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Chimpanzees communicate to two different audiences during aggressive interactions

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Conflict and aggressive interactions are common phenomena in group-living animals and vocal behaviour often plays an important role in determining their outcomes. In some species, vocal signals seem to provide bystanders with information about the nature of an ongoing aggressive interaction, which can be beneficial for the victims. For example, in chimpanzees and some other primates, victims adjust their screams depending on the composition of the by-standing audience, probably to solicit their support. Considerably less is known, however,

about the role of other call types produced by victims of aggression. In this study, we focused on the fact that, immediately after screams, chimpanzee, *Pan troglodytes schweinfurthii*, victims often produce 'waa' barks, but little is known about their function. Our results showed that for screams, but not 'waa' barks, production was dependent on the audience composition with victims being more likely to scream when adult or late-adolescent males were in close proximity. We also found that after 'waa' barking, but not screaming, victims were more likely to retaliate against and less likely to reconcile with their aggressors, and that 'waa' barking was more common after victims had received support from other party members. These results suggest that, in chimpanzees, victims of aggression vocalize with a dual social strategy of attempting to recruit support from bystanders and to repel their attackers by signalling readiness to retaliate. We conclude that victim scream and 'waa' bark calls, although often produced during the same agonistic event, are directed at different audiences and fulfil different social functions, and that these calls can mediate both aggressive interactions and aggressor–victim relationships following aggression.

Key words: agonistic calls, chimpanzee, graded calls, reconciliation, screams, 'waa' barks

Agonistic interactions are a common consequence of group living (Nieburg, 1970), which can bring about substantial costs to the opponents, including severe injuries, mutilations or death. One way to minimize the costs of aggressive interactions is for opponents to communicate their behavioural intentions in order to prevent costly escalations (Smith, 1977). For example, an opponent can signal submission or willingness to retaliate or recruit support from bystanders, with vocal behaviour playing a key role in achieving these goals.

During animal conflicts screams are probably the most common vocalizations and various functions have been attributed to them, such as alerting group members, confusing or dissuading the opponent or attracting help (Hogstedt, 1983; Rohwer, Fretwell, & Tuckfield, 1976). In primates, screams are commonly produced by victims of aggression, apparently to alert and recruit aid from allies (Bernstein & Ehardt, 1985; Cheney, 1977; Gouzoules, Gouzoules, & Marler, 1984). For example, rhesus macaques, *Macaca mulatta*, produce acoustically distinct variants of screams that seem to be related to the identity of the caller, the dominance rank of the opponent, the relatedness between the caller and opponent and the severity of the attack (Gouzoules & Gouzoules, 1990; Gouzoules et al., 1984). Receivers attend differently to different scream variants, suggesting that the calls inform potential supporters about the nature of the aggressive interaction (Gouzoules et al., 1984).

In chimpanzees, *Pan troglodytes schweinfurthii*, recruiting support from bystanders also seems to be an important function of screams. Here, the acoustic structure varies as a function of the severity of the aggression (Slocombe & Zuberbühler, 2007) and these differences seem to be informative for the receiver (Slocombe, Townsend, & Zuberbühler, 2009). Victims and aggressors produce acoustically different screams (Slocombe & Zuberbühler, 2005) enabling the receiver to infer something regarding the nature of the aggressive encounter (Slocombe, Kaller, Call, & Zuberbühler, 2010). Importantly, screams are individually distinctive (Kojima, Izumi, & Ceugniet, 2003) and victims of aggression can modify the acoustic

structure of their screams to exaggerate the aggression received if individuals of equal or higher rank to the opponent are nearby, which is likely to increase the probability of receiving aid (Slocombe & Zuberbühler, 2007).

In chimpanzees, however, victims of aggression often produce another type of call, 'waa' barks. Chimpanzee 'waa' barks belong to an acoustic cluster of bark vocalizations that are given in several contexts, such as hunting or when replying to long-distance calls from other group members or from members of other communities (Crockford & Boesch, 2003; Goodall, 1986; Marler & Tenaza, 1977). 'Waa' barks are also given to alert others about predators (Crockford & Boesch, 2003; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013) or to drive away dangerous animals, such as bush pigs (P. Fedurek, personal observation), suggesting that, although these calls can have subtly different acoustic structure depending on the context of production (Crockford & Boesch, 2003), they are linked to targeted aggressive motivation. 'Waa' barks are also given in agonistic encounters and it has been proposed that they are signals directed at aggressors (Goodall, 1986; Marler & Tenaza, 1977), usually given immediately after screams from which they can grade (Marler, 1976; Marler & Tenaza, 1977). Overall, however, there has been little systematic analysis of the function of this call type in agonistic contexts. One notable exception concerns the observation that, during agonistic interactions, 'waa' barks are sometimes given by allies of the opponents observing the interaction, possibly as a way of expressing support (Newton-Fisher, 2006; Wittig, Crockford, Langergraber, & Zuberbühler, 2014).

