

1 **Chimpanzees communicate to two different audiences during aggressive interactions**

2 Pawel Fedurek ^{a,*}, Katie E. Slocombe ^b, Klaus Zuberbühler ^{a,c}

3 ^aInstitute of Biology, University of Neuchâtel, Neuchâtel, Switzerland

4 ^b Department of Psychology, University of York, York, U.K^c School of Psychology and
5 Neuroscience, University of St Andrews, St Andrews, U.K

6

7

8 Received 3 June 2015

9 Initial acceptance 4 August 2015

10 Final acceptance 21 August 2015

11 MS. number: 15-00475

12 *Correspondence: P. Fedurek, Institute of Biology, University of Neuchâtel, Rue Emile-
13 Argand 11, 2000 Neuchâtel, Switzerland.

14 E-mail address: fedurek@hotmail.co.uk (P. Fedurek).

15

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

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

36 Key words: agonistic calls, chimpanzee, graded calls, reconciliation, screams, ‘waa’ barks

37

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

44 During animal conflicts screams are probably the most common vocalizations and various
45 functions have been attributed to them, such as alerting group members, confusing or
46 dissuading the opponent or attracting help (Hogstedt, 1983; Rohwer, Fretwell, & Tuckfield,
47 1976). In primates, screams are commonly produced by victims of aggression, apparently to
48 alert and recruit aid from allies (Bernstein & Ehardt, 1985; Cheney, 1977; Gouzoules,
49 Gouzoules, & Marler, 1984). For example, rhesus macaques, *Macaca mulatta*, produce
50 acoustically distinct variants of screams that seem to be related to the identity of the caller,
51 the dominance rank of the opponent, the relatedness between the caller and opponent and the
52 severity of the attack (Gouzoules & Gouzoules, 1990; Gouzoules et al., 1984). Receivers
53 attend differently to different scream variants, suggesting that the calls inform potential
54 supporters about the nature of the aggressive interaction (Gouzoules et al., 1984).

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

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

66 In chimpanzees, however, victims of aggression often produce another type of call, ‘waa’
67 barks. Chimpanzee ‘waa’ barks belong to an acoustic cluster of bark vocalizations that are
68 given in several contexts, such as hunting or when replying to long-distance calls from other
69 group members or from members of other communities (Crockford & Boesch, 2003;
70 Goodall, 1986; Marler & Tenaza, 1977). ‘Waa’ barks are also given to alert others about
71 predators (Crockford & Boesch, 2003; Schel, Townsend, Machanda, Zuberbühler, &
72 Slocombe, 2013) or to drive away dangerous animals, such as bush pigs (P. Fedurek, personal
73 observation), suggesting that, although these calls can have subtly different acoustic structure
74 depending on the context of production (Crockford & Boesch, 2003), they are linked to
75 targeted aggressive motivation. ‘Waa’ barks are also given in agonistic encounters and it has
76 been proposed that they are signals directed at aggressors (Goodall, 1986; Marler & Tenaza,
77 1977), usually given immediately after screams from which they can grade (Marler, 1976;
78 Marler & Tenaza, 1977). Overall, however, there has been little systematic analysis of the
79 function of this call type in agonistic contexts. One notable exception concerns the
80 observation that, during agonistic interactions, ‘waa’ barks are sometimes given by allies of
81 the opponents observing the interaction, possibly as a way of expressing support (Newton-
82 Fisher, 2006; Wittig, Crockford, Langergraber, & Zuberbühler, 2014).

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

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

101

102 <H1>Methods

103 <H2>&u>Study site and study subjects

104

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

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

112

113 <H2>Sampling method

114

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

130

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

135 adult and late-adolescent individuals present within 35 m of the focal animal; Newton-Fisher,
136 1999), (2) the identities of individuals present within 5 m of the focal male and (3) the
137 identity of the adult or late-adolescent individual closest to the focal male.

