conducted a bivariate correlation test between the three dependent variables. All correlation coefficients were $r < 0.7$, indicating minimal likelihood of multicollinearity, and, therefore, no need to exclude any variables (Tabachnick and Fidell

2007). In our analysis, we used a matched sample design, testing all three conditions simultaneously using a Friedman test (and a Cochran test for categorical data). If the multivariable test was significant, we conducted Wilcoxon matched-pairs signed-ranks and sign test for categorical data to compare subjects' behaviour between trials (Siegel and Castellan 1988). Due to small sample size, we conducted exact tests (Mundry and Fischer 1998). Because our hypotheses generated clear directional predictions, all tests were one-tailed ($\alpha=0.05$). As we tested the behavioural responses several times in the matched-pair design (responses towards the speaker three times, responses towards aggressor's matriline 4 times), we corrected for multiple testing (Bonferroni correction for Wilcoxon and Sign tests: speaker $\alpha'=0.016$, interaction $\alpha''=0.0125$).

Results

Naturally observed alliances

Overall, we observed 1,409 agonistic interactions, including 149 alliances among adult females. More than half of the alliances (58.4%) consisted entirely of vocal support; 41.6% involved physical support (Table 1). When only physical support was considered, adult females formed alliances at a rate of 4.4%. Of these physical alliances, 29% were formed among kin, whereas 71% included a non-kin supporter. When corrected for the number of kin and non-kin supporters available for each female, females formed significantly more alliances than expected with kin than with non-kin (Table 1).

When all instances of physical and vocal support were combined, the same pattern emerged (Table 1). The frequency of vocal support was, however, 1.4 times greater than that of physical support. If vocal support were to be treated as an alliance, it would increase the total rate of female alliances to 10.6% of all conflicts.

Responses to threat-grunt playbacks

Subjects' responses to the threat-grunt playbacks differed significantly across the three trial types in two of the three measures taken: number of looks towards the speaker (Friedman: $X=6.826$, $df=2$, $N=13$, $P=0.033$; Fig. 1) and likelihood of moving away from the speaker (Cochran: $Q=14.22$, $df=2$, $N=16$, $P=0.001$; Fig. 2). There was no difference across trial types in the duration that subjects looked towards the speaker (Friedman: $X=4.167$, $df=2$, $N=13$, $P=0.125$; Fig. 3).

In our analysis of subjects' behaviour in the hour after playback, we first examined subjects' behavioural interactions with their aggressor, the supporter, and other members of those females' matriline separately and found no significant differences across trial types. However, when we analysed subjects' responses towards the aggressor's (or supporter's) matriline as a whole, significant differences emerged. Subjects showed differences in the latency to tolerate the proximity of any member of the aggressor's matriline (Friedman: $X=9.941$, $df=3$, $N=13$, $P=0.019$; Fig. 4) and in the frequency of submissive behaviour during their first interaction with them (Cochran: $Q=18.574$, $df=3$, $N=16$, $P<0.001$; Fig. 5).

Is vocal kin support effective?

Subjects looked towards the speaker more times (Wilcoxon: $N=13$, $T^+=71$, 1 tie, $P=0.0046$, $\alpha'=0.016$) during the first minute in kin support trials than in no aggression trials. They were also more likely to move away from the speaker (Sign: $N=16$, $k=0$, 8 ties, $P=0.004$, $\alpha'=0.016$). Similarly, during the first hour after the playback, subjects avoided the proximity of all members of the aggressor's matriline for a longer period of time after kin support than after no aggression trials (Wilcoxon: $N=13$, $T^+=68$, 1 tie, $P=0.0105$, $\alpha''=0.0125$). Moreover, when they did come into proximity, subjects were more likely to behave submissively (Sign: $N=16$, $k=0$, 6 ties, $P<0.001$, $\alpha''=0.0125$).

