Bonobos (*Pan paniscus*) vocally protest against violations of social expectations

Zanna Clay[1*], Lucie Ravaux[2], Frans de Waal[3], Klaus Zuberbühler[1, 4]

[1]**Department of Comparative Cognition**, University of Neuchatel, Neuchatel (Switzerland); [2]**Institut Jean Nicod,** Ecole Normale Supérieure, Paris (France); [3]**Living Links, Yerkes National Primate Research Center**, Atlanta (USA), [4]**School of Psychology & Neurosciences**, University of St Andrews (UK)

- Zanna Clay: susanna.clay@unine.ch

Abstract

Research has shown that great apes possess certain expectations about social regularities and both perceive and act according to social rules within their group. During natural and experimentally induced contexts, such as the inequitable distribution of resources, individuals also show protesting behaviours when their expectations about a social situation are violated. Despite broad interest in this topic, systematic research examining the nature of these expectations and the communicative signals individuals use to express their protests to violated expectations remains scant. Here, we addressed this by exploring whether bonobos (*Pan paniscus*) respond to violations of social expectations in naturally occurring social interactions, focussing on the vocal behaviour of victims following socially expected and unexpected aggression. Expected aggression included conflicts over a contested resource and conflicts that were provoked by the victim, while unexpected aggression was any spontaneous, unprovoked hostility towards the victim. For each conflict, we also determined its severity and the composition of the nearby audience. We found that the acoustic and temporal structure of victim screams was individually distinct and varied significantly depending on whether or not aggression could be socially predicted. Certain acoustic parameters also varied as a function of conflict severity, but unlike social expectation, conflict severity did not discriminate scream acoustic structure overall .We found no effect of audience composition. We concluded that, beyond the physical nature of a conflict, bonobos possess certain social expectations

about how they should be treated and will publicly protest with acoustically distinctive vocal signals if these expectations are violated.

Keywords: violation of expectancy; social norm; social conflict; audience effect; protest; scream

Author footnotes

Z. Clay is also affiliated with: [3]Living Links, Yerkes National Primate Research Center, Atlanta (USA)

Corresponding Author: Zanna Clay, Institute of Biologie, University of Neuchatel, Rue Emile-Argand 11, Neuchatel, 2000, Switzerland; +41 032 718 30 64

susanna.clay@unine.ch

Acknowledgements: This work was financially supported by the Living Links Center (Yerkes National Primate Research Center), Emory University's College of Arts and Sciences as well as the European Union's Seventh Framework Programme for research, technological development and demonstration (grant no. 283871). We thank Pitshou Nsele Kayanga for assistance in data collection. We are grateful to Claudine André, Fanny Mehl, Dominique Morel, Valery Dhanani and Pierrot Mbonzo for their collaboration and to the Ministry of Research and the Ministry of Environment in the Democratic Republic of Congo for supporting our research (research permit: MIN.RS/SG/004/ 2009). We thank all the staff of Lola ya Bonobo for their support, particularly to Stany Mokando and Jean-Claude Nzumbi. We thank Brian Hare for his ongoing support.

Introduction

The notion that animals may possess personal expectations about social regularities or what is permissible within social encounters has been a topic of considerable interdisciplinary interest, including those interested in the evolution of morality, justice and fairness (e.g., Bekoff, 2001, 2004; Brosnan & de Waal, 2012, 2014; de Waal, 2014; de Waal & Tyak, 2003). One hypothesis is that animals possess a sense of 'social regularity', i.e., a set of expectations about how they and others should be treated and how resources should be divided (de Waal, 1996).

Experimental research using food rewards has shown that a range of non-human primates (see Price & Brosnan, 2012; Brosnan & de Waal 2014, for reviews), as well as corvids (Wascher & Bugnyar, 2013) and dogs (Range, Horn, Viranyi, & Huber, 2009), possess certain expectations about resource distribution and will protest against distributional inequities of rewards in which they are disadvantaged. For example, capuchins (*Cebus apella*) and chimpanzees (*Pan troglodytes*) will protest by becoming unwilling to trade for low-value food rewards after observing their partner receiving a higher-value reward for no extra effort (Brosnan & de Waal, 2003; Brosnan, Schiff, & de Waal, 2005). More active behavioural protests have also been observed. For example, during the 'Ultimatum Game', an economic game considered to be the hallmark test for a human sense of fairness, chimpanzees protested towards selfish offers proposed by their partner by spitting water and hitting the cage-bars, while human children in the same task made verbalised protests (e.g., "you got more than me") (Proctor, Williamson, Brosnan, & de Waal, 2013). Another study showed that chimpanzees were prepared to 'punish' individuals that stole their food by pulling a rope to cause their reward to fall out of reach

(Jensen, Call, & Tomasello, 2007). So far, most studies showing protest to distributional inequities have been based on paradigms in which subjects are required to perform an effortful trading task to obtain food rewards (Price & Brosnan, 2012). Whether or not these forms of protests to distributional inequities relate to a broader sensitivity to violations of expectation in other social contexts, however, remains less understood.

Beyond experiments with food rewards, research into whether animals are sensitive to inequities and violations of expectations during social encounters has mostly focussed on social play (Bekoff & Pierce, 2009; Pierce & Bekoff, 2012; van Leeuwen, Zimmermann, & Davila-Ross, 2011). In one study, juvenile chimpanzees 163were shown to follow distinct social rules during play, which they used to guide their rates of play signalling and levels of play intensity (Flack, Jeannotte, & de Waal, 2004). For example, juveniles increased their play signalling in the presence of mothers of younger partners, especially as the intensity of play bouts increased, suggesting that they were sensitive to the influence that social pressures and third-parties (i.e. maternal interventions) may have on their interactions and increased play signalling in order to prevent termination of the play bouts.

In the context of aggressive interactions, studies of chimpanzees and rhesus macaques (*Macaca mulatta*) have suggested that, beyond personal expectations involving the actor, individuals may also be sensitive to violations of social rules involving third-parties and are even willing to break up conflicts impartially or sometimes on behalf of the victim (Boehm 1994; de Waal 1984; Flack, Girvan, de Waal, & Krakauer, 2006; Goodall 1986; von Rohr, Burkart, & van Schaik, 2011). For example, Townsend, Slocombe, Emery-Thompson, & Zuberbühler (2007) described a case of a wild adult male chimpanzee interfering against an infanticide attempt by several adult females on a newly immigrated female's newborn infant. Nevertheless, the cognitive mechanisms underlying these kinds of intervention behaviours are not well understood, and there still remains a clear distinction between responses towards violated personal expectations involving the actor itself as opposed to possessing expectations about how third-parties should be treated. Beyond bystander interventions, for example, it is not well understood whether the victim receiving the aggression possesses expectations about how they should be treated, or whether agonistic interactions are guided by social rules.

While the above mentioned studies are valuable in suggesting that animals are sensitive to social inequities and, in some cases, social rules, most of the available evidence only indirectly addresses whether animals possess expectations about how they should be treated in social situations. Moreover, aside from observations of protesting behaviours occurring in response to inequitable outcomes (e.g., chimpanzees spitting water at their partner during inequity experiments, Proctor et al. 2013), evidence on how animals communicatively express their protests to violated expectations remain mostly anecdotal.

