

The form and function of chimpanzee buttress drumming

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Many animal species use vocal and nonvocal acoustic signals to communicate over large distances. Wild chimpanzees, *Pan troglodytes*, drum on the buttress roots of trees, generating low-frequency sounds that can reach distances of over 1 km. Buttress drumming is produced in bouts of beats and is often accompanied by pant hoots, the species-typical long-distance vocalization. We investigated whether individual differences exist in the acoustic structure of drumming bouts produced by male chimpanzees of the Waibira community in the Budongo Forest in Uganda, and whether individual, contextual and social factors affected their use of drumming. We found individual differences in drumming bouts produced by seven male chimpanzees during travel events as well as in their timing within the pant hoot, and discriminated specific patterns of beats for some chimpanzees. In contrast, we found no evidence for individual differences in the acoustic structure of drumming bouts produced by four males during displays. Together these findings suggest that chimpanzees may be able to choose to encode identity within individual drumming 'signatures'. Chimpanzees drummed less frequently as their party size increased. We found no evidence that the age of the signaller or the presence of preferred social partners, higher-ranking males or females in oestrus affected the use of drumming. These findings suggest there may be flexibility in buttress drumming across social and behavioural contexts and provide support for the hypothesis that, by encoding individual identity, long-distance drumming may be used to facilitate chimpanzee fission–fusion social dynamics.

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Acoustic signals transmit as vibrations through the substrate and/or through the air, and serve a wide range of functions for social and solitary species, including mate competition and attraction, advertisement of location and group cohesion (Caldwell, 2014; Furmankiewicz et al., 2011; McComb, 1991; McComb et al., 2003; Spehar & Di Fiore, 2013). Long-distance, acoustic communication occurs in many animals. When individuals move within their environment they may move out of range of the visual and tactile signals used by conspecifics. In contrast, acoustic signals allow highly flexible information to be shared over both short and substantial distances or through visually dense environments (Brown & Waser, 2017; Garstang, 2004; Mitani & Stuht, 1998).

In addition to vocalizations, a diverse range of species use nonvocal acoustic signals, such as drumming, when communicating

over long distances, suggesting that these signals address specific needs across lineages (Hill, 2008; Randall, 2001, 2010). For example, kangaroo rats, *Dipodomys spectabilis*, drum on the ground to advertise territorial ownership or their presence in neighbouring territories and naked mole-rats, *Heterocephalus glaber*, drum to communicate occupation of subterranean burrows (Randall, 1993, 2001; Sherman et al., 2017). Nonvocal acoustic signals are also common in primates. Many ape gestures have audible components, which make them accessible to out-of-sight individuals or those not paying visual attention (Byrne et al., 2017; Call & Tomasello, 2007; Hobaiter & Byrne, 2011). Nevertheless, nonvocal, long-distance acoustic signals are rare in the natural repertoires of primates (Byrne et al., 2017; Geissmann, 2009; Remedios et al., 2009). Two well-described examples are gorilla chest beating and chimpanzee, *Pan troglodytes*, buttress drumming. Gorilla chest beating may travel up to a kilometre (Salmi & Muñoz, 2020), but is typically employed to advertise gorillas' social status, physical strength and body size to individuals in near proximity (Genty et al., 2009; Schaller, 1963;

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Wright et al., 2021). In contrast, chimpanzee buttress drumming seems to function primarily for long-distance communication and can be heard at well over a kilometre, even in dense forest (Arcadi et al., 1998; Babiszewska et al., 2015; Boesch, 1991).

Wild chimpanzees drum by hitting their hands and feet on a variety of substrates, including the ground, their body and resonant human artefacts present in their environment (Arcadi et al., 1998; Arcadi & Wallauer, 2013; Boesch, 1991). However, they most frequently drum on the flange-like buttress roots that support tree trunks, generating low-frequency sounds that can propagate through the forest further than their long-distance vocalization, the pant hoot, and potentially selecting particular buttresses for their resonant properties (Arcadi et al., 1998; Babiszewska et al., 2015; Crook et al., 1997; Fitzgerald et al., 2022; Kalan et al., 2019).

Chimpanzees drum in agonistic displays during which they may also pant hoot, charge, throw and drag objects and shake branches to signal strength and dominance to nearby individuals (Goodall, 1986; Hosaka, 2015; Muller, 2002). But chimpanzees also frequently drum while travelling and often incorporate drums into pant hoots, apparently facilitating information transfer across dispersed individuals and parties within communities (Arcadi et al., 1998; Babiszewska et al., 2015).

Chimpanzee sociality is regarded as higher-level fission–fusion (Amici et al., 2008; Nishida, 1968). Within a clearly defined community, individuals fission and fuse across smaller parties with fluctuating membership, rarely, if ever, coming together as a whole community at any one time (Anderson et al., 2002; Lehmann & Boesch, 2004). Given their dispersed fission–fusion sociality and a typical habitat of visually dense forest, the ability to signal effectively one's identity, location and perhaps activity over large distances could provide significant benefits when navigating social interactions (Arcadi et al., 1998; Mitani et al., 1996; Notman & Rendall, 2005). For example, being identifiable across long distances could aid allies in facilitating reunions when dispersed or in maintaining awareness of potential rivals.

A number of species' long-distance calls reveal identity. For example, white-crowned sparrows, *Zonotrichia leucophrys*, and gibbons possess individually distinctive songs (Nelson & Poesel, 2007; Oyakawa et al., 2007). Chimpanzee pant hoots encode cues to the signaller's identity in their acoustic structure, and receivers appear to be sensitive to these cues (Fedurek et al., 2016; Kojima et al., 2003; Marler & Hobbett, 1975). The acoustic characteristics of voiced calls are, to some extent, restricted by the shape of the vocal apparatus of the signaller and may also depend on physical characteristics, such as age, body size and health (Crockford et al., 2004; Maciej et al., 2013; Taylor & Reby, 2010). In contrast, while the information potential of a single drumming element, a 'beat', is more restricted than that of a single vocal element of a pant hoot and may depend on the substrate on which it is produced, the use of structured temporal features, such as rhythm, patterns or timing within the pant hoots (Arcadi & Wallauer, 2013; Babiszewska et al., 2015) may allow flexibility in whether to incorporate identity. Chimpanzees have flexible voluntary control over their limbs, shown, for example, in their ability to learn artificial manual signs and in their dexterous use of tools (Jensvold and Gardner, 2000; McGrew, 2010). As a result, they may be able to encode information on individual or group identity, as well as on activity, in the sequential features of drumming beats.

Being individually identifiable through drumming, or any other signal, might be beneficial in some contexts but disadvantageous in others (Hobaiter et al., 2017; Tibbetts & Dale, 2007). Previous studies exploring individual differences in the acoustic structure of male chimpanzee drumming have produced contrasting

results. Drumming bouts produced by chimpanzees in the Taï Forest in Côte D'Ivoire and by the Sonso community in the Budongo forest in Uganda revealed individual differences in the acoustic structure and in the timing of integration within the pant hoot (Arcadi et al., 1998; Babiszewska et al., 2015). In contrast, drumming bouts produced by the Kanyawara community from the Kibale forest in Uganda showed no differences (Arcadi et al., 2004). While the drumming bouts analysed from chimpanzees of Taï and Sonso were produced in the context of travelling, those from Kanyawara were recorded from out-of-sight individuals who were presumed to be travelling but might have been engaged in other activities. As such, these mixed results might reflect differences of sampling effort across behavioural contexts.

To understand whether chimpanzee drumming is individually distinctive, we examined the acoustic structure of drumming bouts in different contexts, as well as the impact of individual, contextual and social factors on the use of this signal by male chimpanzees of the Waibira community of the Budongo Forest in Uganda. First, we investigated the acoustic structure of the drumming bouts and, where combined with pant hoots, their timing within the vocalization. To explore whether the behavioural context influences the acoustic features of drumming, we explored the structure of drumming bouts in two general contexts: while travelling and while displaying. We hypothesized that, when used during travel events, drumming will show individually distinctive features, which may aid spatial coordination between dispersed individuals and parties. In contrast, during displays, we hypothesized that drumming will exhibit no individually distinctive features as displays are mainly directed towards nearby individuals who are already aware of the signaller's identity, and signallers may wish to avoid revealing their identity to potentially competitive out-of-sight eavesdroppers.

We assessed the impact of individual, contextual and social factors on the use of drumming by replicating and extending Babiszewska et al.'s (2015) analysis on the drumming behaviour of male chimpanzees in the neighbouring Sonso community. They found that chimpanzees drum more frequently in the context of travelling and that older males drum more frequently than younger ones. Chimpanzee pant hoots show rank-related patterns, with higher-ranking males signalling more often than low-ranking ones (Clark, 1993; Fedurek et al., 2014). Thus, we predicted that drumming would be used more frequently by older and higher-ranking males because they experience lower costs in advertising their identity and location to out-of-sight individuals. The presence of particular individuals in the party can influence chimpanzees' use of calls (Fedurek et al., 2014; Slocombe et al., 2010; Slocombe & Zuberbuhler, 2007); however, in the Sonso community drumming was not influenced by the social composition of the signaller's party (Babiszewska et al., 2015). Moreover, chimpanzees pant hoot more frequently when allies or close associates are in a nearby party, suggesting that pant hoots may function to maintain contact with, or recruit, specific individuals (Mitani & Nishida, 1993). Given its substantial long-distance potential (Arcadi et al., 1998; Crockford et al., 2004), drumming may also be used similarly to facilitate association with distant group members. We predicted that Waibira chimpanzees would drum more often in the context of travelling, which is when individuals are more likely to make grouping decisions, and when individuals are alone or in small groups in order to recruit or maintain contact with group members. We predicted that, given its apparent use as a primarily long-distance signal, drumming would not be influenced by the immediate audience. By exploring the form and function of chimpanzee buttress drumming, this study contributes to our understanding of nonvocal acoustic signals in primate long-distance communication.