138

139 <H2>Data recorded and definitions

140

141 <H3>Screams and ‘waa’ barks

142 For every act of aggression in the focal party, we noted whether or not the victim produced
143 screams and whether or not these were followed by ‘waa’ barks (within 10 min of the end of
144 aggression). Although these two types of calls often grade from one to another, they are
145 acoustically distinguishable. ‘Waa’ barks have an abrupt onset, are typically shorter, and have
146 a lower frequency range and a noisier spectral quality than screams (Fig. 1; Crockford &
147 Boesch, 2003). The call typically starts with a low-frequency ‘w’ introductory phase and
148 culminates with a higher frequency element usually sounding to the human ear as an ‘aow’ or
149 ‘aoo’ sound (Schel et al., 2013). In agonistic contexts, ‘waa’ barks usually grade from
150 screams and occur either immediately after the last call of a scream bout or within a scream
151 bout, in which case they are both preceded and followed by screams (Fig. 1; see
152 Supplementary material Audio S1 and Audio S2 for examples of recordings). We recorded
153 the presence or absence of screams and waa barks during and after each agonistic interaction
154 in real time. High-quality audio recordings were available for a small number of the agonistic
155 events observed and all calls ($N = 142$) from these 16 events were categorized from these
156 audio recordings independently by P.F., K.S. and an independent coder, who was blind to the
157 hypotheses and aims of the study but trained in categorizing chimpanzee calls. There was
158 100% agreement between the three coders on the classification of these calls as screams ($N =$

159 124) or ‘waa’ barks ($N = 18$), indicating that these calls were reliably distinguished in the
160 field.

161

162 <H3>Severe and mild aggression

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

171

172 <H3>Audience

173 We determined all adult and late-adolescent males or females in close proximity to the victim
174 (<15 m away) at the start of aggression. Data on adult and late-adolescent individuals present
175 in the victim’s party were taken from the 15 min scan preceding the aggression.

176

177 <H3>Retaliation

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

180

181 <H3>Support for victim

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

184

185 <H3>Reconciliation

186 Reconciliation between aggressors and victims took place when there was an affiliative
187 interaction, such as sitting in contact, allogrooming, presenting, mounting, genital inspection,
188 embracing, gentle touching or soft biting (Arnold & Whiten, 2001) between the two
189 opponents within 10 min of the end of aggression (e.g. de Waal & Yoshihara, 1983).

190 Reconciliation was also considered to have taken place if during that 10 min period there was
191 a prolonged (i.e. for at least 10 s) close proximity (i.e. equal to or less than 1 m) between the
192 former aggressor and victim initiated by either of the opponents (e.g. Aureli, Cords, & van
193 Schaik, 2002; McFarland & Majolo, 2013).

194

195 <H3>Victim orientation during 'waa' barking

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

198

199 <H3>Preferred social partners

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

204

205 <H3>Dominance status

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

209

210 <H2>Statistical analysis

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

218

219 <H3>Models created

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

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

230 To examine whether the production of screams and ‘waa’ barks was predicted by the distance
231 in terms of dominance rank between the victim and the aggressor, we created two GLMMs,

232 in which we put as the dependent variable whether or not (0/1) screams or ‘waa’ barks
233 occurred during aggression, and as the independent variable the rank distance between the
234 victim and the aggressor. Only data from adult and late-adolescent males, for whom we had
235 accurate dominance data, were considered in this analysis ($N=130$).

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

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

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

256 To investigate whether screams or ‘waa’ barks predicted the occurrence of the victim’s
257 retaliation, we created a GLMM in which we put as the dependent variable whether or not
258 (0/1) retaliation occurred, and as independent variables the occurrence (0/1) of screams and
259 ‘waa’ barks. In this model we also put the type of aggression as another independent variable
260 to control for the effect of aggression type on the occurrence of retaliation ($N=223$).

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

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

271

272 <H1>Results

273 <H2>Rates and context of victim screams and ‘waa’ barks

274 In total, we recorded 223 bouts of aggression (see Table 1 for the summary of data collected).

275 ‘Waa’ barks were always produced during or after, but not before, screaming (56 of 56 ‘waa’
276 bark events). In 80% of cases ($N=45$) ‘waa’ barks occurred during screaming or within 15 s
277 after scream termination. For the remaining 20% ‘waa’ barks occurred between 16 s and 10
278 min after the end of screaming. During ‘waa’ barking victims were always (all 56 events)

279 visually oriented towards aggressors. In addition, while screams typically occurred during the
280 exact time of assault (when the victim was charged, chased, physically attacked, etc.) lasting
281 for up to several minutes after the first attack, ‘waa’ barks were never given during the act of
282 aggression but usually (91%; $N=51$) shortly after the assault when the aggressor was still in
283 visual contact. The mean closest distance between victims and aggressors was smaller during
284 screaming (mean=3.45 m, SD=2.99) than during ‘waa’ barking (mean=10.52 m, SD=5.11;
285 $\beta \pm SE = 7.13 \pm 0.53$, $z = 13.52$, $P < 0.001$).