The aim of this study was to examine the function of victim 'waa' barks and to investigate how victim screams and barks are deployed during aggressor–victim interactions. We hypothesized that 'waa' barks are optional signals directed at the aggressor in specific situations to signal the probability of retaliation.

To address our hypothesis, we tested the following predictions. First, if 'waa' barks were directed at the aggressor rather than a third-party audience, we expected that, in contrast to screams, 'waa' bark production would be independent of the audience composition. We therefore compared the production of both call types as a function of the number of males or females in the party and the presence of at least one affiliated or higher-ranking group member in close proximity to the victim (<15 m) or within the party (e.g. Fedurek & Slocombe, 2013). Second, we predicted that if 'waa' barks were directed at aggressors, victims should be visually oriented towards their aggressors during call production. If 'waa' barking signalled the probability of retaliation, we predicted that utterances containing 'waa' barks would be associated with higher rates of retaliation and lower rates of reconciliation with the aggressor compared to utterances with screams only. Finally, if 'waa' barks expressed aggressive motivation, we predicted that victims would be more likely to produce these signals after rather than before receiving support from third-party individuals, when the risk of renewed aggression from the aggressor is low.

Methods

Study site and study subjects

The study was conducted with the Sonso chimpanzee community of Budongo Forest, Uganda. The group has been under constant observation since 1990 and is well habituated to the presence of human observers (Reynolds, 2005). At the time of the study, the community contained 75 individuals with a home range of around 15 km². Study subjects were adult males and females (N=11: ≥16 years; N=24: ≥15 years; (Goodall, 1986)) and adolescents

(N=3 early males: 8–12 years; N=3 late males: 13–15 years; N=9 early females: 8–10 years old; N=4 late females: 11–14 years).

Sampling method

This study was approved by the Institute of Biology Ethics Committee at the University of Neuchâtel and permission to conduct the study was granted by the Uganda Wildlife Authority and the Uganda National Council for Science and Technology. The study was conducted between June and October 2013, February and September 2014 and January and April 2015. Data were collected between 0700 and 1630 hours local time. Since agonistic interactions were relatively rare, we used all-occurrence sampling (Altmann, 1974). For each aggressive interaction we recorded (1) the identity of the aggressor and victim, (2) the type of aggression, (3) whether or not the victim called and the type of calls given, (4) whether the victim was oriented towards the aggressor if 'waa' barking occurred, (5) the closest distance between aggressor and victim at the beginning of screaming and 'waa' barking, (6) the identities of all audience members within 15 m (relative to the victim at the beginning of aggression), (7) whether or not the victim or aggressor received support from bystanders, (8) whether or not there was a reconciliation between the aggressor and the victim, and (9) whether or not the victim retaliated against the aggressor (see section below for definitions of these behaviours).

In addition, a randomly chosen focal adult or late-adolescent male was followed continuously every day of data collection to obtain data on party composition and male preferred social partners. Instantaneous scan samples (Altmann, 1974) at 15 min intervals were conducted to record (1) the identities of individuals present in the focal individual's party (defined as all

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adult and late-adolescent individuals present within 35 m of the focal animal; Newton-Fisher, 1999), (2) the identities of individuals present within 5 m of the focal male and (3) the identity of the adult or late-adolescent individual closest to the focal male.

Data recorded and definitions

Screams and 'waa' barks

For every act of aggression in the focal party, we noted whether or not the victim produced screams and whether or not these were followed by 'waa' barks (within 10 min of the end of aggression). Although these two types of calls often grade from one to another, they are acoustically distinguishable. 'Waa' barks have an abrupt onset, are typically shorter, and have a lower frequency range and a noisier spectral quality than screams (Fig. 1; Crockford & Boesch, 2003).
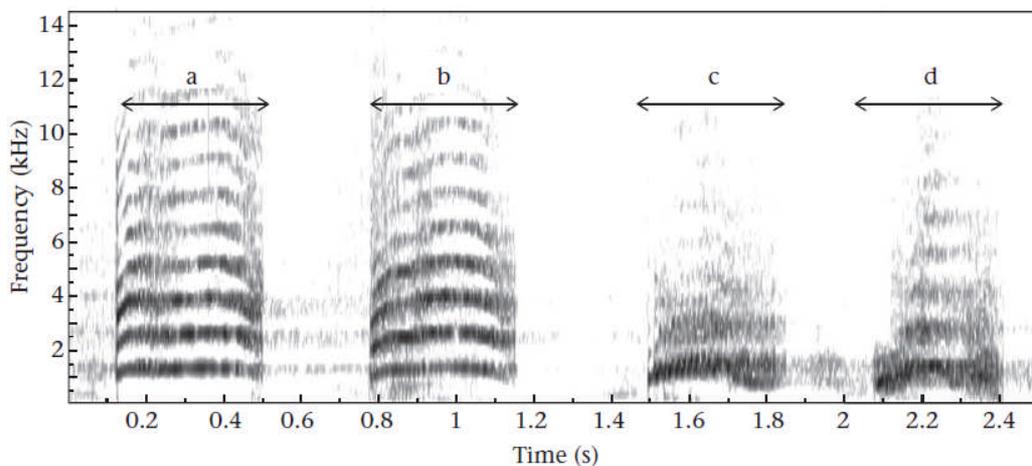

Figure 1. An example time–frequency spectrogram of an utterance consisting of (a, b) two screams followed by (c, d) two waa barks given by an adult male.