Table 1 Number of naturally observed and expected alliances by adult female baboons

	Vocal support		Physical support		Total support	
	Observed	Expected	Observed	Expected	Observed	Expected
Kin	25 ^a	12.2	18 ^b	8.7	43 ^c	20.9
Non-kin	62	74.8	44	53.3	106	128.1
Total	87		62		149	

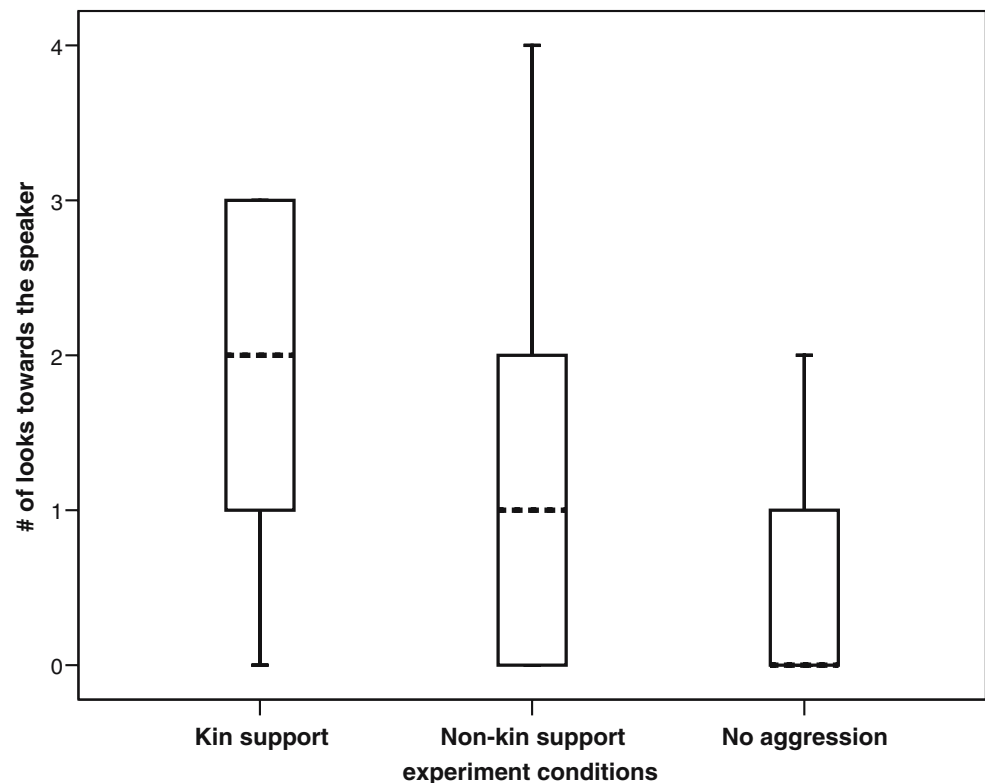
Expected frequencies are calculated on the base of the number of kin and non-kin female dyads.

^a Goodness of fit: $\chi^2=16.1$, $df=1$, $P<0.001$

^b Goodness of fit: $\chi^2=11.6$, $df=1$, $P<0.001$

^c Goodness of fit: $\chi^2=27.2$, $df=1$, $P<0.001$

Fig. 1 The number of times that subjects looked towards the speaker in the first minute after the playback in each of the three test conditions ($N=13$). Median value is shown as *dashed line*. *Box plots* represent second and third quartiles, and *error bars* represent 95% confidence interval



Is vocal non-kin support effective?

Subjects did not look towards the speaker more times (Wilcoxon: $N=13$, $T^+=52.5$, 2 ties, $P=0.0508$, $\alpha''=0.016$) in non-kin support trials than in no aggression trials. Moreover, they were not more likely to move away from the speaker (Sign: $N=16$, $k=1$, 14 ties, NS). In addition, subjects' latency to come into proximity with both the aggressor's matriline and the supporter's matriline in non-kin support trials did not differ from that in no aggression trials (Wilcoxon: supporter's matriline: $N=13$, $T^+=73$, 0

ties, $P=0.0287$, $\alpha''=0.0125$; aggressor's matriline: $N=13$, $T^+=71$, 0 ties, $P=0.0402$, $\alpha''=0.0125$). Similarly, when they did come into proximity, they were not more likely to behave submissively (Sign: supporters' matriline: $N=16$, $k=0$, 13 ties, NS; aggressors' matriline: $N=16$, $k=1$, 9 ties, $P=0.062$, $\alpha''=0.0125$).

Is vocal non-kin support as effective as vocal kin support?

