Audience sensitivity in chimpanzee display pant hoots

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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.

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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

| Term | Definition | Source |
|------|------------|--------|
| Display | Intimidatory behaviour characterised 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 ‘hoot’ vocalizations but are noticeably longer in duration and alternate with inhaled tonal elements | Mitani, 1977; Fischer et al., 2002, 2004; chimpanzees: Fedurek, Slocombe, et al., 2016; Riede et al., 2007. 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
microphone (Sennheiser Electronic GmbH & Co. KG, 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 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 accurate 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](https://ravensoundssoftware.com/)

**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 1.6.3, https://ravensoundssoftware.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 PSSs 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).

Next, 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 0 and standard deviation of 1 (Schieleth, 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. A4), 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%
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: χ² = 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: χ² = 19.70, P* = 0.006). We found that displaying

Table 2

| Term                        | Estimate | SE  | Lower CI | Upper CI | χ²  | 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| -0.482   | 0.482    | 0.007| 0.934  |
| Dominatedness*Directness   | 0.751    | 0.241| 0.223    | 1.269    |      |        |
| Dominance distance*Directness* | 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.
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: $\chi^2 = 10.941$, $P = 0.141$).

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: $\chi^2 = 17.79$, $P = 0.010$). 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: $\chi^2 = 18.95$, $P = 0.010$). 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.

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: $\chi^2 = 54.35$, $P < 0.001$). 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

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

| Term                  | Estimate | SE  | Lower CI | Upper CI | $\chi^2$ | $P$  |
|-----------------------|----------|-----|----------|----------|----------|------|
| Intercept             | -0.132   | 0.407 | -1.041   | 0.788    |          |      |
| Dominance distance    | -0.195   | 0.298 | -0.936   | 0.441    | 0.389    | 0.513|
| 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 | -1.813   | 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 | $\chi^2$ | $P$  |
|-----------------------|----------|-----|----------|----------|----------|------|
| Intercept             | -1.643   | 0.417 | -2.898   | -0.914   | 5.517    | 0.019|
| Dominance distance    | -0.625   | 0.273 | -1.322   | -0.117   | 1.140    | 0.286|
| Number of males       | -0.276   | 0.264 | -0.972   | 0.230    | 0.497    | 0.481|
| Number of females     | -0.205   | 0.295 | -0.564   | 0.395    | 0.124    | 0.289|
| Age displayer         | -0.244   | 0.231 | -0.782   | 0.260    | 0.257    | 0.612|
| Directedness          | 0.228    | 0.452 | -0.720   | 1.249    | 2.918    | 0.002|
| Chorus                | 1.540    | 0.510 | 0.609    | 2.918    | 9.517    | 0.002|

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

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![Figure 3](image-url)  
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.
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 directed 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).

Table 5

| Term                  | Estimate | SE   | Lower CI | Upper CI | χ²   | 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.

Table 6

| Term                  | Estimate | SE   | Lower CI | Upper CI | χ²   | 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   | −0.831   |      |         |
| 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* (Leighly 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 may benefit from making their displays more intimidating by producing fewer pant hoots, 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 phrase 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 hoos’, 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 signalers 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, Fedurek, 2016, the introduction and the climax do not necessarily 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 signalers 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, ‘hootting’ 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 & Zuberbühler, 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=7fed3b5b5164f649299d58d86b3ae1c.

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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.
Table A1 (continued)

| ID  | Sex | Age category start | Age category end | Year of birth |
|-----|-----|--------------------|------------------|---------------|
| 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          |
| JS  | M   | Subadult           | Subadult         | 2006          |
| KA  | F   | Adult              | Adult            | 1998          |
| KB  | F   | Subadult           | *                | 2007          |
| KC  | M   | Subadult           | Subadult         | 2006          |
| KD  | M   | Infant             | Juvenile         | 2014          |
| KE  | F   | Adult              | Adult            | 1998          |
| KJ  | M   | Juvenile           | Juvenile         | 2013          |
| KL  | F   | Adult              | Adult            | 1979          |
| KM  | M   | Infant             | Juvenile         | 2014          |
| KP  | F   | Subadult           | *                | 2008          |
| KQ  | M   | Infant             | Infant           | 2016          |
| KS  | M   | Subadult           | Adult            | 2003          |
| KT  | M   | Adult              | Adult            | 1993          |
| KV  | F   | Adult              | Adult            | 1979          |
| KW  | M   | Infant             | Juvenile         | 2014          |
| KX  | F   | Subadult           | Subadult         | 2007          |
| KY  | F   | Adult              | Adult            | 1983          |
| KM  | M   | Adult              | Adult            | 1985          |
| 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             | Adult            | 2015          |
| NF  | F   | Adult              | Adult            | 1962          |
| OK  | F   | Adult              | Adult            | 1996          |
| OZ  | M   | Infant             | Juvenile         | 2014          |
| PF  | M   | Young adult        | Adult            | 1998          |
| RF  | F   | Subadult           | Subadult         | 2007          |
| RH  | F   | Adult              | Adult            | 1965          |
| RM  | F   | Young adult        | Adult            | 2002          |
| RN  | M   | Infant             | Adult            | 2018          |
| RS  | F   | Adult              | Adult            | 1997          |
| RM  | M   | Infant             | Infant           | 2013          |
| SM  | M   | Adult              | Adult            | 1993          |
| SQ  | M   | Adult              | 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              | Adult            | 1982          |
| ZL  | M   | Adult              | Adult            | 1995          |

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

1 Subjects that died during the study period.

* (Potentially) emigrated females.

Table A2

| 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            |
| Klaue (KC) | 12  | 10                | 1              | 5             |
| Kasiga (KS) | 15  | 14                | 12             | 9             |
| Kato (KT)  | 25  | 37                | 10             | 17            |
| Mbotella (MB) | 26  | 9                | 5              | 6             |
| Musa (MS)  | 26  | 22                | 26             | 19            |
| Pascual (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.

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              | 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           | Adult            | 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          |
Dominance Distance

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:

\[ \text{SRI}_{ab} = \frac{P_{ab}}{P_a + P_b} \]

where \( P_{ab} \) is the number of parties in which both A and B were together, while \( P_a \) is the number of parties in which A was present and \( P_b \) 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):

\[ \text{NN}_{ab} = \frac{1}{\text{focal duration A}} \]

where \( A_{B_{D}} \) 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:

\[ \frac{\text{CFI}_{ab}}{\text{CFI}_{A_{mean}}} = \text{SD of CFI}_A \]

where \( CFI_{ab} \) is the friendship index between the focal individual A and another individual B. The mean CFIa 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 CFIa values. Finally, for each study subject the five highest-scoring individuals were considered preferred social partners (Table A5).

### 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                      |

### 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     |

### 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        | FK         | ZF        | SM         | JN        |
|    | 2      | MS        | KT         | JS        | ZL         | PS        |
|    | 3      | MS        | ZL         | KT        | PS         | FK        |
| HW | 1      | ZF        | MS         | HW        | NB         | KC        |
|    | 2      | SM        | JN         | HW        | KT         | DL        |
|    | 3      | JN        | KS         | ZL        | BS         | MB        |
| KC | 1      | KL        | PS         | NB        | ZF         | ZK        |
|    | 2      | KL        | MS         | IN        | KS         | HW        |
|    | 3      | KL        | CD         | PS        | ZD         | FK        |
| KS | 1      | JL        | HT         | FU         | KA         | KC        |
|    | 2      | DR        | EV         | KJ         | 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        | KS         | ZT         | 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         | KS         | MS         | KS        |
|    | 3      | KU        | JN         | KC         | ML         | ZL        |
| 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.

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 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      | 0        | 0  |
| 0            | 1        | 0      | 0        | 50 |
| 0            | 1        | 0      | 1        | 0  |
| 0            | 1        | 0      | 0        | 3  |
| 0            | 1        | 1      | 0        | 3  |
| 0            | 0        | 1      | 0        | 0  |
| 0            | 0        | 1      | 0        | 0  |
| 0            | 0        | 0      | 1        | 0  |
| Total        | 164      |        |          |    |

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.