The call typically starts with a low-frequency 'w' introductory phase and culminates with a higher frequency element usually sounding to the human ear as an 'aow' or 'aoo' sound (Schel et al., 2013). In agonistic contexts, 'waa' barks usually grade from screams and occur

either immediately after the last call of a scream bout or within a scream bout, in which case they are both preceded and followed by screams (Fig. 1; see Supplementary material Audio S1 and Audio S2 for examples of recordings). We recorded the presence or absence of screams and waa barks during and after each agonistic interaction in real time. High-quality audio recordings were available for a small number of the agonistic events observed and all calls ($N = 142$) from these 16 events were categorized from these audio recordings independently by P.F., K.S. and an independent coder, who was blind to the hypotheses and aims of the study but trained in categorizing chimpanzee calls. There was 100% agreement between the three coders on the classification of these calls as screams ($N = 124$) or 'waa' barks ($N = 18$), indicating that these calls were reliably distinguished in the field.

Severe and mild aggression

We distinguished between two categories of aggression depending on its severity. Severe aggression took place when the aggressor physically attacked the victim (slap, kick, bite, etc.) or when the victim was chased by the aggressor (i.e. the pursuit distance was more than 7 m) but there was no physical contact between them. Mild aggression was defined as instances of aggression such as charge (i.e. the pursuit distance was less than 7 m), displaying towards another individual (i.e. a male runs piloerect towards another individual, and may include shaking vegetation, slapping the ground (Goodall, 1986)), and postural threat such as arm raises or ground slaps directed at the victim (Slocombe & Zuberbuhler, 2007).

Audience

We determined all adult and late-adolescent males or females in close proximity to the victim (<15 m away) at the start of aggression. Data on adult and late-adolescent individuals present in the victim's party were taken from the 15 min scan preceding the aggression.

Retaliation

Retaliation was defined as the victim directing mild or severe aggression towards the aggressor within 10 min after the agonistic interaction had terminated.

Support for victim

Support for the victim took place when one or more individuals aided the victim by directing mild or severe aggression towards the aggressor (e.g. Mitani & Gros-Louis, 1998).

Reconciliation

Reconciliation between aggressors and victims took place when there was an affiliative interaction, such as sitting in contact, allogrooming, presenting, mounting, genital inspection, embracing, gentle touching or soft biting (Arnold & Whiten, 2001) between the two opponents within 10 min of the end of aggression (e.g. de Waal & Yoshihara, 1983). Reconciliation was also considered to have taken place if during that 10 min period there was a prolonged (i.e. for at least 10 s) close proximity (i.e. equal to or less than 1 m) between the former aggressor and victim initiated by ether of the opponents (e.g. Aureli, Cords, & van Schaik, 2002; McFarland & Majolo, 2013).

Victim orientation during 'waa' barking

During 'waa' barking, the victim was oriented towards the aggressor when the victim's face was directed towards the aggressor rather than in other directions.

Preferred social partners

Preferred social partners (PSPs) were identified only for adult and late-adolescent males. PSPs were established on the basis of three different dyadic association measures: simple ratio index (time spent in a party together), 5 m association index and nearest-neighbour association index (Gilby & Wrangham, 2008; see Appendix).

Dominance status

Dominance status was established only for adult and late-adolescent males, using the Elo-rating procedure (Neumann et al., 2011; see Appendix). Rank difference between two male opponents was established by deducting the rank of the aggressor from the rank of the victim.

Statistical analysis

Generalized linear mixed-effect models (GLMM) and linear mixed-effect models (LMM) were used in all the analyses. In all analyses each aggression event was entered as one data point. To avoid the problem of nonindependence of data (e.g. Waller, Warmelink, Liebal, Micheletta, & Slocombe, 2013), we incorporated in the analyses data on entities from which repeated measurements were taken as 'random effects', which in our models concerned the identities of the aggressor and the victim. All statistical analyses were conducted using STATA 12.0 software (StataCorp LP, College Station, TX, U.S.A.).

Models created

In the majority of models the entire data set was used. However, for the analyses concerning dominance rank and PSPs, we used data only on adult and late-adolescent males, for whom we had accurate data on dominance and affiliation relationships.

To examine whether the production of screams and 'waa' barks was predicted by the severity of aggression and the sex of the victim, we created two GLMMs in which we put as the dependent variable whether or not (0/1) screams or 'waa' barks occurred during aggression, and as independent variables the type of aggression (0: mild; 1: severe) and the sex of the victim (0: female; 1: male). Only data from adult and late-adolescent males and females, which were the most common age–sex categories of the victim and aggressor in our data set (Table 1), were incorporated in this analysis (N=216).

Table 1. Summary of the data set examined

Age–sex category of aggressor–victim	Aggression bouts	Bouts of severe aggression	Bouts with screams	Bouts with 'waa' barks	Bouts with retaliation	Bouts with reconciliation
Adult male–adult male	85	22	68	26	3	21
Adult male – late-adolescent male	33	5	33	7	0	3
Adult male–adult female	61	18	58	14	2	17
Adult male – late-adolescent female	5	3	5	0	1	0
Adult male–early adolescent male or female	6	0	5	1	0	1
Late adolescent male–adult male	8	2	5	3	2	2
Late adolescent male – late-adolescent male	4	2	2	1	0	0
Late adolescent male–adult female	16	4	14	4	2	4
Late adolescent male – late-adolescent female	1	0	1	0	0	0
Late adolescent male–early adolescent male or female	1	0	1	0	0	0
Adult female–adult male	2	2	2	0	0	0
Adult female–adult female	1	0	1	0	0	0
Total	223	58	195	56	10	48

The table gives details of the number of aggression bouts and the number of bouts that included severe aggression, screams or 'waa' barks produced by the victim, retaliation by the victim or reconciliation between the interacting animals that we recorded for each of the age–sex categories of the aggressor and victim.

To examine whether the production of screams and 'waa' barks was predicted by the distance in terms of dominance rank between the victim and the aggressor, we created two GLMMs, in which we put as the dependent variable whether or not (0/1) screams or 'waa' barks occurred during aggression, and as the independent variable the rank distance between the victim and the aggressor. Only data from adult and late-adolescent males, for whom we had accurate dominance data, were considered in this analysis (N=130).

To examine whether there was a difference in terms of the distance between the aggressor and the victim during screaming and waa barking, we created an LMM in which we put as the dependent variable the closest distance (m) between the victim and aggressor during calling and as the independent variable whether the call was a scream (0) or a 'waa' bark (1). Since data points with 'waa' barks (N=56) also contained screams, in this model aggression bout ID was set as another random effect in addition to aggressor ID and victim ID. For this analysis, we only included data from aggressive bouts in which either screams or 'waa' barks were produced (N=195).

To examine the effect of audience both in close proximity to the victim and in the victim's party on the probability of screaming or 'waa' barking, we created two GLMMs in which we put as the dependent variable the occurrence (0/1) of screams or 'waa' barks, and as independent variables (1) the number of males in close proximity to the victim, (2) the number of females in close proximity to the victim, (3) the total number of males in the party and (4) the total number of females in the party (N=223).

To investigate whether the presence of a PSP or a higher ranking individual predicted screaming or 'waa' barking, we created two models in which we put either scream (0/1) or 'waa' bark (0/1) as the dependent variable, and the presence of a PSP (0: non-PSP; 1: PSP) and an individual that outranked the aggressor (0: lower ranking; 1: higher ranking) in both close proximity and the party. Only data on adult and late-adolescent males for whom accurate dominance and PSP data were available were considered in these analyses (N=130).

To investigate whether screams or 'waa' barks predicted the occurrence of the victim's retaliation, we created a GLMM in which we put as the dependent variable whether or not (0/1) retaliation occurred, and as independent variables the occurrence (0/1) of screams and

'waa' barks. In this model we also put the type of aggression as another independent variable to control for the effect of aggression type on the occurrence of retaliation (*N*=223).

To examine whether the occurrence of screams or 'waa' barks predicted reconciliation between the opponents, we created a GLMM in which we put as the dependent variable whether or not (0/1) there was reconciliation between the aggressor and the victim, and as independent variables the presence of screams (0/1) and 'waa' barks (0/1). We also put the type of aggression as another independent variable to control for the effect of aggression type on the occurrence of reconciliation (*N*=223).

To investigate whether screams or 'waa' barks were associated with audience support for the victim, we created a GLMM in which we put as the dependent variable whether or not (0/1) the victim received support from the audience, and as the independent variables the occurrence of screams (0/1) and 'waa' barks (0/1) (*N*=223).

Results

Rates and context of victim screams and 'waa' barks

In total, we recorded 223 bouts of aggression (see Table 1 for the summary of data collected). 'Waa' barks were always produced during or after, but not before, screaming (56 of 56 'waa' bark events). In 80% of cases (*N*=45) 'waa' barks occurred during screaming or within 15 s after scream termination. For the remaining 20% 'waa' barks occurred between 16 s and 10 min after the end of screaming. During 'waa' barking victims were always (all 56 events) visually oriented towards aggressors. In addition, while screams typically occurred during the exact time of assault (when the victim was charged, chased, physically attacked, etc.) lasting for up to several minutes after the first attack, 'waa' barks were never given during the act of

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aggression but usually (91%; N=51) shortly after the assault when the aggressor was still in visual contact. The mean closest distance between victims and aggressors was smaller during screaming (mean=3.45 m, SD=2.99) than during 'waa' barking (mean=10.52 m, SD=5.11; β±SE=7.13±0.53, z=13.52, P<0.001).