To explore whether animals communicatively protest against violated personal expectations, we carried out a systematic study in which we focussed on naturally occurring aggressive interactions among bonobos (*Pan paniscus*), a species of great ape closely related to humans (Pruefer et al., 2012). Specifically, we examined the vocal behaviour of victims following socially expected and unexpected aggression. By their nature, aggressive interactions involve conflicts of interests, but they can vary substantially in how much social expectations are violated, especially if the victim is the target of spontaneous aggression and without prior provocation. To address this, we compared the acoustic structure of victim screams produced in response to expected and unexpected aggression, taken from our assessment of the victim's perspective. Expected aggression was defined as any conflict arising over a contested resource, cases in which the victim provoked the conflict, or if the conflict could be anticipated in advance. Unexpected aggression included any spontaneous, unprovoked aggression towards the subject, initiated by another individual.

Like most other primates, bonobos vocalise if they become the target of conspecific aggression. In chimpanzees, the acoustic structure of victim screams conveys something about the severity of the attack, but call structure is also affected by audience composition, with screams indicating more severe aggression in the presence of high- compared to low-ranking audiences, regardless of the physical nature of the attack (Slocombe & Zuberbühler, 2007). This indicates that chimpanzees and probably many other primates (e.g., Gouzoules, Gouzoules, & Marler, 1984) vocalise, not only to influence the attacker, but also to elicit support from bystanders during or after the fight, such as interventions and policing (Flack et al., 2006; von Rohr et al., 2012) as well as consolation, a form of affiliative behaviour offered by bystanders (de Waal & van Roosmalen, 1979), which helps to reduce distress in the victim (Fraser, Stahl, & Aureli, 2008; Clay & de Waal, 2013).

In our study, we were particularly interested in whether protests to perceived violations of social expectations were acoustically conveyed by bonobo victim screams. We also examined whether victim screams could be statistically discriminated based on caller identity, as for these signals to function in an evolutionary sense, they need to be individually distinctive. In addition, we explored whether victim screams varied as a function of conflict severity, as shown for chimpanzees (Slocombe & Zuberbühler, 2007) and rhesus macaques (Gouzoules et al., 1984), and the composition of the nearby audience, as shown for chimpanzees (Slocombe & Zuberbühler, 2007). In chimpanzees, victims appear to exaggerate their screams in the presence of audience members of equal or higher rank than their aggressor (Slocombe & Zuberbühler, 2007), presumably to recruit their alliance support against the aggressor. As bonobo females are socially dominant in most contexts and regularly intervene in conflicts as allies (e.g., Furuichi, 2011; Vervaecke, de Vries, & van Elsacker, 2000), we examined whether victim screams varied as a function of the presence of females of equal or higher rank than the aggressor.

Methods

Behavioural Observations

Observations of bonobos were conducted at the 'Lola ya Bonobo' sanctuary, Kinshasa, DR Congo. All data collected complied with APA ethical standards in the treatment of animal samples, and the study received full ethical clearance from the Lola Ya Bonobo Research and Ethics Coordinator. Most individuals arrived at the sanctuary as wild-caught juvenile or infant orphans as a result of the bush-meat and pet trades. Following several years of rehabilitation with a nursery 'cohort', where each individual was assigned a substitute human mother, individuals were integrated into large, mixed-age social groups. Individuals spent their days ranging outdoors in one of three naturalistic forest enclosures (15–20 ha), which were comprised of rainforest, lake, swamp, streams and open grass areas. At night, individuals slept together inside dormitories (approx. 75 m^2). The bonobos were provisioned 3–4 times per day by caregivers with a variety of fruits and vegetables as well as a daily soymilk supplement. Their daily routines remained the same throughout observation periods.

We collected data during two observation phases (May–August 2011; May-August 2012) and pooled the data to maximise sample size. In both periods, we conducted observations at enclosure 1 (Group 1) and enclosure 2 (Group 2). In 2011, Group 1 comprised of 25 individuals and Group 2 comprised of 17 individuals. In 2012, Group 1 comprised of 22 individuals and Group 2 comprised of 20 individuals (Table 1).

Observations of agonistic interactions were conducted by Z.C. and an assistant throughout the day (Observation hours: 2011: Group 1 = 301h, Group 2 = 152h; 2012: Group 1 = 205h, Group 2 = 187h). Social interactions were recorded from a distance of 3-20m with a Panasonic HD digital camcorder (HDC-SD900) equipped with a directional microphone (Sennheiser MKH 816T).

For each interaction, we recorded the identities of the initial recipient of the aggression, which we will call the 'victim', and the initiator of the conflict, the 'aggressor'. We determined the identities of all visible bystanders within 5 m, the 'audience'. We also recorded the conflict severity as 'mild' or 'severe'. Mild aggression included threats (hand shake, bipedal swagger, threat bark, lunge), directed displays or charges without physical contact, chase pursuits or quick pokes or shoves, and single grabs without biting. Severe aggression included multiple or severe grabs, hits ands bites and any sort of injurious physical attack.

We also determined the social context of the conflict as (1) 'unprovoked aggression': victim is attacked spontaneously and without any obvious prior provocation during feeding, resting or travelling; (2) 'resource competition' in the form of (i) 'contest possession': opponents physically compete aggressively for the same food/object without either having prior possession; (ii) 'lose possession by forced, aggressive removal': individual previously holding/in possession of food/object has it taken away from them by another individual by physical force; (iii) 'win possession': individual forcefully takes food or object from another individual, which results in an aggressive conflict; (3) 'display aggression': victim is attacked by aggressor as part of a male display in the form of (i) 'contest hoot charge display': approaching aggressor produces display vocalisations, known as 'contest hoots' (de Waal, 1988; Genty, Clay, Hobaiter, & Zuberbühler, 2014), before physically contacting the victim; (ii) 'silent display': aggressor does a silent charge out of direct sight from the victim (i.e. from behind) before physically aggressing them; (4) 'play-related aggression': aggressive interventions by mothers following the production of distress vocalisations of her infant during rough play between her infant and the victim, or aggressive attacks received from a play partner following an escalation of rough or aggressive play instigated by the victim; (5) 'redirected aggression': victim is attacked as part of redirected aggression from another agonistic event with which the victim was uninvolved; (6) 'Other': any cases in which the observation conditions of the victim before and during the attack were not clear enough to assess the nature of the conflict.

For each conflict, we also determined whether it could be considered 'expected' or 'unexpected' as taken from our assessment of the victim's perspective, which was informed from existing literature. Unexpected aggression included all cases in which the victim was attacked spontaneously, without prior provocation or warning. This included. (1) 'unprovoked/spontaneous aggression'; (2ii) losing possession by forced, aggressive removal; (3ii) silent display charges/aggression; (5) 'redirected aggression'. We considered 'losing possession by aggressive, forced removal' as a form of 'unexpected aggression' following evidence that across a broad number of primate species, individuals possess a sense of property or possession, behaving as if food or objects belong to the individual in possession of them, even if low-ranking (e.g., Brosnan, 2012; Kummer & Cords, 1990; Sigg & Fallet, 1985). Bonobo males at Lola typically include 'contest hoots' in their directed displays towards specific targets (de Waal, 1988; Genty et al., 2014), therefore as "silent display charges' were rare, we considered them to be unexpected as they occurred without clear behavioural cueing. Redirected aggression was considered to be 'unexpected aggression' based on the finding that rates of redirected aggression in bonobos are generally low (Clay & de Waal, 2013) and in some cases, virtually absent (Palagi & Norscia, 2013). Expected aggression included all cases in which conflict was predictable, provoked by the victim or expected in some way, i.e. (2i) 'contest competition'; (2iii) 'win possession'; (3i) 'vocal charge display'; or (4) 'play-related aggression'. We coded 'play-related' aggression as 'Expected' as during these contexts, the victim was the individual who escalated the play to a more aggressive, rougher play level with an infant or play partner, resulting in the production of distress signals by their play partner and the consequential maternal interventions. While it is possible that previous, unobserved, behaviours of the victim may have resulted in their opponent behaving aggressively towards them in the current encounter (i.e. renewed aggression), we tried to avoid this possibility by restricting our coding of unexpected aggression to those cases in which no prior aggression had occurred between the opponents for 1 hour or more.