Subjects were more likely to move away from the speaker in kin support than in non-kin support trials (Sign: $N=16$,

Fig. 2 The number of trials with subjects that moved away from the speaker in the first minute after the playback in each of the three conditions ($N=16$)

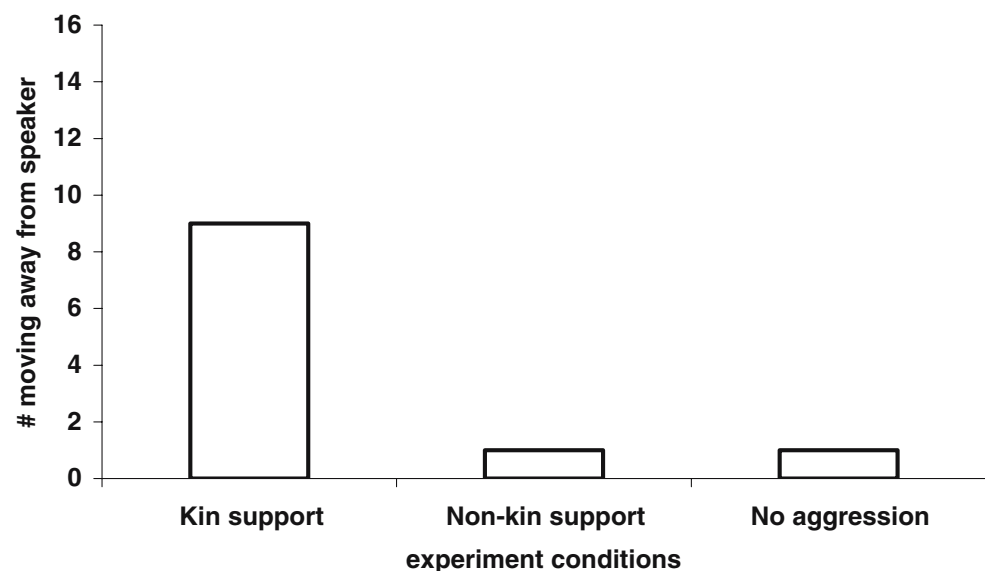
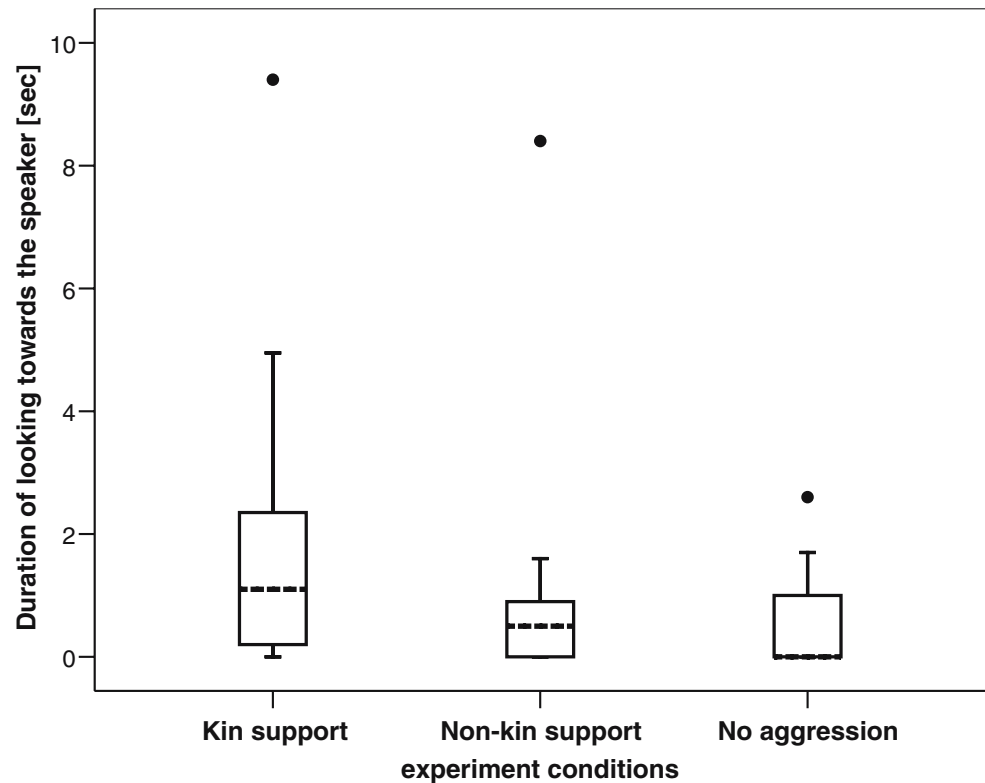


Fig. 3 The duration that subjects looked towards the speaker during the first minute after the playback in each of the three conditions ($N=13$). Dots above the box plots represent outliers. Legend, as in Fig. 1