286 Victim screams occurred in 87% and ‘waa’ barks in 25% of all aggressive bouts ($N=223$;
287 Table 1). Screams ($\beta \pm SE = 3.31 \pm 1.37$, $z = 2.41$, $P = 0.016$) and especially ‘waa’ barks
288 ($\beta \pm SE = 1.18 \pm 0.40$, $z = 2.94$, $P = 0.003$) were more likely to be produced in response to severe
289 rather than mild aggression. When considering adult and late-adolescent individuals, males
290 and females were equally likely to produce screams ($\beta \pm SE = -1.10 \pm 0.68$, $z = -1.62$, $P = 0.105$)
291 and ‘waa’ barks ($\beta \pm SE = 0.58 \pm 0.41$, $z = 1.41$, $P = 0.155$; Table 1). Rank difference between two
292 male opponents did not predict the occurrence of ‘waa’ barks ($\beta \pm SE = -0.08 \pm 0.09$, $z = -1.05$,
293 $P = 0.294$). However, there was a nonsignificant trend showing that the larger the rank
294 distance between the aggressor and the victim was, the more likely the victim was to produce
295 screams ($\beta \pm SE = 0.23 \pm 0.13$, $z = 1.76$, $P = 0.078$).

296

297 <H2>Third-party audience effects on screaming and ‘waa’ barking

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

303 Victims tended to scream ($\beta \pm SE = 2.48 \pm 1.50$, $z = 1.65$, $P = 0.099$) but not ‘waa’ bark ($\beta \pm SE = -$
304 0.35 ± 0.68 , $z = 0.51$, $P = 0.613$) when an individual that was higher ranking than the aggressor
305 was in close proximity. Victims were not more likely to scream ($\beta \pm SE = -1.69 \pm 1.64$, $z = -1.03$,
306 $P = 0.302$) or ‘waa’ bark ($\beta \pm SE = 0.08 \pm 0.74$, $z = 0.10$, $P = 0.917$) when an individual that was
307 higher ranking than the aggressor was in the victim’s party.

308 Victims were not more likely to scream ($\beta \pm SE = -2.49 \pm 1.68$, $z = -1.48$, $P = 0.139$) or ‘waa’ bark
309 ($\beta \pm SE = 0.67 \pm 0.83$, $z = 0.81$, $P = 0.416$) when a PSP of the victim was in close proximity.

310 Likewise, victims were not more likely to scream ($\beta \pm SE = 2.21 \pm 1.68$, $z = 1.31$, $P = 0.190$) or
311 ‘waa’ bark ($\beta \pm SE = -1.02 \pm 0.74$, $z = -1.38$, $P = 0.167$) when a PSP of the victim was in the same
312 party.

313

314 <H2>Victims’ calls and retaliation

315 ‘Waa’ barking (Fig. 3; $\beta \pm SE = 3.18 \pm 1.44$, $z = 2.20$, $P = 0.028$) but not screaming
316 ($\beta \pm SE = 14.72 \pm 1695.73$, $z = 0.01$, $P = 0.993$) was associated with victims retaliating against the
317 aggressor. The type of aggression did not predict the occurrence of retaliation
318 ($\beta \pm SE = 1.77 \pm 1.35$, $z = 1.31$, $P = 0.190$).

319

320 <H2>Victims’ calls and reconciliation

321 Reconciliation between aggressors and victims was less likely after ‘waa’ barking (Fig. 4;
322 $\beta \pm SE = -2.15 \pm 0.70$, $z = -3.09$, $P = 0.002$) but not screaming ($\beta \pm SE = 0.67 \pm 0.63$, $z = 1.07$, $P = 0.284$).
323 The type of aggression did not predict the occurrence of reconciliation ($\beta \pm SE = -0.49 \pm 0.49$,
324 $z = -1.00$, $P = 0.317$).

325

326 <H2>Victims' calls and audience support

327 The production of 'waa' barks ($\beta \pm SE = 2.59 \pm 1.14$, $z = 2.26$, $P = 0.024$) but not screams
328 ($\beta \pm SE = 14.57 \pm 1194.19$, $z = 0.01$, $P = 0.990$) was dependent on whether or not the victim had
329 received support from the audience. Support was usually given by adult or late-adolescent
330 males, who provided 78% of the recorded instances of support for the victim. When one or
331 more individuals in the third-party audience supported the victim by directing mild or severe
332 aggression at the aggressor, the victim was more likely to produce 'waa' barks. Typically, in
333 cases in which bystanders intervened in the interaction, the victim screamed in response to
334 the original aggressive act until the bystander started to direct aggression at the aggressor,
335 then the victim tended to stop screaming and start 'waa' barking.