We used the Matman analysis programme (Noldus, version 1.1) to calculate dominance relationships, and investigated whether the dominance hierarchy was linear by calculating the adjusted linearity index h', which takes into account the number of unknown relationships (Stevens, Vervaecke, de Vries, & van Elsacker, 2006; de Vries, Stevens, & Vervaecke, 2006). These calculations were made of the basis of matrices of agonistic interactions (see Genty et al., 2014) using fleeing from aggression as a marker for dominance (Stevens et al., 2006)

Vocal behaviour.

Bonobos often vocalise during conflicts by producing acoustically complex and often noisy signals, typically a series of screams (see Fig.1). Screams usually consist not only of tonal but also non-tonal sections, caused by non-linear behaviour of the vocal folds during sound production.

Following Riede, Owren, & Arcadi (2004), we used the term 'non-linear phenomena' (NLP) to refer to the presence of *subharmonics, biphonation,* and *deterministic chaos* visible on the spectrogram. *Biphonation* refers to the presence of two simultaneous but independent fundamental frequencies visible in a spectrogram as two distinct and autonomous frequency contours that interact in a non-linear fashion (Riede et al., 2004, see also Brown, Alipour, Berry, & Montequin, 2003; Tokuda, Riede, Neubauer, Owren, & Herzel, 2002; Volodin & Volodin 2003). *Subharmonics* are spectral components additional to the fundamental frequency F0 that appear as sidebands of acoustic energy at evenly spaced intervals below the F0 and its associated harmonics. *Deterministic chaos* refers to periods of non-random noise visible in the spectrogram caused by irregular oscillations in the vocal folds (see Figure 1).

We carried out quantitative acoustic analyses using PRAAT 5.2.21 (www.fon.hum.uva.nl/praat/; settings: pitch range: 1,500-4,500 Hz, optimised for voice analysis; spectrogram settings: analysis window length: 0.03s, dynamic range: 70dB, spectrogram view range: 0-10kHz). We performed pitch analysis using a script written by Michael Owren (pers. comm.). We conducted analyses on a total of 12 temporal and spectral parameters. To standardise the varying number of calls per calling episode, we calculated mean scores for the first analysable three calls within the episode. Calls were examined for the presence of non-linear phenomena through visual inspection of spectrograms.

To describe the overall structure of the screaming episode, we measured the (1) episode duration (s): duration of total vocal episode (i.e. a vocal episode could contain one or more calls) separated from other bouts by at least 30s of silence; (2) N calls within a call episode; (3) inter-call interval (s): duration between call end to the start of the next call; (4) duration of call (s): duration of a single call taken from onset to offset; (5) presence of inter-scream pause: pause of minimum 3sec between scream phases within same episode.

Due to the non-linear nature of bonobo screams, it was not possible to measure many of the spectral parameters that are typically employed for more tonal calls (Clay & Zuberbühler, 2009, 2011). Taking this into account, we used spectral analyses to identify the presence of several forms of NLP within the call, that is: (6) the percentage of the call containing NLP, as well as the presence of three specific forms of NLP that were visually identifiable within the spectrogram: (7) mean duration (s) of sub-harmonic segments; (8) mean duration (s) of biphonation (s) segments; (9) mean duration (s) of chaotic segments (s). See Figure 1.

For calls containing at least one segment with a visible fundamental frequency band, we also measured: (10) mean fundamental frequency (F0): the mean value of the fundamental frequency across the first tonal section of the call (Hz); (11) peak frequency at the start of the call (Hz): location in the frequency domain where maximum acoustic energy occurred in the F0 at the onset of the call and (12) peak frequency at the end of the call (Hz): location in the frequency domain where maximum acoustic energy occurred in the F0 at the offset.

Statistical Analyses

We conducted statistical analyses using SPSS version 22.0 (SPSS Inc., Chicago, IL, USA) and R version 3.1.0 (R Development Core Team 2008), using the software packages 'MASS', 'lme4' and 'lmerTest'. Tests were 2-tailed and significance levels were set to a = 0.05. For small sample sizes, we calculated exact p-values (Mundry & Fischer, 1998).

We screened the data for outliers by producing standardized z-scores (Tabachnik & Fidell, 2001). Next, we regressed all parameters to check for multi-colinearity and singularity among the acoustic variables, removing any parameters with a variance inflation factor >10 (Belsley, Kuh, & Welsch, 1980). Subsequently, we conducted cross-validated Discriminant Function Analyses (DFAs) using the leave-one-out procedure to investigate whether the acoustic variables, when combined together, could generate discriminant functions that correctly discriminated the following factors: Caller Identity; Fight Severity; Audience and Social Expectancy. To test whether the degree of classification was greater than chance, we used two-tailed binomial tests with a corrected level of chance that corresponded to the number of discriminated categories (Mundry & Sommer, 2007). We set the DFA prior probabilities to assume equal group size in order for the model to generate a randomly selected selection of cases to equally represent across individuals.

As the data were two-factorial and contained repeated contributions per individual, conventional DFA methods are considered inadequate to allow valid estimation of the significance of discriminability (Mundry & Sommer, 2007). Therefore, to estimate the significance of the number of correctly classified calls (cross-validated), while controlling for repeated contributions, we conducted a permutated DFA (pDFA; R. Mundry, pers. comm.), entering Caller Identity as a random factor. Following diagnostic nests and tests for multi-collinearity between test factors (using Variance Inflation Factors), we then conducted Linear Mixed Models on each of the non-correlated acoustic parameters to investigate which varied statistically with the factors under scrutiny; Social Expectation, Conflict Severity and Audience presence (Caller Identity entered as a random factor).

Analyses were conducted on victim screams produced by 9 individuals (2 adult males, 1 adult female, 1 adolescent male, 2 juvenile males and 3 juvenile females; Table 1). Samples from other individuals were excluded owing to inadequate sample size of recordings available that were of sufficiently high quality for acoustic analyses. As pDFAs are vulnerable to the erroneous effects of small sample size, we set an inclusion cut-off as a minimum of four call episodes per category per individual. Collecting clean, high-quality recordings is problematic for victim screams because multiple individuals typically vocalise during an agonistic encounter, rendering it difficult to isolate calls.

Results

Caller Identity: Analyses based on a total of 156 calling episodes, produced by 9 individuals (mean $N = 16$ events per individual, range: 9-26) showed that screams could be reliably discriminated based on the identity of the caller (cross-validated DFA: Wilks lambda = .06, $\chi^2(80, N\,\text{callers} = 9) = 410.69$, $p < .001$, see Figure 2 and Table 2). Calls could be reliably classified according to caller identity at a rate significantly greater than chance (correct classification 55.1% (86/156 calls), cross-validated: Binomial test (0.11 chance level): $p < .001$)

---Figure 2 ----

Fight Severity: We compared $N = 87$ screams produced in response to severe agonistic events and $N = 69$ screams produced during mild agonistic events, with each individual ($N = 9$) contributing a minimum of 4 calls per category. A pDFA, which controlled for caller identity, showed that only 58/156 calls were correctly classified according to conflict severity, which was not significantly greater than chance (cross-validated pDFA; $p = .11$).