$k=0$, 8 ties, $P=0.004$, $\alpha'=0.016$). They also behaved, although not significantly, more submissively towards kin supporters than towards non-kin supporters (Sign: supporter's matriline [kin vs non-kin]: $N=16$, $k=1$, 7 ties, $P=0.02$,

$\alpha''=0.0125$; aggressor's matriline [kin vs non-kin]: $N=16$, $k=0$, 11 ties, $P=0.031$, $\alpha''=0.0125$). However, there were no differences between trial types in the number of looks that subjects gave towards the speaker (Wilcoxon: $N=13$,

Fig. 4 The latency with which subjects first tolerated the proximity of members of their aggressor's or supporter's matriline in each of the three conditions ($N=13$). Legend, as in Fig. 1

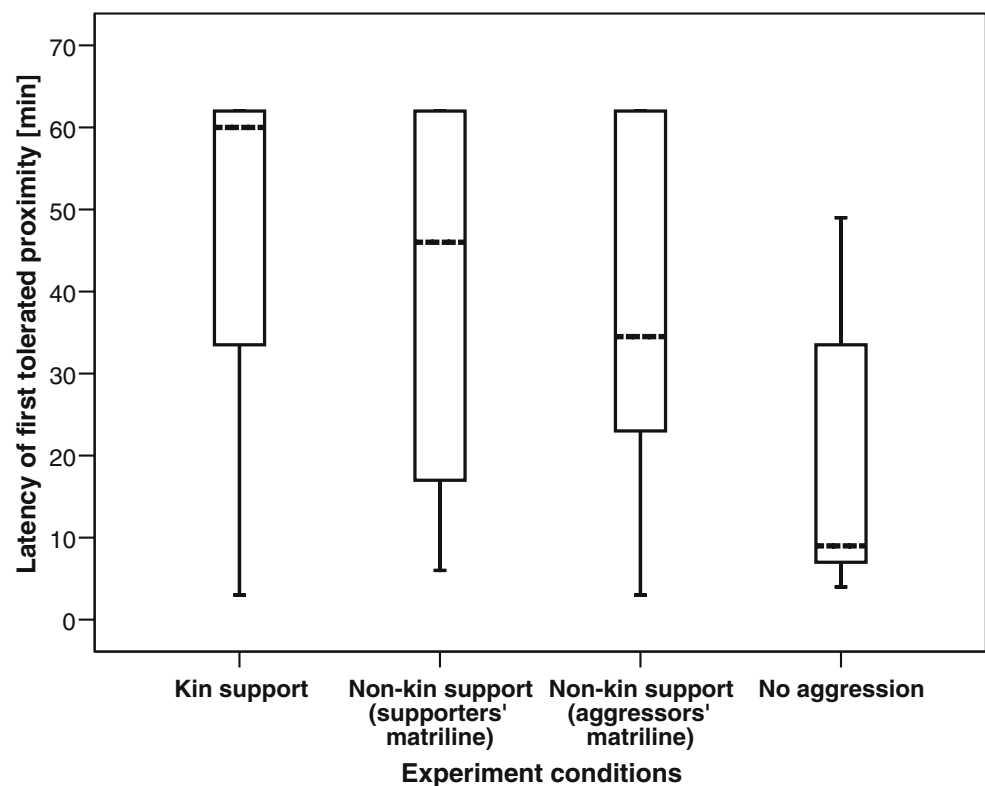
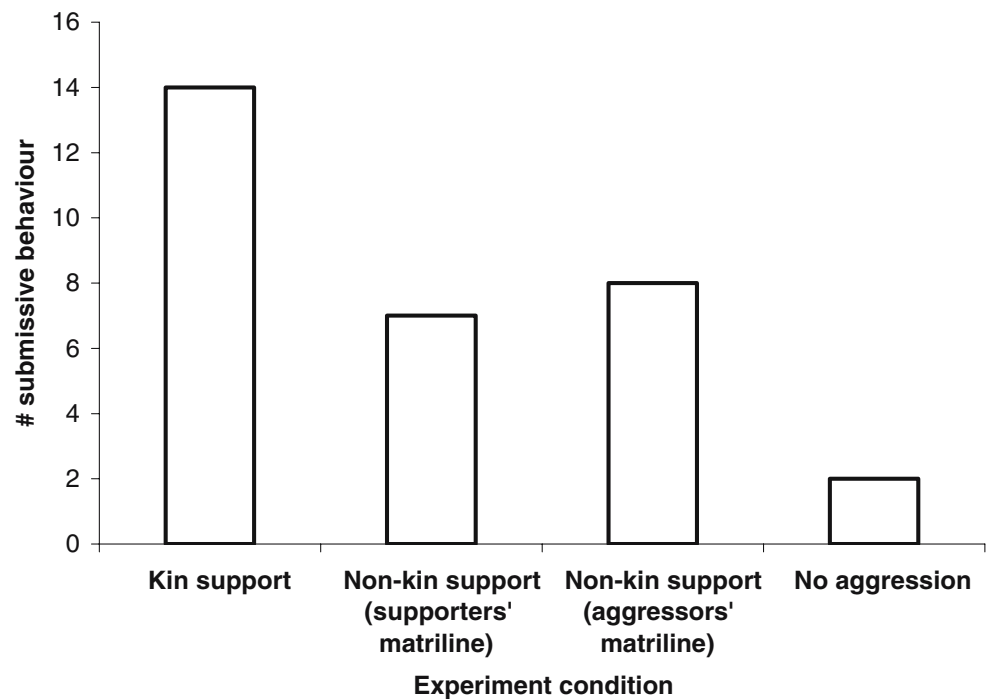


