Do chimpanzees produce context-specific vocal structures in group-specific ways?

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Learning how to link a signal to its appropriate behavioural context in a flexible and meaningful way is foundational to human language, but there is little evidence of this capacity in nonhuman primates. We addressed this by studying chimpanzee, *Pan troglodytes schweinfurthii*, pant hoot contextual use in two communities, Sonso and Kanyawara, from two different wild populations in Uganda. Pant hoots are complex, composite vocal signals, comprising four acoustically distinct phases and produced in different contexts, mostly during travelling and feeding to mediate grouping dynamics. We measured 18 acoustic parameters across phase types and found significant effects of context in all four phases, confirming that pant hoots have the potential to inform others about the caller's behaviour. We also found two inter-action effects between context and community in the final let-down phase: Sonso males produced let-down call elements at higher rates during feeding than travelling and were also more likely to omit the let-down phase entirely during feeding than travelling, than Kanyawara males. We concluded that despite their largely fixed call repertoire, chimpanzees modulate acoustic features according to the behavioural context and, in the case of a few acoustic parameters, do so differently in different populations, with learning potentially involved in this process. Overall, however, the link between most of the acoustic features of chimpanzee calls and context seems to be largely independent of population, which contrasts with human language where different and novel signals are often flexibly attached to different information via social learning.

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Population differences in vocal behaviour are a key feature of human language and a result of advanced vocal learning involving the production of new sounds learned from others, a trait that has nevertheless likely evolved in several animal taxa (Janik & Slater, 1997; Nowicki & Searcy, 2014; Vernes et al., 2021). For example, considerable population differences in vocal production have been documented in different nonhuman animal species, including mammals such as humpback whales, *Megaptera novaeangliae*, and dolphins (Garland et al., 2011; Janik, 2014) as well as birds such as songbirds (Passeriformes) and parrots (Psittaciformes) (Bradbury et al., 2001; Cunningham & Baker, 1983; Wright, 1996).

Another type of vocal learning characterizing human speech is vocal usage learning, learning to produce existing repertoire sounds in novel environmental or social contexts (Janik & Slater, 1997). In contrast to vocal production learning, documented examples of vocal usage learning in nonhuman animals are scarce and come mostly from experimental studies that involve training by humans. For example, European blackbirds, *Turdus merula*, use mobbing calls, which are usually given to predators, when exposed to a stuffed bird (Curio et al., 1978). Similar behaviours have been shown by exper-imental studies on grey seals, *Halichoerus grypus* (Stansbury et al., 2015), bottlenose dolphins, *Tursiops truncatus* (Richards et al., 1984) and carrion crows, *Corvus corone* (Liao et al., 2024), that learned to produce the existing calls when exposed to arbitrary cues.

Despite learning to produce and use sounds being key features of human speech, there is strikingly little evidence of these

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processes in our close evolutionary relatives: nonhuman primates (hereafter: primates), especially in wild populations (Tyack, 2020). The few existing pieces of evidence of vocal production learning include geographical or between-group differences in wild marmoset, *Callithrix* spp. (De la Torre & Snowdon, 2009) and wild orang-utans, *Pongo* spp. (Lameira et al., 2022). Interesting results also come from studies on captive primates, with orangutans acquiring new vocal sounds in controlled settings (Lameira et al., 2013), and marmosets showing group-specific acoustic variants in their calls (Zürcher & Burkart, 2017). There are even fewer clear instances of vocal usage learning from research on primates. One example comes from an experimental study on rhesus monkeys, *Macaca mulatta*, where individuals were trained to produce a specific vocalization in response to an arbitrary visual cue (Hage & Nieder, 2013).

Regarding vocal learning and dialects in our closest living relatives, the long-distance chimpanzee, *Pan troglodytes*, pant hoot vocalization has received considerable attention. Pant hoots are complex vocal sequences that consist of four acoustically distinct phases: the introduction, build-up, climax and let-down, which in turn comprise smaller vocal units labelled as 'call elements' (Fig. 1; Marler & Hobbett, 1975; Mitani & Gros-Louis, 1998). Both Mitani et al. (1992) and Crockford et al. (2004) showed that different chimpanzee populations produce acoustically different pant hoots. Subsequent studies, however, did not detect any between-population and between-group (hereafter: community) differences in this respect, questioning the role and extent of vocal learning in chimpanzees (Desai et al., 2022; Mitani et al., 1999).

Compared with vocal production learning, as with other primates, considerably less research has focused on vocal usage learning in chimpanzees (Vernes et al., 2021). A study on captive chimpanzees showed that after merging chimpanzee groups from two different facilities, one of the groups modified the acoustic structure of their food calls to match that of the other group when exposed to a specific food type (Watson et al., 2015), although the extent of such acoustic changes and the mechanism behind them have been debated (Fischer et al., 2015). Instead, looking at the temporal and structural features (e.g. call duration, presence and number of specific calls within a sequence, call arrangements within sequences) of vocal output, and the context in which calls are produced, may represent a more promising research avenue when exploring primate vocal learning. Primates, including

chimpanzees, despite their limited vocal repertoires, are capable of combining different call types in context-specific ways, and these combinations seem to be meaningful to the receivers (Arnold & Zuberbühler, 2006; Leroux et al., 2023). Recent research on chimpanzees suggests this aspect of vocal communication could be especially relevant. For example, Sonso and Tai populations combine two call types, pant hoots and pant grunts, in a different order when greeting, raising the possibility that chimpanzees may learn how to combine existing calls into different structures in the same context (Girard-Buttoz et al., 2022). Another recent study showed that two populations of wild bonobos, *Pan paniscus*, combine two call types, whistles and high-hoots, in different behavioural contexts (Schamberg et al., 2024). Overall, recent research advances suggest that the structure and usage of ape vocalizations are more flexible than previously assumed and that learning processes might be involved (Slocombe et al., 2022; Townsend et al., 2020).