336

337 <H1>Discussion

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

342 In particular, the production of screams was influenced by the composition of the third-party
343 audience, indicating that these calls were, at least in part, directed at bystanders. The fact that
344 the number of males but not females was a good predictor of screams might be explained by
345 the fact that males are physically more powerful than females and our results, in line with
346 previous studies (e.g. Slocombe & Zuberbühler, 2007), indicate that males are more likely
347 than females to provide support for victims. Victims also tended to scream when a higher

348 rather than lower ranking male than the aggressor was in close proximity. In this respect, our
349 study is in line with work showing that victims of aggression change the acoustic structure of
350 their screams to exaggerate the level of aggression received if high-ranking individuals are in
351 close proximity (Slocombe & Zuberbühler, 2007), suggesting that one function of these calls
352 is to solicit help. We did not find evidence that screams are more likely to be given in the
353 presence of affiliated individuals, but this may have been due to fact that friendship patterns
354 between males were unstable during the study period.

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

366

367 Concerning the screams, our results suggest that apart from alerting the audience, these calls
368 signal the victim's submission and indicate that he is unlikely to retaliate, which might
369 discourage the aggressor from continuing the assault (e.g. Rowell, 1962). Indeed, vocal
370 sequences consisting of screams only tended to be produced more often when the rank
371 distance between the opponents was large. Both screams and 'waa' barks, therefore, are good

372 predictors of the signaller's subsequent behaviour (e.g. Smith, 1977), which may influence
373 the outcome of an aggressive interaction by signalling submission or readiness to retaliate,
374 and by increasing the probability of obtaining support from bystanders.

375 Our results also suggest that calls are used to manage aggressor–victim relationships
376 following aggression. In particular, ‘waa’ barks, but not screams, seem to inhibit the
377 occurrence of reconciliation, probably because the aggressor is less likely to approach the
378 victim and reconcile after the victim has ‘waa’ barked or because victims are unlikely to
379 behave affiliatively towards their aggressors after producing these calls. Owing to the small
380 number of instances of reconciliation following victims’ ‘waa’ barking recorded in this study,
381 we were unable to test between these two hypotheses. None the less, our study suggests that
382 agonistic calls in chimpanzees play an important role in managing relationships between
383 aggressors and victims, including the occurrence of reconciliation, an important element in
384 the sociality of primates and other animals (Aureli & de Waal, 2000). In baboons, it has been
385 shown that affiliative grunts facilitate reconciliation (Wittig, Crockford, Wikberg, Seyfarth,
386 & Cheney, 2007), and to our knowledge this is the first study showing that agonistic calls can
387 also influence the likelihood of reconciliation, albeit in the opposite way.

388 Our study is also relevant for an ongoing debate in the animal communication literature,
389 instigated by Owren and Rendall (1997; 2001). Here, the main argument has been that animal
390 vocalizations can have direct physiological effects on recipients, a plausible proposal for both
391 ‘waa’ barks and screams. Both call types consist of loud and acoustically chaotic sounds
392 which may have direct dissuasive effects on an aggressor (see also Gouzoules & Gouzoules,
393 2000). At the same time, however, our results also suggest that screams are primarily directed
394 at third-party audience members, which is inconsistent with an acoustic repellent function.
395 More generally, it has been proposed that the acoustic features of a call are shaped by natural
396 selection in a way that makes the call effective in fulfilling its function (Morton, 1977; Owren