Fig. 5 The number of trials with first interactions in which subjects showed submissive behaviour towards a member of the aggressor's or supporter's matriline in each of the three conditions ($N=16$)



$T^+ = 40$, 3 ties, $P = 0.1162$, $\alpha' = 0.016$) or in the latency that they came into proximity with members of the aggressor's matriline (Wilcoxon: supporter's matriline: $N = 13$, $T^+ = 28$, 4 ties, $P = 0.2852$, $\alpha'' = 0.0125$; aggressor's matriline: $N = 13$, $T^+ = 38$, 3 ties, $P = 0.1611$, $\alpha'' = 0.0125$).

There was no evidence that subjects' avoidance of their aggressor's matriline in the non-kin support condition was influenced by the relative ranks of the aggressor and her vocal ally or the strength of their social bond. Subjects' responses varied independently of the rank difference between the aggressor and the non-kin supporter (Spearman: $r = 0.039$, $N = 16$, $P = 0.886$) and the rank difference between aggressor and subject (Spearman: $r = 0.328$, $N = 16$, $P = 0.215$). Similarly, subjects' responses appeared to be unaffected by the strength of the social bond between the aggressor and the non-kin supporter: Neither the rate at which the two females groomed each other (Spearman: $r = 0.125$, $N = 16$, $P = 0.646$) nor the relative frequency of their natural alliances (Spearman: $r = 0.289$, $N = 16$, $P = 0.277$) affected subjects' avoidance behaviour.

What caused subjects' avoidance of their aggressor's matriline?

Results suggest that the victims of aggression regarded the threat-grunts of their aggressor's close kin as an alliance against them and a signal of renewed aggression. In contrast, hearing the threat-grunts of females unrelated to their aggressor had less effect on their behaviour. Hearing a threat-grunt after a friendly interaction had no effect on subjects' behaviour.

It remains possible, however, that subjects would have avoided their aggressor and her relatives even in the absence of a threat-grunt signalling vocal support. Thus, the aggressive act alone, and not the aggressive act in combination with vocal support, may have been sufficient to influence subjects' behaviour. If this were the case, subjects should have avoided their aggressor more in non-kin support trials, when they heard the threat-grunts of an unrelated female, than in no aggression trials, when they heard the threat-grunts of the same female but in the absence of aggression. This was not the case: Subjects did not avoid their aggressor more in non-kin support trials than in no aggression trials (non-kin support trials: median avoidance \pm SD = 57 min \pm 16.5; no aggression trials: median avoidance \pm SD = 61 min \pm 19.3; Wilcoxon: $N = 13$, $T^+ = 19$, 5 ties, $P = 0.4727$).

Discussion

Under natural conditions, chacma baboons form both vocal and physical alliances. Although females form alliances with both kin and non-kin, they form alliances with kin at significantly higher rates. Their pattern and rates of physical alliances are similar to those found in other populations of baboons (Silk et al. 2004) and other Old World monkeys (Bernstein and Ehardt 1985; Kaplan et al. 1987; Cheney and Seyfarth 1990; Vasey 1996). Although this is the first study to investigate vocal alliances specifically, there is evidence that they may occur in other Old World monkeys (e.g. *M. fascicularis*: de Waal 1977; *C.*

aethiops: Cheney and Seyfarth 1990) and apes (e.g. *Pan troglodytes*: Wittig and Boesch 2003a).