Looking at the temporal structure of chimpanzee pant hoots and how different features of this vocal sequence are linked to the context of production can be especially promising when investigating between-population differences in call usage. This is because the temporal structure of chimpanzee pant hooting shows a high level of flexibility, with a considerable within-individual variation in terms of the presence and absence of particular pant hoot phases, number of call elements within a phase and element duration (Fedurek, Schel, & Slocombe, 2013, 2017). Furthermore, pant hoots are produced in a variety of behavioural contexts that modulate their temporal structure, with Budongo chimpanzees, for example, often omitting the build-up and let-down phases when feeding but not when travelling (Fedurek, Zuberbühler, & Dahl, 2016; Notman & Rendall, 2005) and omitting up to three phases depending on the social context when displaying (Soldati et al., 2022). Previous research also showed between-population differences in temporal features of pant hooting, such as call element duration and the rate of element production (Mitani et al., 1992, 1999). It is therefore possible that the same temporal arrangements (e.g. pant hoot with no let-down) are produced in different contexts when comparing different populations. If true, it would imply that the same temporal features may have different communicative functions or meanings in different populations, greatly expanding the communicative potential of a fixed vocal repertoire and that social learning may play a role in how these are linked to the context of production.
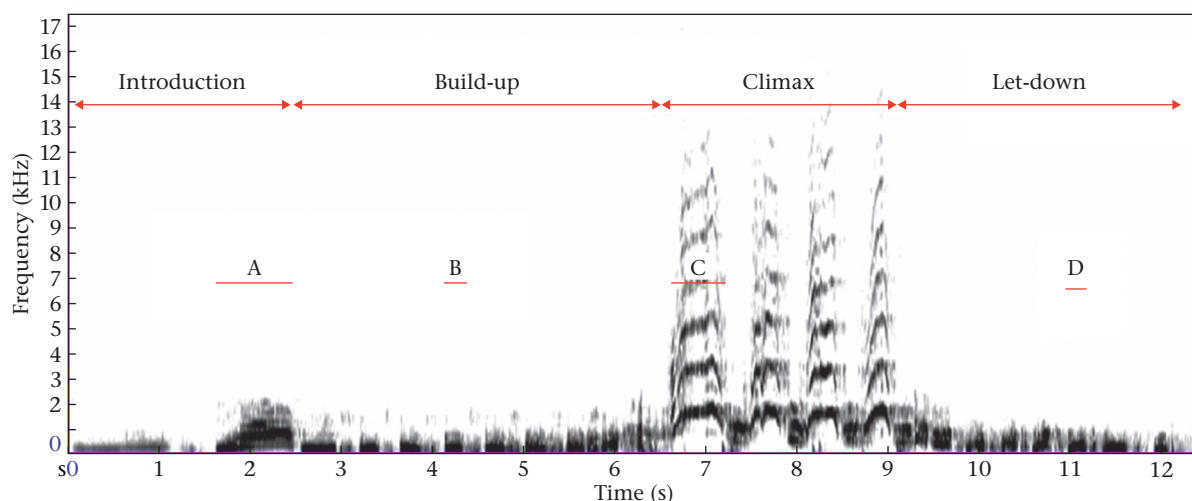

Figure 1. Spectrographic representation of a pant hoot, with the four phases and their call elements. a: an introduction element; b: a build-up element; c: a climax element; d: a let-down element.

This, however, has not been investigated yet. Accordingly, the aim of our study was to compare a range of temporal features of pant hooting, such as the presence of the build-up and the let-down, phase and element duration, the number of elements in a phase and the rate of element production, produced in two different contexts (travel versus feed) between chimpanzees from two wild populations in Uganda: the Sonso community from Budongo Forest and the Kanyawara community from Kibale Forest.

METHODS

Study Site and Subjects

Data were collected on two communities of wild chimpanzees, the Sonso community in the Budongo Central Forest Reserve and the Kanyawara community in the Kibale National Park in Uganda. The Sonso community consisted of 75 individuals, and the Kanyawara community consisted of 54 individuals. Both communities are well habituated and have been studied regularly, Kanyawara since 1987 by the Kibale Chimpanzee Project (Thompson et al., 2020) and Sonso by the Budongo Conservation Field Station since the early 1990s (Reynolds, 2005). Study subjects were 14 Sonso and 11 Kanyawara adult and late adolescent males ($\geq$13 years, Goodall, 1986; see Table A1). As in previous research on chimpanzee pant hoots, including research on between-population differences in this respect (e.g. Desai et al., 2022; Fedurek, Zuberbühler, & Dahl, 2016, 2017), we focused on males to make our study more comparable with the existing literature on the topic (e.g. Crockford et al., 2004; Mitani et al., 1992, 1999).