Social Expectation: We conducted a DFA analysis to compare screams in response to N = 59 socially expected and N = 97 unexpected aggression interactions (minimum N = 4 calling events per individual per category; N events analysed per combination of factors 'Social expectation' and 'Conflict severity': Expected-Severe = 34, Unexpected-Severe = 53, Expected-Mild = 25, Unexpected- Mild = 44). 67.9% of calls could be correctly classified based on whether the conflict was expected or not (Wilks' lambda = 0.76, χ^2 (10) = 40.28, $p < .001$), which was significantly greater than chance (106/156 calls; binomial (0.5); $p < .001$). A subsequent pDFA revealed that calls could be correctly classified on the basic of social expectation when caller identity was controlled (pDFA cross-validated: 53 calls; $p = .02$).

Audience: the structure of victim screams did not differ significantly between events when a female of equal or higher rank than the aggressor was present within 5m (N = 59) compared to when this was not the case (N = 97; DFA: Wilks' lambda = 0.91, χ^2 (10) =13.99, $p = .24$; cross-validated classification: 51.3% of calls: Binomial test (0.5) $p > 0.05$). We were unable to analyse the audience effects of alpha female presence alone, due to insufficient sample size.

We used Linear Mixed Models (LMMs) to identify which of the acoustic variables might be driving the original classification. In this analysis, we included all three variables of interest (social expectation, conflict severity, audience presence) as a fixed factors, as while only social expectation provided significant discrimination at the overall scream structure level, the other two factors have been previously demonstrated to be biologically relevant variables in explaining scream acoustic structure (Gouzoules et al., 1984; Slocombe & Zuberbühler, 2005, 2007). Before commencing, we ran diagnostic tests and examined the Variance Inflation Factors, which revealed no collinearity between the three factors for any of the parameters (all VIFs < 2). LMMs (caller identity as a random factor) showed that both social expectation and fight severity but not audience presence explained a significant amount of the variance in a number of different acoustic parameters, as explained below(see Figure 3 and in Table 3) . However, likelihood ratio tests revealed that there were no significant interactions between the two factors themselves (all $p > 0.05$). As shown in Table 3 and Figure 3, screams produced in response to unexpected aggression were significantly longer in overall calling episode duration, contained significantly more calls per episode, were significantly longer in call duration, contained a significantly higher percentage of non-linear phenomena within a call, possessed a significantly higher peak frequency at the end of the call, contained significantly more biphonation within the call and the vocalising subject was significantly more likely to recommence screaming after a phase break. Compared to mild aggression, victim screams produced in response to severe attacks were also significantly longer in duration, the overall calling episodes were longer, they contained a greater number of calls, a greater percentage of non-linear phenomena and a higher peak frequency. For the variable of mean duration of biphonation segments, likelihood ration tests revealed a significant interaction between conflict severity and audience presence. Examination of the interaction plot revealed that there was more biphonation in screams produced in association with severe, but not mild conflicts in the absence of a dominant female in 5m.The remaining acoustic variables were non-significant for any of the factors.

--Figure 3--

Discussion

Bonobos, as with other social animals, live in sophisticated societies, characterised by a rich set of fluctuating social dynamics (Kano, 1992). In order to navigate their complex social landscapes, individuals need sufficient levels of social awareness and social skills to establish, maintain and restore their social relationships. An underlying component of these social skills appears to be a set of personal expectations that an individual uses to predict how they should be treated by others. Aside from some studies of social play (e.g., Bekoff, 2001 2004), most evidence for social expectations in primates is still indirect, coming from experimental studies of resource competition that have shown that animals are averse to inequitable distribution of resources and will protest in cases where their perceived expectations are violated (Brosnan & de Waal, 2003, 2014; Price & Brosnan, 2012; Proctor et al., 2013; Range et al., 2009, Wascher & Bugnyar, 2013). Results from the current study contribute novel data by showing that violations of social expectations can be distinguished vocally in an ape species in the biologically relevant context of aggressive conflicts. The results suggest that bonobos are both sensitive to perceived violations of self-oriented social expectation in the context of aggressive conflicts and moreover, will publically broadcast their protest through the use of individually distinctive victim screams. Being spontaneously aggressed, without any prior warning, appears to violate certain, self-oriented social expectations relating to how agonistic interactions manifest themselves. The apparent perception of these violations is consequently expressed in the acoustic structure of their screams. This suggests that bonobos possess specific personal expectations about how they should be treated by others (de Waal, 1996; von Rohr et al., 2011); the fact that they vocally signalled this to others suggests that their conspecific audience may be sensitive to it as well.

Evidence that bonobos are sensitive to a form of self-oriented violation of social expectation reflects the rich literature on inequity aversion in primates, which has shown that individuals are typically only sensitive to inequitable resource distributions in cases where they are themselves disadvantaged. This self-orientated inequity aversion differs from more complex forms of other-oriented, 'fairness' behaviours, which extend to a more generalised set of social norms about how others should be treated (Brosnan & de Waal, 2012, 2014; von Rohr et al., 2011).

Nevertheless, it has been suggested that some species may be able to extend their social expectations towards the treatment of third parties in some cases. Evidence that animals take a normative approach to their social relationships has been suggested by a number of social behaviours that function to reduce social conflict among group members, such as impartial third-party policing interactions in agonistic conflicts, reconciliation, preventative conflict resolution and consolation (de Waal, 2014; Flack et al., 2006; von Rohr et al., 2011, 2012).

The possession of social expectations is thought to relate to a capacity to both perceive and act according to social rules, which individuals use to guide their social interactions with others (de Waal, 2014; Flack et al. 2004). This has been demonstrated during social play encounters, which appear to be guided by specific social rules and expectations, and provide an important opportunity to develop normative behaviours and to build trust. For instance, studies of play signalling in apes and canids have demonstrated that individuals adjust their rates of play signalling according to the play partner and surrounding audience, in order to prevent the play from escalating into aggression or terminating due to a third-party intervention (Bekoff, 2001; Cordoni & Palagi, 2011; Flack et al., 2004; Pellis, Pellis, Reinhart & Thierry, 2011).

If screams function to communicate perceived violations of social expectation to others, they must therefore be individually distinct so that recipients can make inferences about the identity of the caller. As predicted, our acoustic analyses also revealed that bonobo victim screams could be reliably discriminated on the basis of caller identity, in contrast to what has been reported from rhesus monkeys (Rendall et al., 1998). Non-linear phenomena were common in our sample, probably proximately explained by the high arousal states triggered by being a target of an agonistic attack. The presence of non-linear phenomena may have increased the level of individual discrimination in these screams (Fitch et al., 2002). Functionally speaking, this is relevant because other acoustic properties of primate screams have been said to be ill suited for providing identity cues (Owren & Rendall, 2001).

In contrast to chimpanzees (Slocombe & Zuberbühler, 2007), we found no evidence that victims exaggerated their screams in the presence of females of equal or higher rank than the aggressor. It is possible that results would have been different with free-ranging bonobos, as the visibility in the forest is much lower than in the sanctuary environment of this study, where most social conflicts were broadly visible to other group members.

