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Audience sensitivity in chimpanzee display pant hoots

Adrian Soldati [a, b, c, *], Pawel Fedurek [c, d], Guillaume Dezecache [c, e], Josep Call [a, 1], Klaus Zuberbühler [a, b, c, 1]

[a] School of Psychology and Neuroscience, University of St Andrews, St Andrews, U.K.
[b] University of Neuchâtel, Department of Comparative Cognition, Neuchâtel, Switzerland
[c] Budongo Conservation Field Station, Masindi, Uganda
[d] University of Stirling, Faculty of Natural Sciences, University of Stirling, Stirling, U.K.
[e] Université Clermont Auvergne, CNRS, LAPSCO, Clermont-Ferrand, France

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Audience effects are key in studies of animal social cognition and are typically investigated during directed social interactions. Male chimpanzees, *Pan troglodytes*, regularly perform aggressive displays in the presence of others, often targeting a specific group member, and combine this agonistic behaviour with acoustic signals. Here, we were interested in whether the production and structure of pant hoots, a long-distance signal, were influenced by audience composition (i.e. presence and absence of specific individuals). We investigated pant hoots produced during displays by adult and subadult males of Budongo Forest, Uganda. We found that males overall called more often when their preferred social partners and females were absent from the party, as well as when more dominant males were present. We then separately analysed the four phases of pant hoots, introduction, build-up, climax and let-down, and found that audience composition and social context could often explain the presence or absence of each phase. In addition, displays were often accompanied by drumming, especially by older males and when male audiences were small. Our study adds to the growing body of literature on audience effects and other social factors and shows their impact on the structure of a sophisticated vocal sequence, which enhances the communicative capacity in a species with limited vocal control.

In animal communication, vocal behaviour is often moderated by the identity of nearby listeners (Evans, 1997; Fichtel & Manser, 2010; Marler et al., 1986), generally referred to as 'audience effects' (Zuberbühler, 2008), with evidence from a wide range of taxa, including birds (chickens, *Gallus gallus*: Evans & Marler, 1994; zebra finches, *Taeniopygia guttata*: Vignal et al., 2004), fish (Siamese fighting fish, *Betta splendens*: Matos et al., 2003; three-spined sticklebacks, *Gasterosteus aculeatus*: Dzieweczynski & Rowland, 2004), and mammals (lions, *Panthera leo*: Grinnell & McComb, 2001; vervet monkeys, *Cercopithecus aethiops*: Hector et al., 1989; yellow mongooses, *Cynictis penicillata*: Le Roux et al., 2008). Audience effects are typically studied during close-range social interactions and their corresponding vocal signals. However, some animal calls, usually referred to as long-distance or loud calls, reach both distant and nearby recipients (Matos & Schlupp, 2005). Consequently, to minimize eventual eavesdropping costs and maximize social benefits, long-distance callers should be sensitive to the audience composition and adjust call production accordingly (Johnstone, 2001; McGregor & Peake, 2000). Arguably, this type of audience sensitivity might indicate goal-directed and flexible call production (Fichtel & Manser, 2010; Fischer & Price, 2017; Schamberg et al., 2018).

There is a consensus that social complexity acts as an evolutionary driver for communicative complexity (Freeberg et al., 2012; McComb & Semple, 2005; Schamberg et al., 2018). Audience effects, that is, when a signaller takes the composition of its audience into account, is considered one such manifestation of complexity (Evans, 1997; Zuberbühler, 2008). In chimpanzees, *Pan troglodytes*, audience effects have been reported in a number of contexts (e.g. predator encounters: Crockford et al., 2012; greeting: Laporte & Zuberbühler, 2010; feeding: Schel, Machanda, et al., 2013; mating: Townsend et al., 2008), in terms of both production rates (e.g. aggression: Fedurek et al., 2015) and call structure (agonistic interaction: Slocombe & Zuberbuhler, 2007). However, it remains unknown whether these effects extend to more complex acoustic structures (sensu Johnstone, 1996), such as calls composed of acoustically distinct components.

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* Corresponding author.
E-mail address: as391@st-andrews.ac.uk (A. Soldati).
[1] These authors contributed equally.

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In this study, we continued this line of investigation by studying whether audience effects were also present in pant hoot vocalizations. Structurally, pant hoots are arguably one of the most complex signals produced by great apes, consisting of four acoustically distinct phases produced in an orderly manner: introduction, build-up, climax and let-down (Marler & Hobbett, 1975; Marler & Tenaza, 1977). The climax is a high-amplitude signal that travels over longer distances than the other phases, which are lower amplitude (Mitani & Gros-Louis, 1998). Individual phases contain different types of information and can be omitted in context-specific ways (Goodall, 1986; Zuberbühler, 2019). In particular, identity is strongly encoded in the introduction and climax (Fedurek, Zuberbühler, & Dahl, 2016; Mitani et al., 1996) and is recognizable to listeners (Kojima et al., 2003; Schel, Machanda, et al., 2013). Age is mainly encoded in the introduction and build-up, social rank in the climax and context mainly in the let-down phase (Fedurek, Zuberbühler, & Dahl, 2016). Given that social status is not a fixed property in chimpanzee societies and physical condition varies with age (Muller & Mitani, 2005; Thompson et al., 2020), advertising these attributes can be beneficial for both callers and receivers (baboons, *Papio cynocephalus ursinus*: Fischer et al., 2002, 2004; chimpanzees: Fedurek, Slocombe, et al., 2016; Riede et al., 2007). At the proximate level pant hoot production could be largely explained as expressions of basic arousal states (Notman & Rendall, 2005); nevertheless, receivers can obtain multiple sets of information about the caller's attributes simultaneously (Fedurek, Zuberbühler, & Dahl, 2016). Although it is unclear which information is used, or prioritized, when multiple sets of information are transmitted, each call element independently encodes different socially important information, consistent with the idea that pant hoots serve multiple social functions (Fedurek, Zuberbühler, & Dahl, 2016).

Pant hoots are generally produced in three distinct behavioural contexts: travel, feeding and displays (Marler & Tenaza, 1977; Nishida et al., 1999). During displays, pant hoots are combined with exaggerated locomotion, piloerection and throwing or shaking objects, for example during visually impressive agonistic interactions by males seeking to assert their social status while challenging the status of others (Goodall, 1986; Muller, 2002). In addition, males often accompany displays with drumming, an acoustic signal produced by pounding hands and feet against the buttress roots of trees (Arcadi et al., 1998; Arcadi & Wallauer, 2013). While during travelling drumming is used to communicate over long distances and is often combined with pant hoots (Babiszewska et al., 2015), during displays, males may use drumming to intimidate competitors and acquire social status (Goodall, 1986). Although intimidating, display behaviours rarely lead to physical attacks, injuries or death (Fawcett & Muhumuza, 2000; Muller & Mitani, 2005). Display pant hoots can be given jointly with others which appears to play a role in social bonding (Gilby et al., 2013; Mitani & Gros-Louis, 1998; Muller & Mitani, 2005). Indeed, males can adjust the build-up phase of display pant hoots in a coordinated way with audience members which then results in chorusing (Fedurek, Schel, & Slocombe, 2013). This coordinated calling is also seen in the climax phase and signals social bonding (Fedurek, Machanda, et al., 2013). Not all displays contain pant hoots, with nonvocal displays mostly directed at specific individuals in contrast to nondirected vocal displays (Goodall, 1986), which may be directed towards distant individuals (Bygott, 1979; Muller, 2002). Given that pant hoots are produced across several social contexts, different functional hypotheses have been proposed (signalling social status: Clark & Wrangham, 1994; signalling social bonds: Fedurek, Machanda, et al., 2013; Mitani & Brandt, 1994; signalling subgroup formation: Fedurek et al., 2014). During long-distance communication, pant hoots are mainly used to maintain spatial contact between conspecifics and to recruit associates (Mitani & Nishida, 1993) or group members (Kalan & Boesch, 2015). Overall, high-ranking males tend to pant hoot more often than low-ranking individuals, in line with the idea that pant hoots are involved in male–male competition (Clark, 1993; Fedurek, Slocombe, et al., 2016; Riede et al., 2007). Importantly, when callers use pant hoots depends on the composition of the nearby audience to, for example, signal dominance and bonded relationships towards party members (e.g. Bouchard & Zuberbühler, 2022; Fedurek et al., 2014; Fedurek, Machanda, et al., 2013; Mitani & Nishida, 1993). Furthermore, several social functions of pant hoots are linked to fine details of their acoustic structure (e.g. Fedurek, Zuberbühler, & Dahl, 2016; Notman & Rendall, 2005).

The aim of this study was to examine the factors mediating male pant hoot production during displays. First, we tested whether pant hoot production is affected by the identity of nearby individuals (immediate audience composition) and varies according to the type of display (i.e. directed versus nondirected, see Table 1). Because signalling social status during a display may provoke aggression from other individuals, we predicted that dominant males would be more likely to pant hoot when displaying than lower-ranking individuals. Similarly, considering that displays increase the risk of aggression from males in the audience, displaying callers might seek to solicit social partners for support. Therefore, we predicted that males would pant hoot more often when preferred social

Table 1
Descriptions and definitions of behaviours and vocalizations produced by chimpanzees during displays investigated in this study

Term	Definition	Source
Display	Intimidatory behaviour characterized by piloerection, exaggerated locomotion, branch shaking, object throwing, stomping, vocalizing, or drumming	Hosaka, 2015; Nishida et al., 1999
Directed display	Aggression including charges (pursuit distance < 7 m) and chases (pursuit distance > 7 m) towards one specific victim. The body and behaviour of the focal are oriented towards one victim throughout the display. Directed displays are considered 'mid-severity'	Fedurek et al., 2015; Muller, 2002
Nondirected display	Display without a specific target. Nondirected displays are considered 'low severity'	Goodall, 1986
Vocal display	Display accompanied by a pant hoot	Nishida et al., 1999
Pant hoot	Complex vocal signal composed of up to four acoustically distinctive phases produced in the sequence introduction, build-up, climax and let-down	Marler & Hobbett, 1975; Marler & Tenaza, 1977; Mitani et al., 1992; Notman & Rendall, 2005
Introduction	Series of low-amplitude, low-frequency tonal elements that acoustically resemble 'hoo' vocalizations but are noticeably longer in duration and alternate with inhaled tonal elements	
Build-up	Series of short low-amplitude and low-frequency elements produced during both inhalations and exhalations in rapid rhythm which can increase in intensity and frequency as the call proceeds	
Climax	One or more scream-like high-amplitude and high-frequency elements	
Let-down	Series of low-amplitude and low-frequency acoustic elements which acoustically resemble the build-up phase but tend to progressively decrease in intensity and frequency over time	

partners are absent in the caller's party. We also predicted that males would be more likely to pant hoot when their displays are not targeted at another individual since these nondirected displays could serve to communicate to distant individuals. The second aim of our study was to test whether phase production is influenced by audience composition, the type of display (directed versus nondirected), and whether another individual choruses with the displaying male. Since omitting the high-amplitude phase of the call may limit eavesdropping by distant competitors, we predicted that males would be more likely to produce the low-amplitude introduction, and less likely to produce the loud climax, during displays directed at nearby individuals as opposed to nondirected displays. In addition, since the climax is related to signalling social status, we predicted that higher-ranking males would produce the climax phase more often than lower-ranking individuals. Given that joint pant hoots and chorusing are important signals in male–male competition, we expected the build-up and climax phases to be more likely to be chorused. Finally, we examined whether drumming is also influenced by the social context. We hypothesized that, due to its loud and visually impressive features which might function to intimidate others, drumming would be more often produced by more dominant individuals.