397 & Rendall, 2001; Wiley & Richards, 1978; Zahavi, 1979). For example, in mammals and
398 birds, high-frequency, tonal sounds are often signals of submission, while low-frequency,
399 noisy calls are more likely to be produced by hostile individuals (Hauser, 1993; Morton,
400 1977; Ordóñez-Gómez et al., 2015). Our results are consistent with this interpretation. In
401 particular, ‘waa’ barks are lower pitched than screams and victim retaliation was associated
402 with ‘waa’ barking but not screaming. However, ‘waa’ barks are given not only during
403 aggressive interactions but also in other dangerous contexts, for example, when encountering
404 bush pigs or other dangerous animals (P. Fedurek, personal observation), probably to repel
405 them. Interestingly, chimpanzees exposed to python models directed their ‘waa’ barks at
406 preferred social partners that were ignorant about the snake (Schel et al., 2013), as if to drive
407 them away from the danger. Evidence from a range of contexts, therefore, indicates that
408 ‘waa’ barks function to repel others and, on a proximate level, seem to reflect an individual’s
409 confidence and willingness to behave aggressively. Importantly, barking may have a similar
410 function in other species, such as domestic dogs, *Canis familiaris* (Lord, Feinstein, &
411 Coppinger, 2009; Yin & McCowan, 2004), Arctic foxes, *Alopex lagopus* (Frommolt,
412 Goltsman, & Macdonald, 2003), roe deer, *Capreolus capreolus* (Reby, Cargnelutti, &
413 Hewison, 1999) and sea lions, *Zalophus californianus* (Schusterman & Dawson, 1968).

414 In conclusion, our results show that victim screams and ‘waa’ barks, although often produced
415 during the same agonistic events and as part of the same vocal sequence, are directed at
416 different types of audiences and fulfil different social functions. ‘Waa’ barks are signals
417 directed at the aggressor and indicate the probability of retaliation. Screams, on the other
418 hand, are calls primarily directed at the third-party audience to attract support. The use of
419 these two types of calls aids the victim to manage aggressive interactions by signalling either
420 submission or the probability of retaliation, as well as by influencing the probability of
421 reconciliation or receiving support from bystanders. We conclude that agonistic calls play an

422 important role in mediating agonistic interactions and aggressor–victim relationships
423 following aggression, and that the graded system of chimpanzee vocal production is capable
424 of generating complex signals with multiple functions.

425 **Acknowledgments**

426 We thank the management and staff of the Budongo Conservation Field Station for their
427 support and assistance. We also thank the Uganda Wildlife Authority and the Uganda
428 National Council for Science and Technology for permission to conduct the study. We are
429 grateful to Anne Schel for blind coding the recorded calls and Christof Neumann for his help
430 with Elo-rating calculations. P.F. was funded by Swiss National Science Foundation and
431 European Research Council project grants to K.Z. (PRILANG 283871).

432

433

434 Supplementary Material

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

436

437 References

438 Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour*, 49(3-
439 4), 227-267. doi: 10.1163/156853974x00534

440 Arnold, K., & Whiten, A. (2001). Post-conflict behaviour of wild chimpanzees (*Pan*
441 *troglydites schweinfurthii*) in the Budongo Forest, Uganda. *Behaviour*, 138(5), 649-
442 690. doi: doi:10.1163/156853901316924520

443 Aureli, F., Cords, M., & van Schaik, C. P. (2002). Conflict resolution following aggression in
444 gregarious animals: a predictive framework. *Animal Behaviour*, 64(3), 325-343. doi:

445 Aureli, F., & de Waal, F. (2000). *Natural conflict resolution*. Berkeley, CA.: California
446 University Press.

447 Bernstein, I. S., & Ehardt, C. L. (1985). Agonistic aiding: kinship, rank, age, and sex
448 influences. *American Journal of Primatology*, 8(1), 37-52. doi:
449 10.1002/ajp.1350080105

450 Bygott, J. D. (1979). Agonistic behaviour, dominance, and social structure in wild
451 chimpanzees of the Gombe National Park. In D. A. Hamburg & E. R. McCown
452 (Eds.), *The great apes* (pp. 405-428). Menlo Park, CA: Benjamin/Cummings.

453 Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indexes. *Animal*
454 *Behaviour*, 35, 1454-1469. doi: 10.1016/s0003-3472(87)80018-0

455 Cheney, D. (1977). The acquisition of rank and the development of reciprocal alliances
456 among free-ranging immature baboons. *Behavioral Ecology and Sociobiology*, 2(3),
457 303-318. doi: 10.1007/BF00299742

458 Clark AP, Wrangham RW (1994) Chimpanzee arrival pant-hoot- Do they signify food or
459 status? *International Journal of Primatology* 15:185-205

460 Crockford, C., & Boesch, C. (2003). Context-specific calls in wild chimpanzees, *Pan*
461 *troglydites verus*: analysis of barks. *Animal Behaviour*, 66, 115-125. doi:
462 10.1006/anbe.2003.2166

463 de Waal, F., & Yoshihara, D. (1983). Reconciliation and redirected affection in rhesus
464 monkeys. *Behaviour*, 85(3), 224-241. doi: doi:10.1163/156853983X00237

465 Elo, A. E. (1978). *The rating of chess players, past and present*. New York, NY: Arco.

466 Fedurek, P., Machanda, Z., Schel, A. M., & Slocombe, K. E. (2013). Pant hoot chorusing and
467 social bonds in male chimpanzees. *Animal Behaviour*, 86, 189-196.

