Re-emergence of a socio-cultural gesture and its association with male chimpanzee loud calls (#24776)

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Re-emergence of a socio-cultural gesture and its association with male chimpanzee loud calls

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Loud calls are used by many species as long-distance signals for group defense, mate attraction, and inter- and intragroup spacing. Chimpanzee loud calls, or pant hoots, are used in a variety of contexts including group coordination and during male contests. Here, we observed an alpha male takeover in wild chimpanzees (*Pan troglodytes verus*) during which the leaf clipping gesture re-emerged after disappearing for almost two years in this community. Leaf clipping only occurred in males and almost always preceded a pant hoot vocalization, as has been observed in other chimpanzee communities of the Taï forest in Côte d'Ivoire. Therefore, we hypothesized that leaf clipping may be important for male-male competition by affecting variation in the loud calls of chimpanzee males. We therefore investigated whether pant hoots preceded by leaf clipping differed acoustically from those without, while also testing the influence of social context on pant hoot variation, namely male dominance rank and hierarchy instability, i.e., before, during and after the alpha takeover. We found that pant hoots preceded by leaf clipping were longer, contained more call elements and drum beats, lower fundamental frequencies and higher peak frequencies. Moreover, during the alpha takeover pant hoots were shorter, contained fewer drum beats and higher fundamental frequencies. Additionally, pant hoot and aggression rates were also highest during the alpha takeover with leaf clipping more likely to occur on days when pant hooting rates were high. Overall social rank had limited effects on pant hoot variation. We suggest that elevated arousal and aggression during the alpha takeover triggered the re-emergence of leaf clipping and the associated acoustic changes in pant hoots. Further research should focus on the potential mechanisms by which leaf clipping is connected to variation in pant hoots and cross-population comparisons of the behaviour.

Re-emergence of a socio-cultural gesture and its association with male chimpanzee loud calls

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Abstract

Loud calls are used by many species as long-distance signals for group defense, mate attraction, and inter- and intragroup spacing. Chimpanzee loud calls, or pant hoots, are used in a variety of contexts including group coordination and during male contests. Here, we observed an alpha male takeover in wild chimpanzees (*Pan troglodytes verus*) during which the leaf clipping gesture re-emerged after disappearing for almost two years in this community. Leaf clipping only occurred in males and almost always preceded a pant hoot vocalization, as has been observed in other chimpanzee communities of the Taï forest in Côte d'Ivoire. Therefore, we hypothesized that leaf clipping may be important for male-male competition by affecting variation in the loud calls of chimpanzee males. We therefore investigated whether pant hoots preceded by leaf clipping differed acoustically from those without, while also testing the influence of social context on pant hoot variation, namely male dominance rank and hierarchy instability, i.e., before, during and after the alpha takeover. We found that pant hoots preceded by leaf clipping were longer, contained more call elements and drum beats, lower fundamental frequencies and higher peak frequencies. Moreover, during the alpha takeover pant hoots were shorter, contained fewer drum beats and higher fundamental frequencies. Additionally, pant hoot and aggression rates were also highest during the alpha takeover with leaf clipping more likely to occur on days when pant hooting rates were high. Overall social rank had limited effects on pant hoot variation. We suggest that elevated arousal and aggression during the alpha takeover triggered the re-emergence of leaf clipping and the associated acoustic changes in pant hoots. Further research should focus on the potential mechanisms by which leaf clipping is connected to variation in pant hoots and cross-population comparisons of the behaviour.

Keywords: male competition, male signaling, multimodal communication, leaf clipping, pant hoot, tool use, animal vocalizations