Victim screams occurred in 87% and 'waa' barks in 25% of all aggressive bouts (N=223; Table 1). Screams (β±SE=3.31±1.37, z=2.41, P=0.016) and especially 'waa' barks (β±SE=1.18±0.40, z=2.94, P=0.003) were more likely to be produced in response to severe rather than mild aggression. When considering adult and late-adolescent individuals, males and females were equally likely to produce screams (β±SE=-1.10±0.68, z=-1.62, P=0.105) and 'waa' barks (β±SE=0.58±0.41, z=1.41, P=0.155; Table 1). Rank difference between two male opponents did not predict the occurrence of 'waa' barks (β±SE=-0.08±0.09, z=-1.05, P=0.294). However, there was a nonsignificant trend showing that the larger the rank distance between the aggressor and the victim was, the more likely the victim was to produce screams (β±SE=0.23±0.13, z=1.76, P=0.078).

Third-party audience effects on screaming and 'waa' barking

The production of screams was dependent on the number of adult and late-adolescent males, but not the number of adult and late-adolescent females, in close proximity (<15 m; Table 2, Fig. 2). The number of males or females in the party (<35 m) had no effect (Table 2). In contrast, 'waa' bark production was not affected by the number of males or females in close proximity or in the party (Table 3).

Table 2. The relationship between the production of screams and various types of audience (independent variables)

Independent variables	Coefficient	SE	z	P	95% Confidence interval	
Number of males within 15 m	0.58	0.26	2.25	0.024	0.07	1.08
Number of females within 15 m	0.18	0.37	0.49	0.622	−0.55	0.91
Total number of males in party	−0.08	0.13	−0.61	0.542	−0.33	0.17
Total number of females in party	0.16	0.17	0.93	0.354	−0.18	0.50

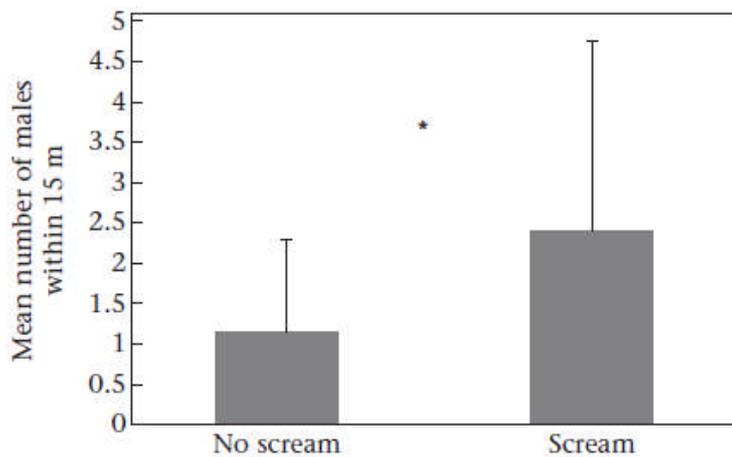GLMM; Dependent variable: scream (0/1); Random effects: aggressor ID and victim ID.

Figure 2. The relationship between the mean number of males present in close proximity to the victim and whether or not the victim produced screams (GLMM; *$P \leq 0.05$; random effects: aggressor ID and victim ID; error bars represent 1 SD).

Victims tended to scream ($\beta \pm SE = 2.48 \pm 1.50$, $z = 1.65$, $P = 0.099$) but not 'waa' bark ($\beta \pm SE = -0.35 \pm 0.68$, $z = 0.51$, $P = 0.613$) when an individual that was higher ranking than the aggressor was in close proximity. Victims were not more likely to scream ($\beta \pm SE = -1.69 \pm 1.64$, $z = -1.03$, $P = 0.302$) or 'waa' bark ($\beta \pm SE = 0.08 \pm 0.74$, $z = 0.10$, $P = 0.917$) when an individual that was higher ranking than the aggressor was in the victim's party.
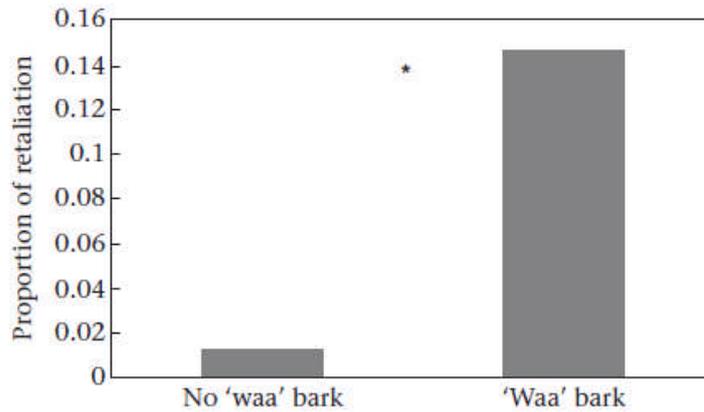
Figure 3. The relationship between 'waa' bark production and retaliation (GLMM; *P≤0.05; random effects: aggressor ID and victim ID).