468 Fedurek, P., & Slocombe, K. E. (2013). The social function of food-associated calls in male
469 chimpanzees. *American Journal of Primatology*, 75, 726-739.

470 Frommolt, K., H., Goltsman, M., E., & Macdonald, D., W. (2003). Barking foxes, *Alopex*
471 *lagopus*: field experiments in individual recognition in a territorial mammal. *Animal*
472 *Behaviour*, 65(3), 509-518.

473 Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (*Pan*
474 *troglydites schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology*
475 *and Sociobiology*, 62(11), 1831-1842. doi: 10.1007/s00265-008-0612-6

476 Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior*. Cambridge, MA:
477 Harvard University Press.

478 Gouzoules, H., & Gouzoules, S. (1990). Matrilineal signatures in the recruitment screams of
479 pigtail macaques, *Macaca nemestrina*. *Behaviour*, 115(3), 327-347. doi:
480 doi:10.1163/156853990X00635

481 Gouzoules, H., & Gouzoules, S. (2000). Agonistic screams differ among four species of
482 macaques: the significance of motivation-structural rules. *Animal Behaviour*, 59(3),
483 501-512.

484 Gouzoules, H., Gouzoules, S., & Marler, P. (1984). Rhesus monkey (*Macaca mulatta*)
485 screams: Representational signalling in the recruitment of agonistic aid. *Animal*
486 *Behaviour*, 32, 182-193.

487 Hauser, M. (1993). The evolution of nonhuman primate vocalizations: effects of phylogeny,
488 body weight, and social context. *American Naturalist*, 142, 528-542.

489 Hogstedt, G. (1983). Adaptation unto death: function of fear screams. *American Naturalist*,
490 121, 562-570.

491 Kojima, S., Izumi, A., & Ceugniet, M. (2003). Identification of vocalizers by pant hoots, pant
492 grunts and screams in a chimpanzee. *Primates*, 44(3), 225-230. doi: 10.1007/s10329-
493 002-0014-8

494 Lord, K., Feinstein, M., & Coppinger, R. (2009). Barking and mobbing. *Behavioural*
495 *Processes*, 81(3), 358-368.

496 Marler, P. (1976). Social organization, communication and graded signals: the chimpanzee
497 and the gorilla. In P. P. Bateson & R. A. Hinde (Eds.), *Growing points in ethology*
498 (pp. 239–277). Cambridge, U.K.: Cambridge University Press.

499 Marler, P., & Tenaza, R. R. (1977). Signalling behavior of apes with special reference to
500 vocalisation. In T. A. Sebeok (Ed.), *How animals communicate* (pp. 965-1033).
501 Bloomington, IN: Indiana University Press.

502 McFarland, R., & Majolo, B. (2013). The importance of considering the behavioral form of
503 reconciliation in studies of conflict resolution. *International Journal of Primatology*,
504 34(1), 15-29. doi: 10.1007/s10764-012-9643-y

505 Mitani, J. C., & Gros-Louis, J. (1998). Chorusing and call convergence in chimpanzees: Tests
506 of three hypotheses. *Behaviour*, 135, 1041-1064.

507 Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in
508 some bird and mammal sounds. *American Naturalist*, 111, 855-869.

509 Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild
510 chimpanzees: a test of the ' challenge hypothesis '. *Animal Behaviour*, 67, 113-123.
511 doi: 10.1016/j.anbehav.2003.03.013

512 Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., . . . Engelhardt, A.
513 (2011). Assessing dominance hierarchies: validation and advantages of progressive
514 evaluation with Elo-rating. *Animal Behaviour*, 82(4), 911-921.