Data Collection

Data, including both observational and audio data, at Sonso were collected between May 2013 and October 2015 by P.F. and between September 2018 and March 2020 by A.S. Data at Kanyawara were collected between October 2010 and September 2011 by P.F. We used focal animal sampling with a randomly chosen individual that was followed for half a day (up to 5 h; P.F. in Sonso) or a full day (P.F. in Kanyawara; A.S. in Sonso; Table A1). In addition to recording all pant hoots produced by the focal individual, we collected additional ad libitum recordings from other individuals in the same party as the focal animal. Parties are temporary groups formed by chimpanzees in their societies with a high degree of fission—fusion dynamics (Aureli et al., 2008), and we defined them as individuals within 30 m of the focal individual (Newton-Fisher, 1999). A.S. collected audio recordings using a Sennheiser MKH416 directional microphone (www.sennheiser.com) with a Marantz PMD661 MkII solid-state recorder (www.marantzpro.com). P.F. collected audio recordings using a Marantz Professional PMD661 solid-state recorder and a Sennheiser ME67 directional microphone. We selected for analysis focal or ad libitum pant hoots from audio recordings that met the following criteria: (1) the context of call production was known, (2) the pant hoot was not chorused by other individuals (i.e. solo call) since chorusing can affect the acoustic structure of these calls (Fedurek, Schel, & Slocombe, 2013; Mitani & Gros-Louis, 1998) and (3) the pant hoot recording was complete and included both the introduction and climax phases. In total, 346 pant hoots produced by Sonso males and 105 pant hoots produced by Kanyawara males were analysed. Although some of the recordings were used in our previously published studies (e.g. Fedurek, Schel, & Slocombe, 2013; Fedurek, Slocombe, et al., 2016; Soldati et al., 2022), they were used to answer different research questions and therefore analysed differently than in this comparative study.

Data Extraction

Acoustic measurements were extracted manually using Praat software (version 6.2.03; www.praat.org). We measured phase duration from the start of the first exhalation sound (i.e. element) to the end of the last element (in seconds), the number of elements in each phase, the mean duration of all elements for each phase (in seconds), the production rate of elements of each phase (the number of elements divided by the duration of the phase) and the presence of the build-up and the let-down phases. Measurements were taken from a phase and included in the analysis only if this phase was present in a pant hoot.

Dominance Rank

Each male was assigned a linear ordinal rank. In the Kanyawara data and Sonso data collected by P.F., the rank was based on the direction of pant grunts and the outcome of dyadic agonistic interactions. 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 determine ordinal dominance ranks the Matman Software Package (version 1.1, Noldus Information Technology, Wageningen, Netherlands) was used, and all male dominance hierarchies were significantly linear using a two-step randomization procedure with 10 000 iterations (De Vries et al., 1993, see also Fedurek, Machanda, et al., 2013). For the Sonso data collected by A.S., the dominance hierarchy was assessed by calculating Eloratings for each individual using the R package 'EloRating' (version 0.46.11; Neumann & Kulik, 2014, see also Soldati et al., 2022). Scores were first calculated from pant grunts produced by or towards the focal animal as recorded by field assistants during focal follows throughout the whole study period (Neumann et al., 2011) and then ordered to determine the linear ordinal rank.

Statistical Analyses

All statistical analyses were conducted using the software R (version 4.3.0; R Core Team, 2014). We used a theory-driven approach to formulate statistical models on the basis of the existing literature and previous findings. Candidate models were subsequently compared using likelihood-ratio tests (LRT; Fox & Weisberg, 2018; Lewis et al., 2011). More specifically, we ran 18 models using the R package lme4 (version 1.1—23; Bates et al., 2012): models 1—8 and 13—16 were linear mixed-effect models run with a normal distribution. Models 9—12 were generalized linear mixed-effect models run with a Poisson distribution. Models 17 and 18 were generalized linear mixed-effect models run with a binomial distribution. We included the duration of each pant hoot phase (models 1—4), the mean duration of elements of a phase (models 5—8), the number of elements in a phase (models 9—12), the rate of element production in a phase (models 13—16) and the presence of build-up and let-down phases (models 16—18) as dependent variables. To investigate if the investigated temporal features of pant hoots varied between chimpanzee communities depending on the context in which they were produced (Fedurek, Zuberbühler, & Dahl, 2016; Notman & Rendall, 2005), we included an interaction between communities (Kanyawara = 0, Sonso = 1) and context (travel = 0, feed = 1). If the interaction was significant, we conducted post hoc tests where we created two data subsets, one for each level of the fixed factor 'community', while keeping other factors from the model the same and then interpreted the effect of the fixed factor 'context'. Nonsignificant interaction terms were removed from the model so that main effects

could be interpreted. Rank and age of the caller were included as control factors because they can impact chimpanzee pant hoots (Clark & Wrangham, 1993; Fedurek, Zuberbühler, & Dahl, 2016). Prior to analysis, we z-transformed the numeric fixed effects and control variables [i.e. centred around 0 and SD of 1] to improve the accuracy of the parameter estimates and achieve standardized effect sizes (Schielzeth, 2010). The identity of the focal individual was included as a random effect. 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 LRT (Faraway, 2016). We controlled for the false discovery rate by adjusting the P values of each LRT when comparing the model against its null model using the Benjamini and Hochberg methods. We report the corrected P values (P*) for each LRT, which are compared against the standard alpha level of 0.05. Once LRTs identified full models that were significantly different from null models in explaining the variation in the data, we then report standard P values for parameters within these models (alpha level of 0.05). If the interaction term between 'context' and 'community' was not significant, it was removed so the main effects could be interpreted. We report estimates, SEs, lower and upper bounds of the 95 % CI, odds ratios, lower and upper bounds of the 95 % CI for the odds ratios, significance test results and P values for each model parameter. Test results and P values of the intercept were omitted due to limited interpretation. We used the 'performance' package (version 0.5.1; Lüdecke et al., 2021) to assess the variance inflation factor (VIF) between the examined independent variables to measure collinearity. There were no concerning levels of multicollinearity in any of the models (maximum VIF: 1.19).