Table 3. The relationship between 'waa' barking and various types of audience (independent variables)

Independent variables	Coefficient	SE	z	P	95% Confidence interval	
Number of males within 15 m	0.09	0.10	0.85	0.393	−0.11	0.29
Number of females within 15 m	−0.15	0.15	−1.01	0.310	−0.43	0.14
Total number of males in party	−0.01	0.08	−0.09	0.929	−0.17	0.15
Total number of females in party	0.11	0.10	1.10	0.271	−0.08	0.30

GLMM; Dependent variable: 'waa' bark (0/1); Random effects: aggressor ID and victim ID.

Victims were not more likely to scream ($\beta\pm SE$=-2.49±1.68, z=-1.48, P=0.139) or 'waa' bark ($\beta\pm SE$=0.67±0.83, z=0.81, P=0.416) when a PSP of the victim was in close proximity. Likewise, victims were not more likely to scream ($\beta\pm SE$=2.21±1.68, z=1.31, P=0.190) or 'waa' bark ($\beta\pm SE$=-1.02±0.74, z=-1.38, P=0.167) when a PSP of the victim was in the same party.

Victims' calls and retaliation

'Waa' barking (Fig. 3; β±SE=3.18±1.44, z=2.20, P=0.028) but not screaming (β±SE=14.72±1695.73, z=0.01, P=0.993) was associated with victims retaliating against the aggressor. The type of aggression did not predict the occurrence of retaliation (β±SE=1.77±1.35, z=1.31, P=0.190).

Victims' calls and reconciliation

Reconciliation between aggressors and victims was less likely after 'waa' barking (Fig. 4; β±SE=-2.15±0.70, z=-3.09, P=0.002) but not screaming (β±SE=0.67±0.63, z=1.07, P=0.284). The type of aggression did not predict the occurrence of reconciliation (β±SE=-0.49±0.49, z=-1.00, P=0.317).
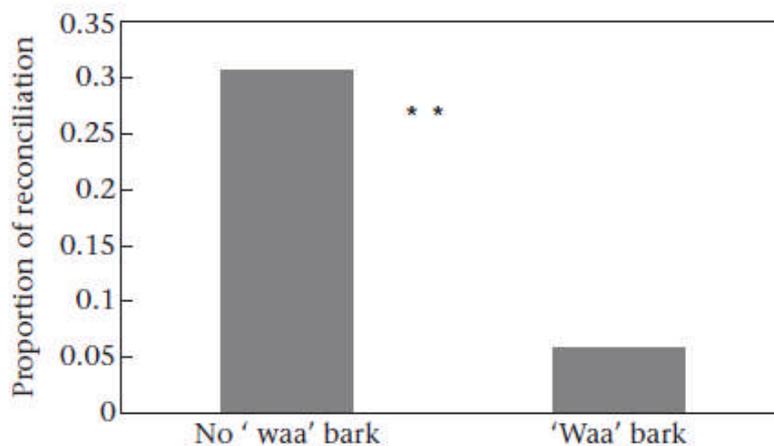

Figure 4. The relationship between 'waa' bark production and reconciliation (GLMM; **P≤0.01; random effects: aggressor ID and victim ID).

Victims' calls and audience support

The production of 'waa' barks (β±SE=2.59±1.14, z=2.26, P=0.024) but not screams (β±SE=14.57±1194.19, z=0.01, P=0.990) was dependent on whether or not the victim had

received support from the audience. Support was usually given by adult or late-adolescent males, who provided 78% of the recorded instances of support for the victim. When one or more individuals in the third-party audience supported the victim by directing mild or severe aggression at the aggressor, the victim was more likely to produce 'waa' barks. Typically, in cases in which bystanders intervened in the interaction, the victim screamed in response to the original aggressive act until the bystander started to direct aggression at the aggressor, then the victim tended to stop screaming and start 'waa' barking.

Discussion

Wild chimpanzees that have become victims of physical aggression can utter two basic call types, screams and 'waa' barks. While all utterances are initiated by screams, some of them also contain 'waa' barks after the screams. In our study, we were able to show that the two calls are directed at two different audiences and so serve different social functions.

In particular, the production of screams was influenced by the composition of the third-party audience, indicating that these calls were, at least in part, directed at bystanders. The fact that the number of males but not females was a good predictor of screams might be explained by the fact that males are physically more powerful than females and our results, in line with previous studies (e.g. Slocombe & Zuberbühler, 2007), indicate that males are more likely than females to provide support for victims. Victims also tended to scream when a higher rather than lower ranking male than the aggressor was in close proximity. In this respect, our study is in line with work showing that victims of aggression change the acoustic structure of their screams to exaggerate the level of aggression received if high-ranking individuals are in close proximity (Slocombe & Zuberbühler, 2007), suggesting that one function of these calls is to solicit help. We did not find evidence that screams are more likely to be given in the

presence of affiliated individuals, but this may have been due to fact that friendship patterns between males were unstable during the study period.