515 Newton-Fisher, N. E. (1999). Association by male chimpanzees: a social tactic? *Behaviour*,
516 136(6), 705-730. doi: doi:10.1163/156853999501531

- 517 Newton-Fisher, N. E. (2006). Female coalitions against male aggression in wild chimpanzees
518 of the Budongo Forest. *International Journal of Primatology*, 27(6), 1589-1599. doi:
519 10.1007/s10764-006-9087-3
- 520 Nieburg, H. L. (1970). Agonistics—rituals of conflict. *The Annals of the American Academy*
521 *of Political and Social Science*, 391(1), 56-73. doi: 10.1177/000271627039100106
- 522 Ordóñez-Gómez, J. D., Dunn, J. C., Arroyo-Rodríguez, V., Méndez-Cárdenas, M. G.,
523 Márquez-Arias, A., & Santillán-Doherty, A. M. (2015). Role of emitter and severity
524 of aggression influence the agonistic vocalizations of Geoffroy's spider monkeys
525 (*Ateles geoffroyi*). *International Journal of Primatology*, 36(2), 429-440. doi:
526 10.1007/s10764-015-9833-5
- 527 Owren, M. J., & Rendall, D. (1997). An affect-conditioning model of nonhuman primate
528 vocal signaling. In D. H. Owings, M. D. Beecher, & N. S. Thompson (Eds.),
529 *Perspectives in Ethology: Vol. 12. Communication* (pp. 299–346). New York, NY:
530 Plenum Press.
- 531 Owren, M. J., & Rendall, D. (2001). Sound on the rebound: bringing form and function back
532 to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary*
533 *Anthropology: Issues, News, and Reviews*, 10(2), 58-71. doi: 10.1002/evan.1014
- 534 Reby, D., Cargnelutti, B., & Hewison, A. J. M. (1999). Contexts and possible functions of
535 barking in roe deer. *Animal Behaviour*, 57(5), 1121-1128.
- 536 Reynolds, R. (2005). *The chimpanzees of Budongo Forest: ecology, behaviour and*
537 *conservation*. Oxford, U.K.: Oxford University Press.
- 538 Rohwer, S., Fretwell, S. D., & Tuckfield, R. C. (1976). Distress screams as a measure of
539 kinship in birds. *American Naturalist*, 96, 418-430.
- 540 Rowell, T. E. (1962). Agonistic noises of the rhesus monkey (*Macaca mulatta*). *Symposia of*
541 *the Zoological Society of London*, 8, 91-96.

542 Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013).
543 Chimpanzee alarm call production meets key criteria for intentionality. *PLoS One*,
544 8(10), e76674. doi: 10.1371/journal.pone.0076674

545 Schusterman, R. J., & Dawson, R. G. (1968). Barking, dominance, and territoriality in male
546 sea lions. *Science*, 160(3826), 434-436. doi: 10.1126/science.160.3826.434

547 Slocombe, K. E., Kaller, T., Call, J., & Zuberbühler, K. (2010). Chimpanzees extract social
548 information from agonistic screams. *PLoS One*, 5(7), e11473. doi:
549 10.1371/journal.pone.0011473

550 Slocombe, K. E., Townsend, S. W., & Zuberbühler, K. (2009). Wild chimpanzees (*Pan*
551 *troglydites schweinfurthii*) distinguish between different scream types: evidence from
552 a playback study. *Animal Cognition*, 12(3), 441-449. doi: 10.1007/s10071-008-0204-x

553 Slocombe, K. E., & Zuberbühler, K. (2005). Agonistic screams in wild chimpanzees (*Pan*
554 *troglydites schweinfurthii*) vary as a function of social role. *Journal of Comparative*
555 *Psychology*, 119(1), 67-77. doi: 10.1037/0735-7036.119.1.67

556 Slocombe, K. E., & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a
557 function of audience composition. *Proceedings of the National Academy of Sciences*
558 *of the United States of America*, 104(43), 17228-17233.

559 Smith, W. J. (1977). *The behavior of communicating: An ethological approach*. Cambridge,
560 MA: Harvard University Press.

561 Waller, B. M., Warmelink, L., Liebal, K., Micheletta, J., & Slocombe, K. E. (2013).
562 Pseudoreplication: a widespread problem in primate communication research. *Animal*
563 *Behaviour*, 86(2), 483-488.