Upon hearing the threat-grunts of their aggressor's close relative after a recent dispute, subjects responded more strongly to the call playback, avoided coming into proximity with members of their aggressor's matriline for a longer period of time, and behaved more submissively towards these individuals than they did after hearing the same female's threat-grunts in the absence of recent aggression. Subjects appeared to take into account the signaller's identity, her relationship with the aggressor, and the nature of recent interactions when inferring whether or not threat-grunts were directed at them. The threat-grunts of kin, therefore, function as vocal alliances.

In contrast, there was little evidence that the threat-grunts of unrelated females serve a similar function. After correcting for multiple testing, none of the measures revealed a difference between non-kin support and no aggression conditions. There were, however, several measures that differentiated the kin support from the other two conditions. Subjects were significantly more likely to move away from the speaker after hearing the threat-grunts of their aggressor's relative than after hearing the threat-grunts of an unrelated dominant female. They were also more likely to behave submissively towards members of the aggressor's matriline than towards members of the unrelated supporter's matriline. Although subjects appeared to infer that the threat-grunts of their aggressor's kin were targeted at them and thus directly related to the recent dispute, they did not appear to make similar inferences about the threat-grunts of unrelated dominant females. Results from previous experiments (Engh et al. 2006a) indicate that female baboons do not respond to a more dominant female's threat-grunts unless that female has recently threatened them. In a similar manner, females in these experiments may have assumed that threat-grunts given by females unrelated to their aggressor were directed at someone else.

It also remains possible that female baboons do regard the threat-grunts of unrelated females as a vocal alliance directed against them, but our experiments were not able to detect this effect. For most measures, females' responses in the non-kin support condition were intermediate to those in the kin support and no aggression conditions (Figs. 1, 3, 4 and 5), and significance levels were borderline due to correction for multiple testing. The females whose threat-grunts were used in non-kin support trials were selected opportunistically, without regard to the strength and quality of their relationship with the supporter. We were not able to detect any effects of rank, alliance history, or the strength of social bonds in subjects' responses in non-kin support trials, but larger sample sizes may yet reveal such effects.

Although we cannot exclude the possibility that small sample size was the primary reason for the apparent lack of efficacy of non-kin support in our experiments, it seems likely that kin support is generally more effective than non-kin support in female baboons' alliances. Silk et al. (2006a,b) have shown that female baboons prefer maternal sisters to paternal sisters as grooming partners. They have also shown that female baboons have the strongest and most enduring relationships with close maternal kin and stronger relationships with more distantly related maternal kin than with paternal kin. It therefore seems plausible that partners with the closest bonds are also the most effective supporters.

Similarly, other studies have shown that aggressive interactions negatively affect a female's relationship not only with her aggressor but also with her aggressor's matriline (Wittig et al. in review), and that females alter their behaviour towards the relatives of their own kin's opponent (Cheney and Seyfarth 1999). The pooled data suggest that a female who has sequentially been threatened by two close female relatives attempts to avoid further interactions with all members of those females' matriline. Avoidance of an entire matriline is not unexpected in nepotistic monkey species.

Although most physical alliances among female Old World monkeys are conservative and target individuals who are already lower-ranking than the aggressor and the supporter (reviewed by Walters and Seyfarth 1987), physical intervention—even on behalf of a higher-ranking aggressor—is not entirely without potential cost. Although rare, occasional upheavals in the female dominance hierarchy do occur (Samuels et al. 1987; Engh et al. 2006b), and there is therefore always a potential for injury when a female intervenes in a dispute. In contrast, vocal alliances signal the willingness to intervene physically if the dispute is not settled quickly, but they occur at low cost to the signaller herself. Theory predicts that animals should always attempt to settle disputes through low cost displays that allow contestants to assess each other's competitive ability and likelihood of support before the fight escalates and results in potential injury (Maynard Smith 1982; Bradbury and Vehrencamp 1998; Wittig and Boesch 2003b). Vocal alliances, therefore, should be widespread in social animals.

Female baboons form vocal alliances at roughly one and a half times the frequency of physical alliances. Although similar data are not yet available for other species of Old World monkeys, it seems probable that female macaques and vervets also provide vocal support in their relatives' disputes. Vocal support reinforces relatively infrequent physical intervention and may help females to acquire and maintain their dominance ranks. Given the generally positive, if weak, correlation between rank and reproductive

success in female Old World monkeys (reviewed by Silk 2002b; Cheney et al. 2004), it seems likely that vocal support ultimately functions to enhance the signaller's inclusive fitness.

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