In terms of conflict severity, we replicated previous findings in chimpanzees (Slocombe & Zuberbühler, 2007), by showing that a number of acoustic variables varied significantly as a function of conflict severity if we controlled for caller identity. While conflict severity appeared to be a biologically relevant variable in explaining some aspects of scream structure, it was nevertheless unable to statistically discriminate scream structure overall, unlike the more psychological variable of social expectation. The relationship between scream structure and conflict severity was weaker than expected, suggesting that the manner in which conflict severity was categorised in this study may not have adequately reflected how it is perceived by bonobos. Alternatively, a weaker relationship between conflict severity and scream structure may have reflected the fact that bonobo aggressiveness is considered as generally reduced and less severe compared to that of chimpanzees (Hare, Wobber, & Wrangham, 2012), and so may be less likely to trigger extreme differences in vocal responses.

Our main finding was that our assessment of interactions involving violations of expectations (that appeared to also be perceived as such by the bonobos) had the strongest explanatory power regarding overall scream acoustic structure, suggesting that the underlying cause of a conflict, and its adherence to social rules, may have been psychologically important to bonobos beyond simply the physical experience alone. However, while there were no interactions between the two factors, there was nevertheless considerable overlap in the acoustic variables discriminating social expectation and conflict severity, suggesting that both factors play an important role in shaping call acoustic structure. Future research using playback experiments will need to determine whether receivers attend more strongly to the perceived social rules governing the fight or its severity.

Overall, by showing that great apes can be sensitive to and communicate about the underlying cause of an aggressive interaction, beyond its physical nature alone, we have revealed something about the underlying social motivation in naturally occurring aggressive conflicts. Further research should investigate the phylogenetic distribution of such capacities, especially in species that have already demonstrated inequity aversion during feeding competition. Moreover, further research is needed to investigate the nature of the underlying social expectations demonstrated here, for instance whether individuals possess expectations about treatment by specific individuals in their group, such as close affiliative partners, as compared to treatment by those they do not share close social ties. The fact that bonobos vocally broadcasted their assessments in the form of individually distinctive screams opens up new research avenues to determine whether receivers can distinguish such screams and, if so, what adaptive benefits victims might attain. In some primates, some individuals play a policing role of others' social interactions within their group, thus it is possible that screams signalling perceived unfairness may facilitate such interventions (Flack et al., 2006; von Rohr et al., 2012). Similarly, bonobos have been demonstrated to offer consolation to distressed parties in order to reduce their distress (Clay & de Waal, 2013; Palagi, Paoli, & Tarli, 2004) and so communicating this distress via victim screams may facilitate the offering of third-party affiliation.

References

Bekoff, M. (2001). Social Play Behaviour: Cooperation, Fairness, Trust, and the Evolution of Morality. *Journal of Consciousness Studies*, *8*, 81–90.

Bekoff, M. (2004). Wild justice and fair play: cooperation, forgiveness, and morality in animals. *Biology and Philosophy*, *19*, 489–520.

Bekoff, M., & Pierce, J. (2009). *Wild justice: The moral lives of animals.* Chicago: Chicago University Press.

Belsley, D. A., Kuh, E. & Welsch, R. E. (1980). *Regression Diagnostics: Identifying Influential Data and Sources of Collinearity*. New York: J. Wiley,

Boehm, C. (1994). Pacifying interactions at Arnhem Zoo and Gombe. In R.W. Wrangham, R., W. C., McGrew, F. B. M., de Waal, P. G., Heltne, (Eds.) *Chimpanzee Cultures* (pp. 211–226). Cambridge, Mass: Harvard University Press.

Brosnan, S. F. (2011). Property in Nonhuman Primates. In H. Ross & O. Friedman (Eds.), *Origins of ownership of property. New Directions for Child and Adolescent Development, 132*, 9-22.

Brosnan, S. F., & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature, 425*, 297–299.

Brosnan, S. F., & de Waal, F. B. M. (2012). Fairness in animals: where to from here? *Social Justice Research, 25*, 336–351

Brosnan, S. F. & de Waal, F. B. M. (2014). Evolution of responses to (un)fairness. *Science, 346,* 6207.

Brosnan, S. F., Schiff, H. C., & de Waal, F. B. M. (2005). Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of The Royal Society* B: *Biological Sciences 272*, 253–258.

Brown, C., Alipour, F., Berry, D.A., & Montequin, D. 2003. Laryngeal biomechanics and vocal communication in the squirrel monkey (Saimiri boliviensis). *Journal Acoustical Society America, 113*, 2114–2126.

Clay, Z., & de Waal, F. B. M. (2013). Bonobos Respond to Distress in Others: Consolation across the Age Spectrum. *PLoS ONE*, *8*, e55206.

Clay, Z. & Zuberbühler, K. (2009). Food-associated calling sequences in bonobos. *Animal Behaviour, 77,* 1387–1396.

Clay, Z. & Zuberbühler, K. (2011). The Structure of Bonobo Copulation Calls During Reproductive and Non-Reproductive Sex. *Ethology, 117*, 1158-1169.

Cordoni, G., & Palagi, E. (2011). Ontogenetic trajectories of chimpanzee social play: Similarities with humans. *PLoS ONE*, *6,* 27344.

de Vries, H., Stevens, JMG., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour, 71*, 585-592.

de Waal, F. B. M. (1984). Sex differences in the formation of coalitions among chimpanzees. *Ethology and Sociobiology*, *5*, 239-255.

de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (Pan paniscus) compared to that of chimpanzees. *Behaviour, 106,* 183-251.

de Waal, F. B. M. (2014). Natural normativity: The “ is ” and “ ought ” of animal behavior. *Behaviour*, *151*, 185–204.

de Waal, F.B.M. (1996). *Good Natured: The Origins of Right and Wrong in Humans and Other Animals.* Cambridge, Mass.: Harvard University Press.

de Waal, F. B. M. & Tyack, P. L. (2003). *Animal Social Complexity: Intelligence, Culture, and Individualized Societie*s. Cambridge, Mass: Harvard University Press.

de Waal, F. B. M., & van Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology*, 5, 55–66.

Fitch, T. W., Neubauer, J., Herzel, H. (2002). Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour, 63*, 407–418.

Flack, J. C., Girvan, M., de Waal, F. B. M. & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature, 439*, 426-429.

Flack, J. C., Jeannotte, L. A., & de Waal, F. B. M. (2004). Play signalling and the perception of social rules by juvenile chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 118*, 149–159.

Fraser, O., Stahl, D. Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences USA, 105*, 8557-8567.

Furuichi, T. (2011). Female contributions to the peaceful nature of bonobo society. *Evolutionary Anthropology*, *20*, 131–142.

Genty, E., Clay, Z., Hobaiter, C., & Zuberbühler, K. (2014). Multi-Modal use of a socially directed call in bonobos. *PloS One*, *9*, e84738.

Goodall, J. (1986). The Chimpanzees of Gombe:Patterns of behaviour. Cambridge, Mass: Belknapp Press of Harvard University.

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

Hare, B., Wobber,V., & Wrangam, R. (2012). The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour,* 83, 573-585.

Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are vengeful but not spiteful. *Proceedings of the National Academy of Sciences USA*, *104*, 13046–13050.

Kano, T. (1992). *The Last Ape: Pygmy chimpanzee behaviour and ecology*. Stanford: Stanford University Press.

Kummer, H. & Cords, M. (1990). Cues of ownership in long-tailed macaques, Macaca fascicularis. *Animal Behaviour, 42*, 529-549.

Mundry, R. & Fischer, J. (1998) Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values: examples from Animal Behaviour. *Animal Behav*iour, *56*, 256.

Mundry, R., & Sommer, C. (2007). Discriminant function analysis with nonindependent data: consequences and an alternative. *Animal Behav*iour, *74,* 965-976.

Owren M. J., Rendall, D. (2001). Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocalization. *Evolutionary Anthropology, 10*, 58–71.

Palagi, E. & Norscia, I. (2013). Bonobos protect and console kin.*PLoS One, 8,* e79290.

Palagi, E., Paoli, T., & Tarli, S. B. (2004). Reconciliation and Consolation in Captive Bonobos (*Pan paniscus*). *American Journal of Primatology*, *62*, 15–30.

Pellis, S. M., Pellis, V. C., Reinhart, C. J., & Thierry, B. (2011). The use of the bared-teeth display during play fighting in Tonkean macaques (*Macaca tonkeana*): Sometimes it is all about oneself. *Journal of Comparative Psychology,* 125*,* 393-403.

Pierce, J., & Bekoff, M. (2012). Wild Justice Redux: What We Know About Social Justice in Animals and Why It Matters. *Social Justice Research, 25*, 122–139.

Price, SA. & Brosnan, S. F. (2012). To Each According to his Need? Variability in the Responses to Inequity in Non-Human Primates. *Social Justice Research*, *25*, 140-169.

Proctor, D., Williamson, R. A., Brosnan, S. F., & de Waal, F. B. M. (2013). Chimpanzees play the Ultimatum Game. *Proceedings for the National Academy of Sciences USA*, *6*, 2070-2075.

Prüfer, K., Munch, K., Hellmann, I., Akagi, K., Miller, J. R., Walenz, B., … Pääbo, S. (2012). The bonobo genome compared with the chimpanzee and human genomes. *Nature, 486,* 527-531.

Range, F., Horn, L., Viranyi, Z., & Huber, L. (2009). The absence of reward induces inequity aversion in dogs. *Proceedings for the National Academy of Sciences USA*, 106, 340–345.

Rendall, D., Owren, M. J. & Rodman, P. S. (1998). The role of vocal tract filtering in identity cueing in rhesus monkey vocalizations. *Journal of the Acoustical. Society of Am*erica, *103*, 602–614.

Riede, T., Owren, M. J., & Arcadi, A. C. (2004). Nonlinear Acoustics in Pant Hoots of Common Chimpanzees (*Pan troglodytes*): Frequency Jumps, Subharmonics, Biphonation, and Deterministic Chaos. *American Journal of Primatology*, *64*, 277-291.

Sigg, H. & Falett, J. (1985). Experiments on the respect of possession and property in hamydryas baboons (*Papio hamydryas*). *Animal Behaviour, 33,* 978-984.

Slocombe, K.E. & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings for the National Academy of Sciences USA*, *104*, 17228-17233.

Stevens, J. M. G., Vervaecke, H., de Vries, H., & van Elsacker, L. (2006). Social structures in Pan paniscus: Testing the female bonding hypothesis. *Primates, 47*, 210-217.

Tabachnick, B. G. & Fidell, L. S. (2001). *Using Multivariate Analysis*. London: Allyn Bacon.

Tokuda, I., Riede, T., Neubauer, J., Owren, MJ., & Herzel, H. (2002). Nonlinear analysis of irregular animal vocalizations. *Journal of the Acoustical. Society of America, 111*, 2908–2919.

Townsend, S. W., Slocombe, K. E., Emery Thompson, M., & Zuberbühler, K. (2007). Female-led infanticide in wild chimpanzees. *Current Biology,* 17, R355-356.

Van Leeuwen, E., Zimmermann, E., & Davila-Ross, M. (2011). Responding to inequities: Gorillas try to maintain their competitive advantage during play fights. *Biology Letters*, 7, 39–42.

Vervaecke, H., Vries, H., & Elsacker, L. (2000). Function and distribution of coalitions in captive bonobos (Pan paniscus). *Primates, 41, 249-265.*

Volodin, I.A., & Volodin, E.V. (2003). Biphonation as a prominent feature of the Dhole

Cuos alpinus sounds. *Bioacoustics* 13, 105–120.

von Rohr, C.R., Burkart, J.M., van Schaik, C.P. (2011). Evolutionary precursors of social norms in chimpanzees: a new approach. *Biology & Philosophy*, *26*, 1-30.

von Rohr, C.R., Koski, S.E., Burkart, J.M., Caws, C., Fraser, O. N,. Ziltener, A., van Schaik, C. P. (2012). Impartial Third-Party Interventions in Captive Chimpanzees: A Reflection of Community Concern. *PLoS One,* **7**, e32494.

Wascher, C. A., & Bugnyar, T. (2013). Behavioral responses to inequity in reward distribution and working effort in crows and ravens. *PloS One, 8*, e56885.

Tables

Table 1

Study Group composition at Lola ya Bonobo Sanctuary in 2011-2012

ID code	Age 2012	Group membership 2011-2012	ID Code	Age 2012	Group membership 2011-2012
		Females			
OP $^{(PO)}$	17	1-1	MY$^{+ (BS)}$	19	2-2
SW$^{+ (EK)}$	15	1-1	KL$^{+ (ML)}$	14	1-2
BD $^{(WO)}$	15	1-1	KS^{+}	13	1-2
SL $^{(KM)}$	14	1-1	LI^{+}	11	2-2
***LS**$^{+}$	11	1-1	MU	8	x-2
***KT**	8	1-1	***SK**	7	2-2
EK	7	1-1	ML	5	1-2
***WK**	6	1-1	MS	6	1-2
KM	3	1-1			
		Males			
MN	18	1-1	KZ	20+	2-2
KW	14	1-1	MX	26	2-2
FZ	13	1-1	MD	10	2-2
***LM**	13	2-1	BL	11	2-2
***AP**	12	x-1	IB	10	2-2
MA	12	1-1	***YL**	8	2-2
DL	11	1-1	BS	7	2-2
***KG**	10	1-1	EL	7	2-2
MB	9	1-1			
***PO**	7	1-1			
WO	4	1-1			

Bold asterisks indicate the individuals included in the acoustic analyses. "+" symbol indicates the presence of a dependent infant and ID codes in superscript indicate the identity of independent offspring. Group membership is represented as a two number code, the first being Group in 2011 (i.e. 1 = Group 1) and the second being group in 2012. X indicates cases when the bonobo was not housed in either enclosure.

As exact birth dates for orphaned apes are generally unknown, we used age estimates made by sanctuary veterinarians upon arrival, based on measurements of weight and patterns of dental emergence according to known patterns of ape development (Wobber & Rosati, Pers. Comm). This was validated by the known exact ages of individuals born at the sanctuaries, which we also used.

Table 2

Percentage correct classification (cross-validated) per individual caller in the DFA analysis of bonobo victim screams

Caller Identity	% correct classification (cross validated)
1	64.3
2	87.0
3	47.8
4	55.6
5	75.0
6	18.8
7	61.5
8	36.8
9	42.9

Table 3

Results from LMMs of the significant effects of three factors on victim scream acoustic structure

	Social expectation				Conflict severity				Dominant female Audience			
	Est.	*SE*	*t*	*p*	Est.	*SE*	*t*	*p*	Est.	*SE*	*t*	*p*
Episode duration	14.75	2.87	5.15	< .001	-6.49	2.86	-2.27	0.02	-0.52	2.82	-0.19	.85
N of calls	12.90	2.76	4.67	< .001	-5.83	2.76	-2.11	.04	2.78	2.72	1.02	.31
Call duration	.24	.07	3.26	.001	-.13	.07	-1.74	.08	.04	.07	.53	.60
% NLP	14.62	4.75	3.08	.003	-17.74	4.77	-3.71	<.001	6.36	4.64	1.37	.17
Phase break	.24	0.07	3.26	.001	-.13	.07	-1.74	.08	.03	.07	.53	.60
Biphonation	.12	0.04	3.37	< .001	**.18*	*.07*	*2.48*	*.01*				
Peak frequency	209.99	58.43	3.59	< .001	-158.26	59.0	-2.68	.008	76.75	56.9	1.35	.18

Results in Italics with * indicate the output for a significant interaction between Conflict Severity and Audience for the parameter of 'Mean duration of biphonation'.

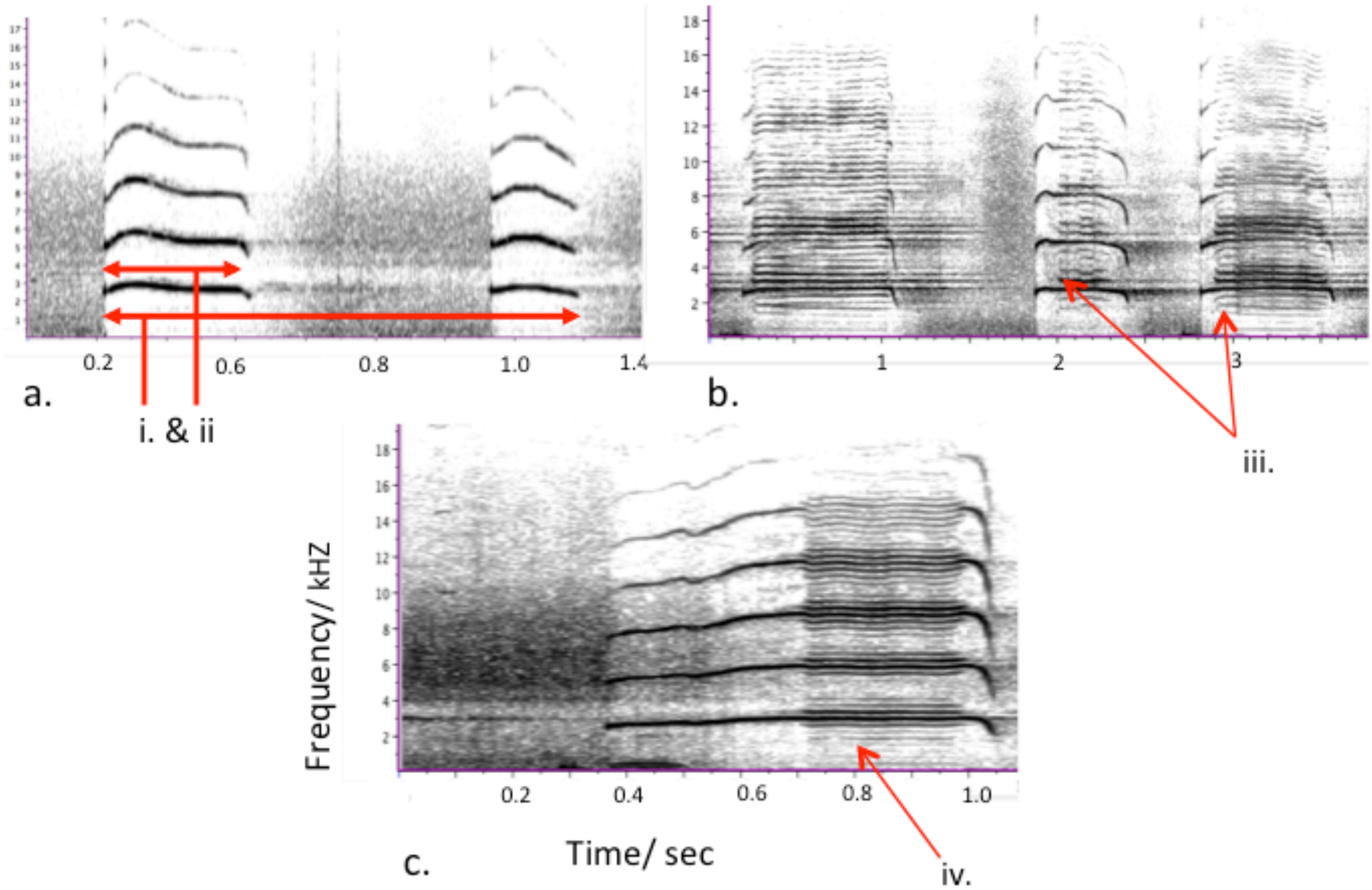
Figure Captions

Figure 1. Time-frequency Spectrograms of bonobo victim screams produced by the same individual in response to (a) socially expected and (b + c) socially unexpected aggression. Red lines and arrows indicate some of the acoustic measures analysed, and the presence of some different forms of non-linear phenomena. (i) duration of the call episode (s), (ii) is the duration of a call, (iii) points to two sections of biphonation (as depicted by a frequency band that does not relate to the F0); and (iv) points to subharmonics (side-bands relating to the F0).

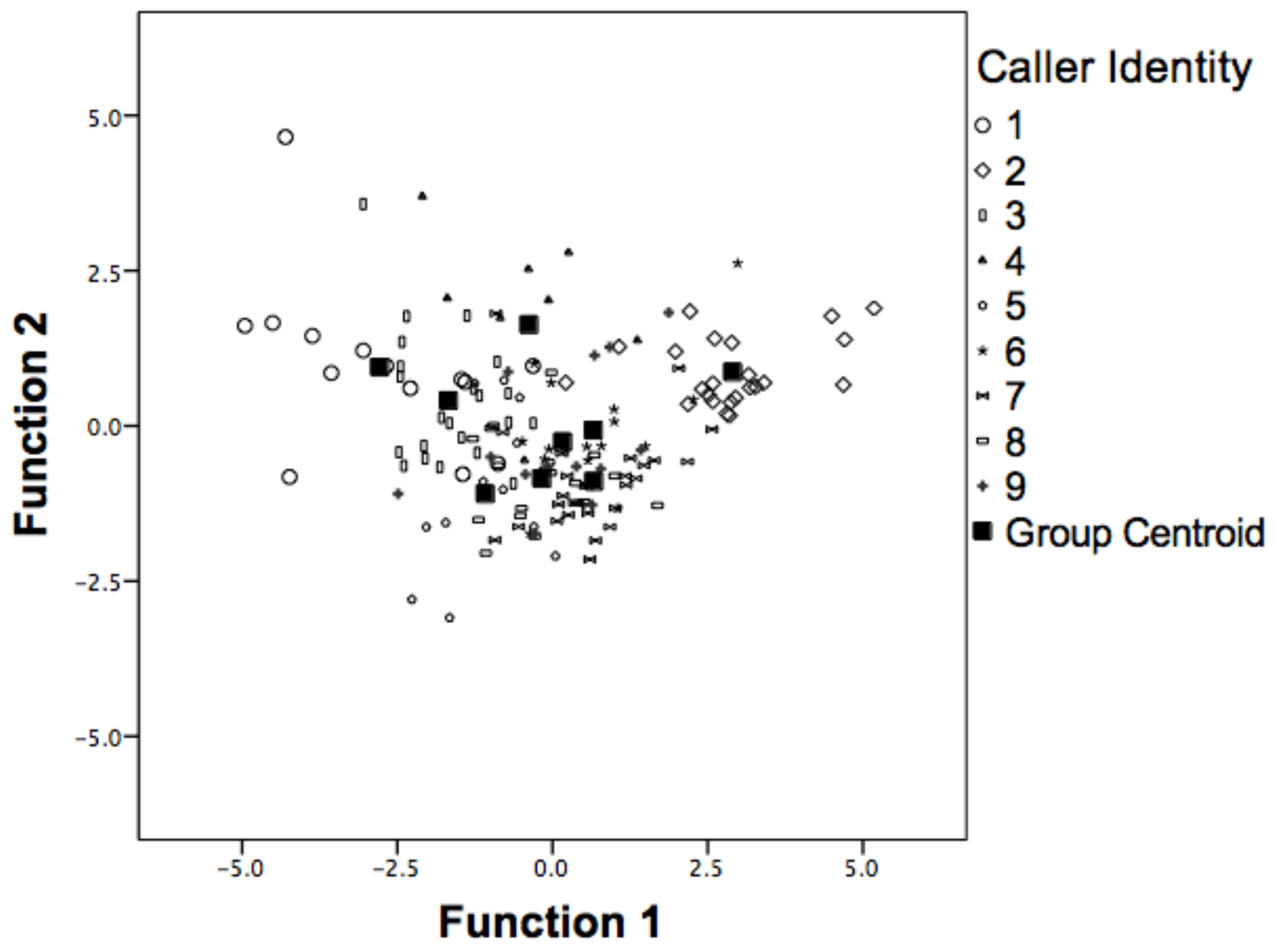
Figure 2. Distribution of discriminant scores for victim screams produced by n = 9 bonobos following aggressive encounters. The discriminant scores lie along two canonical discriminant functions established to discriminate caller identity. The caller