In contrast to screams, 'waa' bark production was not dependent on audience composition, and these calls were given after rather than before receiving support from bystanders. Moreover, 'waa' barking victims were visually oriented towards aggressors and likely to retaliate, suggesting that these calls do not function to recruit support from bystanders but to repel the attacker .The ultimate function of 'waa' barking, therefore, may be to discourage the attacker from future aggression. This hypothesis, however, requires further testing, ideally with postconflict data collected over longer timescales. Nevertheless, our interpretation is consistent with the results of a recent experimental study showing that individuals avoid barks of former aggressors' associates (Wittig et al., 2014), suggesting that these calls are aversive to listeners and function to repel them, probably because they reflect an aggressive attitude of the producer.

Concerning the screams, our results suggest that apart from alerting the audience, these calls signal the victim's submission and indicate that he is unlikely to retaliate, which might discourage the aggressor from continuing the assault (e.g. Rowell, 1962). Indeed, vocal sequences consisting of screams only tended to be produced more often when the rank distance between the opponents was large. Both screams and 'waa' barks, therefore, are good predictors of the signaller's subsequent behaviour (e.g. Smith, 1977), which may influence the outcome of an aggressive interaction by signalling submission or readiness to retaliate, and by increasing the probability of obtaining support from bystanders.

Our results also suggest that calls are used to manage aggressor–victim relationships following aggression. In particular, 'waa' barks, but not screams, seem to inhibit the

occurrence of reconciliation, probably because the aggressor is less likely to approach the victim and reconcile after the victim has 'waa' barked or because victims are unlikely to behave affiliatively towards their aggressors after producing these calls. Owing to the small number of instances of reconciliation following victims' 'waa' barking recorded in this study, we were unable to test between these two hypotheses. None the less, our study suggests that agonistic calls in chimpanzees play an important role in managing relationships between aggressors and victims, including the occurrence of reconciliation, an important element in the sociality of primates and other animals (Aureli & de Waal, 2000). In baboons, it has been shown that affiliative grunts facilitate reconciliation (Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007), and to our knowledge this is the first study showing that agonistic calls can also influence the likelihood of reconciliation, albeit in the opposite way.

Our study is also relevant for an ongoing debate in the animal communication literature, instigated by Owren and Rendall (1997; 2001). Here, the main argument has been that animal vocalizations can have direct physiological effects on recipients, a plausible proposal for both 'waa' barks and screams. Both call types consist of loud and acoustically chaotic sounds which may have direct dissuasive effects on an aggressor (see also Gouzoules & Gouzoules, 2000). At the same time, however, our results also suggest that screams are primarily directed at third-party audience members, which is inconsistent with an acoustic repellent function. More generally, it has been proposed that the acoustic features of a call are shaped by natural selection in a way that makes the call effective in fulfilling its function (Morton, 1977; Owren & Rendall, 2001; Wiley & Richards, 1978; Zahavi, 1979). For example, in mammals and birds, high-frequency, tonal sounds are often signals of submission, while low-frequency, noisy calls are more likely to be produced by hostile individuals (Hauser, 1993; Morton, 1977; Ordóñez-Gómez et al., 2015). Our results are consistent with this interpretation. In particular, 'waa' barks are lower pitched than screams and victim retaliation was associated

with 'waa' barking but not screaming. However, 'waa' barks are given not only during aggressive interactions but also in other dangerous contexts, for example, when encountering bush pigs or other dangerous animals (P. Fedurek, personal observation), probably to repel them. Interestingly, chimpanzees exposed to python models directed their 'waa' barks at preferred social partners that were ignorant about the snake (Schel et al., 2013), as if to drive them away from the danger. Evidence from a range of contexts, therefore, indicates that 'waa' barks function to repel others and, on a proximate level, seem to reflect an individual's confidence and willingness to behave aggressively. Importantly, barking may have a similar function in other species, such as domestic dogs, *Canis familiaris* (Lord, Feinstein, & Coppinger, 2009; Yin & McCowan, 2004), Arctic foxes, *Alopex lagopus* (Frommolt, Goltsman, & Macdonald, 2003), roe deer, *Capreolus capreolus* (Reby, Cargnelutti, & Hewison, 1999) and sea lions, *Zalophus californianus* (Schusterman & Dawson, 1968).