Ethical Note

Permission to conduct the study was granted by the Uganda Wildlife Authority and the Uganda National Council for Science and Technology. The study complied with the current laws of Uganda. This study was approved by, and carried out in accordance with, the Ethics Committee at the University of York, the University of St Andrews and the University of Neuchatel. The study was purely observational and noninvasive. We followed the disease trans/mission prevention protocols established by the Budongo Conservation Field Station and the Kibale Chimpanzee Project. We complied with the relevant international, national and institutional guidelines for the care and use of animals.

RESULTS

We compared five measures taken from the introduction, build-up, climax and let-down pant hoot phases across two behavioural contexts and in two chimpanzee communities. We provide the descriptive statistics of all measurements per community and context in Table 1.

For the following seven of 18 models, the full model containing context and population did not explain any more variation in the dependent variables than the null model: duration of the introduction phase (LRT: $\chi^2_2 = 5.78$, $P* = 0.083$), duration of the build-up phase (LRT: $\chi^2_2 = 5.78$, $P* = 0.083$), duration of the climax phase (LRT: $\chi^2_2 = 4.10$, $P* = 0.154$), mean duration of build-up elements (LRT: $\chi^2_2 = 2.80$, $P* = 0.278$), mean duration of let-down elements (LRT: $\chi^2_2 = 4.58$, $P* = 0.130$), number of elements in the introduction phase (LRT: $\chi^2_2 = 1.87$, $P* = 0.415$) and rate of build-up elements (LRT: $\chi^2_2 = 5.62$, $P* = 0.083$). Instead, for 11 models, we found that the independent variables explained a significant amount of variation in the dependent variables (Table 2).

Context predicted the temporal features of pant hooting in ten models. During travelling, chimpanzees were more likely than when feeding to produce longer let-down phases (Table 2, Fig. 2a), shorter introduction elements (Table 2, Fig. 2b), shorter climax elements (Table 2, Fig. 2c), more build-up elements (Table 2, Fig. 2d), more let-down elements (Table 2, Fig. 2e), introduction elements at a higher rate (Table 2, Fig. 2f) and climax elements at a higher rate (Table 2, Fig. 2g) and to produce the build-up phase (Table 2, Fig. 2i).

There were community differences in the presence of the build-up phase: Sonso chimpanzees were more likely to produce the build-up than Kanyawara males (Table 2, Fig. 2j). There was an interaction between community and context in terms of how these two variables predicted the presence of the let-down phase (Table 2, Fig. 2k): Sonso males were more likely to produce it during travelling (LRT: $\chi^2_2 = 32.68$, $P < 0.001$), whereas its production was not significantly affected by the context in Kanyawara (LRT: $\chi^2_2 = 3.51$, $P = 0.061$). There was also an interaction between community and context in terms of how these variables predicted the production rate of let-down elements (Table 2, Fig. 2h): Sonso

Table 1
Mean ± SD for continuous variables, proportion for binary variables and count for the presence of phases

Community	Kanyawara		Sonso	
Context	Travel	Feed	Travel	Feed
Introduction duration	3.91 ± 1.71	4.50 ± 1.72	5.15 ± 2.23	5.46 ± 2.14
Build-up duration	2.91 ± 1.56	2.62 ± 1.38	2.35 ± 1.17	2.04 ± 0.91
Climax duration	1.53 ± 0.96	1.42 ± 0.68	1.37 ± 0.67	1.50 ± 0.77
Let-down duration	1.54 ± 1.13	0.86 ± 0.51	1.50 ± 1.14	0.67 ± 0.52
Mean duration of introduction elements	0.54 ± 0.23	0.63 ± 0.28	0.59 ± 0.30	0.61 ± 0.28
Mean duration of build-up elements	0.23 ± 0.05	0.25 ± 0.08	0.27 ± 0.07	0.26 ± 0.07
Mean duration of climax elements	0.59 ± 0.25	0.72 ± 0.25	0.64 ± 0.31	0.73 ± 0.33
Mean duration of let-down elements	0.23 ± 0.08	0.24 ± 0.04	0.23 ± 0.04	0.23 ± 0.06
No. of introduction elements	4.45 ± 2.01	4.78 ± 2.17	5.45 ± 2.90	5.51 ± 2.60
No. of build-up elements	6.93 ± 3.83	5.94 ± 3.33	4.98 ± 2.56	4.69 ± 2.30
No. of climax elements	2.10 ± 1.14	1.75 ± 0.77	1.84 ± 0.79	1.88 ± 0.94
No. of let-down elements	3.85 ± 2.83	2.19 ± 1.03	3.70 ± 2.49	1.89 ± 1.10
Rate of introduction element	1.20 ± 0.43	1.08 ± 0.39	1.07 ± 0.39	1.01 ± 0.28
Rate of build-up element	2.43 ± 0.51	2.29 ± 0.52	2.18 ± 0.56	2.30 ± 0.48
Rate of climax element	1.56 ± 0.51	1.35 ± 0.55	1.47 ± 0.51	1.35 ± 0.45
Rate of let-down element	2.70 ± 0.64	2.95 ± 0.83	2.70 ± 0.62	3.39 ± 1.09
Presence of build-up (proportion)	41/49 (0.83)	32/56 (0.57)	164/174 (0.94)	116/172 (0.67)
Presence of let-down (proportion)	40/49 (0.82)	43/56 (0.77)	167/174 (0.96)	118/172 (0.69)

Durations are in seconds and rates represent the number of elements produced per second.

Table 2
The relationship between the investigated dependent variables and community, context of production, age and dominance rank of the caller

Independent variable and model number	Estimate	SE	Lower CI	Upper CI	Odds ratio	Lower CI (odds)	Upper CI (odds)	χ^2	P
Model 4: Let-down duration (LRT: χ^2_2 = 51.02, P^* < 0.001)									
Intercept	1.330	0.133	1.193	1.963	4.840	3.243	7.222		
Community	−0.005	0.250	−0.476	0.466	0.995	0.610	1.622	0	0.983
Context	−0.763	0.104	−0.970	−0.563	0.466	0.380	0.572	53.675	**<0.001**
Age	−0.020	0.091	−0.191	0.151	0.980	0.820	1.171	0.049	0.824
Rank	−0.072	0.100	−0.275	0.149	0.930	0.765	1.131	0.524	0.469
Model 5: Mean introduction element duration (LRT: χ^2_2 = 11.60, P^* = 0.007)									
Intercept	0.579	0.070	0.445	0.713	1.784	1.554	2.047		
Community	0	0.089	−0.170	0.169	1.000	0.841	1.189	0	0.998
Context	0.085	0.025	0.036	0.132	1.089	1.038	1.143	12.068	**0.001**
Age	−0.002	0.027	−0.055	0.051	0.998	0.945	1.053	0.007	0.933
Rank	0.035	0.030	−0.022	0.093	1.036	0.977	1.098	1.363	0.243
Model 7: Mean climax element duration (LRT: χ^2_2 = 23.61, P^* < 0.001)									
Intercept	0.604	0.068	0.475	0.732	1.829	1.602	2.088		
Community	0.019	0.084	−0.140	0.178	1.020	0.865	1.201	0.053	0.817
Context	0.143	0.029	0.085	0.199	1.154	1.090	1.221	24.292	**<0.001**
Age	0.028	0.028	−0.024	0.082	1.029	0.974	1.087	1.047	0.306
Rank	0.050	0.031	−0.009	0.109	1.051	0.989	1.118	2.578	0.108
Model 10: No. of build-up elements (LRT: χ^2_2 = 7.80, P^* = 0.036)									
Intercept	1.708	0.123	1.451	1.950	5.516	4.339	7.014		
Community	−0.095	0.151	−0.398	0.220	0.910	0.676	1.224	0.390	0.532
Context	−0.149	0.055	−0.258	−0.041	0.861	0.773	0.960	7.277	**0.007**
Age	0.019	0.052	−0.084	0.124	1.019	0.921	1.128	0.129	0.719
Rank	−0.077	0.057	−0.190	0.048	0.926	0.828	1.035	1.847	0.174
Model 12: No. of let-down elements (LRT: χ^2_2 = 63.95, P^* < 0.001)									
Intercept	1.330	0.133	1.071	1.603	3.780	2.912	4.907		
Community	−0.035	0.164	−0.375	0.303	0.965	0.700	1.331	0.046	0.829
Context	−0.611	0.077	−0.749	−0.463	0.543	0.466	0.632	62.253	**<0.001**
Age	−0.030	0.062	−0.149	0.086	0.970	0.860	1.095	0.240	0.624
Rank	−0.039	0.066	−0.177	0.092	0.962	0.844	1.096	0.340	0.560
Model 13: Introduction rate (LRT: χ^2_2 = 9.81, P^* = 0.015)									
Intercept	1.166	0.104	0.969	1.364	3.211	2.616	3.940		
Community	−0.023	0.133	−0.274	0.229	0.977	0.754	1.267	0.030	0.862
Context	−0.105	0.033	−0.169	−0.039	0.900	0.843	0.961	9.920	**0.002**
Age	−0.038	0.040	−0.113	0.038	0.963	0.891	1.041	0.914	0.339
Rank	−0.017	0.043	−0.099	0.064	0.042	0.904	1.069	0.167	0.683
Model 15: Climax rate (LRT: χ^2_2 = 21.20, P^* < 0.001)									
Intercept	1.537	0.097	1.354	1.720	4.650	3.848	5.620		
Community	−0.040	0.118	−0.262	0.182	0.961	0.763	1.210	0.116	0.733
Context	−0.225	0.048	−0.316	−0.128	0.798	0.727	0.877	22.165	**<0.001**
Age	−0.030	0.041	−0.109	0.047	0.970	0.895	1.051	0.556	0.456
Rank	−0.096	0.046	−0.184	−0.008	0.908	0.829	0.995	4.311	**0.038**
Model 16: Let-down rate (LRT: χ^2_3 = 32.36, P^* < 0.001)									
Intercept	2.726	0.160	2.425	3.022	15.275	11.158	20.912		
Community	−0.020	0.189	−0.369	0.331	0.980	0.676	1.421	1.968	0.161
Context	0.092	0.187	−0.260	0.473	1.096	0.760	1.582	26.648	<0.001
Age	−0.087	0.067	−0.210	0.037	0.917	0.804	1.045	1.680	0.195
Rank	−0.069	0.070	−0.204	0.062	0.933	0.814	1.070	0.971	0.324
Community*context	0.539	0.218	0.121	0.962	1.715	1.120	2.627	6.147	**0.013**
Model 17: Build-up presence (LRT: χ^2_2 = 28.98, P^* < 0.001)									
Intercept	1.916	0.506	0.669	2.951	6.791	2.518	18.316		
Community	1.429	0.612	0.121	2.705	4.176	1.257	13.872	5.447	**0.020**
Context	−1.621	0.333	−2.252	−0.788	0.198	0.103	0.380	23.623	**<0.001**
Age	0.292	0.217	−0.222	0.683	1.340	0.876	2.048	1.823	0.177
Rank	−0.555	0.269	−1.101	−0.014	0.574	0.339	0.972	4.271	**0.039**
Model 18: Let-down presence (LRT: χ^2_3 = 49.82, P^* < 0.001)									
Intercept	2.090	0.489	1.192	3.163	8.087	3.104	21.067		
Community	1.160	0.646	−0.149	2.430	3.189	0.899	11.311	0.002	0.961
Context	−0.807	0.573	−2.001	0.294	0.446	0.145	1.370	28.461	<0.001
Age	−0.455	0.150	−0.765	−0.145	0.634	0.472	0.852	9.159	**0.002**
Rank	−0.376	0.184	−0.764	−0.004	0.687	0.479	0.985	4.172	**0.041**
Community*context	−1.754	0.727	−3.189	−0.321	0.173	0.042	0.719	5.821	**0.016**