Introduction

Long-distance vocalizations in animals primarily function in group spacing, defense and mate competition (Ryan & Kime, 2003; Delgado, 2006). In mammals, long-distance 'loud calls' are central to male displays that are used to deter potential competitors and attract mates, where listeners can obtain information about the quality of a male signaler from its loud call (Fischer et al., 2004; Reby et al., 2005; Pitcher et al., 2014; Benítez et al., 2016). Given the source-filter theory for vocal sound production (Fitch & Hauser, 2003), larger males are expected to produce lower pitched calls which can serve as reliable cues of their body size and thus competitive strength (Davies & Halliday, 1978; Fitch, 1997). Support for this relationship has been observed in a variety of birds (Searcy & Andersson, 1986; Gil & Gahr, 2002; Nolan & Hill, 2004), frogs (Davies & Halliday, 1978; Searcy & Andersson, 1986; McClelland, Wilczynski & Ryan, 1996) and mammals (Fitch, 1997; Reby & McComb, 2003; Sanvito, Galimberti & Miller, 2007; Vannoni & McElligott, 2008; Neumann et al., 2010; Puts et al., 2016). Numerous studies have also demonstrated that males in better physical condition usually produce a larger number of calls, call at higher rates or with a longer duration than conspecific males of a lower quality (birds (Searcy & Andersson, 1986; Gil & Gahr, 2002; Nolan & Hill, 2004), frogs (Searcy & Andersson, 1986; Welch, Semlitsch & Gerhardt, 1998), primates (Mitani, 1985; Clark, 1993; Kitchen et al., 2003; Wich et al., 2003; Neumann et al., 2010; Barelli et al., 2013; Benítez et al., 2016), hyenas (East & Hofer, 1991) and deer (Reby et al., 2005; Pitcher et al., 2014)). However, studies on non-human primates ('primates' hereafter) have provided mixed results on male traits and vocalization parameters (Ey, Pfefferle & Fischer, 2007; Puts et al., 2016). For example, high quality males have been associated with low fundamental frequencies (Neumann et al., 2010; Benítez et al., 2016) ~~but also~~ higher fundamental frequencies (Fischer et al., 2004; Barelli et al., 2013).

The chimpanzee loud call, the 'pant hoot', is acoustically sexually dimorphic with males pant hooting more often than females and having more pronounced pant hoots (Marler & Hobbett, 1975; Clark, 1993; Puts et al., 2016), as well as being individual (Mitani & Brandt, 1994; Kojima, Izumi & Ceugniet, 2003; Notman & Rendall, 2005) and group specific (Crockford et al., 2004). The pant hoot functions in coordinating group movement (Mitani & Nishida, 1993; Fedurek, Donnellan & Slocombe, 2014) and territory defense (Wilson & Wrangham, 2003) while little is known about its role in regulating within group male-male competition (Muller & Mitani, 2005). The pant hoot is a compound call traditionally described as consisting of four phases: introduction, build-up, climax and let down (Marler & Hobbett, 1975; Crockford et al., 2004; Notman & Rendall, 2005). Male chimpanzees often incorporate buttress drumming into the climax phase of their pant hoot, where the soles of the hands and feet are hit repeatedly against buttress roots of trees and this occurs more frequently in Taï chimpanzees than in other populations (Arcadi, Robert & Boesch, 1998). The highest ranking male, the alpha, is often the most vocal (Clark, 1993; Fedurek et al., 2016), as in other mammals (Pitcher et al., 2014), but little is known about the variation in acoustic properties of the pant hoot beyond individual differences (Marler & Hobbett, 1975; Mitani & Brandt, 1994; Kojima, Izumi & Ceugniet, 2003; Notman & Rendall, 2005). A recent study showed that pant hoot rates of male chimpanzees were positively correlated with urinary testosterone levels and males with higher testosterone produced higher peak frequencies in the climax phase (Fedurek et al., 2016).

Here, we documented the re-emergence of the leaf clipping gesture during an alpha male takeover in a habituated chimpanzee community of the Taï forest in Côte d'Ivoire (Boesch & Boesch-Achermann, 2000). Almost two years had passed since the last time leaf clipping was observed in this group. Leaf clipping is a tool-use gesture where a chimpanzee detaches leaves and rips the leaf blade repeatedly between pressed lips or teeth without ingesting it, often producing an audible 'ripping' sound (Nishida, 1980; Boesch, 1995). Leaf clipping has been documented in multiple chimpanzee populations where it appears to be used in different contexts (Nishida, 1980; Sugiyama, 1981; Boesch, 1995; Watts, 2007) and is therefore considered to be one of many cultural variants present in wild populations (Whiten et al., 1999; Boesch, 2012). At Taï, leaf clipping is primarily produced by adult males in contexts of social frustration where it is done immediately preceding a pant hoot vocalization and is rarely produced on its own (Boesch, 1995). To our knowledge, leaf clipping occurs in both sexes in other chimpanzee populations and appears to be disassociated from the pant hoot vocalization altogether (Boesch, 2012). For example, in Mahale, males and estrus females use leaf clipping to initiate copulations (Nishida, 1980), and this is similarly observed in Budongo (Hobaiter & Byrne, 2014), Gombe and Ngogo (Watts, 2007). Meanwhile, male and female chimpanzees in Bossou, Guinea have been observed to engage in leaf clipping in a variety of contexts including frustration, copulation and play (Sugiyama, 1981). However, due to its relatively low rate of occurrence in wild populations (Boesch, 1995; Watts, 2007), it is hitherto a poorly understood socio-cultural trait in wild chimpanzees ~~due to the lack of information about this nuanced behaviour.~~