In conclusion, our results show that victim screams and 'waa' barks, although often produced during the same agonistic events and as part of the same vocal sequence, are directed at different types of audiences and fulfil different social functions. 'Waa' barks are signals directed at the aggressor and indicate the probability of retaliation. Screams, on the other hand, are calls primarily directed at the third-party audience to attract support. The use of these two types of calls aids the victim to manage aggressive interactions by signalling either submission or the probability of retaliation, as well as by influencing the probability of reconciliation or receiving support from bystanders. We conclude that agonistic calls play an important role in mediating agonistic interactions and aggressor–victim relationships following aggression, and that the graded system of chimpanzee vocal production is capable of generating complex signals with multiple functions.

Acknowledgments

Supplementary Material

Supplementary material associated with this article can be found in the online version at doi.

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Appendix

Male preferred social partners

PSPs were established on the basis of three different dyadic association measures. The first measure, simple ratio index (SRI), reflects the total proportion of scans in which both individuals were together in the same party (Cairns & Schwager, 1987), or

$$SRI_{AB} = \frac{P_{AB}}{P_A + P_B - P_{AB}}$$

where P_{AB} = the number of parties containing both A and B, P_A = the number of parties containing A, P_B = the number of parties containing B.

The second dyadic association measure is the '5 m association index' (5M) (Gilby & Wrangham, 2008) which measures the frequency with which a dyad was observed within 5 m

of one another, given that one of the individuals was present in the party and another one was a focal animal:

$$5M_{AB} = \frac{A_f(B_5) + B_f(A_5)}{A_f(B_p) + B_f(A_p)}$$

where $A_f(B_5)$= the number of instances in which A was the focal animal and B was within 5 m of A, $B_f(A_5)$= the number of instances in which B was the focal animal and A was within 5 m, $A_f(B_p)$= the number of instances A was the focal animal and B was in the same party, $B_f(A_p)$= B was the focal animal and A was in the same party.

The third employed dyadic association measure is the 'nearest-neighbour association index' (NN) (Gilby & Wrangham, 2008), which reflects the frequency with which two individuals were observed as nearest neighbours, provided that one was the focal animal and the other was within 5 m, or

$$NN_{AB} = \frac{A_f(B_{nn}) + B_f(A_{nn})}{A_f(B_5) + B_f(A_5)}$$

where $A_f(B_{nn})$= the number of instances A was the focal animal and B was the nearest neighbour and $B_f(A_{nn})$= the number of instances B was the focal animal and A was the nearest neighbour.

For a given index (SRI, 5M and NN) individuals A and B were classified as 'mutual associates' if the value was one-third of a standard deviation larger than the averages of both A and B. We classified a dyad as mutual preferred social partners (mutual PSP) if they were mutual associates for at least two of the three different indexes (Gilby & Wrangham, 2008). Since association dynamics in chimpanzees change on a temporal basis (e.g. Fedurek et al., 2013), we conducted association calculations for four separate periods with durations

between 4 and 5 months: between June and October 2013, February and May 2014, June and September 2014 and January and April 2015. Using this procedure we identified eight for the first (mean ±SD=1.15±0.8/focal individual, range 0–3), seven for the second (mean ±SD=1.08±0.76/focal individual, range 0–2), seven for the third (mean ±SD=1.08±1.32/focal individual, range 0–3) and six (mean ±SD=0.92±0.95/focal individual, range 0–3) mutual PSP dyads for the fourth period of the study. The remaining dyads were classified as neutral social partners (non-PSPs).

Dominance status

Dominance status was established only for adult and late-adolescent males, using the Elo-rating procedure. This method is based on a sequence in which interactions between individuals occur rather than on an interaction matrix (Neumann et al., 2011). At the onset of the process each individual is given the same rating of a value 1000. After each agonistic or submissive interaction the score is updated with the winner of the interaction gaining whereas the loser loses points (Neumann et al., 2011). The number of points gained or lost by two interacting individuals is dependent on the expected outcome which in turn depends on previous interactions between these two individuals (Elo, 1978). In our study the scores were based on interactions such as pant grunts (i.e. vocalizations given by males to other males that outrank them) combined with the outcomes of dyadic win–lose agonistic interactions (i.e. physical attack, chase, charge, displacements, etc.; Goodall, 1986; Bygott, 1989; Muller & Wrangham, 2004) recorded during the study period. Since dominance relationships between male chimpanzees change on a temporal basis (Gilby & Wrangham, 2008), we calculated Elo-rating scores for four periods: between June and October 2013, June 2013 and May 2014, June 2013 and September 2014 and June 2013 and April 2015. The Elo-rating scores were then converted into rank orders for each male (from 1 to 14, with 1 representing the highest

ranking male). The Elo-rating method has several advantages over more traditional methods such as sensitivity to short-term demography changes, effectiveness in tracking hierarchy dynamics on short-term scales and more effective evaluation of relative hierarchy position between individuals with undecided interactions (Neumann et al., 2011). We believe that this method was especially effective in establishing dominance positions of the Sonso males, since the hierarchy was unstable throughout the study period with no clear alpha male after one of the males had lost his alpha status prior to the study period. Elo-rating scores were calculated using R v.3.1.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org).