Shown are the results of models where the full-null model comparison was significant are shown. Interactions are indicated with an asterisk and significant results are in bold.

males produced let-down elements at higher rates during feeding (LRT: χ^2_2 = 30.08, P < 0.001), whereas the rate was not affected by the context in Kanyawara (LRT: χ^2_2 = 0.70, P = 0.403).

In addition, in both communities, low-ranking males were more likely to produce the build-up and let-down phases than high-ranking males, and younger males were more likely to produce the let-down phase than older males (Table 2).

DISCUSSION

We examined whether chimpanzees from two wild populations produced pant hoots differently in terms of their temporal features in two different contexts. Of 18 models, an interaction between the context of call production and community was found in only two models. In contrast, we found contextual differences in calling
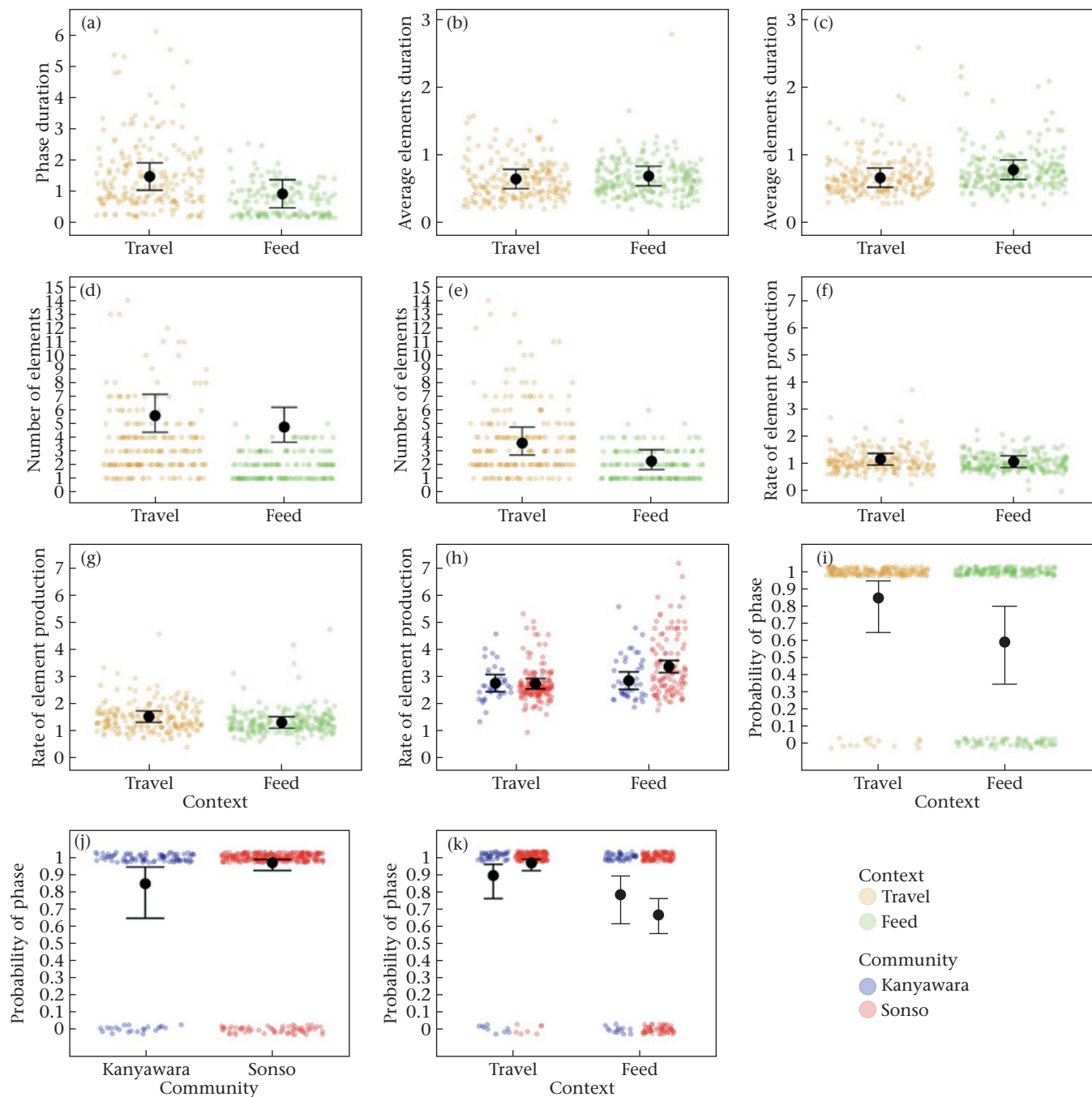
Figure 2. Relationship between the dependent and the significant independent variables in the statistically significant models (full-null comparisons). (a) Model 4: Let-down; (b) model 5: Introduction; (c) model 7: Climax; (d) model 10: Build-up; (e) model 12: Let-down; (f) model 13: Introduction; (g) model 15: Climax; (h) model 16: Let-down; (i) model 17: Build-up; (j) model 17: Build-up and (k) model 18: Let-down. Model estimates are displayed with 95 % confidence intervals. Dots represent raw data.

shared by both communities in eight models. In addition, we found between-community differences in pant hooting independent of context in one model. Together, these results show that, overall, context-dependent calling is similar between the two chimpanzee populations while population differences, although present, are less prevalent.