METHODS

Study Site

We collected data between June and July 2019 and between January and March 2020 in the Waibira chimpanzee community of the Budongo Forest Reserve in Uganda. The 793 km² reserve contains 482 km² of medium-altitude and semideciduous tropical rain forest between 1°35' and 1°55'N and 31°08' and 31°42' (Eggeling, 1947). The habituation of the Waibira chimpanzee community started in 2011 and most independent chimpanzees are now habituated to human observation (Samuni et al., 2014). The community is estimated to have a total of 120 individuals with 95 identified members; including at least 22 adult males, nine sub-adult males, 31 adult females, two subadult females and 31 juveniles and infants. Following Reynolds (2005), we categorized individuals above 15 years old or females with infants as adults, individuals between 10 and 15 years old as subadults, those between 5 and 10 years old as juveniles and those younger than 5 years old as infants. Because most adult individuals were born before habituation of the community started, we estimated ages using physical features such as body size, muscle mass, the development of secondary sexual characteristics and other indications of ageing (Reynolds, 2005). Most adult individuals in the neighbouring Sonso community have birth dates that are known to within a few weeks and provided a source of reference for age estimation in this population. The specificity for age estimations varies across maturity, with specific age typically easier to discriminate in immaturity (six focal individuals were first encountered as immature individuals). We provide an indication of estimated accuracy along with individual ages in Table 1.

We considered the sampling bias in our study in relation to the STRANGE framework (Rutz & Webster, 2021; Webster & Rutz, 2020). The size of the Waibira community at ca. 120 individuals is considerably larger than that of most other communities. Typically, chimpanzee communities consist of between 30 and 70 individuals, ranging from seven to 144 individuals with a median of 42 across the three subspecies (Wilson et al., 2014). Party size may be constrained by food competition and their large size may lead them to split into a larger number of parties. The Waibira territory of 11 km² is relatively small compared with other communities (Badihi et al., 2021; Herbiner et al., 2001), which may influence ranging patterns and the use of long-distance communication. As a consequence chimpanzees may use buttress drumming to regulate their fission–fusion dynamics. We discuss our results in relation to those found in a previous study on the neighbouring Sonso

community living in a more typically sized community of around 70 individuals, but who also range within a particularly small territory of 7 km².

Of the 22 adult males, we selected eight focal males for behavioural data collection (1) on the basis of individuals who could be reliably located and followed, and (2) in order to include the full range of social ranks and ages (see next section). While all adult males in the community are habituated, the patterns of male chimpanzee association in this community are distinctive, with central clique(s) and more peripheral satellite individuals (Badihi et al., 2021). Our data may include a bias towards males who associated more often with other individuals, and who were, thus, easier to locate daily. We discuss the possible implications of sampling biases on the use of long-distance communication in our discussion.

Finally, while ad libitum acoustic data were recorded from all available individuals (from 16 of the 22 adult males in the community) the challenges of this type of data collection in the field resulted in a relatively small number of individuals retained per context within our analyses: seven in travel, four in displays. Acoustic analyses require clean recordings with relatively little overlap in signals. We discarded data from acoustic analysis where (1) overlap across individuals prevented reliable discrimination of acoustic information, for example when two males displayed at the same time, (2) drums comprised a single beat alone and (3) the individual contributed fewer than five separate drumming events, to describe reliable patterns of individual identity. These relatively small sample sizes in terms of both number of drums and number of individuals mean we interpret the generalizability of our findings to other individuals with caution, in particular in the context of display.

Focal Behavioural Data Collection

We recorded behavioural data using a focal behaviour sampling method with a bespoke Cybertracker behavioural database application version 3.501 (Altmann, 1974; CyberTracker GPS Field Data Collection System—Home, <http://www.cybertracker.org/>). To explore the effect of individual factors on the use of buttress drumming, we included eight adult males as focal individuals to follow for the duration of the study to include a range of ages (16–34 years; total community range among adult males: 16–44 years) and ordinal linear social ranks (1–24, with 1 representing the alpha male; total community range of adult and subadult males: 1–31) that represent the range present within the community (see Table 1). We calculated for each adult and subadult male chimpanzee in the community ($N = 31$) their social rank via the Elo-rating method using pant grunt vocalizations (Neumann et al., 2011). These vocalizations are given by subordinate individuals towards more dominant ones and are often used to assess linear dominance relationships in a chimpanzee community (Clark, 1993). The hierarchy in a community of chimpanzees can be determined via the Elo-rating method by considering pant grunts in terms of winner–loser interactions (Elo, 1978; Neumann et al., 2011). We calculated Elo-ratings for each pant grunt interaction collected for the field site's long-term data between November 2017 and December 2019. We calculated the rank by averaging the Elo-rating scores across the 3 months prior to the two data collection periods: March–June 2019 for the data collection period June–July 2019 and October–January 2019 for the data collection period January–March 2020. For males with no data available in the 3 months prior to data collection we averaged the data collected in the 3 months prior. We assigned each male a rank from 1 to 31 from the individual with the highest Elo-rating score to the one with the lowest score (Table 1).

Table 1
Focal individual demography and social rank

Focal male	Focal duration	Period 1		Period 2	
		Age (years) ^a	Rank	Age (years) ^a	Rank
BEN (Ben)	36:12	27 ± 2	1	28 ± 2	1
TRS (Tristan)	40:54	33 ± 5	4	34 ± 5	3
ALF (Alf)	19:56	21 ± 1	5	22 ± 1	5
MAC (Macallan)	41:28	21 ± 1	8	22 ± 1	7
SAM (Sam)	17:29	20 ± 1	11	21 ± 1	9
ILA (Ila)	25:26	20 ± 1	16	21 ± 1	13
FID (Fiddich)	24:52	17 ± 1	22	18 ± 1	16
LAF (Lafroig)	15:05	16 ± 1	24	17 ± 1	20

Focal individuals' ($N = 8$) age and rank were calculated at the start of data collection for each period (Period 1: June – July 2019; Period 2: January – March 2020). 'Age' and 'rank' represent the estimated age (years) and social rank (1 = highest; 24 = lowest). 'Focal duration' represents the total observation hours and minutes collected per individual.

^a As the exact year of birth was unknown for adult individuals born before habituation of the community, we provide an indication of estimated accuracy.

We collected observations on the Waibira community between 0600 and 1800 hours. We followed focal males from their location in the early morning to the late afternoon. If more than one potential focal individual was present, we selected the focal individual to follow throughout the day based on availability of data across focal individuals and by opportunity for further ad libitum acoustic data. We then prioritized males with fewer acoustic data available. We preferred males that were already accompanied by other males over solitary males because the chance of obtaining ad libitum recordings of drumming was increased. However, we followed individuals continuously, even where they remained alone. We followed an individual for a whole day, but the data collected could consist of multiple periods if we lost him and found him again. If we lost an individual for more than 1 h, we selected another focal individual. We collected a total of ca. 221 h of behavioural data across 45 days within the study period (see [Table 1](#)).

We kept a continuous record of the focal individuals' behaviour for all behaviour that lasted more than 30 s, which we assigned to one of six general behavioural contexts: feeding, displaying, resting, travelling, other, unknown. Feeding comprised consuming food on the ground, on a feeding tree or on a nonfeeding tree, or arriving at a feeding tree ([Babiszewska et al., 2015](#)). Displaying was a social display that typically included behaviour such as running with piloerection, throwing objects, using gestures or calling while other individuals were located nearby. Travelling comprised moving on the ground or on a tree (e.g. moving in the canopy). Resting occurred when the individual was on the ground or on a tree and was not involved in any other activity (for example self- or social grooming, etc.). Other was recorded when the individual was engaging in another behaviour and Unknown when the individual's location was known but his specific behaviour was not visible. In addition, we defined 'travel events' as when the focal individual was either travelling or resting during ongoing travelling, including pauses on the ground between periods of travelling that lasted for longer than 30 s, but that did not include other activities such as feeding on the ground, self- or social grooming, etc. We continuously recorded the identity of other individuals within a 35 m radius of the focal individual, representing the 'party composition' ([Newton-Fisher, 2004](#)), as well as the presence of females in oestrus. Oestrous level can be estimated by the sexual swellings that female chimpanzees exhibit when they ovulate ([Deschner et al., 2003](#)), which was graded with a score between '0' and '4' by an experienced field assistant familiar with the individuals, with '0' representing the presence of no swelling.

During each focal follow we recorded each communication event that included a pant hoot, pant hoot with drumming or drumming, termed 'long-distance communication', produced by the focal individual when on the ground. Although drumming can occur on different substrates, we restricted drumming data collection to drumming events on buttress roots, which have the resonant properties for effective long-distance communication ([Arcadi et al., 1998](#)). As a result, we recorded long-distance communication events only when males were on the ground and had the opportunity to deploy either signal type.

We examined all party compositions and marked whether the preferred social partner of an individual male was present. We assessed the preferred social partners of each focal individual by calculating three indexes using the field site's long-term focal observational data collected on associations, grooming and proximity in the 12 months prior to the data collection periods: 'grooming rate index' (GR_{AB}), 'party level association index' (PLA_{AB}), and the 'nearest-neighbour' spatial proximity index (NN_{AB}) ([Babiszewska et al., 2015](#); [Schel et al., 2013](#)). Following [Babiszewska \(2015\)](#), we considered preferred social partners those males having

values of at least two of the three indexes (GR_{AB} , PLA_{AB} , NN_{AB}) greater than one-quarter of a standard deviation of the mean.

Grooming rate index (GR_{AB}) represents the rate at which a male (B) groomed with the focal individual (A) in the period examined. We determined this index using all grooming events between the focal individual and other males collected when the focal individual was being followed to calculate the following proportion:

$$GR_{AB} = \frac{A_f B_g}{A_m}$$

$A_f B_g$ is the duration of grooming (min) in which the focal individual (A) and another male (B) were grooming each other when the focal individual was being followed. A_m is the total focal observation time (min) for the focal individual for the period June 2018 to May 2019 and January to December 2019.

Party level association index (PLA_{AB}) represents the rate at which a male (B) was in the focal individual's (A) party ([Cairns & Schwager, 1987](#)). We determined this index using 15 min scan samples of the identity of all males in the focal individual's party available in the long-term data to calculate the following proportion:

$$PLA_{AB} = \frac{P_{AB}}{P_A + P_B - P_{AB}}$$

P_{AB} represents the number of parties in which A and B were together, P_A the number of parties with A and P_B the number of parties with B.

Nearest-neighbour index (NN_{AB}) represents the rate at which a male was the closest to the focal individual when the focal individual was being followed. We determined this index using the 15 min scan samplings of the identity of the males in the party that were closest to the focal individual available in the long-term data to calculate the following proportion:

$$NN_{AB} = \frac{A_f B_{nn}}{A_h}$$

$A_f B_{nn}$ is the number of 15 min scans in which a male (B) was the nearest neighbour to the focal individual (A) when the focal individual was being followed. A_h is the total focal observation time (h) for A for the period June 2018 to May 2019 and January to December 2019.