The aim of this study was therefore to assess acoustic variation in the pant hoot with respect to the occurrence of leaf clipping while also considering the potential effects of male dominance rank and male-male competition during the alpha takeover period on chimpanzee loud calls. We specifically investigated acoustic cues typically associated with male competitive ability and predicted that leaf clipping and high ranking males would produce pant hoots with lower fundamental frequencies, a longer duration, and contain more call elements and buttress drumming, the latter component being particularly salient to observers. Additionally, since disruptions in the dominance hierarchy are expected to increase male-male competition (Muller & Mitani, 2005; Georgiev, 2012) we predicted that the alpha male takeover provided a critical social context for signals associated with male loud calls to be modulated, including pant hoots and leaf clipping at Taï. Therefore, we further tested whether male pant hooting and aggression rates were also affected by the period of instability (i.e., before, during and after the alpha takeover) and the occurrence of leaf clipping.

Materials & Methods

All data were collected between July 2011 and May 2012 in the Taï National Park in Côte d'Ivoire. The study subjects were five males from one chimpanzee community, the South group (Boesch, 2012), including 3 adult males (16, 18 and 18 years of age) and 2 sub-adult males both 13 years of age. The sub-adult males were included in the study once it became clear they held important rank positions in the chimpanzee hierarchy due to the small group size (19 adults and sub-adult individuals plus 5 infants). All day focal follows were conducted on the five males with the help of a field assistant for a total of 666 hours of observation during which all behavioural activities, social interactions, and vocalizations were continuously noted (Table S1). All data were collected on wild chimpanzees using non-invasive, observational methods only.

In the field, we noted whether a pant hoot was directly preceded by leaf clipping (<3s before the start of a pant hoot and often the leaf was falling out of the mouth when the pant hoot began). Leaf clipping observations and recordings of pant hoots (see Acoustic Analysis) were collected during focal follows and *ad libitum* throughout the study period whenever target males were present. The dominance rank of each male changed throughout the study period due to the alpha male takeover and the disappearance of one male in January 2012 (Utan). The ranks were assigned by continuous observations of the directionality of pant grunting vocalizations among males since the chimpanzee pant grunt is uniquely produced towards dominant individuals (Boesch & Boesch-Achermann, 2000; Muller & Mitani, 2005).

The study duration was divided into three periods: 'before' (3 months), 'during' (1 month) and 'after' (6 months) the alpha male takeover to describe the relative instability in the male hierarchy based on critical observations of physical aggression (fight between the alpha and beta male on October 16, 2011) and the alpha male conceding to the beta male by clearly pant grunting to him on November 19, 2011. Therefore, the duration of each period had to be deduced *post hoc* for this analysis according to the behaviour of the males. Permissions for field research were granted by the Ministère de la Recherche Scientifique, the Ministère de l'Environnement et des Eaux et Forêts and the Office Ivorien des Parcs et Reserves of Côte d'Ivoire (Ref: 11/MINEF/OIPR/DT/CAT).

Acoustic Analysis

Recordings of pant hoot vocalizations were made by AK using a Marantz PMD661 solid state recorder and a Sennheiser ME66/K6 directional microphone handheld with a windshield using a 44 kHz sampling frequency at 24 bits/s. Only recordings where the caller's identity was certain were used and the pant hoot had to be free of any other individual's vocalizations. All pant hoots were recorded at a distance of 3 to 10m from the vocalizing chimpanzee and were recorded during focal follows but also *ad libitum* throughout the study period. Pant hoots were recorded while chimpanzees were feeding or arriving at feeding tree (n=42), resting (n=46), or traveling (n=124). For this analyses we did not distinguish between each of these contexts due to ~~the lack of~~ sample size per individual per category and because it was not directly related to our hypotheses. In the field it was noted whether any portion of the call was missing from the recording (incomplete) or whether the pant hoot was recorded in its entirety (complete). Incomplete recordings occurred for 88 of the 212 pant hoots used in this analysis for multiple reasons: noisy recording due to microphone or cable damage, caller moving quickly while vocalizing, background noise or other chimpanzees calling, but in all cases at least one of the three phases was recorded in its entirety.

All pant hoot analyses were conducted using the speech analysis freeware Praat version 5.3 (Boersma, 2001). We measured acoustic parameters that have already been shown to vary with male quality or dominance in other mammals (see Introduction) as well as chimpanzees (Marler & Hobbett, 1975; Clark, 1993; