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Bonobos (*Pan paniscus*) Vocally Protest Against Violations of Social Expectations

Zanna Clay
University of Neuchatel and Emory University

Lucie Ravaux
Institut Jean Nicod, Ecole Normale Supérieure, Paris, France

Frans B. M. de Waal
Emory University

Klaus Zuberbühler
University of Neuchatel and University of St. Andrews

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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 behaviors 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 them remains scant. Here, we addressed this by exploring whether bonobos (*Pan paniscus*) respond to violations of social expectations in naturally occurring social interactions, focusing on the vocal behavior of victims following socially expected and unexpected aggression. Expected aggression included conflicts over a contested resource and conflicts that were provoked by the victim. Unexpected aggression was any spontaneous, unprovoked hostility toward 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 conflict, audience effect, protest, scream

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 & Tyack, 2003). One hypothesis is that animals possess a sense of "social regularity," that is, 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 nonhuman primates (Brosnan & de Waal, 2014; Price & Brosnan, 2012), as well as corvids (Wascher & Bugnyar, 2013) and canines (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

Zanna Clay, Department of Comparative Cognition, University of Neuchatel, and Living Links, Yerkes National Primate Research Center, Psychology Department, Emory University; Lucie Ravaux, Institut Jean Nicod, Ecole Normale Supérieure, Paris, France; Frans B. M. de Waal, Living Links, Yerkes National Primate Research Center, Psychology Department, Emory University; Klaus Zuberbühler, Department of Comparative Cognition, University of Neuchatel, and School of Psychology and Neurosciences, University of St. Andrews.

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Correspondence concerning this article should be addressed to Zanna Clay, who is now at the School of Psychology, University of Birmingham, Hills Building, Birmingham B15 2TT, United Kingdom. E-mail: z.clay@bham.ac.uk

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receiving a higher value reward for no extra effort (Brosnan & de Waal, 2003; Brosnan, Schiff, & de Waal, 2005). More active behavioral 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 toward selfish offers proposed by their partner by spitting water and hitting the cage-bars (Proctor, Williamson, de Waal, & Brosnan, 2013). In the same task in the same study, human children made verbalized protests, for example, by saying, "you got more than me." 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 remains less understood.

Beyond experiments with food rewards, research into whether animals are sensitive to violations of expectations during social encounters has mostly focused on social play (Bekoff & Pierce, 2009; Pierce & Bekoff, 2012; Van Leeuwen, Zimmermann, & Ross, 2011). In one study, juvenile chimpanzees were shown to follow distinct social rules during play, which they used to guide their rates of play signaling and levels of play intensity (Flack, Jeannotte, & de Waal, 2004). For example, juveniles increased their play signaling 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 signaling 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, and 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. However, the underlying cognitive mechanisms of these kinds of intervention are not well understood, and there remains a clear distinction between responses toward violated personal expectations involving the self as opposed to expectations about how third-parties should be treated. Beyond observations of bystander interventions, it is not well understood how individuals respond to violated expectations involving the self, that is, whether victims receiving aggression possess expectations about how they should be treated, or whether they perceive agonistic interactions as guided by social rules.

Although these studies suggest that animals may be sensitive to social inequities, most of the available evidence indirectly only addresses whether animals possess expectations about how they themselves should be treated. Moreover, aside from protesting 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 focused on naturally occurring aggressive interactions among bonobos (*Pan paniscus*), a species of great ape closely related to humans (Prüfer et al., 2012). Specifically, we examined the vocal behavior of victims following socially expected and unexpected aggression. By their nature, aggressive interactions involve conflicts of interest, but they can vary substantially in how much social expectations are violated, especially if the victim is the target of spontaneous aggression 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 toward the subject, initiated by another individual.

Like most other primates, bonobos vocalize 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-ranking audiences compared to low-ranking audiences, regardless of the physical nature of the attack (Slocombe & Zuberbühler, 2007). This behavior indicates that chimpanzees and probably other primates (e.g., Gouzoules, Gouzoules, & Marler, 1984) vocalize, not only to influence the attacker, but also to elicit support from bystanders during or after the fight in the form of interventions or policing (Flack et al., 2006; von Rohr et al., 2012) as well as consolation, a form of affiliative behavior offered by bystanders (de Waal & van Roosmalen, 1979), which helps to reduce distress in the victim (Clay & de Waal, 2013; Fraser, Stahl, & Aureli, 2008).

We were 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: If these signals are to function in recruiting support, they need to be individually distinctive. In addition, we explored whether victim screams varied as a function of two other biologically relevant variables—conflict severity—as shown for chimpanzees (Slocombe & Zuberbühler, 2005, 2007) and rhesus macaques (Gouzoules et al., 1984)—and 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 support against the aggressor. Because 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.

Materials and Method

Behavioral Observations

Observations of bonobos were conducted at the Lola ya Bonobo Sanctuary, Kinshasa, DR Congo. 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 three to four 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 maximize 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 (see Table 1).

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

For each interaction, we recorded the identities of the initial recipient of the aggression, termed "victim," and the initiator of the conflict, termed "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 and bites and any sort of injurious physical attack.

We also determined the social context of the conflict as (a) *unprovoked aggression*: victim is attacked spontaneously and without any obvious prior provocation during feeding, resting or traveling; (b) *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; (c) *display aggression*:

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			

Note. Bold asterisks indicate the individuals included in the acoustic analyses. "+" 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, personal communication, 2011). This was validated by the known exact ages of individuals born at the sanctuaries, which we also used.

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victim is attacked by aggressor as part of a male display in the form of (i) *contest hoot charge display*: approaching aggressor produces display vocalizations, 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; (d) *play-related aggression*: aggressive interventions by mothers following the production of distress vocalizations 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; (e) *redirected aggression*: victim is attacked as part of redirected aggression from another agonistic event with which the victim was uninvolved; (f) *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.

We also determined whether each conflict was "expected" or "unexpected" as taken from our assessment of the victim's perspective. Following the existing literature we categorized unexpected aggression as any case in which the victim was attacked spontaneously, without prior provocation or warning. This included (a) unprovoked/spontaneous aggression; (bii) losing possession by forced, aggressive removal; (cii) silent display charges/aggression; (e) 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, 2011; Kummer & Cords, 1990; Sigg & Falett, 1985). Bonobo males at Lola ya Bonobo Sanctuary typically include "contest hoots" in their directed displays toward specific targets (Genty et al., 2014). These "silent display charges" were rare, so we considered them to be unexpected as they occurred without clear behavioral 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, that is, (bi) contest competition, (biii) win possession, (ci) vocal charge display, or (d) 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. Although it is possible that previous and unobserved behaviors of the victim may have resulted in their opponent behaving aggressively toward 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 one hour or more.

Vocal Behavior

Bonobos often vocalize during conflicts by producing acoustically complex and often noisy signals, typically a series of screams (see Figure 1). Screams usually consist of both tonal and nontonal sections, caused by nonlinear behavior of the vocal folds during sound production.

Following Riede, Owren, and Arcadi (2004), we used the term *nonlinear phenomena* (NLP) to refer to the presence of *subharmonics, biphonation* (see Figure 1), and/or *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 nonlinear fashion (Brown, Alipour, Berry, & Montequin, 2003; Riede et al., 2004; 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 nonrandom noise visible in the spectrogram caused by irregular oscillations in the vocal folds.

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, optimized for voice analysis; spectrogram settings: analysis window length: 0.03s, dynamic range: 70dB, spectrogram view range: 0–10 kHz). We performed pitch analysis using a script written by Michael Owren (personal communication, 2007). We conducted analyses on a total of 12 temporal and spectral parameters. To standardize the varying number of calls per calling episode, we calculated mean scores for the first three analyzable calls within the episode. Calls were examined for the presence of NLP through visual inspection of spectrograms. A coder, blind to the scream categories under analysis, conducted all of the acoustic analyses following thorough acoustic analysis training and an interobserver reliability test (Cohen's $\kappa > 0.85$).

To describe the overall structure of the screaming episode, we measured the (a) 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 30 s of silence, (b) *N* calls within a call episode, (c) intercall interval (s): duration between call end to the start of the next call, (d) duration of call (s): duration of a single call taken from onset to offset, (e) presence of interscream pause: pause of minimum 3 s between scream phases within same episode.

Due to the nonlinear 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 (see Figure 1), that is (f) 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: (g) mean duration (s) of subharmonic segments, (h) mean duration (s) of biphonation (s) segments, (i) mean duration (s) of chaotic segments (s).

For calls containing at least one segment with a visible fundamental frequency band, we also measured (j) mean fundamental frequency (F0): the mean value of the fundamental frequency across the first tonal section of the call (Hz), (k) 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 (l) 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.

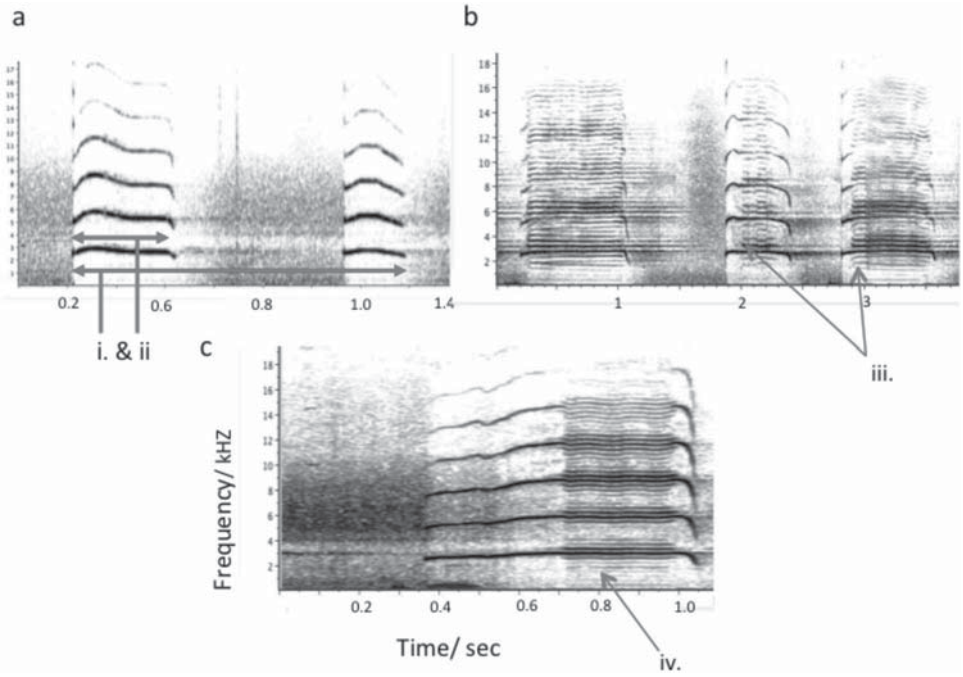


Figure 1. Time-frequency spectrograms of bonobo victim screams produced by the same individual in response to (a) socially expected and (b and c) socially unexpected aggression. Grey lines and arrows indicate some of the acoustic measures analyzed, and the presence of some different forms of nonlinear phenomena. (i) Duration of the call episode (s), (ii) 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).

Statistical Analyses

We conducted statistical analyses using SPSS version 22.0 and R version 3.1.1 (R. Core Team, 2014), using the software packages MASS, lme4, and lmerTest. Tests were two-tailed and significance levels were set to $\alpha = .05$. For small sample sizes, we calculated exact p values (Mundry & Fischer, 1998).

We screened the data for outliers by producing standardized z scores (Tabachnick & Fidell, 2001). Next, we regressed all parameters to check for multicollinearity and singularity among the acoustic variables, removing any parameters with a variance inflation factor (VIF) > 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, personal communication, 2008), entering Caller Identity as a random factor. Following diagnostic tests and tests for multicollinearity (using VIFs), we conducted linear mixed models (LMMs) on each of the noncorrelated 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). This approach follows the information theory approach, which relies on estimates of the distances of different models from full reality rather than null hypothesis significance testing (Burnham & Anderson, 2002).

We conducted analyses on victim screams produced by nine individuals (two adult males, one adult female, one adolescent male, two juvenile males, and three 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 vocalize during an agonistic encounter, rendering it difficult to isolate calls.

We used the Matman analysis program (Noldus, version 1.1) to calculate social 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;

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de Vries, Stevens, & Vervaecke, 2006). These calculations were made on 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).

Results

Caller Identity

Analyses based on a total of 156 calling episodes, produced by nine 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 (1/9 = 0.11 chance level): $p < .001$).

Conflict 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 four calling events per category (minimum $N = 4$ calling events per individual per category; N events analyzed per combination of factors Social Expectation and Conflict Severity: expected-severe = 34, unexpected-severe = 53, expected-mild = 25, unexpected-mild = 44). A pDFA, which controlled for caller identity, showed that only 37.2% (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 to compare screams in response to $N = 59$ socially expected and $N = 97$ unexpected aggressive interactions. 67.9% of calls could be correctly classified based on whether the conflict was expected or not, Wilks' $\lambda = 0.76$, $\chi^2(10) = 40.28$, $p < .001$, 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 basis of social expectation when caller identity was controlled (pDFA cross-validated: 53 calls; $p = .02$).

Audience Presence

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' $\lambda = 0.91$, $\chi^2(10) = 13.99$, $p = .24$; cross-validated classification: 51.3% of calls: Binomial test (0.5) $p > .05$. We were unable to analyze the audience effects of alpha female presence alone due to insufficient sample size.

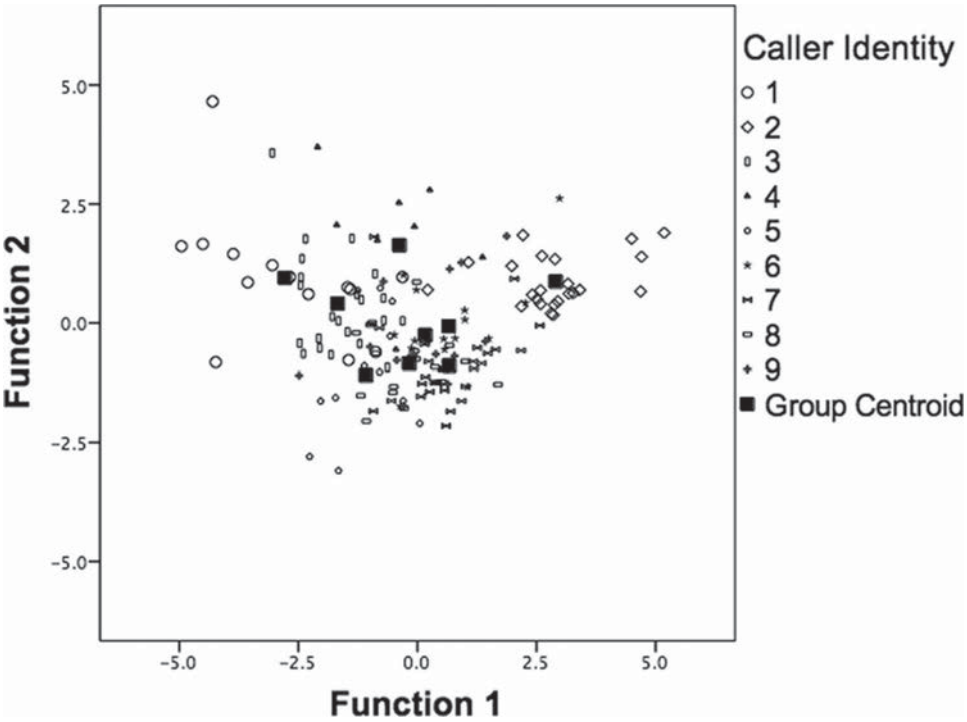


Figure 2. Distribution of discriminant scores for victim screams produced by $N = 9$ bonobos following aggressive encounters. The discriminant scores lie along two canonical discriminant functions established to discriminate caller identity. The caller identities overlay the discriminant function scores and black squares indicate the group centroids per individual caller.

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Table 2
Percentage Correct Classification (Cross-Validated) per Individual Caller in the Discriminant Function 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

Comparing Factors

We used 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 fixed factors. Although only social expectation provided significant discrimination at the overall scream structure level, the other two factors of biological interest have been previously demonstrated to influence scream acoustic structure in other primate species (Gouzoules et al., 1984; Slocombe & Zuberbühler, 2005, 2007), which is why we included them. Before commencing, we ran diagnostic tests and standardized the variables in order to compare effect sizes using the regression coefficients. We examined the VIFs, 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 conflict 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 $p > .05$). 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 NLP within a call, possessed a significantly higher peak frequency at the end of the call, contained significantly more biphonation within the call and the vocalizing subject was significantly more likely to recommence screaming after a phase break. Compared to mild aggression, the overall victim scream episodes produced in response to severe attacks were significantly longer and contained a greater number of calls. The victim screams themselves contained a significantly greater percentage of NLP with a higher peak frequency (see Table 3). The screams themselves were also longer in duration with more phase breaks, although not significantly so. For the variable of mean duration of biphonation segments, likelihood ratio 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 within 5m. The remaining acoustic variables were nonsignificant for any of the factors.

Discussion

Bonobos live in social groups characterized 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 skills to establish, maintain and restore their social relationships. Underlying these social skills appears to be a set of personal expectations that an individual uses to predict how to be treated by others. Aside from some studies of social play (e.g., Bekoff, 2001, 2004), most evidence for social expectations in primates has been indirect, coming from experimental studies showing that animals are averse to inequitable distribution of resources (Brosnan & de Waal, 2003, 2014; Price & Brosnan, 2012; Proctor et al., 2013; Range et al., 2009; Wascher & Bugnyar, 2013). The current study contributes novel data by showing that great apes mark violations of social expectations vocally in the biologically relevant context of aggressive conflicts. Bonobos appear sensitive to perceived violations of self-oriented social expectation in the context of aggressive conflicts and publically broadcast their protest through the use of individually distinctive victim screams. Being the victim of spontaneous aggression 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 signaled 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 sensitive only to inequitable resource distributions in cases where they are themselves disadvantaged. This differs from more complex forms of other-oriented, "fairness" behaviors, which extend to a more generalized 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 toward the treatment of third parties. Evidence that animals take a normative approach to their social relationships has been suggested by a number of social behaviors that function to reduce social conflict among group members, such as impartial third-party policing 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 behaviors and to build trust. For instance, studies of play signaling in apes and canids have demonstrated that individuals adjust their rates of play signaling according to the

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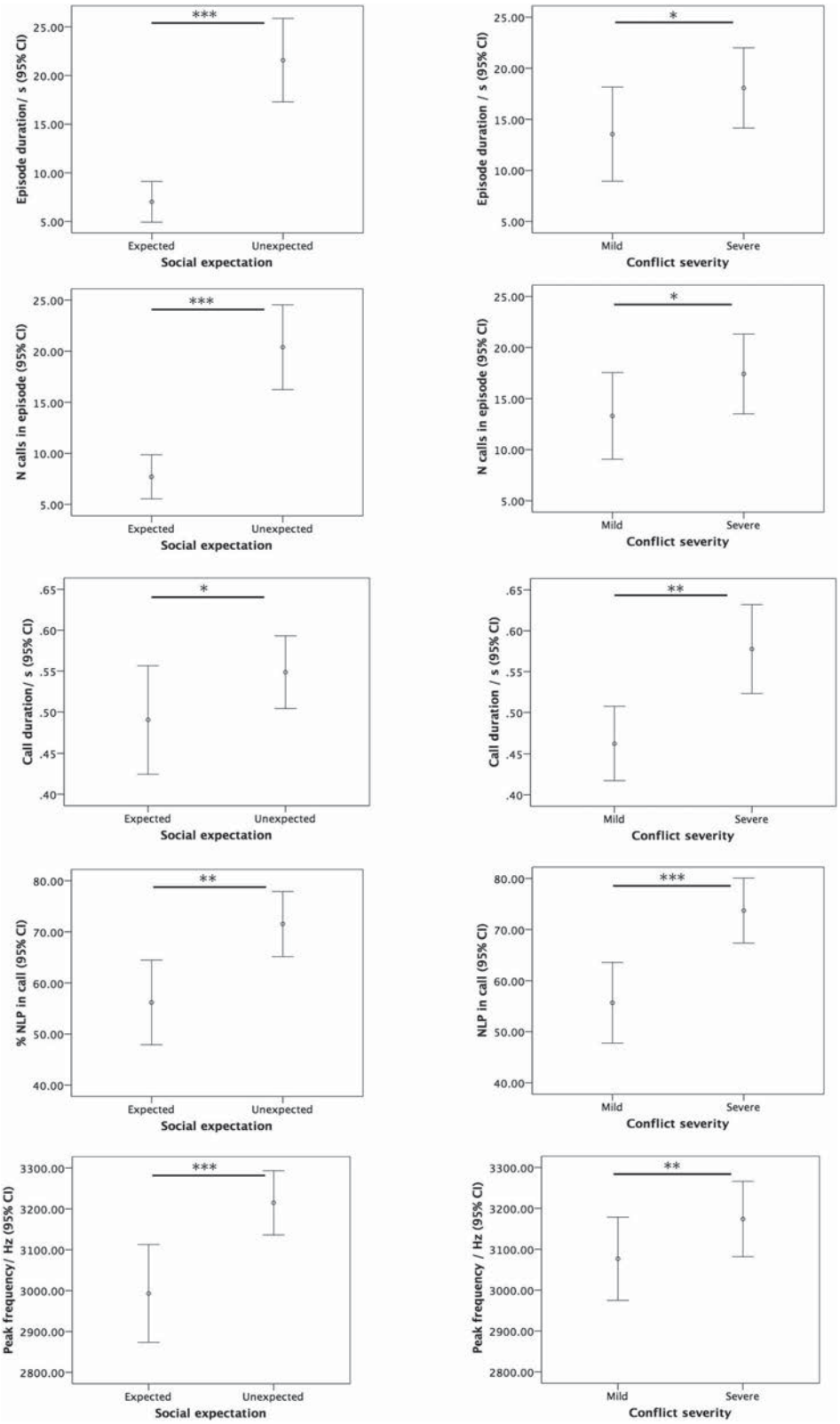


Figure 3. Mean and 95% confidence intervals for five acoustic parameters for victim screams produced in response to agonistic conflicts that varied significantly according to social expectation (left side) and/or physical severity (right side). Asterisks indicate p values in linear mixed models (* $p < .05$. ** $p < .01$. *** $p < .001$.).

Table 3
Results From LMMs of the Significant Effects of Three Factors on Victim Scream Acoustic Structure

	Social expectation				Conflict severity				Dominant female audience			
Standardized variables	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	.02	−.52	2.82	−.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	.03	.02	2.21	.03	−.05	.02	−3.01	.003	.0001	.02	−.01	.99
% NLP	14.62	4.75	3.08	.003	−17.74	4.77	−3.71	<.001	6.36	4.64	1.37	.17
Peak frequency	209.99	58.43	3.59	<.001	−158.26	59.0	−2.68	.008	76.75	56.9	1.35	.18
Biphonation	*.12*	*.04*	*3.37*	*<.001*	**.18*	.07	2.48	.01				
Phase break	.24	.07	3.26	.001	−.13	.07	−1.74	.08	.03	.07	.53	.60

Note. Results in italics with * indicate the output for a significant interaction between conflict severity and audience for the parameter of "mean duration of biphonation."

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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, they must therefore be individually distinct so that recipients can make inferences about the caller's identity. As predicted, our analyses 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, Owren, & Rodman, 1998). NLP were common in our sample, probably proximately explained by the high arousal states triggered during agonistic attacks. The presence of NLP may have increased the level of individual discrimination in these screams (Fitch, Neubauer, & Herzel, 2002) which, functionally speaking, 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 lower than in the sanctuary environment of this study, where most social conflicts were broadly visible.

Although conflict severity appeared to be a biologically relevant variable in explaining some aspects of scream structure, as previously shown for chimpanzees (Slocombe & Zuberbühler, 2005, 2007), it was unable to statistically discriminate scream structure overall, unlike the 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 categorized 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 generally reduced and less severe compared to that of chimpanzees (Hare, Wobber, & Wrangam, 2012), and so may be less likely to trigger extreme differences in vocal responses.

Our main finding was that our assessment of aggressive interactions involving violations of expectations (that appeared to also be perceived as such by the bonobos) had the strongest explanatory power regarding scream acoustic structure, as indicated by the significant discrimination in the pDFA and higher regression coefficients in the LMMs as compared to conflict severity. This suggests that the underlying cause of a conflict may be psychologically important to bonobos, beyond the physical experience alone. In regards to perception of screams, these data do not enable us to draw firm conclusions about how receivers interpreted this vocal information. As both conflict severity and social expectation independently explained scream structure, it is possible that listeners either perceived this variation as a continuum (such as unexpected severe > unexpected mild > expected severe > expected mild) or alternatively, as indicative of two orthogonal factors. Future research using playback experiments can determine whether receivers attend more strongly to the perceived social rules governing the aggressive conflict or its severity.

Overall, by showing that great apes can be sensitive to and communicate about the underlying cause of an aggressive interaction, we have revealed something about the underlying social motivation in naturally occurring aggressive conflicts. Further research should investigate the phylogenetic distribution of such capacities as well as the nature of the underlying social expectations; for instance, whether an individual's expectations about treatment by others vary according to social affiliation. The fact that bonobos vocally broadcasted their social assessments opens up new research avenues to determine what adaptive benefits victims might attain. In some primates, some individuals play a policing role in social interactions within their group; thus it is possible that screams signaling perceived unfairness may facilitate such interventions (Flack et al., 2006; von Rohr et al., 2012). Similarly, communicating distress may facilitate the offering of third-party affiliation, something that has already been demonstrated in bonobos (Clay & de Waal, 2013; Palagi, Paoli, & Tarli, 2004).

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