METHODS

Study Site

The study was conducted with the Sonso community (*P. t. schweinfurthii*) of the Budongo Forest in Western Uganda. The community is well habituated to human observers with research ongoing since the early 1990s (Reynolds, 2005). At the beginning of the study (September 2018) the community consisted of 74 individuals (11 adult males, 25 adult females, 15 subadults, eight juveniles and 15 infants). At the end of the study (March 2020), the community consisted of 68 individuals (nine adult males, 26 adult females, 15 subadults, nine juveniles and eight infants; Appendix Table A1).

Study Subjects

Study subjects were 12 male individuals: four subadults (10–15 years old), three young adults (16–20 years old) and five adults (>20 years old; Appendix Table A2). We initially sampled all subadult and adult males, but three males died during the study period. We did not include juveniles and infants since they were unable to produce complete pant hoots and did not engage in displays, other than during play (Pusey, 1990).

Data Collection

Data were collected between September and December 2018, February and July 2019 and November 2019 and March 2020, for a total of 15 months. We used focal animal sampling as the main method of data collection, following a different individual each day from 0700 to 1630 hours, approximately 5.5 days a week, together with a field assistant. We avoided following the same individual on consecutive days while at the same time balancing the sampling time across individuals. Audio recordings of display events and pant hoots were collected using a Sennheiser MKH416 directional microphone (Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) with a Marantz PMD661 MkII (Marantz, Kanagawa, Japan) solid-state recorder (sample rate 44.1 kHz, resolution 32 bits, 'wav' format). We collected a total of 302 h of focal data, with a mean of 25.2 h (range 13.7–34.6) per subject (Appendix Table A3). Because of the rarity of display events, we also collected display data opportunistically from other individuals in the same party. Information regarding behavioural context, identity of displaying male and target, type of display, communicative signals, other participants, outcome and continuous party composition were either dictated into the microphone or noted using CyberTracker (version 3.496) on a Samsung Xcover 4 portable device (Samsung Group, Seoul, South Korea). The identification of the displaying individual, target and type of display (Table 1) were determined in agreement between A.S. and the field assistant. Whenever a display was performed by more than one individual (i.e. joint display), we collected data only from the individual that initiated the behaviour. We focused on pant hoot vocalizations (Table 1) associated with displays from the perspective of the signaller only.

Ethical Note

The project adhered to the ASAB guidelines for the treatment of animals during behavioural studies. The study was approved by the Uganda Wildlife Authority (UWA/COD/96/5), the Uganda National Council for Science and Technology (NS 637) and the research ethic committees of both the Universities of Neuchâtel and St Andrews (38/2019-B; N. 171). Data collection was terminated on 17 March 2020, due to the Covid-19 pandemic, to avoid putting the health of the study animals at risk (Matsuzawa, 2020; Patrono et al., 2018), a decision subsequently reinforced by The Ugandan Wildlife Authority (25 March 2020; UWA ref: EDO/73/01).

Data Analyses

Dominance distance

The dominance hierarchy was assessed by calculating Elo-ratings for each individual using the R package 'EloRating' (version 0.46.11, Neumann & Kulik, 2020) in R Studio (version 3.6.3, R Core Team, 2020). Scores were calculated from pant grunts produced by or towards the focal animal as recorded by field assistants during focal follows thorough the whole study period (Neumann et al., 2011). Pant grunts are vocal signals produced by subordinate chimpanzees towards dominant ones and are widely considered a reliable indicator of dominance relations (Fedurek et al., 2021; Newton-Fisher, 2017). To take the possibility of changes in group dynamics and their effects on rank (e.g. loss of individuals or natural changes in social dynamics) into account, we calculated the Elo-ratings for each individual for three separate periods of approximately 6 months each (Appendix Table A4). We then calculated dominance distance as the difference in Elo-rating between the agent (i.e. the individual conducting the display) and the patient (i.e. the party member with the highest Elo-rating; negative distance: agent lower ranking than patient; positive distance: agent higher ranking than patient).

Preferred social partners

Preferred social partners (PSP) were identified using a modified social index from Gilby and Wrangham (2008), further developed by Schel, Townsend et al. (2013; see Appendix for details on the procedure and Appendix Table A5). We used long-term data on focal follows collected by field assistants as a basis of the social index: 15 min scan samples with the following information: party composition (identity of all individuals present in the focal party), the focal individual's nearest neighbour (identity of the closest individual to the focal) and the focal individual's grooming interactions (partner identity and duration). Party composition was defined as all individuals present within a radius of approximately 35 m with the focal individual as the radius centre (Newton-Fisher, 1999). For each individual, dyadic affiliative relationships were established using a composite social index based on three different dyadic association measures: a simple ratio index, a nearest-neighbour association index and a grooming index. The composite index, as with dominance distance, was calculated separately for the three 6-month periods.

Acoustic data

Recordings of display pant hoots were visually inspected using spectrograms generated by Adobe Audition software (version 12.0.1) at a sampling rate of 22 kHz and acoustically assessed using Sennheiser HD650 headphones (Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany). This procedure was only used for visualization and did not modify the original recordings used in the acoustic analyses (see below). A.S. classified pant hoot calls and pant hoot phases following previous definitions (Table 1). We only used recordings where the caller's identity could be established and, in the case of choruses, where overlapping elements from a second caller (chorus) allowed us to determine the individual call structure. Chorusing from another individual in the audience always occurred after the initial call from the subject performing the vocal display. Whenever more than one pant hoot was produced during the same display event, we only coded the first occurrence. In addition, we carried out an interobserver reliability test for classification of each phase. P.F. independently classified the presence or absence of the four pant hoot phases in 20% of randomly selected calls from the original set ($N = 33$). P.F.'s classification showed very high levels of agreement with A.S.'s classification (Cohen's $k = 0.91$; 95% agreement).

As mentioned (Table 1, Fig. 1), pant hoots are usually defined as long-distance calls comprising up to four distinct phases (Marler & Hobbett, 1975), although there is no consensus as to whether the term ‘pant hoot’ should also be used when one or more phases are missing. For example, some authors require the presence of at least two phases (Notman & Rendall, 2005), at least a climax (Arcadi, 1996; Fedurek et al., 2014; Mitani & Brandt, 1994), at least an introduction and a climax (Mitani et al., 1999), or at least an introduction and a build-up (Crockford & Boesch, 2005). In this study, we used the broadest possible definition, by including any utterance with up to three phases missing, regardless of which phase(s) was/were missing. Example recordings of display pant hoots are available as Supplementary Material (Audio S1–S5) and as figures (Appendix Figs A1–A5).

Statistical Analysis

To determine whether the acoustic structure of single phases differed from the same phases produced as part of a multiphase pant hoot, we performed crossed permuted discriminant function analyses (pDFA; Mundry & Sommer, 2007). We selected nine calls composed of a single introduction phase, 17 multiphase pant hoots including an introduction, 11 calls composed of a single build-up phase and 22 multiphase pant hoots including a build-up that were suitable for acoustic parameter extraction from five adult individuals combined (Appendix Table A6). To ensure an acceptable signal-to-noise ratio for the analyses, we selected the first available tonal element that did not contain background noise and that did not overlap with other calls. From each element, we extracted a series of spectral and temporal acoustic parameters (Appendix Table A7) using a custom-built script in Praat (version 6.0.42, see Briefer et al., 2019; Leroux et al., 2021; Watson et al., 2018). We compared the extracted F0 contour to the F0 from the spectrogram to guarantee accurate pitch tracking. For each phase type, we assessed multicollinearity to avoid including correlated acoustic parameters. We removed seriatim the parameter with the highest variance inflation factor (VIF) until we obtained a set of five acoustic parameters, the same as the number of individuals tested. In the final set, the highest VIF for introduction calls was 1.20 and the highest VIF for build-up calls was 1.11. We assessed the normal distribution of the data and when variables were not normally

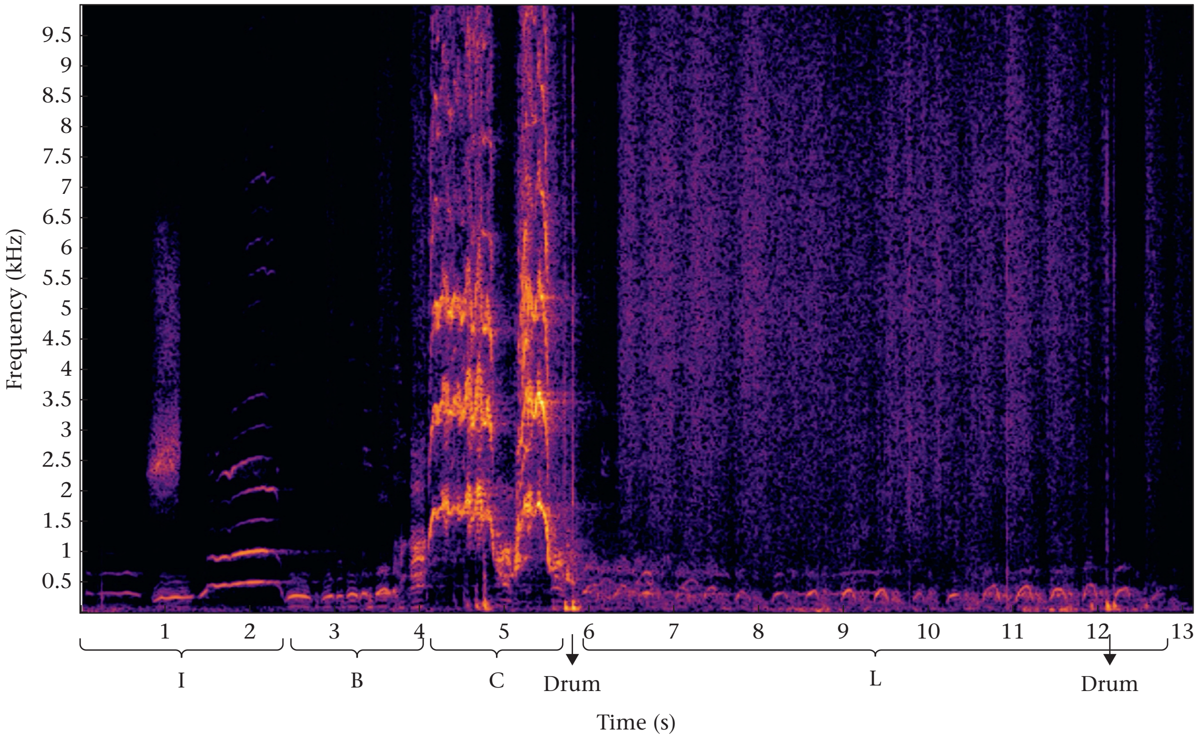

Figure 1. Spectrographic illustration of a pant hoot produced by a subadult male chimpanzee (JS). The vocalization includes all four phases (I = introduction, B = build-up, C = climax, L = let-down) and is combined with a series of drumming beats (Drum). The figure was created using Raven Pro (version 1.6.1, https://ravensoundsoftware.com/).

distributed and could be improved, we applied a log transformation. To test whether the acoustic structure of each single phase differed significantly from the same phase produced as part of a multiphase pant hoot we used pDFA with 1000 permutations (Mundry & Sommer, 2007). In comparison with a conventional DFA, a pDFA allows the inclusion of repeated data points per individual (nonindependence) and controls for unbalanced data sets at the same time. We included the 'ID' of the caller as a control factor. Statistical analyses were conducted in R studio (version 1.2.5033, R Core Team, 2020).

To investigate whether certain components of displays were affected by the audience composition and display features, we created six generalized linear mixed models (GLMM) with a binomial error structure using the R package 'lme4' (version 3.6.3, Bates et al., 2015).

First, in the 'pant hoot model' we considered whether a pant hoot vocalization was present (0/1) during a display as the dependent variable. As independent variables, we included the number of males in the party, the number of females in the party, the number of PSPs in the party, the age of the displaying individual (years), whether the display was directed (0/1) and the dominance distance ($N = 392$ displays, 132 of which were vocal).

Second, we created a model for each of the four pant hoot phases. As the dependent variable we put the presence (0/1) of the introduction phase ($N = 122$ displays, 79 of which had an introduction), build-up phase ($N = 122$ displays, of which 110 had a build-up), climax phase ($N = 125$ displays, of which 26 had a climax) and let-down phase ($N = 122$ displays, of which 25 had a let-down). We kept the same independent variables as in the 'pant hoot model' but added whether it was chorused with a pant hoot by another adult individual or not (0/1). Finally, in the 'drumming model' the dependent variable was whether drumming occurred or not (0/1) and the independent variables were the same as in the 'pant hoot model' ($N = 394$ displays, of which 140 included drumming).

Since we had repeated observations from the same individuals, the identity of the displaying individual was included as a random effect to control for replicated observations (Pinheiro & Bates, 2000; Waller et al., 2013). Before running the models and to improve the accuracy of the parameter estimates (McElreath, 2016) we z-transformed the distribution of quantitative variables into a distribution with mean of 0 and standard deviation of 1 (Schielzeth, 2010). To assess the significance of the test predictors, we compared each model with a 'null' model comprising only the intercept, control variables and random effects, using a likelihood ratio test (LRT; Faraway, 2006). We controlled for the false discovery rate by adjusting the P values of each LRT using the Benjamini and Hochberg method and we report the corrected P values (P^*). To explore whether the directedness of display interplayed with other predictors and test previous hypotheses, we included interactions between the independent variables and the directedness of a display (0: nondirected; 1: directed).

Subsequently, nonsignificant interactions (estimates with $P > 0.05$) were removed seriatim from the model. To avoid high correlations among predictor variables causing unreliable estimates of the regression coefficients, when the expected correlation of the regression coefficients was greater than 0.5, we ran two models one with each variable removed and kept the variable that was associated with the lowest Akaike information criterion value of the model (i.e. best fit for the model; Akaike, 1974). Variance inflation of variables in each linear model without random effects and interactions was assessed using the function vif of the R package 'car' (version 3.0.3, Fox & Weisberg, 2011), which represented a sensitive measure of collinearity (Field, 2005) and was considered acceptable when < 4.0 (Quinn & Keough, 2002).

There was no collinearity between the examined independent variables (maximum VIF values in each model: pant hoot = 2.51; introduction = 1.57; build-up = 1.49; climax = 1.53; let-down = 1.54; drumming = 1.55). The response variable was not overdispersed (dispersion parameter in each model: pant hoot = 0.971; introduction = 0.932; build-up = 1.189; climax = 1.088; let-down = 0.987; drumming = 1.027). The P values of the fixed effects were calculated with likelihood ratio tests comparing the full model with the respective reduced models using the 'drop1' function of the R package 'stats' (version 4.0.2, R Core Team, 2020).

We report coefficient estimates, standard errors, confidence intervals (95%) and significance tests for each investigated variable after dropping the levels of random effects one at a time, and P values for all effects from models that contained explanatory power. Test results and P values of intercept and single interaction terms were omitted because of limited interpretation. All analyses were carried out using R Studio (version 1.2.5033, R Core Team, 2020). Figures were created using the R packages 'ggplot2' (version 3.3.0, Wickham et al., 2018) and 'interactions' (version 1.1.3, Long, 2019).

RESULTS

Acoustic Analysis

Males produced eight of 15 possible pant hoot variants (Fig. 2, Appendix Tables A8 and A9). In particular, the climax phase was never produced without either an introduction and/or a build-up phase. Similarly, the let-down phase was never produced on its own but always followed the climax phase. Callers revealed most variability in whether they produced introduction and build-up phases, both of which were also produced on their own: 6.7% of vocalizations were composed of a series of repeated introduction elements ($N = 11$; Appendix Fig. A5), while 30.5% of vocalizations were composed of a series of repeated build-up elements ($N = 50$; Appendix Fig. A4). We tested whether the vocal elements of the introduction and build-up phases, produced alone or in combination, were acoustically different and found no such evidence (introduction elements: expected correctly cross-classified: 52.76%, $P = 0.662$; build-up elements: expected correctly cross-classified: 51.28%, $P = 0.575$), suggesting that they should be considered as pant hoot variants.

Descriptive Results

We analysed data on 454 vocal and nonvocal display events produced by 12 males (Appendix Table A2). Of these, 51% were directed at another individual ($N = 220$), while the remaining 49% were not directed ($N = 209$). Females were the target of 58% of all directed displays ($N = 124$) and on average there were slightly fewer females than males in the party during directed displays (party composition: mean number of males: 4.27, range 0–12; mean number of females: 4.01, range 0–18). Only 2% of displays were associated with physical aggression ($N = 9$). Only 6% of displays were performed by more than one individual simultaneously ('joint display' or 'coalitionary aggression', $N = 24$), half of which were vocal ($N = 12$).

Of all pant hoots produced (i.e. both during displays and in other contexts) by the study subjects during focal following ($N = 542$), 6.5% were produced as part of a display. Regarding the pant hoots produced in display contexts, males accompanied 38.1% of their displays with a pant hoot vocalization ($N = 173$). Of all the display pant hoots, 62.2% were targeted at another individual ($N = 97$), of which 52.2% were directed towards males ($N = 47$) and 47.8%

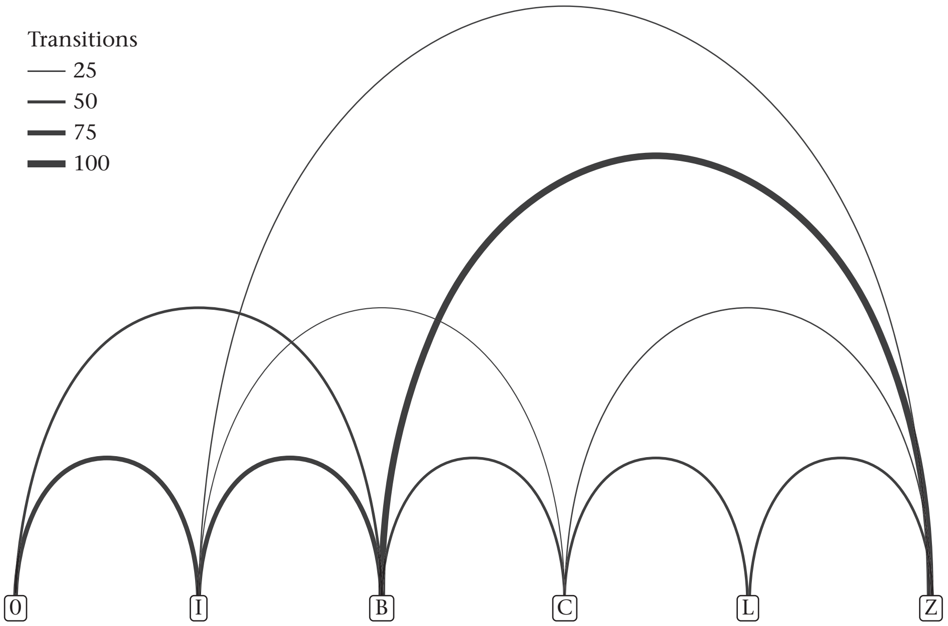

Figure 2. Arc diagram visualization of the order of succession of pant hoot phases in a vocal sequence. Arc lines show the transition probabilities of the inclusion of each phase (I = introduction, B = build-up, C = climax, L = let-down) and the number of transitions is represented by their thickness. Arcs starting from '0' indicate which phase occurred as the first component in the structure. Arcs ending in 'Z' indicate which phase was produced as the last component in the structure. For example, arcs from point '0' to point 'I', from 'I' to 'B' and from 'B' to 'Z', represent a pant hoot structure composed of introduction and build-up (I–B). See Appendix for details.

towards females ($N = 43$). The phases present in the structure of display pant hoots varied: 63.4% contained an introduction ($N = 104$), 91.5% a build-up ($N = 150$), 28.7% a climax ($N = 47$) and 20.7% a let-down ($N = 34$).

Overall, 62.8% of pant hoots ($N = 103$) were two-, three- or four-phase structures, whereas the remaining 37.2% ($N = 61$) had a single phase (either introduction or build-up). Of all single-phase pant hoots, 57.3% were targeted at another individual ($N = 34$), while 42.7% were not targeted at others ($N = 27$). During directed display pant hoots, 30.8% of calls contained a climax ($N = 28$), while during nondirected display pant hoots 23.2% of calls included a climax ($N = 13$). Of all display pant hoots, 24.1% were chorused with another individual ($N = 39$). Males accompanied 33.8% ($N = 154$) of the vocal and nonvocal displays with drumming. Specifically, drumming was produced during 21.2% of vocal displays ($N = 58$) and during 35.0% of nonvocal displays ($N = 97$). Vocalizations and drumming were produced in combination during 7.5% of displays ($N = 30$).

The Pant Hoot Model

In a first analysis, we investigated what factors best explained whether males produced pant hoots during displays, irrespective of their sequential structure. We tested whether audience composition and type of display (directed or nondirected) affected call production. Overall, the difference between the full and null models was significant (LRT: $\chi^2_7 = 33.47$, $P^* < 0.001$). More specifically, males were more likely to call as the number of other males in the party increased (Table 2). The opposite effect was observed for females and preferred social partners: as their numbers increased, male displays were less likely to be vocal (Table 2). We found an interaction effect between the directedness of a display and the dominance distance between the displaying male and the most dominant male in the party (Fig. 3): during nondirected displays, higher-ranking males relative to the most dominant male in the party were less likely to be vocal whereas lower-ranking males were more likely to be vocal. During directed displays, the pattern was reversed: higher-ranking males relative to the most dominant male in the party were more likely to be vocal whereas lower-ranking males were less likely to be vocal. Finally, we found no effect of age of the displaying male (Table 2).

The Introduction Phase Model

In a second analysis, we investigated what factors best explained whether males produced an introduction phase in their pant hoots. The difference between the full and null models was significant (LRT: $\chi^2_6 = 19.70$, $P^* = 0.006$). We found that displaying

Table 2
Relationship between the production of display pant hoots and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	*P*
Intercept	−1.309	0.287	−1.977	−0.750		
Dominance distance	−0.479	0.231	−1.016	0.003		
Number of males	0.400	0.196	−0.046	0.866	4.123	**0.042**
Number of females	−0.376	0.143	−0.697	−0.094	7.419	**0.006**
Number of PSP	−0.389	0.176	−0.792	−0.053	4.851	**0.028**
Age displayer	−0.021	0.233	−0.492	0.482	0.007	0.934
Directedness	0.751	0.241	0.223	1.269		
Dominance distance*Directedness	0.581	0.239	0.097	1.117	5.931	**0.015**

CI: confidence interval; PSP: preferred social partner. Significant results are depicted in bold.

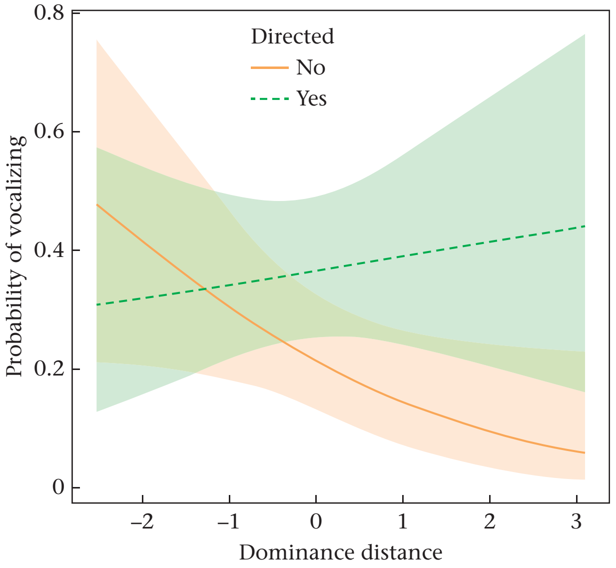

Figure 3. Likelihood of vocalizing depending on the interaction between the dominance distance and the directedness of a display. The fitted model line is presented with confidence bands for the fitted values based on standard errors (95%). Dominance distance values are z-standardized.

males were more likely to produce an introduction phase as the number of males in the audience increased. Directed displays were more likely to contain an introduction phase than nondirected ones (Table 3). Finally, the number of females, age of displaying male, dominance distance and chorusing, had no effect (Table 3). As the variable ‘Number of PSP’ was colinear with the variable ‘Number of males’ we removed it from the model.

The Build-up Phase Model

In a third analysis, we investigated what factors best explained whether males produced a build-up phase in their pant hoots. We failed to find an impact of the test predictors on the probability of producing a build-up phase. The difference between the full and null models was not significant (LRT: $\chi^2_7 = 10.941$, $P^* = 0.141$).

The Climax Phase Model

In a fourth analysis, we investigated what factors best explained whether males produced the climax phase in their pant hoots. The difference between the full and null models was significant (LRT: $\chi^2_7 = 17.79$, $P^* = 0.010$). We found that males were more likely to produce a climax if they were lower ranking relative to the most dominant male in the party and if another individual joined in a chorus (Table 4). However, we did not find an effect of the number of males, number of females, directedness of displays and age of displaying male (Table 4). The variable ‘Number of PSP’ was colinear with the variable ‘Number of males’ and therefore not considered.

The Let-down Phase Model

In a fifth analysis, we investigated what factors best explained whether males produced the let-down phase in their pant hoots. The difference between the full and null models was significant (LRT: $\chi^2_7 = 18.95$, $P^* = 0.010$). Here, males were more likely to produce a let-down if another individual chorused with the displaying male (Table 5). We found an interaction effect between the directedness of a display and the age of the displaying male (Fig. 4): younger individuals were more likely to produce a let-down phase during nondirected displays, while older individuals were more likely to produce it during directed displays. We did not find a significant effect of the number of males, the number of females and the dominance distance (Table 5). The variable ‘Number of PSP’ was colinear with the variable ‘Number of males’ and therefore removed from the model.

Table 3
Relationship between the production of the introduction phase and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	*P*
Intercept	−0.132	0.407	−1.041	0.788		
Dominance distance	−0.195	0.298	−0.936	0.441	0.389	0.533
Number of males	0.713	0.323	0.082	1.544	4.833	**0.028**
Number of females	−0.100	0.274	−0.693	0.569	0.126	0.722
Age displayer	−0.212	0.303	−0.883	0.430	0.426	0.514
Directedness	1.538	0.467	0.611	2.656	11.236	**0.001**
Chorus	−0.477	0.527	−1.613	0.613	0.794	0.373

CI: confidence interval. Significant results are depicted in bold.

Table 4
Relationship between the production of the climax phase and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	*P*
Intercept	−1.643	0.417	−2.898	−0.914		
Dominance distance	−0.625	0.273	−1.322	−0.117	5.517	**0.019**
Number of males	−0.276	0.264	−0.972	0.230	1.140	0.286
Number of females	−0.205	0.295	−0.964	0.395	0.497	0.481
Age displayer	−0.244	0.231	−0.782	0.260	1.124	0.289
Directedness	0.228	0.452	−0.720	1.249	0.257	0.612
Chorus	1.540	0.510	0.609	2.918	9.517	**0.002**

CI: confidence interval. Significant results are depicted in bold.

The Drumming Model

In a final analysis, we investigated which factors best explained whether males accompanied their vocal and nonvocal displays with drumming. The difference between full model and null model was significant (LRT: $\chi^2_6 = 54.35$, $P^* < 0.001$). Here, males were more likely to drum as the number of males present in the party decreased (Table 6). We found an interaction effect between age and directedness (Fig. 5). Specifically, older males were more likely to drum during directed displays, while the pattern was opposite for younger males (Fig. 5). We found no effect of dominance distance and of the number of females (Table 6). The ‘Number of PSP’ was colinear with ‘Number of males’ and therefore removed from the model.

DISCUSSION

The aim in this study was to investigate whether audience features such as the number of males, females and preferred social partners, as well as the displaying male's social status, predict the production of pant hooting, including each of its four phases, and drumming, during displays. We also considered the displaying male's age, whether displays were directed at another individual and whether pant hoots were given as part of a chorus. During directed displays, higher-ranking males were more likely to pant hoot than lower-ranking males. For nondirected displays, the pattern was reversed. Males were more likely to pant hoot in the

Table 5
Relationship between the production of the let-down phase and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	*P*
Intercept	−2.430	0.537	−4.513	−1.659		
Dominance distance	−0.484	0.301	−1.377	0.144	2.633	0.105
Number of males	0.032	0.283	−0.729	0.677	0.012	0.911
Number of females	−0.177	0.321	−1.049	0.475	0.314	0.575
Age displayer	−0.838	0.419	−2.163	0.025		
Directedness	0.602	0.544	−0.395	2.275		
Chorus	1.784	0.569	0.746	3.610	10.250	**0.001**
Age displayer*Directedness	1.006	0.477	0.031	2.640	4.638	**0.031**

CI: confidence interval. Significant results are depicted in bold.

presence of small numbers of preferred social partners and females. Regarding the structure of pant hooting, whether males produced the introduction depended on the number of other males in the audience and on whether the display was directed. We found that the climax was mainly produced by lower-ranking males and during chorusing. Let-down was mainly produced by younger males during nondirected displays and during chorusing. Finally, drumming was more likely to occur in the absence of other males and to be produced by older males during directed display, while the opposite was the case for nondirected displays.

Males were less likely to produce display pant hoots as the number of females increased. Previous studies have also reported effects of the presence of females but in opposite directions. In the Mahale group, males did not increase pant hoot rates in the presence of oestrous females (Mitani & Nishida, 1993), whereas in the Kanyawara group they did so in the presence of (parous) oestrous females (Fedurek et al., 2014). Given that pant hoots were mostly recorded during feeding and travelling in previous studies, it is possible that audience effects on pant hoots vary based on the context of production. Considering that females are frequent targets of displays, often as part of sexual coercion (Muller & Mitani, 2005; Smuts & Smuts, 1993), it is unlikely that display pant hoots function to attract females. Instead, suppressing pant hoots during displays may be a strategic decision that some males take, for example, to avoid alienating females or to conceal their identity and location to distant competitors (Fichtel & Manser, 2010), a pattern also seen in other species (e.g. lions: Grinnell & McComb, 2001). In line with our observation, in Budongo Forest, chimpanzee males preferentially use low-amplitude gestures during consortships, presumably to keep their mating efforts concealed (Hobaiter & Byrne, 2012).

Similar to the presence of females, males were less likely to produce display pant hoots when their preferred social partners were in the audience. A possible interpretation is that displaying males were trying to attract their partners to support them during competitive display episodes. The introduction and climax phases

Table 6
Relationship between the production of drumming and the investigated independent variables

Term	Estimate	SE	Lower CI	Upper CI	χ^2	*P*
Intercept	−0.007	0.155	−0.324	0.332		
Dominance distance	−0.091	0.141	−0.394	0.178	0.413	0.520
Number of males	−0.542	0.151	−0.876	−0.259	12.080	**0.001**
Number of females	−0.011	0.123	−0.262	0.241	0.008	0.927
Age displayer	−0.300	0.188	−0.696	0.068		
Directedness	−1.215	0.233	−1.757	−0.801		
Age displayer* Directedness	0.674	0.240	0.203	1.229	8.298	**0.004**

CI: confidence interval. Significant results are depicted in bold.

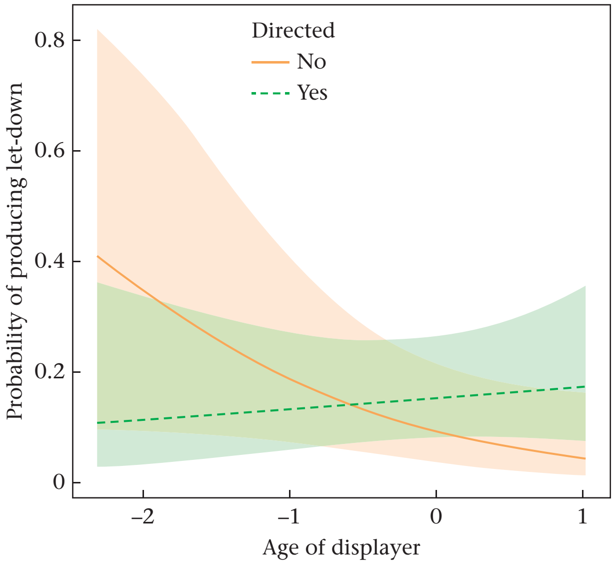

Figure 4. Likelihood of producing a let-down phase depending on the interaction between the age of the displaying male and the directedness of a display. The fitted model line is presented with confidence bands for the fitted values based on standard errors (95%). Age values are z-standardized.

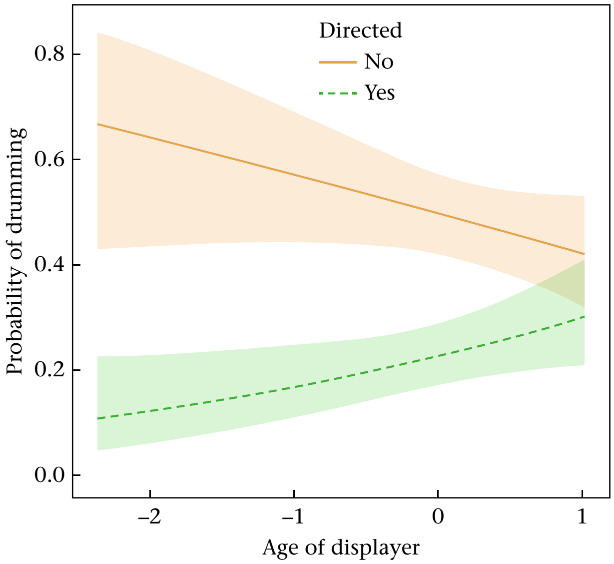

Figure 5. Likelihood of drumming depending on the interaction between the age of the displaying male and the directedness of a display. The fitted model line is presented with confidence bands for the fitted values based on standard errors (95%). Age values are z-standardized.

are individually distinctive, suggesting that the identity of the caller is revealed to receivers provided they produce one of these two phases (Fedurek, Zuberbühler, & Dahl, 2016; Kojima et al., 2003; Mitani et al., 1996). In our analyses it was not possible to investigate whether introduction and climax phases were affected by the number of preferred partners, due to collinearity problems. However, in other studies, it has been concluded that males use pant hoots to maintain spatial contact between conspecifics, especially with social partners (Wrangham & Smuts, 1980), and call more when their social partners are absent in the party but nearby (Mitani & Nishida, 1993).

Males tend to stop pant hooting once reunited with group members (Fedurek et al., 2014). It is important to point out that in this study we only analysed display pant hoots and that pant hoots produced in travelling and feeding contexts may operate under different social mechanisms. Generally, however, the notion of long-distance calls as a way to promote cohesion has been established in other social animal species, such as bonobos, *Pan paniscus* (White et al., 2015), elephants, *Loxodonta africana* (Leighty et al., 2008) and lions (McComb et al., 1994). An alternative interpretation is that the presence of social partners in the audience could represent a form of support to the displaying male. In their absence, males would benefit from making their displays more intimidating by producing a pant hoot, similarly to how lower-ranked males displayed in the presence of more dominant males (see below).

We found multiple dominance effects in our data, in particular in determining whether a displaying male also produced a pant hoot. Here, calling was common in males that were lower ranking than other party males, but only in nondirected displays. For higher-ranking males, we found the opposite pattern. Dominance also impacted the phase structure of pant hoots, with lower-ranking males being more likely to produce a climax than higher-ranking males. Lower-ranking males may follow this strategy as a way to make their displays more impressive or intimidating while avoiding more dangerous directed display. In a similar way, chimpanzees and bonobos incorporate the use of objects, such as dragging and throwing, to amplify their displays (Nishida et al., 1999; Schamberg et al., 2017). Given that previous studies have come to the conclusion that higher-ranking males not only pant hoot more often (Fedurek et al., 2014; Mitani & Nishida, 1993) but also produce more climax phases (Fedurek, Slocombe, et al., 2016; Fedurek, Zuberbühler, & Dahl, 2016; Riede et al., 2007), in contrast to what we found in this study, it would be relevant to extend our analyses to pant hoots given in feeding and travelling contexts. The comparison with bonobos is interesting: males produce ‘contest hoots’, a multiphase call that can also be produced in directed or nondirected ways, to challenge other males and dominant females (Genty et al., 2014). In this sense, the vocal component of chimpanzee displays might have a similar function to bonobo contest hoos. On the other hand, more dominant males may be able to afford the costs associated with signalling during more severe displays, similar to how older males drummed more during severe displays. Note that, in previous studies, dominance was represented as an ordinal or categorical rank, an absolute measure of dominance, while in our study we used a relative measure of dominance, potentially producing different results. Alternatively, given that previous studies only considered calls produced in travelling or feeding contexts, the patterns found in this study may be characteristic of displays.

In our study, similarly to the use of pant hoots during displays, males were also less likely to accompany displays with drumming as the number of males in the party increased. This is in contrast to a previous study (Babiszewska et al., 2015), where the authors did not include the display context, suggesting that drumming is affected by the audience in different ways depending on context. However, in line with their conclusions, our results do not support the hypothesis that drumming was used by dominant males to assert social status. Instead, it was mainly used by young males during nondirected displays and by older males during directed displays. Given that younger males are often subject to aggression (Pusey, 1990; Sabbi et al., 2021), drumming during directed displays may be too costly for them. Interestingly, dominance distance, but not age, affected vocal production during directed displays and the effect of males in the audience on pant hoot production was the opposite to drumming. Consequently, although both vocal and nonvocal acoustic signals allow distant community members to identify and locate signallers during travelling (Babiszewska et al., 2015; Mitani & Nishida, 1993), their functions are likely to be context dependent. Note that buttress trees are common in the Budongo forest (Eleuteri, 2019) and males usually encountered multiple trees during a display event; thus, it is unlikely that tree availability affected drumming. More research is needed to investigate the function of drumming during displays.

We could not test factors influencing the production of the build-up phase, probably because modulation by the audience could not be reliably assessed due to its presence in most display pant hoots. However, given that a significant proportion of display pant hoots were build-up-only calls, which, in contrast to the introduction and the climax, do not primarily signal the identity of the caller (Fedurek, Zuberbühler, & Dahl, 2016), it is unlikely that receivers can extract the identity of displaying males from this component alone. Considering that drumming in male chimpanzees lacks individual acoustic signatures when produced during displays, but not when produced during travelling (Eleuteri et al., in press), the frequent use of build-up-only calls as well as drumming in displays may prevent signallers from revealing their identity to out-of-sight competitors and eavesdroppers while still benefiting from the use of impressive acoustic signals. On the other hand, our results showed that the presence of climax and let-down phases was associated with chorusing. Because the chorused call from a member in the audience always followed the pant hoot from the displaying male, the presence of a specific phase influenced chorusing rather than the other way around. Since let-downs always follow climaxes in the structure of pant hoots (Fedurek, Zuberbühler, & Dahl, 2016; Notman & Rendall, 2005), it is unlikely that they promote chorusing. Instead, chorusing was likely to be associated with climax production. Signalling caller's identity via this call phase may increase the likelihood of others chorusing a display pant hoot. Males flexibly modify the climax phase to prolong and coordinate chorusing, which reflects short-term bonds (Fedurek, Machanda, et al., 2013; Fedurek, Schel, & Slocombe, 2013). Consequently, joining the displaying male's call in a chorus can either be used as a form of support to the displaying male by nearby social partners or to promote coalition formation against other males (e.g. Fedurek, Machanda, et al., 2013).

Males were more likely to produce the introduction phase during directed display pant hoots and as the number of males increased. Because the introduction is associated with the caller's identity and is considered a low-amplitude call component (Fedurek, Zuberbühler, & Dahl, 2016), it could be used to recruit others to join the display. However, given that the inclusion of the introduction was not affected by the number of social partners or by chorusing, and since most display pant hoots were not joint, it is unlikely that this phase was used as an invitation to join. In contrast with previous studies from Gombe and Kanyawara where display pant hoots were rarely directed (Goodall, 1986; Muller, 2002), we observed that around half of the displays were. Vocal signals, in particular those including the introduction phase, were typically produced at the onset of directed displays (A. Soldati, personal observation), which could allow receivers to avoid confrontation costs (Laidre & Johnstone, 2013; Zahavi, 1975). As an example, songbirds produce low-amplitude songs during aggressive encounters (Dabelsteen et al., 1998), which indicate an incoming attack (Akçay et al., 2011; Searcy et al., 2006). Indeed, in captive chimpanzees, 'hooting' during displays has been interpreted as a warning and predictor of aggression (de Waal & Hoekstra, 1980), while bonobo 'contest hoots' indicated incoming aggression (de Waal, 1988). Thus, low-amplitude calls may be used to attract attention from nearby conspecifics or alert conspecifics about an incoming directed display. Because the loud climax phase was similarly produced in directed and nondirected displays and was not produced in the absence of specific individuals (e.g. social partners), our study does not support the idea that its main function is to communicate to distant audiences. Instead, we suggest that males can afford to use a long-distance signal for short-distance communication and that by doing so they signal confidence or dominance. Consequently, pant hoot structures composed of long- and short-distance phases play an important role in short-distance communication and are likely to be directed at nearby individuals too.

Although we were not able to investigate the proximate processes underlying vocal production, our study is consistent with the view that chimpanzee vocal production is flexibly adjusted to highly variable social contexts. While the structure of primate vocalizations is largely constrained (Fischer & Hammerschmidt, 2020), callers do have a certain degree of control over when and which call types they produce (Seyfarth et al., 2010; Townsend et al., 2020). Because vocal production can be modulated according to fine details of the composition of the audience during high-arousal events (e.g. aggression: Slocombe & Zuberbuhler, 2007; copulation: Townsend et al., 2008; feeding: Fedurek & Slocombe, 2013; snake encounter: Crockford et al., 2012), arousal processes do not preclude but contribute to vocal flexibility (Cheney & Seyfarth, 2018; Dezecache et al., 2013; Seyfarth & Cheney, 2003; Snowdon, 2009). Our results, showing audience-based vocal flexibility during a high-arousal context, support this view. The primary concern in our study was not to explore the proximate mechanisms driving call production, while important, but rather to explore ultimate functions of vocal production. Since obtaining data on wild animals' internal states is notoriously difficult, to study the extent to which arousal levels drive vocal production new methods such as infrared thermography might be beneficial (Ioannou et al., 2014; Tattersall, 2016).

Acoustic flexibility can be increased through changes in the acoustic structure of repertoire calls as well as through combinations of different call types (Engesser & Townsend, 2019; Zuberbühler, 2018; Zuberbühler & Lemasson, 2014). In chimpanzees, despite their relatively small repertoire with a fixed number of distinct call types (Slocombe & Zuberbühler, 2010), the capacity to convey multiple information and to elicit several specific responses from receivers is likely to be enhanced through the use of multicomponent vocal structures such as pant hoots. Our study supports the idea that pant hoots are in fact combinatorial structures (Crockford, 2019; Zuberbühler, 2020), for example by demonstrating production of two phases in isolation and as part of multiphase structures. In addition, we have shown that compositional structures that include different phases are affected differently according to the social context, corroborating the idea that different phases are associated with different types of information (Fedurek, Zuberbühler, & Dahl, 2016). However, further testing is necessary to confirm the syntactic-like properties of this call. Because in primates call receivers show more flexibility in vocal behaviour than call producers (Seyfarth & Cheney, 2003; Seyfarth et al., 2010), future studies should focus on the perspective of receivers when investigating the function of complex vocal structures.

The production of vocal and nonvocal signals, including that of acoustically distinctive components in a complex call, is influenced by specific social factors, such as the composition of the audience. Our findings underscore the view that primate vocal structures are flexible and vary in response to fine social factors. Our analyses were limited to the presence or absence of a particular phase within a pant hoot sequence, without taking into consideration specific multiphase combinations and their potential communicative value. Future research should help clarify whether such combinations add to the flexibility of chimpanzee communication. Our study adds to the growing body of evidence that complex vocal structures enhance the communicative potential of vocal signals in species with limited vocal repertoires and allow the signalling of multiple types of information while targeting multiple audiences.

Author Contributions

Adrian Soldati: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing; **Pawel Fedurek**: Conceptualization, Methodology, Writing – original draft, Writing – review & editing; **Guillaume Dezecache**: Conceptualization, Methodology, Writing – original draft, Writing – review & editing; **Josep Call**: Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing – original draft, Writing – review & editing; **Klaus Zuberbühler**: Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing – original draft, Writing – review & editing.

Data Availability

The research data and code used in the analyses in this paper are available at https://osf.io/wzbea/?view_only=7fed3b5b516f4f649299d58d8683ae1c.

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Supplementary Material

Supplementary material associated with this article is available, in the online version at https://doi.org/10.1016/j.anbehav.2022.05.010.

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Appendix

Study Subjects

Table A1
List of all individuals from the Sonso community

ID	Sex	Age category start	Age category end	Year of birth
AC	F	Infant	Infant	2017
AN	F	Adult	Adult	1990
BC	F	Adult	†	1976
BG	F	Subadult	*	2004
CD	F	Young adult	Young adult	2003
DL	F	Young adult	Young adult	2002
DB	F	Infant	Infant	2018
DR	F	Subadult	Young adult	2004
ER	F	Infant	Infant	2019
EV	F	Subadult	Young adult	2004
FA	F	Subadult	Subadult	2006
FH	F	Juvenile	Juvenile	2013
FL	F	Adult	Adult	1979
FK	**M**	**Young adult**	**Adult**	**1999**
GF	M	Juvenile	Juvenile	2013
GH	F	Infant	Infant	2020
GL	F	Adult	Adult	1976
GR	F	Subadult	*	2006
HD	M	Infant	Infant	2017
HM	F	Juvenile	Juvenile	2013
HR	F	Juvenile	Subadult	2009
HT	F	Adult	Adult	1978
HW	**M**	**Adult**	**Adult**	**1993**
IN	F	Young adult	Adult	1999
IS	F	Infant	Infant	2017
JA	F	Infant	Infant	2018
JB	M	Juvenile	Juvenile	2011
JL	F	Adult	Adult	1990
JN	F	Adult	Adult	1984
JS	**M**	**Subadult**	**Subadult**	**2006**
KA	F	Adult	Adult	1998
KB	F	Subadult	*	2007
KC	**M**	**Subadult**	**Subadult**	**2006**
KH	F	Subadult	Subadult	2008
KF	M	Infant	Juvenile	2014
KG	F	Adult	Adult	1998
KJ	M	Juvenile	Juvenile	2013
KL	F	Adult	Adult	1979
KO	M	Infant	Juvenile	2014
KP	F	Subadult	*	2008
KQ	M	Infant	Infant	2016
KS	**M**	**Subadult**	**Adult**	**2003**
KT	**M**	**Adult**	**Adult**	**1993**
KU	F	Adult	Adult	1979
KV	M	Infant	Juvenile	2014
KW	F	Adult	Adult	1981
KX	F	Subadult	Subadult	2007
KY	F	Adult	Adult	1983
KZ	M	Adult	†	1995
MB	**M**	**Juvenile**	**Subadult**	**2009**
MI	F	Subadult	Subadult	2007
MK	F	Adult	Adult	1980
ML	F	Adult	Adult	1975
MS	**M**	**Adult**	**Adult**	**1992**
MZ	M	Infant	Infant	2015
NB	F	Adult	Adult	1962
OK	F	Adult	Adult	1996
OZ	M	Infant	Juvenile	2014
PS	**M**	**Young adult**	**Adult**	**1998**
RF	F	Subadult	Subadult	2007
RH	F	Adult	Adult	1965
RM	F	Young adult	Young adult	2002
RN	M	Infant	†	2018
RS	F	Adult	Adult	1997
RY	M	Infant	†	2013
SM	**M**	**Adult**	**Adult**	**1993**
SQ	M	Adult	†	1991
ST	F	Subadult	*	2007
TJ	F	Adult	Adult	1984
TW	F	Juvenile	Subadult	2010
UP	F	Adult	Adult	1999
ZD	**M**	**Young adult**	**Young adult**	**2001**
ZF	M	Adult	†	1982
ZL	**M**	**Adult**	**Adult**	**1995**

F: female; M: male. Study subjects are in bold.

[†] Subjects that died during the study period.

[*] (Potentially) emigrated females.

Table A2
List of study subjects with number of vocal, nonvocal and drum displays recorded

Individual	Age	Nonvocal displays	Vocal displays	Drum displays
Frank (FK)	19	48	24	15
Hawa (HW)	25	51	37	29
James (JS)	12	9	20	10
Klauce (KC)	12	10	1	5
Kasigwa (KS)	15	14	12	9
Kato (KT)	25	37	10	17
Mbotella (MB)	9	13	5	6
Musa (MS)	26	22	26	20
Pascal (PS)	20	20	19	18
Simon (SM)	25	21	10	11
Zed (ZD)	17	19	4	9
Zalu (ZL)	23	16	6	5
Total		280	174	154

Age (in years) was calculated at the beginning of the study.

Table A3
List of focal individuals with total focal duration (h) and number of separate focal following events

ID	Focal duration	Number of focal events
FK	30.0	12
HW	32.8	8
JS	27.0	7
KC	20.6	6
KS	13.7	6
KT	34.6	10
MB	20.1	7
MS	33.9	10
PS	25.5	10
SM	29.0	5
ZD	14.8	7
ZL	20.1	6
Total	302.1	94
Mean	25.2	8

Dominance Distance

Table A4
Elo-ratings for each subject divided by three 6-month periods

ID	Period 1	Period 2	Period 3
FK	1797	1799	1920
HW	2150	2248	2200
JS	916	1107	1192
KC	860	927	961
KS	1173	1224	1087
KT	1408	1428	1452
MB	887	833	860
MS	1807	1943	1870
PS	1402	1397	1301
SM	1412	1549	1558
ZD	1228	1199	1191
ZL	1447	1508	1575

Preferred Social Partners Index

Long-term preferred social partners (PSP) were established using a modified social index from Gilby and Wrangham (2008) that was developed by Schel, Townsend, et al. (2013). Dyadic affiliative relationships were determined using a composite social index based on three different dyadic association measures for periods of 6 months (same as those used for dominance).

The first association measure is the simple ratio index (SRI), which represents the proportion of time that a dyad (chimpanzees ‘A’ and ‘B’) was observed in the same party:

$$\mathrm{SRI_{ab}} = \mathrm{P_{ab}} / (\mathrm{P_a} + \mathrm{P_b} - \mathrm{P_{ab}})$$

where $\mathrm{P_{ab}}$ is the number of parties in which both A and B were together, while $\mathrm{P_a}$ is the number of parties in which A was present and $\mathrm{P_b}$ the number of parties containing B. The second association measure is based on nearest-neighbour data, which calculates the rate of spatial proximity between the focal individual (A) and another individual (B):

$$\mathrm{NN_{ab}} = \mathrm{A_f B_g} / \text{ focal duration A}$$

where $\mathrm{A_f B_g}$ represents the number of 15 min scans in which A was the focal individual and B its nearest neighbour. The denominator is the total focal observation time of A. The third dyadic association measure is the grooming rate between the focal individual and another individual (B):

$$\mathrm{Grooming_{ab}} = \mathrm{A_f B_g} / \text{focal duration A}$$

where $\mathrm{A_f B_g}$ is the total duration of grooming between the focal individual A and another individual B. The direction of grooming was not considered, which means that receiving, giving and reciprocating grooming were all included. The denominator is the total focal time of A.

After each of the three measures was calculated for each individual, we divided it by the mean of the measures of all other dyads of individuals for a given period to standardize each value, following Gilby and Wrangham (2008). This was done to balance measures before combining them. We then combined the three measures in a composite friendship index (CFI) by averaging them together. For each individual, we calculated mean and standard deviation from all their dyadic composite friendship indexes. These were used to calculate standard z scores which better represent the magnitude and direction of a dyadic relationship and also control an individual's level of gregariousness to associate with others. The following score represents the strength of the bond between the focal individual and another individual relative to all his other bonds:

$$(\mathrm{CFI_{ab}} - \text{ mean } \mathrm{CFI_a}) / \text{ SD of } \mathrm{CFI_a}$$

where $\mathrm{CFI_{ab}}$ is the friendship index between the focal individual A and another individual B. The mean $\mathrm{CFI_a}$ is obtained by averaging the CFI values between the focal individual A and all other individuals of the community. The denominator is the standard deviation of the $\mathrm{CFI_a}$ values. Finally, for each study subject the five highest-scoring individuals were considered preferred social partners (Table A5).

Table A5
List of the five highest scoring preferred social partners (PSP) for each study subject divided by the three 6-month periods

ID	Period	First PSP	Second PSP	Third PSP	Fourth PSP	Fifth PSP
FK	1	DL	HW	JN	SM	KZ
	2	JN	PS	HW	SM	OK
	3	HW	JN	KX	RS	MS
HW	1	MS	FK	ZF	SM	JN
	2	MS	KT	JS	ZL	PS
	3	MS	ZL	KT	PS	FK
JS	1	ZF	MS	HW	NB	KC
	2	SM	JN	HW	KT	DL
	3	JN	KX	KU	RS	MB
KC	1	KL	PS	NB	ZF	KZ
	2	KL	MS	IN	KS	HW
	3	KL	CD	PS	ZD	FK
KS	1	JL	HT	KU	KA	KG
	2	DR	EV	KU	KA	FK
	3	IN	OK	JN	CD	HW
KT	1	MS	OK	HW	HT	FK
	2	HW	FK	MS	EV	KC
	3	HW	RS	MS	OK	ZL
MB	1	HW	KZ	ZL	KC	ML
	2	ZD	KS	MS	ML	ZL
	3	ML	FK	PS	DL	HW
MS	1	NB	HW	PS	SQ	KU
	2	NB	HW	KC	FK	ZL
	3	NB	HW	PS	KT	ZL
PS	1	HW	MS	KC	KT	IN
	2	ZL	ZD	HW	FK	KS
	3	MS	KC	HW	SM	JN
SM	1	JN	HW	KT	SQ	NB
	2	HW	ZL	JN	ZD	MS
	3	HW	FK	KS	MS	KL
ZD	1	JN	FK	ZL	DL	KS
	2	ZL	SM	ST	KS	MS
	3	KU	JN	KX	ML	KT
ZL	1	HW	JN	MS	KT	ZF
	2	PS	ZD	MS	HW	DL
	3	HW	FK	MS	SM	ZD

Acoustic Analyses

Table A6
Summary of the number of calls used for the acoustic analyses divided by individual, call type (introduction, build-up) and call structure (single = single calls, multi = multiphase pant hoots)

ID	Introduction single	Introduction multi	Build-up single	Build-up multi
FK	2	4	1	3
HW	2	4	5	10
JS	2	3	3	4
KT	1	3	1	3
PS	2	3	1	2
Total	9	17	11	22

Table A7
List of acoustic parameters used for the analyses for each phase

Acoustic parameter	Definition
Introduction phase	
F0 variation *	Mean variation in the F0 contour (Hz) divided by duration
% Time of max. intensity *	Percentage of the total element duration during which F0 was at its maximum
AM var	Mean variation per s of the intensity contour, calculated as the cumulative variation in amplitude divided by duration
AM rate	Number of complete cycles of amplitude modulation per second of intensity contour
Jitter *	Mean of absolute difference between frequencies of consecutive F0 periods divided by mean F0
Build-up phase	
Sound duration	Duration of the element (s)
F0 absolute slope *	The mean absolute slope of F0
Q75%	The frequency values at the upper limit of the third quartiles of energy, measured on a linear amplitude spectrum
% EFpeak	The percentage of the total duration where energy value of the frequency with the highest energy was maximum
Shimmer	The mean absolute difference between the amplitudes of consecutive F0 periods divided by the mean amplitude of F0

From Watson et al., 2018.

[*] Parameters that have been log-transformed to be normally distributed.

Table A8
List of possible phase combinations with number of observed cases (*N*)

Introduction	Build-up	Climax	Let-down	*N*
1	0	0	0	11
1	1	0	0	56
1	1	1	0	7
1	1	1	1	27
1	1	0	1	0
1	0	1	0	3
1	0	1	1	0
1	0	0	1	0
0	1	0	0	50
0	1	0	1	0
0	1	1	0	3
0	1	1	1	7
0	0	1	0	0
0	0	1	1	0
0	0	0	1	0
Total				164

Transition Probabilities

We used transitional probabilities to model the sequences of possible states (i.e. pant hoot phases) derived from our sample, where the transition from one step to another is not dependent on the previous state. Probabilities were calculated by dividing the count for each transitional state by the total number of observations (Table A8). This model allowed us to predict transitions between phases including the start and the end of a sequence (Table A9), and to visualize transitions using an arc diagram (Fig. 2).

Table A9
Matrix table of the transitional probabilities (%) between pant hoot phases

	Introduction (I)	Build-up (B)	Climax (C)	Let-down (L)	End (Z)
Onset (O)	63	37	0	0	0
Introduction (I)	0	55	2	0	7
Build-up (B)	0	0	27	0	65
Climax (C)	0	0	0	21	8
Let-down (L)	0	0	0	0	21

Each number represents the probability of change from one state to the next state, with the direction following the sequential order of pant hoot phases (I – B – C – L). For example, the probability that a pant hoot started with a build-up phase (O–B) was 37% ($N = 60$), and the probability that a pant hoot ended with a build-up phase (B–Z) was 65% ($N = 106$).

Pant Hoot Examples

In Figs A1–A5 we reduced the sampling frequency of the original recording from 44.1 kHz to 10 kHz to visualize a frequency resolution that makes the acoustic structure recognizable. Figures were extracted using Praat software (version 6.0.42, Boersma, 2001). We transformed calls with the Fourier function using a Hanning window function and 1024 time steps. Recordings of the calls are available as Supplementary material.

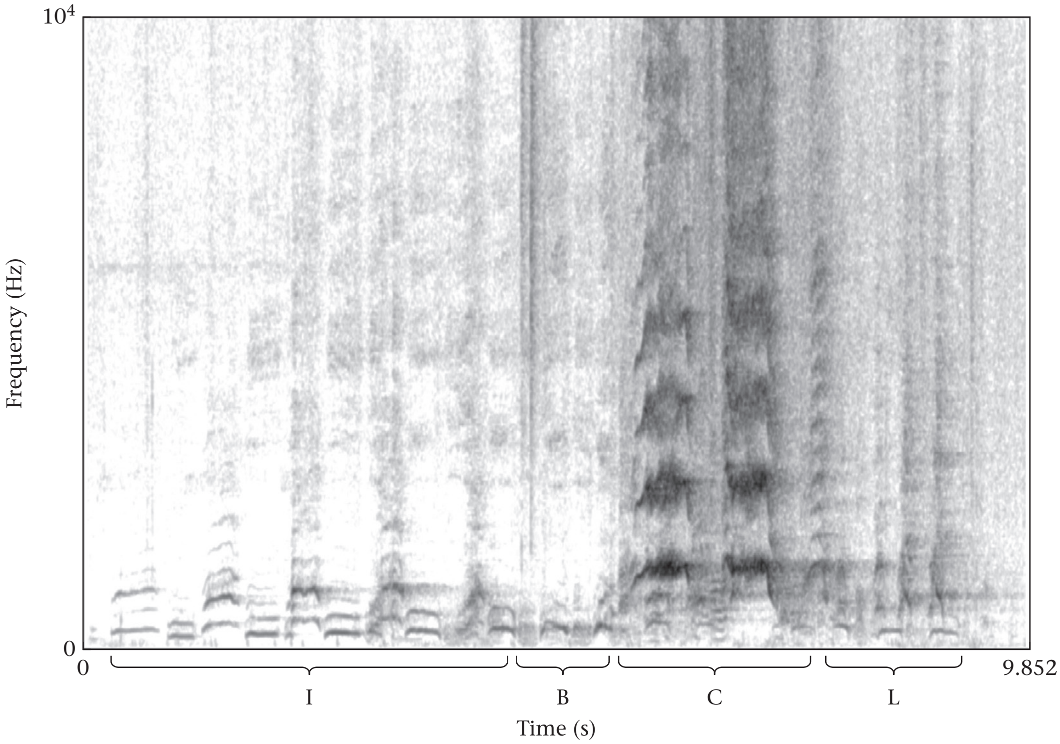

Figure A1. Acoustic spectrogram of a pant hoot produced by ZL during a display. The vocalization includes all four phases (I = introduction, B = build-up, C = climax, L = let-down).

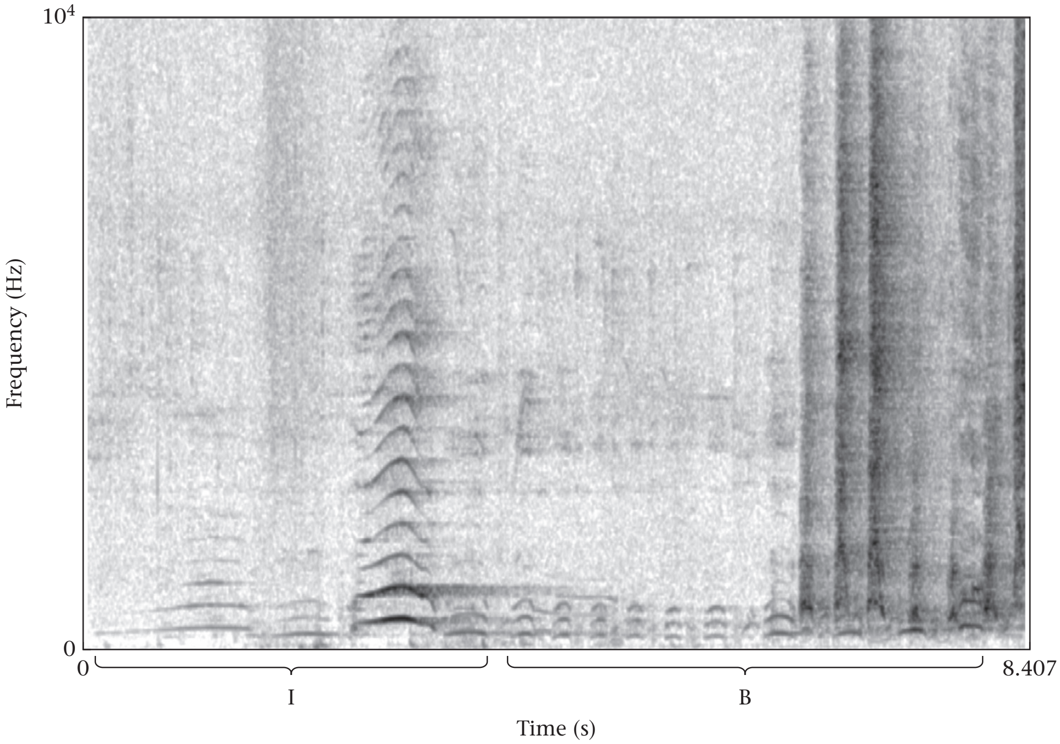

Figure A2. Acoustic spectrogram of a pant hoot produced by MS during a display. The vocalization includes two phases (I = introduction, B = build-up). Screams from the target audience of the display are co-occurring (higher pitch and amplitude) towards the end of the build-up.

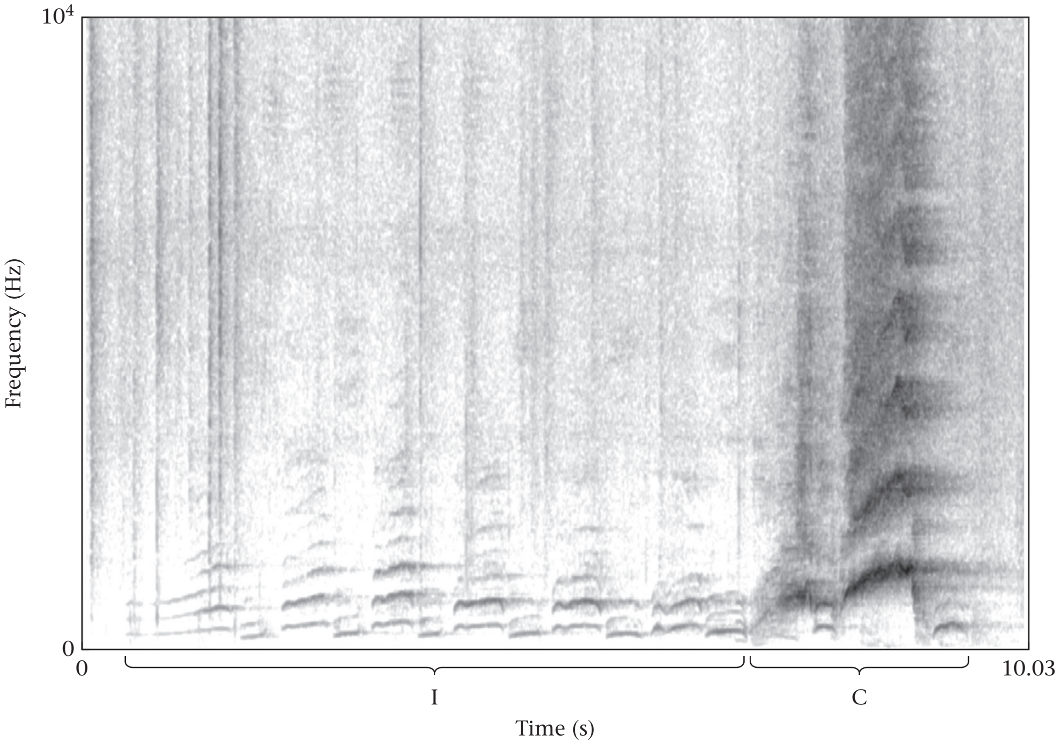

Figure A3. Acoustic spectrogram of a pant hoot produced by PS during a display. The vocalization includes two phases (I = introduction, C = climax).

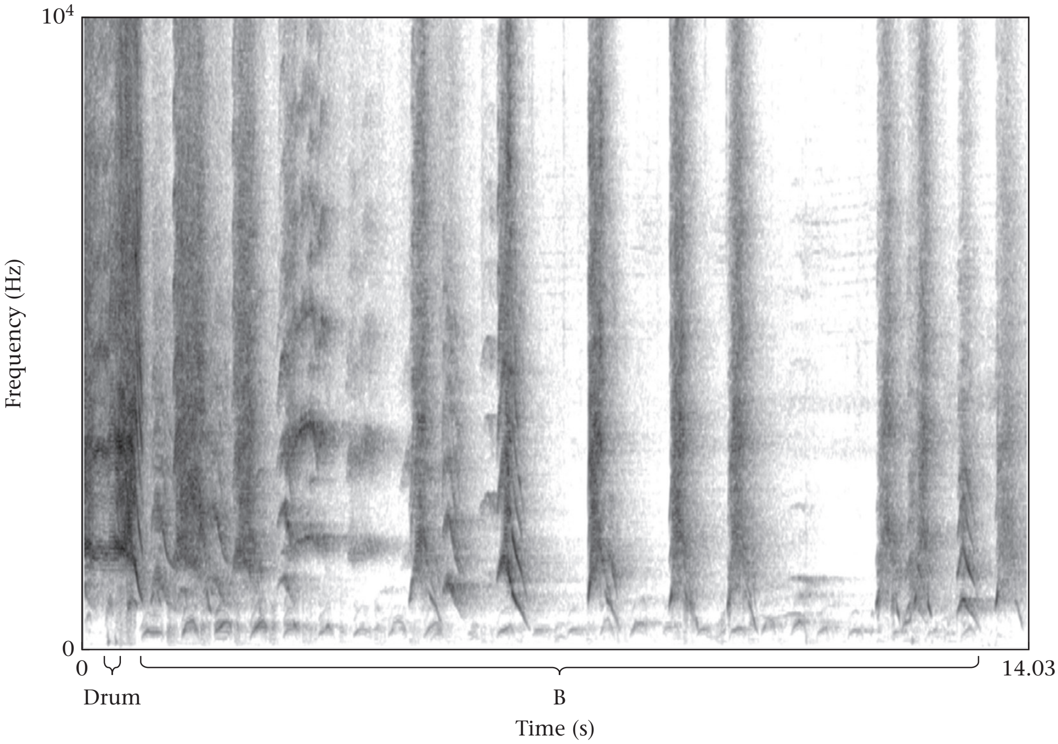

Figure A4. Acoustic spectrogram of pant hoot and drum display produced by MS. The vocalization includes one phase (B = build-up) and drumming (Drum). Screams and barks from the target audience of the display are co-occurring (higher pitch and amplitude) throughout the call.

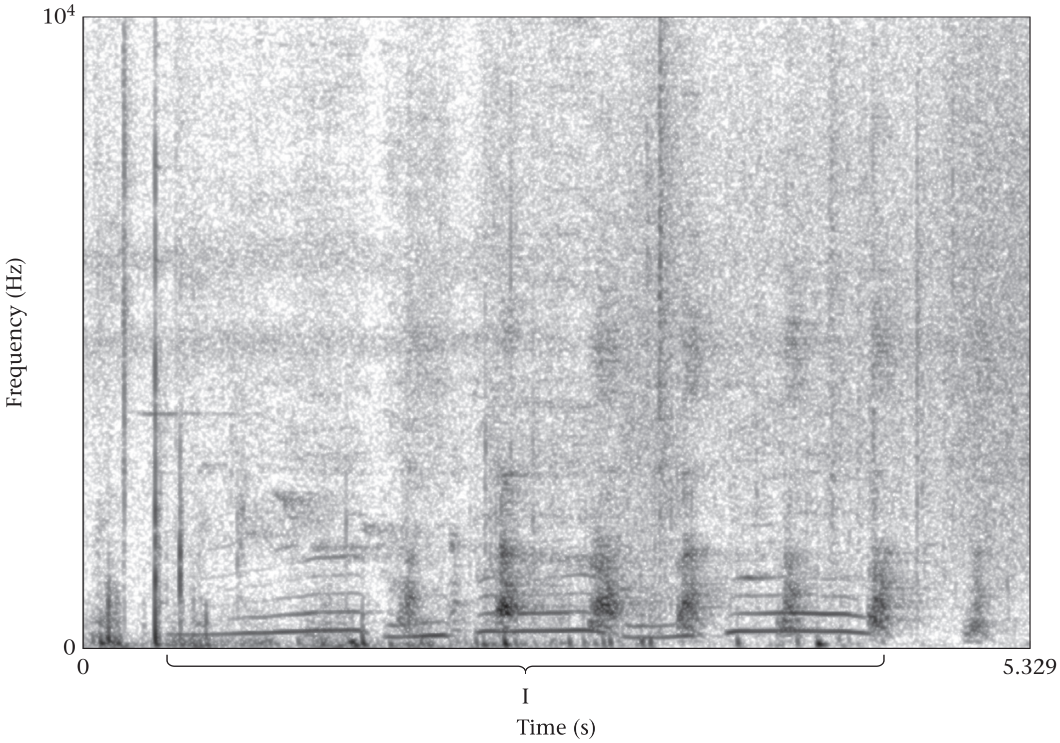

Figure A5. Acoustic spectrogram of a pant hoot produced by PS during a display. The vocalization includes one phase (I = introduction). Pant grunts from the target audience of the display are co-occurring (noisy short call units) throughout the call.