Despite a number of mammalian and avian species modifying the temporal structure of their calls depending on the context of production (Demartsev et al., 2016; Galeotti et al., 1997; Koren & Geffen, 2009; Rehsteiner et al., 1998), little is known about

between-population differences in this respect. The temporal features of chimpanzee pant hooting show a considerable within-individual variation (Fedurek, Schel, & Slocombe, 2013, 2017), making them suitable signals for encoding contextual and population information. Indeed, we found several temporal features of pant hooting that were mediated by the behavioural context in the same way in both populations. Pant hoots produced in the travelling context differed from those produced in the feeding context in several temporal features, such as having longer let-down phases, shorter introduction and climax elements, more build-up and let-

down elements and introduction and climax elements produced at a higher rate. These results are consistent with previous research on the impact of context on the temporal structure of chimpanzee pant hoots, including the omission of specific phases (Fedurek, Zuberbühler, & Dahl, 2016; Notman & Rendall, 2005; Soldati et al., 2022). However, our study additionally shows that the temporal features of all four phases are affected by the behaviour of the caller. The context-dependent aspects of pant hooting ranged from relatively subtle features, such as element duration, to more pronounced ones, such as inclusion or omission of a phase altogether. This suggests that information about the context of production is encoded across the entire pant hoot sequence, implying signalling contextual information is an important function of pant hooting.

Since both relatively low-amplitude (introduction, build-up and let down) and high-amplitude (climax) components of pant hooting are context-dependent, information about the context of production can be targeted at both nearby and distant receivers. Contextual information encoded across multiple features and phases within a call sequence may reinforce the transmission of this information similar to how multimodal communication provides redundant information through multiple communication channels to reduce uncertainty (Partan & Marler, 2005). This might be especially beneficial when communicating to group members through dense forest vegetation to reduce sound degradation (Waser & Brown, 1986). Our findings complement studies on functionally referential animal calls which largely focused on alarm and food calls targeted at nearby audiences (Scarantino & Clay, 2015), by showing that calls produced in less urgent situations and in long-distance vocal exchanges also have the potential to provide listeners with important information about ongoing behavioural contexts. On the proximate level, the context-dependent differences in the acoustic structure of pant hooting may result from different body movements associated with different activities (that is, travelling versus feeding). Further research is needed to examine if listeners are sensitive to the context-specific acoustic variation within pant hoots in their responses. Since context effects on temporal features were similar in both populations, this aspect of pant hooting seems to be rather conserved across populations, either due to genetic similarities or to specific physiological effects on calling that are tightly linked to a specific behaviour, such as feeding and travelling (e.g. Fedurek, Slocombe, et al., 2016). Indeed, across animal species, including chimpanzees, calling rate typically increases during feeding (Clay et al., 2012; Hauser, 1993). These effects, like individual signatures (e.g. Desai et al., 2022), seem to be more prevalent than group differences even if one does not exclude the other. These consistent context effects on pant hooting largely independent of population appear inconsistent with the view that context-dependent usage of this call is socially learned.

Nevertheless, we did find that two acoustic features related to the context of production differ in the two populations of eastern chimpanzees. Sonso males were more likely than Kanyawara males to omit the let-down phase when feeding compared with travelling. Sonso males also produced the let-down elements at a higher rate in the feeding than in the travelling context, whereas Kanyawara males produced it at comparable rates in both contexts. Given that pant hoot phases are associated with information about the behaviour of the signaller (Fedurek, Zuberbühler, & Dahl, 2016), these two results suggest that the same acoustic component of pant hooting can encode information differently in different populations. Although direct between-population comparisons were previously absent, our results are consistent with previous studies showing that in contrast to Kanyawara males (Clark & Wrangham, 1993; Fedurek et al., 2014), Sonso male chimpanzees tend to omit the let-down phase during feeding (Notman & Rendall, 2005). Our

direct between-site comparison corroborates the idea that production of this phase is both context- and population-dependent. Our results are in line with a recent study showing that two populations of wild bonobos produce whistle, high-hoot call combinations in two different contexts, with the Kokolopori community producing these combinations more often in feeding contexts while the Lui Kotale in resting contexts (Schamberg et al., 2024). It is therefore possible that learning is involved in some aspects of ape call sequence usage, although the underlying learning processes need to be determined, for example, by looking at how its structure changes during ontogeny as a function of exposure to others' calls. It is possible that during development, or as adults, chimpanzees modify acoustic features within the same call type to match that of other community members. The magnitude of such vocal modification is considerably lower than in species, such as humpback whales and dolphins (Garland et al., 2011; Janik, 2014) or songbirds and parrots (Bradbury et al., 2001; Cunningham & Baker, 1983; Wright, 1996), where individuals learn to produce novel songs or call types. Nevertheless, such modification is an example of a simple form of vocal learning commonly found in mammals including primates (Briefer & McElligott, 2012; Fischer et al., 2015; Watson et al., 2015). Importantly, considering the little existing evidence of vocal usage learning in primates, especially in wild populations, our study provides a valuable contribution in this respect.