564 Wiley, R. H., & Richards, D. G. (1978). Physical constraints on acoustic communication in
565 the atmosphere: implications for the evolution of animal vocalizations. *Behavioral*
566 *Ecology and Sociobiology*, 3(1), 69-94. doi: 10.1007/bf00300047

- 567 Wittig, R. M., Crockford, C., Langergraber, K. E., & Zuberbühler, K. (2014). Triadic social
568 interactions operate across time: a field experiment with wild chimpanzees.
569 *Proceedings of the Royal Society B: Biological Sciences*, 281(1779). doi:
570 10.1098/rspb.2013.3155
- 571 Wittig, R. M., Crockford, C., Wikberg, E., Seyfarth, R. M., & Cheney, D. L. (2007). Kin-
572 mediated reconciliation substitutes for direct reconciliation in female baboons.
573 *Proceedings of the Royal Society B: Biological Sciences*, 274(1613), 1109-1115. doi:
574 10.1098/rspb.2006.0203
- 575 Yin, S., & McCowan, B. (2004). Barking in domestic dogs: context specificity and individual
576 identification. *Animal Behaviour*, 68(2), 343-355.
- 577 Zahavi, A. (1979). Why shouting. *American Naturalist*, 113(1), 155-156.

578

579 Appendix

580 Male preferred social partners

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

$$584 \quad \text{SRI}_{AB} = \frac{P_{AB}}{P_A + P_B - P_{AB}}$$

585

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

588

589 The second dyadic association measure is the ‘5 m association index’ (5M) (Gilby &
590 Wrangham, 2008) which measures the frequency with which a dyad was observed within 5 m
591 of one another, given that one of the individuals was present in the party and another one was
592 a focal animal:

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

593

594

595 where $A_f(B_5)$ = the number of instances in which A was the focal animal and B was within 5
596 m of A, $B_f(A_5)$ = the number of instances in which B was the focal animal and A was within 5
597 m, $A_f(B_p)$ = the number of instances A was the focal animal and B was in the same party,
598 $B_f(A_p)$ = B was the focal animal and A was in the same party.

599

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

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

604

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

608 For a given index (SRI, 5M and NN) individuals A and B were classified as ‘mutual
609 associates’ if the value was one-third of a standard deviation larger than the averages of both
610 A and B. We classified a dyad as mutual preferred social partners (mutual PSP) if they were
611 mutual associates for at least two of the three different indexes (Gilby & Wrangham, 2008).

612 Since association dynamics in chimpanzees change on a temporal basis (e.g. Fedurek et al.,
613 2013), we conducted association calculations for four separate periods with durations
614 between 4 and 5 months: between June and October 2013, February and May 2014, June and
615 September 2014 and January and April 2015. Using this procedure we identified eight for the
616 first (mean \pm SD=1.15 \pm 0.8/focal individual, range 0–3), seven for the second (mean
617 \pm SD=1.08 \pm 0.76/focal individual, range 0–2), seven for the third (mean \pm SD=1.08 \pm 1.32/focal
618 individual, range 0–3) and six (mean \pm SD=0.92 \pm 0.95/focal individual, range 0–3) mutual
619 PSP dyads for the fourth period of the study. The remaining dyads were classified as neutral
620 social partners (non-PSPs).

621

622 Dominance status

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

637 June 2013 and September 2014 and June 2013 and April 2015. The Elo-rating scores were
638 then converted into rank orders for each male (from 1 to 14, with 1 representing the highest
639 ranking male). The Elo-rating method has several advantages over more traditional methods
640 such as sensitivity to short-term demography changes, effectiveness in tracking hierarchy
641 dynamics on short-term scales and more effective evaluation of relative hierarchy position
642 between individuals with undecided interactions (Neumann et al., 2011). We believe that this
643 method was especially effective in establishing dominance positions of the Sonso males,
644 since the hierarchy was unstable throughout the study period with no clear alpha male after
645 one of the males had lost his alpha status prior to the study period. Elo-rating scores were
646 calculated using R v.3.1.1 (The R Foundation for Statistical Computing, Vienna, Austria,
647 <http://www.r-project.org>).

648

649

650 Figure Legends

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

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

656 Figure 3. The relationship between ‘waa’ bark production and retaliation (GLMM; $*P \leq 0.05$;
657 random effects: aggressor ID and victim ID).

658 Figure 4. The relationship between ‘waa’ bark production and reconciliation (GLMM;
659 $**P \leq 0.01$; random effects: aggressor ID and victim ID).

660

661

662

663 **Table 1.** Summary of the data set examined

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

664

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

669

670 **Table 2.** The relationship between the production of screams and various types of audience

671 (independent variables)

672

673

Independent variables	Coefficient	SE	<i>z</i>	<i>P</i>	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

674

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

676

677 **Table 3.** The relationship between ‘waa’ barking and various types of audience (independent
 678 variables)

Independent variables	Coefficient	SE	<i>z</i>	<i>P</i>	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

679

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

681

682