Acoustic Data Collection

We filmed and recorded drumming events by any adult male ad libitum with a Sennheiser MKE 400 directional microphone (audio sample rate: 44.1 kHz; 16 bits per sample) mounted on a Panasonic HC-V700 video-camera. We then transferred videos and audio recordings to a MacBook Pro and converted them to WAV audio files with Wondershare UniConverter Software 10.5.0 before conducting acoustic analyses with PRAAT software version 6.0.50 ([Boersma & Weenink, 1992-2022](#)).

Acoustic Data Coding

In addition to the ad libitum audio recordings of drumming bouts collected during the study period, we extracted drumming bouts from archival audio and video records of chimpanzee communication collected between 2012 and 2020. Only drumming bouts in which all beats could be clearly discriminated were retained for analyses. We defined a 'Drumming bout' as a series of beats produced by the same individual by hitting the buttress roots

Table 2
Acoustic measures used to examine the acoustic structure of drumming bouts

Measure	
Number of beats	Number of beats present in a drumming bout
Bout duration (s)	Length of a drumming bout measured from the middle of the first beat to the middle of the last beat in the bout (see Fig. 3)
Mean interbeat interval (s)	Mean duration of all interbeat intervals within a drumming bout. Each interbeat interval was measured from the middle of the first beat to the middle of the second beat
Shortest interbeat interval (s)	The shortest interbeat interval in a drumming bout
Longest interbeat interval (s)	The longest interbeat interval in a drumming bout

Interbeat interval = latency between two consecutive beats.

of one tree with hands and/or feet (following Arcadi & Wallauer, 2013). We coded five acoustic measures for analysis of acoustic structure: number of beats, bout duration, mean interbeat duration, shortest interbeat interval, longest interbeat interval (Table 2).

Pant hoots have a compound structure of different vocal elements combined into up to four subsequent phases (Goodall, 1986; Marler & Hobbett, 1975): introduction, build-up, climax and let-down. For all drumming bouts we noted the start and end points of the drumming bout relative to the phases of any accompanying pant hoot (Arcadi, 1996; Fedurek et al., 2016; Goodall, 1986; see Fig. 1).

Statistical Analyses

Individual variation in the acoustic structure of drumming

Because previous studies suggest that drumming while displaying may include a distinct function compared to drumming in

other contexts (Babiszewska et al., 2015; Goodall, 1986), we distinguished drumming bouts during displays from those during travel events in our analyses of acoustic structure. We recorded too few drumming bouts in the context of feeding or other behaviours outside of travel and display to conduct acoustic analyses. We collected and extracted the acoustic information for drumming bouts produced by 16 adult males. However, to ensure that individual drumming styles represented an individual, we included in the statistical analyses only those individuals with at least five drumming bouts with two or more beats.

We used discriminant function analyses (DFA) to assess whether the acoustic measures of drumming bouts were sufficient to discriminate individual identity. A total of 105 drumming bouts recorded during travel events from seven individuals were included in the first DFA, of which five individuals were also focal individuals (travel event; Appendix Table A1). A total of 36 drumming bouts recorded while displaying from four individuals were included in the second DFA, all of whom were also focal individuals (display; Appendix Table A1). We used discriminant function scatterplots to explore visually which individuals' drumming styles differed, by looking at the distances between individual centroids (following Field 2005).

Prior to conducting the DFA, we checked whether within-individual residuals met the assumption of normality and whether between-individual data met the assumption of homogeneity of variance for all acoustic measures. Shapiro–Wilk's test revealed that within-individual residuals were normally distributed for five of 19 individuals' acoustic measures for drumming bouts produced while displaying, and for 10 of 35 individuals' acoustic measures for drumming bouts produced during travel events (see Appendix Table A2). Levene's test revealed that between-individual variance was homogeneous for four of five acoustic measures for drumming bouts produced during displays and for one of five measures for drumming bouts produced during

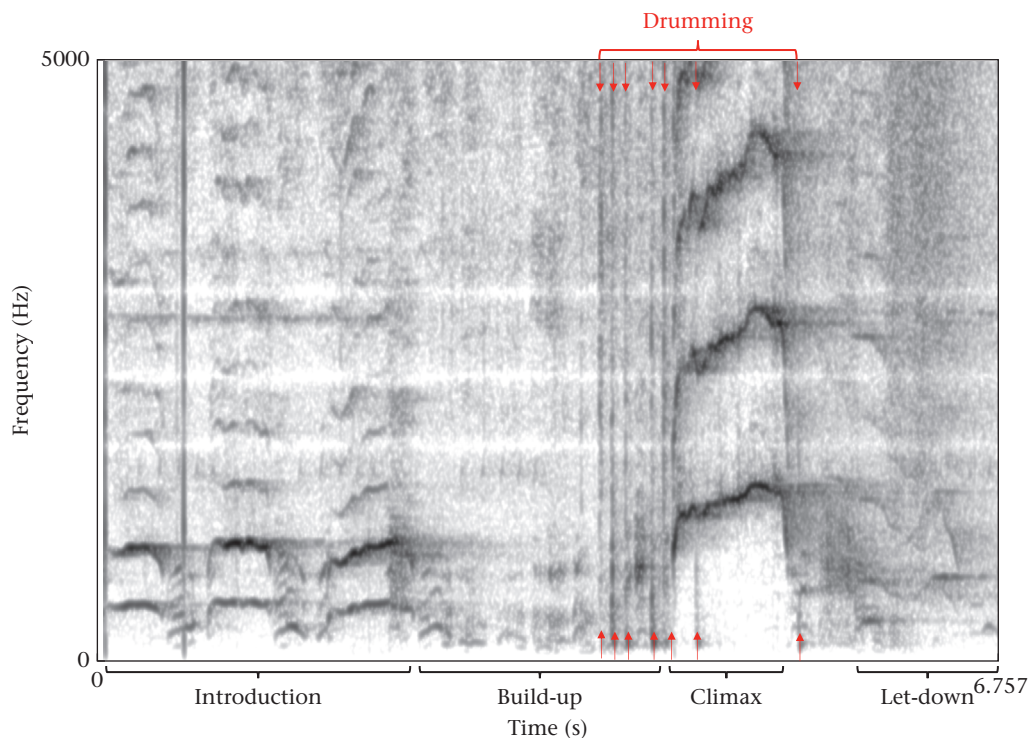


Figure 1. Spectrogram of a drumming bout produced within a pant hoot vocalization. The drumming bout starts in the build-up phase of the pant hoot and ends after the climax phase and is composed of seven beats. The 'Introduction', 'Build-up', 'Climax' and 'Let-down' phases are indicated by the black brackets. The drumming bout is indicated by the red bracket and the drumming beats by the red arrows.

travel events (see [Appendix Table A3](#)). The criterion P value for all statistical analyses was set at $\alpha = 0.05$ and DFAs were conducted on IBM SPSS version 24 (IBM, Armonk, NY, U.S.A.).

We further explored whether individuals use specific drumming patterns more frequently than others by plotting and visually inspecting the beats of each drumming bout acoustically analysed (see Results). Moreover, we explored whether individuals differed in the most frequent range of duration(s) of the drumming bouts' interbeat intervals by creating cumulative probability plots of all interbeat intervals used by each individual (See Results). Lastly, to explore whether individuals varied in the timing of their drumming bouts in the pant hoot, we calculated the proportion of times each individual started and ended the drumming before, during and after the climax phase of the pant hoot. We only calculated these for drumming bouts produced during travel events, as the majority of drumming bouts collected during displays were produced without a pant hoot. We produced all plots in R version 4.0.2 ([R Core Team, 2020](#)).

Effect of individual, social and contextual factors on drumming

To understand whether the drumming behaviour of the Waibira chimpanzees depends on individual, social and contextual variables, we fitted three generalized linear mixed models ([Baayen, 2008](#)) with a binomial error structure and logit link function. In addition, to compare more directly the drumming behaviour of Waibira chimpanzees to that described in an earlier study on the neighbouring Sonso community by [Babiszewska et al. \(2015\)](#), we ran two other simplified models that more closely replicated their statistical analyses (see [Appendix](#)). In all models the binary response variable represented whether a focal chimpanzee produced a long-distance communication while on the ground that included drumming. Drumming alone or pant hoot with drumming was coded as Drum = '1' and a pant hoot alone as Drum = '0'. We included only focal individuals from which a minimum of four of these communications were collected. Because the sample was composed of signals collected from the same individuals, to avoid pseudoreplication, we fitted the identity of the focal chimpanzee producing the communication as a random effect. We z-standardized all covariates, i.e. age, rank and group size, before running the analyses. Before z-standardizing it, we scaled rank from '0', representing the lowest-ranking male, to '1', representing the highest-ranking male, for ease of interpretation of the directionality of the results. To keep the Type I error rate at the 5% nominal level, we built maximal models in which we included all random slopes that were theoretically identifiable ([Barr et al., 2013](#); [Schielzeth & Forstmeier, 2009](#)). We dummy coded and centred all categorical fixed effects before including them in the random slopes; fixed effects were context, period, presence of females in oestrus, presence of preferred social partners and presence of higher-ranking males.

To explore the effect of the fixed effects we used a likelihood ratio test to compare the full model with the null model without all fixed effects but including the control fixed effects and all random effects ([Dobson & Barnett, 2018](#)). We checked for multicollinearity using variance inflation factors (VIFs; [Field et al., 2012](#)). We assessed model stability by comparing the full model estimates with those from models from which random effects were removed one at a time ([Nieuwenhuis et al., 2012](#)). We fitted all models using the statistical software R version 4.0.2 with the package lme4 version 1.1–23 ([Bates et al., 2014](#); [R Core Team, 2020](#)). We computed effect sizes using the function `r.squaredGLMM` of the package MuMIn version 1.43.17 ([Bartoń, 2020](#)). We computed P values of the fixed effects with likelihood ratio tests comparing the full model with the respective reduced models using the `drop1` function of the package stats version 4.0.2 and P values for separate

levels of context with the `cftest` function of the package multcomp ([Hothorn et al., 2008](#); [R Core Team, 2020](#)). We present the bootstrapped 95% confidence intervals.

Do age, rank, context and group size influence drumming?

The sample consisted of 273 long-distance communications collected from eight focal chimpanzees. We entered age, social rank of the focal individual and the behavioural context of the communication as well as the number of individuals in the focal individual's party, termed 'group size', as fixed effects, while the period of data collection, coded as '1' for June–July 2019 and '2' for January–March 2020, as a control fixed effect. We included the theoretically identifiable random slopes for age, rank, group size, period and context within focal individual. We removed correlations among intercepts and slopes because some were unidentifiable, as indicated by absolute correlation parameters being close to 1/–1 ([Matuschek et al., 2017](#)). All fixed effects had VIFs close to 1.0 except for age and rank, which had VIFs of 2.278 and 2.480, respectively, suggesting they were correlated with one another. The model was unstable with respect to the contexts of feeding and display (see Results).

Do oestrous females and preferred social partners affect drumming?

The sample size consisted of 273 long-distance communications collected for eight focal chimpanzees. We included the fixed effects of presence of females in oestrus and presence of preferred social partners in the focal chimpanzee's party. Control fixed effects included the social rank of the focal chimpanzee, the behavioural context of the communication and the number of individuals in the focal individual's party, termed 'group size'. We included the theoretically identifiable random slopes for presence of females in oestrus, presence of preferred social partners, rank, context and group size within focal individual. We removed the correlations among intercepts and slopes as some were unidentifiable being close to 1 or –1 ([Matuschek et al., 2017](#)). All VIFs were close to 1, suggesting the variables were not correlated. The model was unstable with regard to the contexts display and feeding. As mentioned above, for ease of comparison with the findings of [Babiszewska et al. \(2015\)](#) on the neighbouring Sonso community, we ran an additional model for the effect of the presence of females in oestrus and of preferred social partners on the use of drumming, which more closely replicated their analyses. This additional model differed in that it did not include the control fixed effects of rank, context or group size (see [Appendix](#) for full details and the results of the additional model).

Do higher-ranking males affect drumming?

We excluded the highest-ranking male in the community from these analyses because he had no males of higher rank to him. As a result, the sample size consisted of 216 long-distance communications collected for seven focal chimpanzees. We entered as a fixed effect whether higher-ranking males were present or not in the focal chimpanzee's party. We entered the social rank of the focal chimpanzee, the behavioural context of the communication and the number of individuals in the focal individual's party, termed 'group size', as control fixed effects. We included the theoretically identifiable random slopes for presence of higher-ranking males, rank, context and group size within focal individual. We removed the correlations among intercepts and slopes as some were unidentifiable being equal to 1 or –1 ([Matuschek et al., 2017](#)). All VIFs were close to 1, suggesting the variables were not correlated. The model was unstable for the contexts of feeding and display. Again, to compare better our results with those of [Babiszewska et al. \(2015\)](#), we ran an additional model exploring the effect of the presence of higher-ranking males on the use of drumming, which

more precisely replicated their analysis. This additional model differed in that it did not include the control fixed effects of rank, context and group size (see Appendix for full details and the results of the additional model).

Ethical Note

Data collection followed the ASAB/ABS guidelines for the treatment of animals and the Code of Best Practices for Field Primatology established by the International Primatological Society. Permission was granted by the Ugandan National Council for Science and Technology (permit NS179), the Ugandan Wildlife Authority and the Budongo Conservation Field Station. Ethical approval for the study ('Gestural Communication in Wild Chimpanzees in Budongo, Uganda') was given by the School of Psychology and Neuroscience of the University of St Andrews Ethics Committee on 5 May 2019. We ended data collection on 17 March 2020 due to the covid-19 pandemic to mitigate any risk of disease transmission to the study animals through our continued presence.

RESULTS

Individual Variation in Acoustic Structure of Travel Drumming

The first DFA conducted on drumming bouts produced during travel events revealed five discriminant functions (DFs). The first two functions explained a considerable amount of variation in the acoustic structure of the drumming bouts, with the first explaining 62% of the variance (canonical $R^2 = 0.716$) and the second 31% of

the remaining variance (canonical $R^2 = 0.587$). These two DFs significantly discriminated the drumming bouts produced by the seven individuals (DF 1: $\Lambda = 0.284$, $\chi^2_{30} = 123.463$, $P < 0.001$; DF 2: $\Lambda = 0.582$, $\chi^2_{20} = 52.998$, $P < 0.001$).

The discriminant function scatterplot clearly discriminated four individuals, BEN, URS, MAC and TRS, from a cluster of the other three individuals DAU, ALF and ILA (Fig. 2). Along DF 1, TRS's centroid is the most distant from those of the other individuals, followed by MAC's centroid. Along DF 2, BEN's centroid is most distant, separated from URS, MAC and TRS, who are again separated from DAU, ILA and ALF. In general, DAU, ALF and ILA show considerable overlap in the scatterplot, represented by the proximity of their centroids on both DFs, and which is most likely caused by the frequent use of double beats by all three individuals (Fig. 3).

Visual inspection of the drumming bouts further revealed how some individuals differed in the patterns used in the drumming bouts produced during travel events (Fig. 3). While DAU, ILA and ALF were difficult to discriminate within the DFs produced in the DFA, ALF almost exclusively produced drumming bouts with double beats whereas ILA frequently produced double beats or started and/or finished longer drumming bouts with a double beat. This subtle distinction can also be seen in the cumulative probability plot in Fig. 4, which suggests a much wider use of interbeat intervals and a second zone of preference for a longer interval in ILA compared to ALF. Visual inspection of Fig. 3 also shows clear patterns for BEN, who often produced double beats followed by one or more single beats more distantly separated, and for TRS, who generally produced very long drumming bouts of regularly interspaced beats.

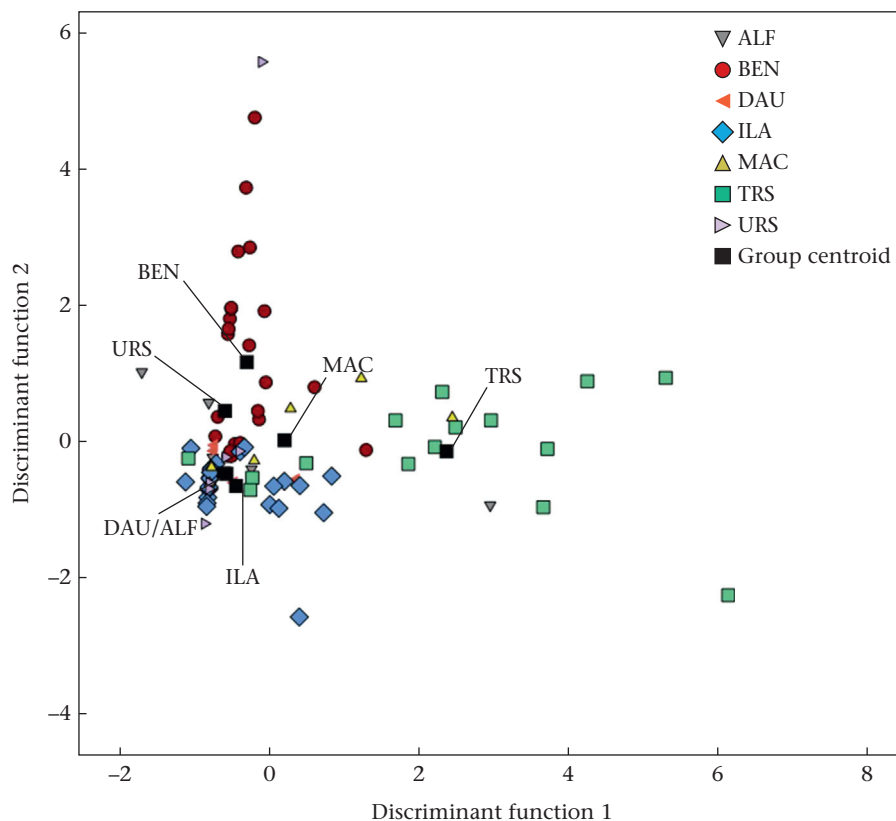


Figure 2. Scatterplot showing the distribution of the drumming bouts produced by the individual chimpanzees on two discriminant functions. The drumming bouts displayed were produced by seven individuals during travel events. The black squares represent the centroids of each group, here each one an individual male. The horizontal distance between the centroids represents the discrimination of drumming bouts produced by the individuals on discriminant function 1, while the vertical distance represents the discrimination of drumming bouts produced by the individuals on discriminant function 2. The greater the distance is the more dissimilar the individuals are. Note that ALF's centroid is hidden behind DAU's centroid.

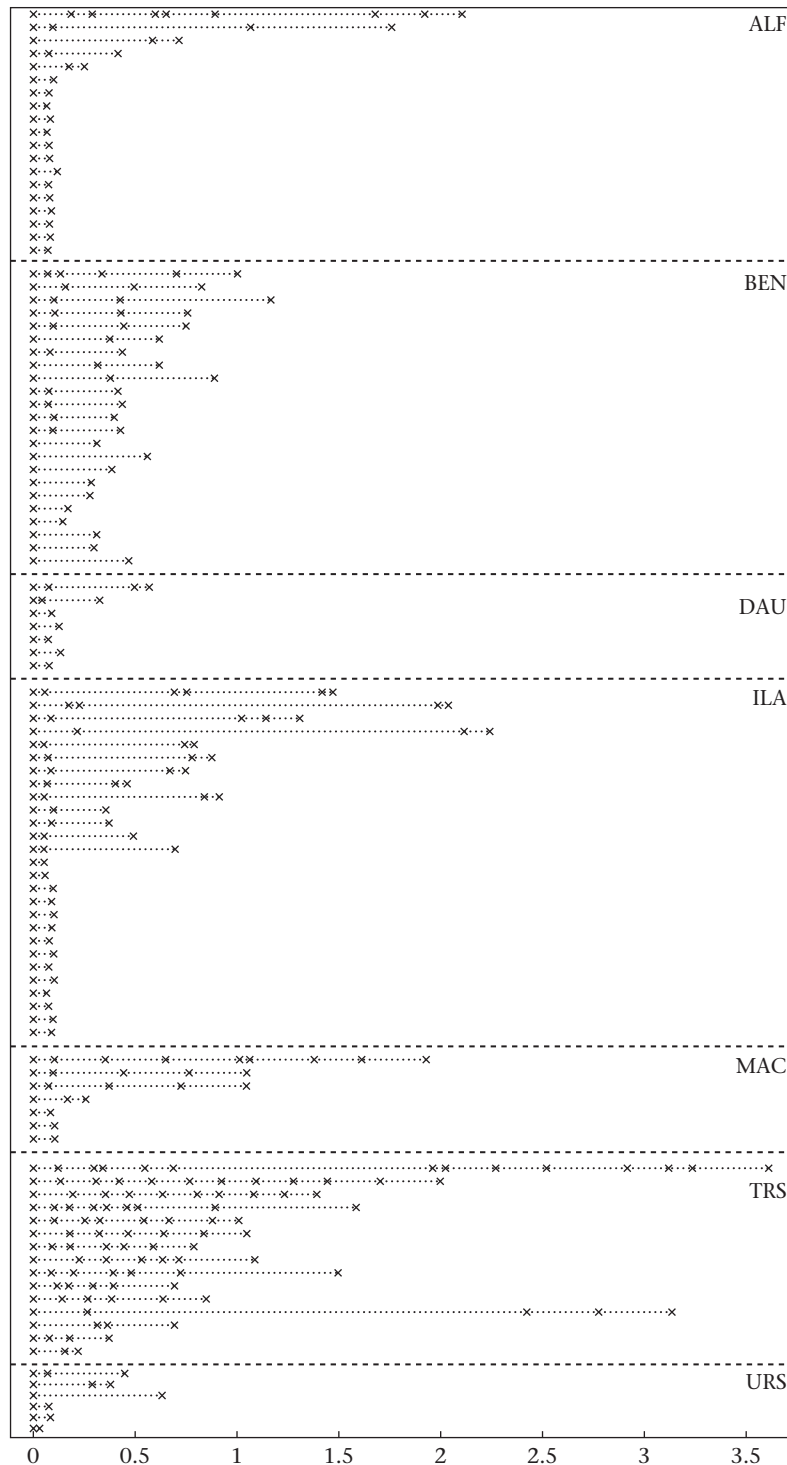


Figure 3. Visualization of the drumming bouts produced by the individual chimpanzees. The drumming bouts displayed were produced by seven individuals during travel events. The rows represent each drumming bout and 'x' represents each drumming beat within the bout. The x axis shows the duration (s) of drumming bouts since the onset of the first beat. The y axis represents the individuals producing the drumming bouts.

Fig. 4 shows the cumulative likelihood and range of durations of interbeat intervals produced by a particular individual, allowing us to describe particular zones of preferred use in interbeat intervals. This figure shows that some individuals produced particular interbeat intervals more frequently than others. Four individuals appeared to have a single zone of preference, indicated by a single steep step, but which occurred at different durations of the

interbeat interval. Again the four individuals clearly separated in the DFA showed distinctive use of interbeat intervals here. BEN's total range varied from 0.06 to 0.74 s, but included two clear zones of preference (0.06–0.13 s and 0.30–0.40 s). MAC's total range varied from 0.05 to 0.36 s and also included two clear zones of preference, the first overlapping with BEN's but the second at a shorter and tighter interval (0.07–0.13 s and 0.28–0.32 s). URS's

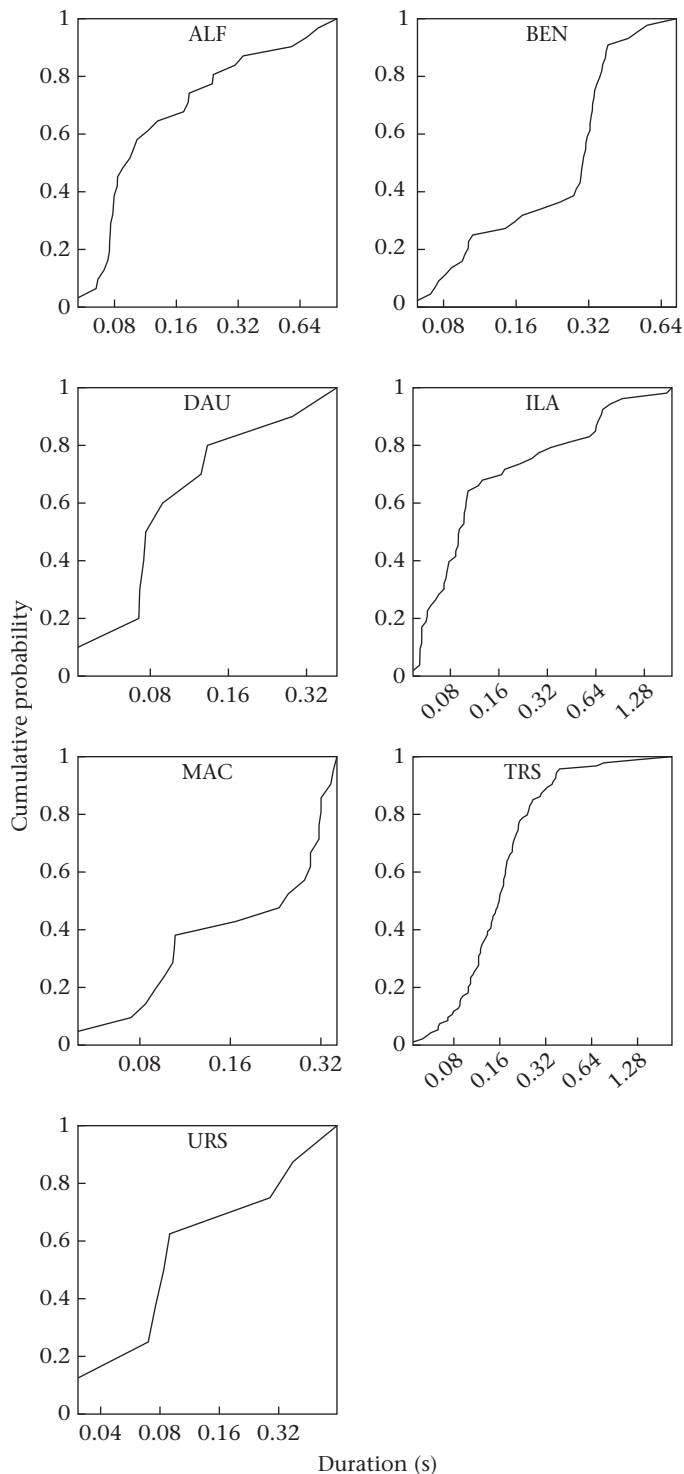


Figure 4. Cumulative probability plots of interbeat interval durations within the drumming bouts produced by the individual chimpanzees. The drumming bouts were produced by seven individuals during travel events. The x axes show the durations (s) of the interbeat intervals for each individual. The y axes show the cumulative probability with which these intervals were produced by each individual. Lines show the use across the full range of intervals, steep vertical 'steps' show frequent use of interbeat intervals at that specific duration and plateaux show limited use of interbeat intervals at that duration.

total range varied from 0.03 to 0.63, again with two apparent zones of preference (0.07–0.10 s and 0.38–0.40 s). TRS's interbeat intervals showed the widest range, from 0.04 to 2.15 s, but were concentrated in the 0.10–0.35 s zone. Of the three individuals that

were more difficult to discriminate in the DFA, we see subtle but consistent differences here, with the three of them sharing a similar zone of preference at a very short interval, likely the result of their frequent use of double beats, but with ILA showing a small second step and DAU a narrower total range of intervals (ALF's interbeat intervals ranged from 0.05 to 0.97 s, but were concentrated in the 0.06–0.18 s zone, DAU's interbeat intervals ranged from 0.04–0.42 s, but were concentrated in the 0.07–0.14 s zone and ILA's interbeat intervals ranged from 0.05 to 1.89 s, but were concentrated in the 0.05–0.14 s zone). Taken together, the DFA plot, the visual inspection of the drumming bouts and the cumulative probability plots reveal individual differences in the acoustic structure of drumming bouts produced in the context of travel.

Finally, individuals also varied with respect to the timing of their drumming bouts relative to accompanying pant hoot phases. For example, ALF and MAC started the drumming bout during the climax more than in any other phase, while ILA, TRS and URS most frequently started the drumming bout before the climax, typically in the build-up phase (Fig. 5a). Moreover, ALF, MAC and TRS most frequently ended the drumming bout during the climax, while ILA and URS most frequently ended it before the climax (Fig. 5b).

Individual Variation in the Acoustic Structure of Display Drumming

The second DFA revealed three DFs that did not significantly discriminate the drumming bouts with two or more beats produced by the four individuals during displays (DF 1: $\Lambda = 0.641$, $\chi^2_{15} = 13.584$, $P = 0.557$; DF 2: $\Lambda = 0.807$, $\chi^2_8 = 6.522$, $P = 0.589$).

Considering drumming bouts of any length produced by the males while displaying ($N = 4$) or travelling ($N = 7$), we found a greater proportion of one- or two-beat drums used while displaying than during travelling (two-proportion z test: $z = -2.811$, $P = 0.005$). During displays 81% ($N = 30$ of 37) of drums were composed of either one or two beats while other drums ranged from three to eight beats. In contrast, during travel 55% ($N = 67$ of 121) of drums were composed of one or two beats, while other drums ranged from three to 14 beats.

Given these combined results, we did not conduct any visual inspection of beat patterns within the drumming bouts or of the cumulative distribution of the interbeat interval durations in the context of display.

Effect of Individual, Social and Contextual Factors on Drumming

Do age, rank, context and group size influence drumming?

The first model assessed the effect of individual age, social rank, behavioural context and group size on the use of drumming by male focal chimpanzees in the Waibira community (Table 3). Overall, these fixed effects did influence the probability of drumming (likelihood ratio test comparing full and null models: $\chi^2_6 = 36.656$, $P < 0.001$). More specifically, as group size increased by one standard deviation, the probability of drumming decreased by 29% (estimate = -0.874 ; Table 4, Fig. 6). Context also influenced the use of drumming ($\chi^2_3 = 23.029$, $P < 0.001$). Compared to resting, drumming occurred 99% (estimate = 4.276) more often in the context of display and 87% (estimate = 1.888) more often in the context of travelling (Table 5, Fig. 7). However, the probability of drumming was unaffected by age or rank, and no difference was found between the contexts of resting and feeding. The model explained a medium proportion of variance (marginal $R^2 = 0.52$, conditional $R^2 = 0.57$).

Do oestrous females and preferred social partners affect drumming?

The second model did not show an influence of the presence of preferred social partners and females in oestrus in the focal

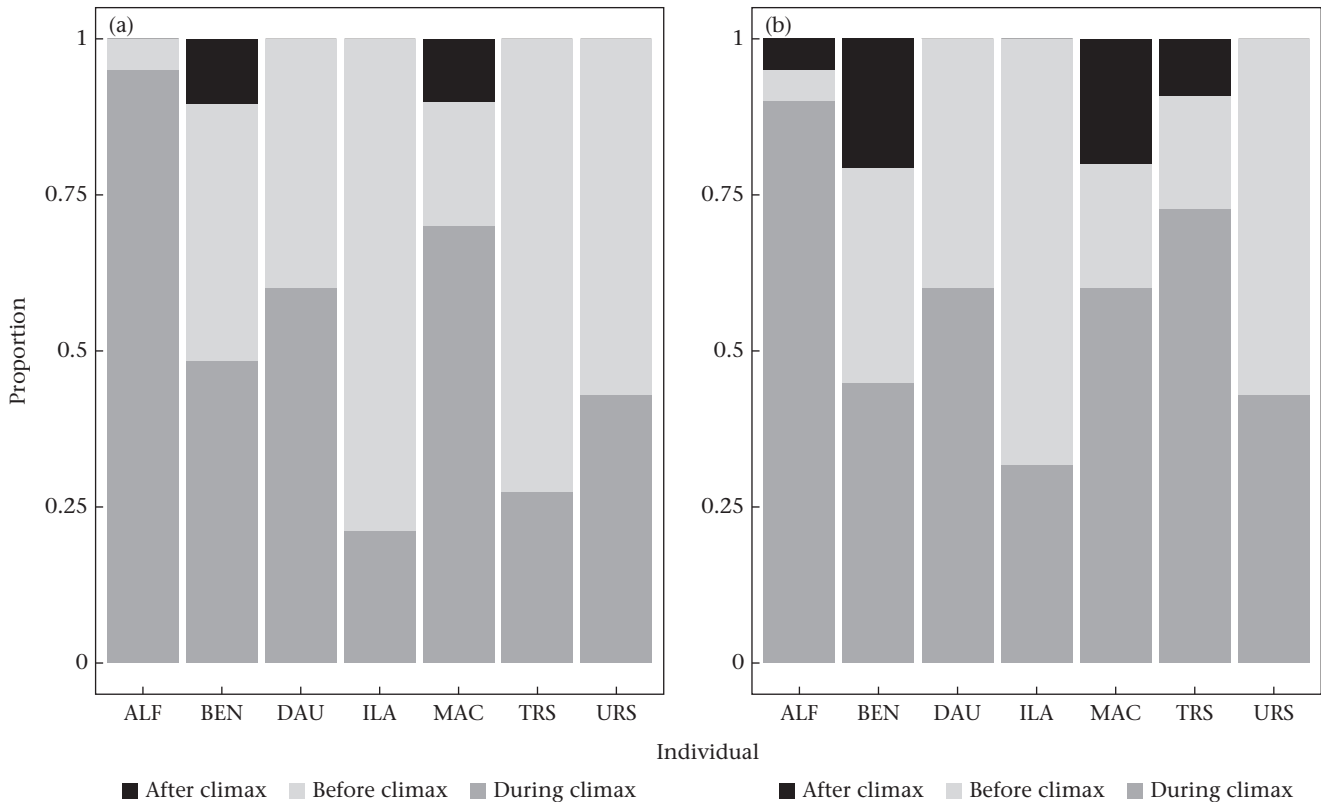


Figure 5. Plots of the timing of drumming bouts in the pant hoot. The drumming bouts were produced during travel events by seven individuals. The percentage of drumming bouts that (a) started and (b) ended before, during and after the climax is shown.

chimpanzee's party on the use of drumming (likelihood ratio test comparing full and null models: $\chi^2_2 = 0.911$, $P = 0.634$).

Do higher-ranking males affect drumming?

No effect of the presence of higher-ranking males in the focal chimpanzee's party on the use of drumming was found in the third model (likelihood ratio test comparing full and null models: $\chi^2_1 = 3.541$, $P = 0.060$).

DISCUSSION

Our study supports the hypothesis that buttress drumming is used as a long-distance signal to mediate chimpanzee fission–fusion social dynamics (Arcadi et al., 1998; Babiszewska et al., 2015). Chimpanzees drummed most frequently in the context of travelling

and in smaller party sizes, and drumming bouts produced during travel events showed individual differences, suggesting that drumming during spatial movements might serve to recruit or maintain contact with distant group members. Moreover, we found preliminary evidence of flexibility between contexts of production that suggests drumming may serve more than one function. Most social displays with long-distance acoustic signals contained drumming, which suggests that drumming is an important component of displays. However, while we found individual differences in the acoustic structure of drums and in their timing within the pant hoot during travel events, we found no evidence of individual differences in drumming bouts produced by some of the same individuals during displays, which suggests a potential alternative function of drumming in this context. Our sample of individuals in our analyses of display drums was small and may be influenced by individual differences and/or a lack of power. However, we also found that a greater proportion of drums during display than drums during travelling were produced with just one or two beats and, thus, have more limited potential for encoding individual identity. Given this additional support, we suggest that flexibility in the production of individual signatures across contexts is promising and merits further investigation.

Our study is consistent with a wide range of research that finds that individual differences are frequently encoded in long-distance calls and nonvocal acoustic signals across species, such as chimpanzee pant hoots, orang-utan long-calls and elephant rumbles (Fedurek et al., 2016; McComb et al., 2003; Spillmann et al., 2010), and kangaroo rat and male ruffed grouse, *Bonasa umbellus*, drumming (Garcia et al., 2012; Randall, 2010). Previous research exploring individual variation in chimpanzee drumming was inconclusive, with studies in the Tai and Sonso communities, but not in the Kanyawara community, finding individual differences (Arcadi et al.,

Table 3
Percentage of 'long-distance communications' with drumming

Focal male	Communications with drumming	Communications without drumming	% Communications with drumming
BEN	21	36	37 ($N = 57$)
TRS	16	57	22 ($N = 73$)
ALF	17	21	45 ($N = 38$)
MAC	16	23	41 ($N = 39$)
SAM	8	3	73 ($N = 11$)
ILA	18	7	72 ($N = 25$)
FID	12	10	55 ($N = 22$)
LAF	4	4	50 ($N = 8$)

The table includes communications by focal individuals ($N = 8$) for which a minimum of four communications produced on the ground were collected ($N = 273$). 'Communications with drumming' include drumming produced on its own and pant hoots integrated with drumming. 'Communications without drumming' are pant hoots produced on their own.

Table 4

Results of the model exploring the effect of age, social rank, behavioural context and group size on the use of drumming by the focal male chimpanzees

	Estimate	SE	z	χ^2	df	P	Lower CI	Upper CI	Minimum	Maximum
Intercept	-1.499	0.410	-3.654			(1)	-2.583	-0.863	-1.665	-0.987
Age	-0.420	0.287		1.938	1	0.164	-1.057	0.185	-0.557	0.910
Rank	-0.006	0.283		0.001	1	0.982	-0.545	0.602	-0.518	0.128
Group size	-0.874	0.294		7.754	1	0.003	-1.629	-0.406	-1.172	-0.761
Period	-0.155	0.414		0.139	1	0.709	-0.978	0.734	-0.481	0.024
Context display	4.276	1.174	3.643		1	<0.001	2.729	14.563	3.809	21.265
Context feeding	-2.734	2.634	-1.038		1	0.299	-11.315	0.040	-18.811	-1.679
Context travelling	1.888	0.458	4.121		1	<0.001	1.078	2.913	1.552	2.049

'Age', 'rank' and 'group size' were z-transformed before entering the model, whereas 'period' and the contexts were dummy coded and centred before entering random slopes in the model. The table shows estimates, standard errors, test results, degrees of freedom, bootstrapped confidence intervals (CI) as well as minimum and maximum of the model stability estimates after removing levels of random effects one at a time. Significant results are highlighted in bold. ('1') Not indicated because of limited interpretation.

1998, 2004; Babiszewska et al., 2015). Our suggestion that the presence of individual signatures may vary among the same individuals offers one possible explanation for the inconsistencies among the previous studies: variation in behavioural context. The studies conducted in Tai and Sonso described drums produced during travel events, while in Kanyawara information on the behavioural context of the signaller was unavailable and drumming bouts may have included those produced within displays.

During travel, drumming may allow chimpanzees to communicate their identity and location across dispersed parties and individuals, aiding them in facilitating or avoiding particular social interactions across greater distances than their pant hoots (Arcadi et al., 1998; Babiszewska et al., 2015; Boesch, 1991). In contrast, because displays are typically used to showcase dominance or strength for individuals who are nearby (Goodall, 1986; Muller, 2002; Nishida, 1983), chimpanzees may not need to advertise their identity by encoding it in the structure of their drumming bouts. Indeed, they may benefit from not doing so, to avoid revealing their identity while displaying to nearby but out-of-sight higher-ranking individuals or other competitors who might subsequently approach and challenge them. In Waibira, display drums tended to be composed of one or two beats, which have less potential to express individual differences or signature patterns than drumming bouts with more beats. Moreover, while drumming was frequently produced during displays, pant hoots, a signal in which chimpanzees may not be able to mask their identity as easily (Fedurek et al., 2016), were almost entirely absent from displays.

Another study showed that pant hoots during displays were present, but only infrequently, in the neighbouring Sonso community, and that 70% of these pant hoots did not contain the climax, which is the phase heard at larger distances and carrying identity information believed to be informative for distant parties (Fedurek et al., 2016; Soldati et al., 2022). This pattern of findings suggests that, when signalling during displays, chimpanzees may not benefit from revealing their identity to other parties.

Arcadi and Wallauer (2013) suggested that, rather than representing individual differences, patterns of drumming bouts may be a consequence of chimpanzee physiology. For example, their study found that in Gombe (Tanzania) drumming was influenced by the galloping gait chimpanzees used when approaching buttress roots to drum on (Arcadi & Wallauer, 2013). However, this study also did not control for the behavioural context of production. Outside of displays, we regularly observed chimpanzees approaching drumming trees at a walking pace or producing drums from standing, rather than galloping (V. Eleuteri & C. Hobaiter, personal observations). Given this, we argue that drumming rhythm in Waibira is unlikely to be simply a consequence of chimpanzee galloping gait. Arcadi and Wallauer (2013) also suggested that drumming patterns may depend on the geometrical properties of the buttress roots. If true, individual signatures are still possible if chimpanzees select drumming trees that allow them to express a particular style, or if they have a preference for a particular type of buttress that shapes their drum as a result. Chimpanzees appear to select specific buttresses for drumming (Fitzgerald et al., 2022) and more resonant buttresses for accumulative stone throwing (Kalan et al., 2019), suggesting that they are aware of the acoustic properties of buttresses.

Chimpanzees drummed across contexts, but predominantly when travelling. In the neighbouring Sonso community in the Budongo forest, Babiszewska et al. (2015) found no effect of rank or social factors, such as the size of the party or the presence of particular individuals, on the probability of drumming, but they did find that older individuals were more likely to drum. In contrast, in

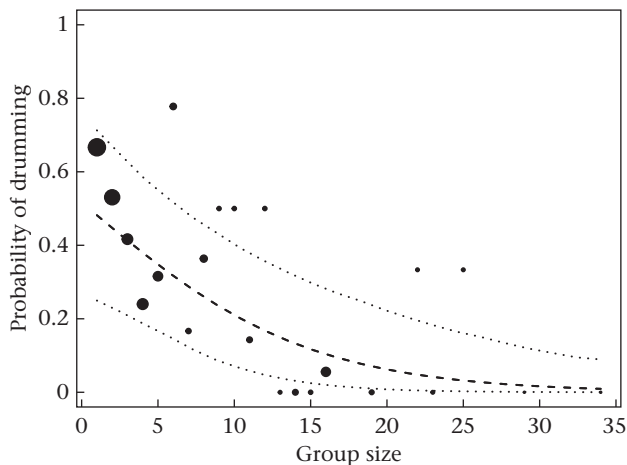


Figure 6. Probability of long-distance communications including drumming as a function of group size. Communications were included from eight focal individuals for which a minimum of four communications produced on the ground were collected ($N = 273$). The area of the dots represents the number of parties at that group size represented in the data set. The dashed line represents the fitted model with all predictors centred. The dotted lines represent the bootstrapped confidence intervals.

Table 5

Frequency of 'long-distance communications' with and without drumming in different behavioural contexts

	Drumming	Pant hoot drumming	Pant hoot	% Communications with drumming
Resting	5	15	97	17 ($N = 117$)
Display	15	2	1	94 ($N = 18$)
Feeding	0	1	24	0 ($N = 25$)
Travelling	5	69	39	65 ($N = 113$)
N	20	87	161	39 ($N = 273$)

The table includes communications by focal individuals ($N = 8$) for which a minimum of four communications produced on the ground was collected ($N = 273$). Communications with drumming include 'drumming' and 'pant hoot drumming'. Communications without drumming are 'pant hoot', indicating pant hoots produced on their own.

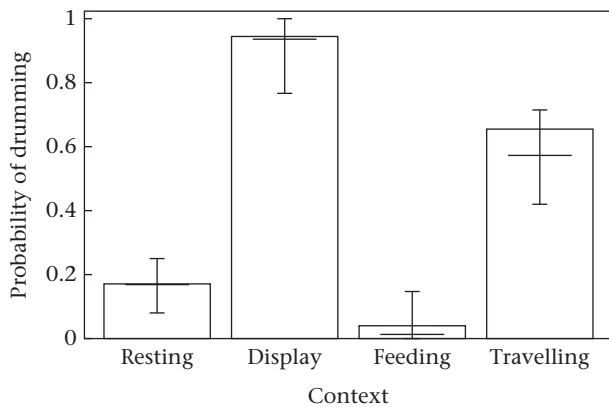


Figure 7. Probability of long-distance communications including drumming in the context of resting, display, feeding and travelling. Communications were included from eight focal individuals for which a minimum of four communications produced on the ground were collected ($N = 273$). The bars represent the probability of drumming in each context. The horizontal lines with error bars depict the fitted model lines and their bootstrapped confidence intervals for each context.

Waibira, having incorporated a wide range of ages in our choice of focal individuals, we found no effect of age, but we did find that males were more likely to drum when in smaller parties. One explanation for these group differences is that while these two communities share a similar neighbouring forest landscape, and regular immigration events occur between them, their social landscape and the size of their territory are very different. The Sonso community of chimpanzees is typically sized (see Wilson et al., 2014) with around 70 individuals and 13 independent males who are relatively cohesive and occupy one of the smallest territories reported for a wild community ($<7 \text{ km}^2$; Newton-Fisher, 2003; Badihi et al., 2021). In contrast, the Waibira community has over 120 individuals with around 30 independent males and occupies a territory of around 11 km^2 (Badihi et al., 2021). If typical party sizes are constrained by shared ecological factors such as food patch size, Waibira chimpanzees are more likely to be dispersed from other males throughout the day and may be more likely to employ long-distance drumming to regulate their opportunities to interact with other individuals. Increased use of drumming when in smaller parties supports this hypothesis.

Chimpanzee drumming can travel further than their alternative long-distance signal, the pant hoot (Arcadi et al., 1998; Babiszewska et al., 2015). Our results show that during travel events chimpanzee buttress drumming reveals individual differences and that chimpanzees drum most frequently while travelling and when in smaller parties. This pattern of use suggests that, when produced during travelling, drumming serves as a long-distance signal to facilitate chimpanzee fission–fusion spatial dynamics, specifically to promote fusion with other individuals.

The fusion function of long-distance signals has also been shown in chimpanzee pant hoots, which are produced more before than after fusion with group members (Fedurek et al., 2014; Goodall, 1986), as well as in a range of other species. Bonobos, *Pan paniscus*, produce long-distance ‘low hoot–high hoot’ combinations that are more likely to recruit others than hoots on their own (Schamberg et al., 2017). In white-bellied spider monkeys, *Ateles belzebuth*, groups that produce loud calls are more likely to fuse with others after calling than groups that do not (Spehar & Di Fiore, 2013). Spotted hyaenas, *Crocuta crocuta*, are more likely to move after hearing ‘recruitment’ whoop bouts than display whoop bouts (Gersick et al., 2015). Elephants use rumble vocalizations to reunite

with herd members after separation (Leighty et al., 2008). Future studies may further explore whether chimpanzee drumming is used to facilitate fusion by examining whether chimpanzees drum more frequently before or after fusion, as well as the extent to which drumming varies with physical properties of the landscape that may alter signal transmission across longer distances. One study described an alpha male chimpanzee in the Tai community using specific sequences of pant hoot drumming events to communicate apparently precise information relating to group spatial movements, which was suggested to represent symbolic and syntactic capacities (Boesch, 1991; Gabrić, 2022). Future studies should systematically explore drumming production and recipient reaction to understand the potential of drumming in regulating grouping dynamics.

We suggest that drumming may serve a different function when produced during displays, where we found no evidence that individual identity is encoded, and where drumming bouts were more frequently composed of just one or two beats and were typically produced without the individually distinctive pant hoot vocalizations. This pattern of use may suggest a possible alternative short-distance function of drumming during display, as well as the ability to flexibly modify the structure of this signal and the information it encodes. For example, display drums might be used to show dominance and strength rather than individual identity (Babiszewska et al., 2015; Goodall, 1986). To understand better the potentially diverse functions of chimpanzee drumming, future studies should explore whether recipients are more likely to respond or approach when they hear travelling drumming compared with display drumming, as well as compare the acoustic structure and features across more diverse social and ecological contexts. This study reveals the importance of nonvocal acoustic signals in chimpanzee communication and the need for research to explore further this understudied type of signal use.

Author Contributions

Vesta Eleuteri: Conceptualization, Investigation, Methodology, Data collection and curation, Statistical analysis, Writing – original draft; **Adrian Soldati:** Provision of archive data, Writing – review and editing; **Matthew Henderson:** Data collection, Writing – review and editing; **Gal Badihi:** Data collection, Writing – review and editing; **Klaus Zuberbühler:** Resources, Writing – review and editing; **Catherine Hobaiter:** Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing – original draft.

Declaration of Interest

The authors have no interests to declare.

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Appendix

Additional Models

Effect of particular individuals on drumming

To compare the drumming behaviour of Waibira chimpanzees more effectively with that of published data from the neighbouring Sonso community, we used our data to replicate more closely the statistical analyses conducted in that study. These are included here for ease of comparison, but note that these models do not include the control fixed effects social rank and behavioural context in the second and third models in the main text. We fitted two generalized linear mixed models (Baayen, 2008) with a binomial error structure and logit link function. In both models ‘Drum’ was the binary dependent variable coded as: Drum = 1 and No Drum = 0, representing whether a long-distance communication produced on the ground by the focal chimpanzees included drumming or not. The samples consisted of communications collected from the same individuals. As a result, to avoid pseudoreplication, in both models the identity of the focal chimpanzee producing the communication was entered as a random effect. Moreover, we included all random slopes that were theoretically identifiable to keep the Type I error rate at the nominal value of 5% (Barr et al., 2013; Schielzeth & Forstmeier, 2009). All categorical fixed effects, females in oestrus, preferred social partners, higher-ranking males and period, were dummy coded and centred before entering the random slopes. To explore the effect of the fixed effects we used a likelihood ratio test comparing the full model with the null model without all fixed effects but keeping the control fixed effect of period and all random effects (Dobson & Barnett, 2018). We checked for multicollinearity with VIFs (Field et al., 2012) and for model stability by comparing the full model estimates with estimates from models from which the random effects were removed one at a time (Nieuwenhuis et al., 2012).

Do oestrous females and preferred social partners affect drumming?

The sample size consisted of 273 long-distance communications collected from eight focal chimpanzees. We entered presence of

females in oestrus and presence of preferred social partners, both coded as absent = 'FALSE', present = 'TRUE', as fixed effects, while period of data collection, coded as '1' for June–July 2019 and '2' for January–March 2020, as a control fixed effect. We included the theoretically identified random slopes for presence of females in oestrus, presence of preferred social partners and period within focal individual. We removed correlations among intercepts and slopes because some were unidentifiable as their absolute correlation parameters were close to 1/−1 (Matuschek et al., 2017). There was no issue of multicollinearity as VIFs were all close to 1.0, and the model was fairly stable (see Table A4).

Do higher-ranking males affect drumming?

The highest-ranking male in the community (BEN) was excluded from the analyses as there were no males of higher rank to him, which resulted in a sample of 216 communications collected from seven focal chimpanzees. We entered presence of higher-ranking males as a fixed effect, coded as absent = 'FALSE', present = 'TRUE', and the period of data collection, coded as '1' for June–July 2019 and '2' for January–March 2020, as a control fixed effect. We entered the theoretically identified random slopes for presence of higher-ranking males and period within focal individual. We removed correlations among intercepts and slopes as some were unidentifiable because they were close to 1/−1 (Matuschek et al., 2017). There was no multicollinearity issue as all VIFs were approximately 1.0 and the model was fairly stable (see Table A5).

Results: Effect of Particular Individuals on Drumming

Do oestrous females and preferred social partners affect drumming?

Overall, the presence of particular individuals impacted chimpanzees' probability of drumming (likelihood ratio test comparing full and null models: $\chi^2_2 = 8.229, P = 0.016$). Specifically, when preferred social partners were present rather than absent in the party, the probability of drumming decreased by 25% (estimate = −1.127; Table A4). In contrast, the presence of females in oestrus did not impact the probability of drumming. The model explained a small proportion of variance (marginal $R^2 = 0.10$, conditional $R^2 = 0.16$; Nakagawa et al., 2017). Note that these results may have been driven by party size, as in our main model, where group size was included, we did not find these effects.

Do higher-ranking males affect drumming?

The presence of males of higher rank to the focal male in the party affected chimpanzees' probability of drumming (likelihood ratio test comparing full and null models: $\chi^2_1 = 13.035, P < 0.001$). When higher-ranking males were present compared to absent, the probability of drumming decreased by 17% (estimate = −1.555; Table A5). The model explained a small proportion of variance (marginal $R^2 = 0.11$, conditional $R^2 = 0.25$; Nakagawa et al., 2017). Again, note that when we controlled for group size in our main model these effects disappeared.

Table A1
Means and standard deviations of the acoustic measures describing drumming bouts

	ID	Number of drumming bouts	Mean bout duration (s)	Mean number of beats (s)	Mean of mean interbeat interval (s)	Mean shortest interbeat interval (s)	Mean longest interbeat interval (s)
Drumming bouts during travel events	ALF	19	0.33 (SD 0.59)	2.63 (SD 1.64)	0.14 (SD 0.13)	0.08 (SD 0.02)	0.21 (SD 0.27)
	BEN	24	0.46 (SD 0.25)	2.83 (SD 1.01)	0.28 (SD 0.11)	0.22 (SD 0.14)	0.35 (SD 0.13)
	DAU	7	0.20 (SD 0.18)	2.43 (SD 0.79)	0.12 (SD 0.04)	0.088 (SD 0.032)	0.17 (SD 0.13)
	ILA	27	0.52 (SD 0.62)	2.96 (SD 1.19)	0.20 (SD 0.16)	0.08 (SD 0.02)	0.41 (SD 0.49)
	MAC	7	0.52 (0.71)	4.00 (SD 2.58)	0.17 (SD 0.08)	0.09 (SD 0.02)	0.22 (SD 0.13)
	TRS	15	1.24 (SD 1.00)	7.20 (SD 3.10)	0.22 (SD 0.16)	0.09 (SD 0.05)	0.51 (SD 0.55)
	URS	6	0.27 (SD 0.25)	2.33 (SD 0.52)	0.21 (SD 0.22)	0.16 (SD 0.23)	0.25 (SD 0.23)
Drumming bouts during displays	ALF	7	0.12 (SD 0.11)	2.00 (SD 0.00)	0.12 (SD 0.11)	0.12 (SD 0.11)	0.12 (SD 0.11)
	BEN	5	0.30 (SD 0.38)	3.20 (SD 2.68)	0.14 (SD 0.10)	0.12 (SD 0.11)	0.16 (SD 0.11)
	ILA	10	0.27 (SD 0.31)	2.40 (SD 0.70)	0.15 (SD .010)	0.10 (SD 0.07)	0.22 (SD 0.24)
	MAC	14	0.34 (0.35)	2.50 (SD 1.09)	0.21 (SD 0.11)	0.18 (SD 0.11)	0.24 (SD 0.14)

The means and standard deviations of the acoustic measures ('bout duration', 'number of beats', 'mean interbeat interval', 'shortest interbeat interval', 'longest interbeat interval') were calculated separately for drumming bouts produced by seven chimpanzees during travel events and drumming bouts produced by four chimpanzees while displaying, respectively.

Table A2
Results of Shapiro–Wilk's tests

	Acoustic measure	Individual	W	df	P	
Drumming bouts during displays	Z score bout duration	ALF	0.571	7	<0.001	
		BEN	0.713	5	0.013	
		ILA	0.747	10	0.003	
		MAC	0.700	14	<0.001	
		.	.	7	.	
	Z score number of beats	ALF	.	.	7	.
		BEN	0.552	5	<0.001	
		ILA	0.650	10	<0.001	
		MAC	0.527	14	<0.001	
		.	.	7	.	
	Z score mean interbeat interval	ALF	0.571	7	<0.001	
		BEN	0.726	5	0.018	
		ILA	0.855	10	0.067	
		MAC	0.925	14	0.255	
		.	.	7	.	
	Z score shortest interbeat interval	ALF	0.571	7	<0.001	
		BEN	0.671	5	0.005	
		ILA	0.789	10	0.011	
		MAC	0.873	14	0.046	
		.	.	7	.	
	Z score longest interbeat interval	ALF	0.571	7	<0.001	
BEN		0.778	5	0.053		
ILA		0.736	10	0.002		
.		.	7	.		

(continued on next page)

Table A2 (continued)

	Acoustic measure	Individual	W	df	P
Drumming bouts during travel events	Z score bout duration	MAC	0.921	14	0.224
		ALF	0.520	19	<0.001
		BEN	0.948	24	0.249
		DAU	0.743	7	0.011
		ILA	0.757	27	<0.001
		MAC	0.698	7	0.004
	Z score number of beats	TRS	0.853	15	0.019
		URS	0.879	6	0.266
		ALF	0.444	19	<0.001
		BEN	0.775	24	<0.001
		DAU	0.646	7	0.001
		ILA	0.786	27	<0.001
	Z score mean interbeat duration	MAC	0.811	7	0.052
		TRS	0.941	15	0.398
		URS	0.640	6	0.001
		ALF	0.602	19	<0.001
		BEN	0.953	24	0.317
		DAU	0.927	7	0.525
	Z score shortest interbeat interval	ILA	0.784	27	<0.001
		MAC	0.799	7	0.040
		TRS	0.550	15	<0.001
		URS	0.783	6	0.041
		ALF	0.884	19	0.025
		BEN	0.883	24	0.010
	Z score longest interbeat interval	DAU	0.918	7	0.455
		ILA	0.928	27	0.061
		MAC	0.902	7	0.343
		TRS	0.757	15	0.001
		URS	0.582	6	0.000
		ALF	0.591	19	<0.001
		BEN	0.893	24	0.015
		DAU	0.787	7	0.030
		ILA	0.725	27	<0.001
		MAC	0.788	7	0.031
		TRS	0.655	15	<0.001
		URS	0.888	6	0.308

The tests were performed to check for normality of within-individual residuals for each acoustic measure ('bout duration', 'number of beats', 'mean interbeat interval', 'shortest interbeat interval', 'longest interbeat interval') extracted from 105 drumming bouts produced by seven chimpanzees during travel events and 36 drumming bouts produced by four chimpanzees during displays.

Table A3

Results of Levene's tests

	Acoustic measure	F	df	P
Drumming bouts during display	Bout duration	1.169	3, 32	0.337
	Number of beats	5.908	3, 32	0.003
	Mean interbeat interval	0.252	3, 32	0.860
	Shortest interbeat interval	1.242	3, 32	0.311
	Longest interbeat interval	1.606	3, 32	0.207
Drumming bouts during travel events	Bout duration	4.154	6, 98	0.001
	Number of beats	4.530	6, 98	<0.001
	Mean interbeat interval	1.225	6, 98	0.300
	Shortest interbeat interval	16.561	6, 98	<0.001
	Longest interbeat interval	4.734	6, 98	<0.001

The tests were performed to check for homogeneity of variance for each acoustic measure ('bout duration', 'number of beats', 'mean interbeat interval', 'shortest interbeat interval', 'longest interbeat interval') extracted from 105 drumming bouts produced by seven chimpanzees during travel events and 36 drumming bouts produced by four chimpanzees during displays.

Table A4

Results of the additional model exploring the effect of presence of females in oestrus and of preferred social partners on the use of drumming by the focal male chimpanzees

	Estimate	SE	z	χ^2	df	P	Upper CI	Lower CI	Minimum	Maximum
Intercept	0.418	0.365	1.145			(1)	-0.255	1.196	0.260	0.615
Females in oestrus	-0.592	0.488		1.288	1	0.256	-1.692	0.260	-0.867	0.040
Preferred social partners	-1.127	0.378		6.537	1	0.011	-1.874	-0.530	-1.449	-0.964
Period	0.027	0.362		0.005	1	0.942	-0.705	0.746	-0.298	0.345

'Period', 'females in oestrus' and 'preferred social partners' were dummy coded and centred before entering the random slopes in the model. The table reports estimates, standard errors, test results, degrees of freedom, bootstrapped confidence intervals (CI) as well as minimum and maximum of the model stability estimates after removing levels of random effects one at a time. Significant results are highlighted in bold. '(1)' not indicated because of limited interpretation.

Table A5

Results of the additional model exploring the effect of higher-ranking males on the use of drumming by the focal male chimpanzees

	Estimate	SE	<i>z</i>	χ^2	<i>df</i>	<i>P</i>	Lower CI	Upper CI	Minimum	Maximum
Intercept	0.832	0.490	1.697			(1)	−0.131	1.821	0.687	1.235
Higher-ranking males	−1.555	0.359		13.035	1	<0.001	−2.299	−0.851	−1.871	−1.475
Period	−0.095	0.360		0.069	1	0.793	−0.819	0.547	−0.323	0.257

'Period' and 'higher-ranking males' were dummy coded and centred before entering the random slopes in the model. In the table are estimates, standard errors, test results, degrees of freedom, bootstrapped confidence intervals (CI) as well as minimum and maximum of the model stability estimates after removing levels of random effects one at a time. Significant results are highlighted in bold. '(1)' Not indicated because of limited interpretation.