It is interesting that both community-specific contextual features relate to the let-down phase, indicating that this element of pant hoots may be less stereotyped and more open to vocal learning processes. Indeed, preliminary observations suggest that very immature chimpanzees do not produce the let-down as part of pant hooting (Soldati et al., 2023), opening the possibility for vocal usage learning in this phase. On the ultimate level, subtle acoustic convergence might promote social bonding and cohesiveness within chimpanzee communities (Mitani & Gros-Louis, 1998). Nevertheless, the adaptive significance of such fine forms of learning in chimpanzees and other animal species needs to be investigated further. The use of comparable methods would greatly benefit quantitative as well as qualitative comparisons of vocal learning abilities across species. Similarly, whether the population and context-dependent features of pant hooting are informative to the receivers in their respective populations needs to be determined with playback experiments for example. Considering that most evidence of vocal usage learning in nonhuman animals comes from experimental research (e.g. Curio et al., 1978; Liao et al., 2024; Richards et al., 1984; Stansbury et al., 2015), our observational study on wild chimpanzees provides a promising, ecologically relevant approach to this line of research. Importantly, ecological or genetic differences between the two groups could also account for population differences in pant hoot usage to a certain extent (Mitani et al., 1999), something that also needs to be examined in more detail by future research. Future studies should also address female pant hooting, including between-community or population differences in this respect, a vastly understudied topic.

In addition to the two acoustic features that were linked differently to the context of production in the two populations, we found that pant hoots produced by Sonso chimpanzees were more likely to include the build-up phase than the Kanyawara pant hoots. Because regional or between-population variation in acoustic features of calls is one of the key features of vocal learning, it is possible that the fine temporal structure of chimpanzee pant hooting can be to some extent learned and lead to the appearance of dialects (Crockford et al., 2004; Mitani et al., 1992). Although a previous study did not find between-population differences in pant hooting (Desai et al., 2022), it is important to note that the authors did not include the Budongo population in their analysis and did

not explore context-specific usage. It appears that population differences in pant hooting exist between some but not other populations, which might not be apparent if only a few populations are included in such analysis. The stereotypical structure of pant hooting, with the four distinct phases, is to a large extent innately rooted as in the case of other chimpanzee calls and calls of other nonhuman primate species (Fitch, 2010). However, chimpanzees start producing different components of pant hoots at different life stages (Soldati et al., 2023), suggesting that the group differences in pant hooting found in this study, such as the presence of specific phases, may be shaped during development. Similar processes have been observed in the development of vocal sequences in avian species including the budgerigar, *Melopsittacus undulatus,* and white-crowned sparrows, *Zonotrichia leucophrys nuttalli,* and mammalian species such as bottlenose dolphins (Berg et al., 2012; Jones et al., 2020; Marler, 1970). Although the role of genetic or ecological factors needs to be established before attributing learning to nonhuman animals, it is becoming increasingly apparent that vocal learning is a capacity that is shown by different species to different degrees rather than being a discrete capacity with some species having it and others not (Fischer & Hammerschmidt, 2020; Janik & Knörnschild, 2021; Petkov & Jarvis, 2012).

Since different pant hoot phases are linked to different information (Fedurek, Zuberbühler, & Dahl, 2016), our findings suggest that chimpanzees use some features of context-specific vocal structures in group-specific ways. In this sense, there may be some similarities between chimpanzee and human communication in terms of associating the same sounds with different information in different populations. However, overall, the link between the temporal structure of the signal and context seems to be largely fixed in chimpanzees, as is their vocal repertoire, which contrasts greatly with human communication where individuals learn how to flexibly link different and novel signals to different meanings leading to variation over time and space.

Author Contributions

Josep Call: Writing — review & editing, Supervision, Funding acquisition. **Pawel Fedurek:** Writing — review & editing, Supervision, Writing — original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Katie Slocombe:** Writing — review & editing, Supervision. **Adrian Soldati:** Writing — review & editing, Writing — original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Erik P. Willems:** Writing — review & editing, Visualization, Formal analysis. **Klaus Zuberbühler:** Writing — review & editing, Supervision, Resources, Funding acquisition.

Data Availability

The data set and R code used in the analyses are available at https://1drv.ms/f/s!AmjUIFZKkJFNiiqU_3Elb4QQMwPR?e=dSeROC.

Declaration of Interest

The authors declare no competing interests.

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Appendix

Table A1
Age, dominance rank and number of pant hoots produced by the focal males per community

ID	Community	Age	Rank	No. of pant hoots
AJ	Kanyawara	36*	3	7
BB	Kanyawara	44*	4	3
ES	Kanyawara	16	6	18
FD	Sonso	19−20	6, 7	8
FK	Sonso	14−16, 19−21	3, 5−7	46
HW	Sonso	20−22, 25−27	1, 2	32
KK	Kanyawara	25	1	18
KT	Sonso	21, 22, 25−27	3, 5, 7, 8	25
KZ	Sonso	18−20, 23	10, 11, 13	32
LK	Kanyawara	27, 28*	2	9
MS	Sonso	22−24, 27, 28*	1, 2	23
NK	Sonso	31−33*	4, 6	17
PB	Kanyawara	15	10	1
PG	Kanyawara	22	7	9
PS	Sonso	15−17, 20−22	9, 10−12	59
SM	Sonso	21, 26, 27	5, 10	3
SQ	Sonso	22−24, 27*	3, 4	18
ST	Kanyawara	55*	8	11
TJ	Kanyawara	15	5	22
TU	Kanyawara	50*	9	2
YB	Kanyawara	37*	11	5
ZD	Sonso	17, 18	11	10
ZF	Sonso	31−33, 36*	5, 8, 9	19
ZG	Sonso	16	12	2
ZL	Sonso	18−20, 23−25	7, 8	52

Since data were collected during different time periods, some individuals were sampled at different ages and rank.

* Estimated age.