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Chimpanzees communicate to two different audiences during aggressive interactions

Pawel Fedurek [a, *], Katie E. Slocombe [b], Klaus Zuberbühler [a, c]

[a] *Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland*
[b] *Department of Psychology, University of York, York, U.K.*
[c] *School of Psychology and Neuroscience, University of St Andrews, St Andrews, U.K.*

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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.

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,

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* Correspondence: P. Fedurek, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland.
E-mail address: fedurek@hotmail.co.uk (P. Fedurek).

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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 km^2. 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 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). 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.