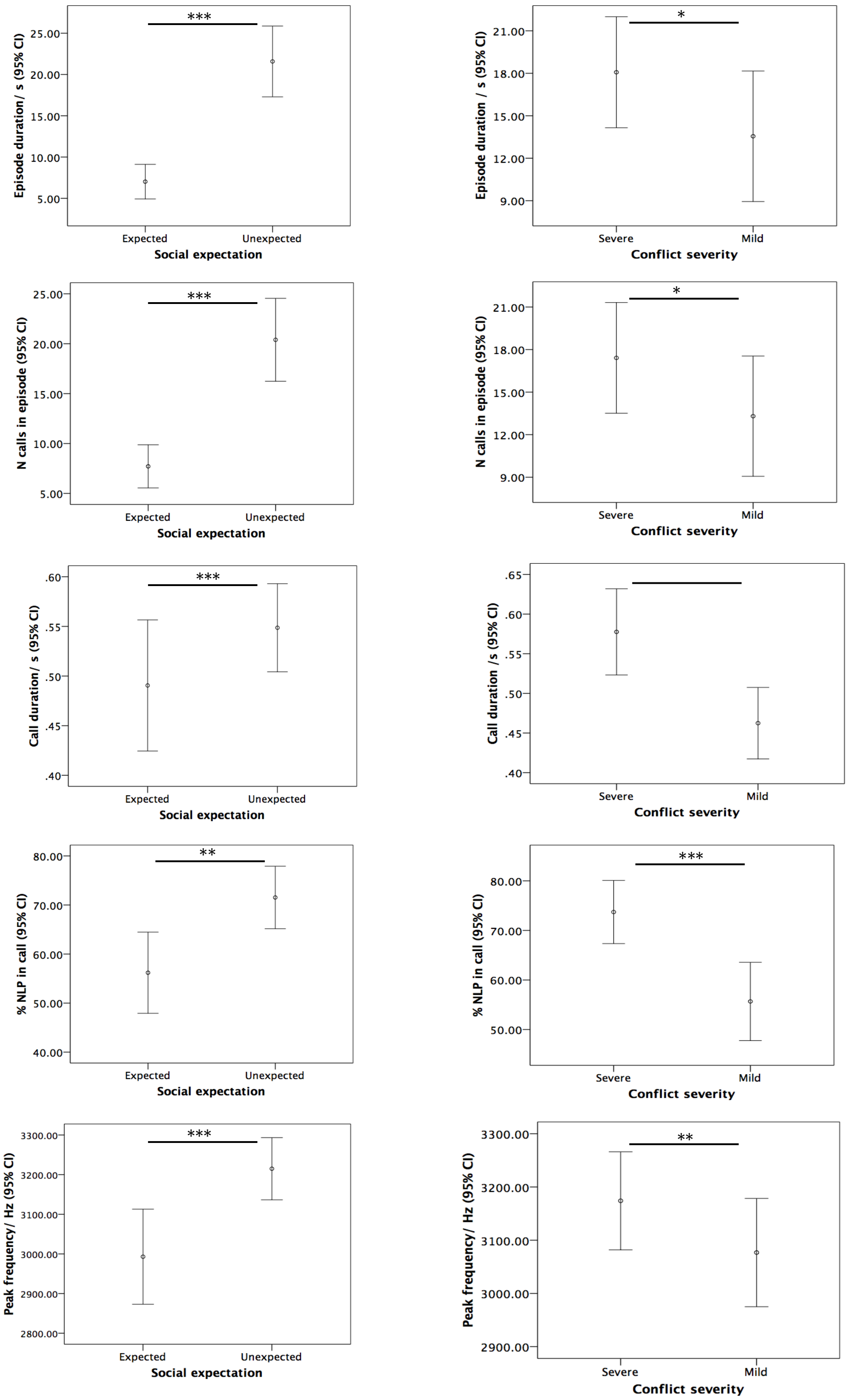
identities overlay the discriminant function scores and black squares indicate the group centroids per individual caller.

Figure 3. Mean and *SE* for five acoustic parameters for victim screams produced in response agonistic conflicts that varied significantly according to social expectation (left side) and/or physical severity (right side). Asterisks indicate p values in LMMs (*** = $p < .001$, ** = $p < .01$, * = $p < .05$)



0.2
0.6
0.8
1.0
1.4
a.
i. & ii
18
16
14
12
10
8
6
4
2
1
2
3
b.
iii.
Frequency/ kHZ
0.2
0.4
0.6
0.8
1.0
Time/ sec
c.
iv.


Caller Identity
1
2
3
4
5
6
7
8
9
Group Centroid
Function 1
Function 2
-5.0
-2.5
0.0
2.5
5.0



***
Episode duration/ s (95% CI)
25.00
20.00
15.00
10.00
5.00
Expected
Unexpected
Social expectation
*
Episode duration / s (95% CI)
21.00
18.00
15.00
12.00
9.00
Severe
Mild
Conflict severity
***
N calls in episode (95% CI)
25.00
20.00
15.00
10.00
5.00
Expected
Unexpected
Social expectation
*
N calls in episode (95% CI)
21.00
18.00
15.00
12.00
9.00
Severe
Mild
Conflict severity
***
Call duration/ s (95% CI)
.60
.55
.50
.45
.40
Expected
Unexpected
Social expectation
Call duration /s (95% CI)
.65
.60
.55
.50
.45
.40
Severe
Mild
Conflict severity
**
% NLP in call (95% CI)
80.00
70.00
60.00
50.00
40.00
Expected
Unexpected
Social expectation
***
% NLP in call (95% CI)
80.00
70.00
60.00
50.00
Severe
Mild
Conflict severity
***
Peak frequency/ Hz (95% CI)
3300.00
3200.00
3100.00
3000.00
2900.00
2800.00
Expected
Unexpected
Social expectation
**
Peak frequency/ Hz (95% CI)
3300.00
3200.00
3100.00
3000.00
2900.00
Severe
Mild
Conflict severity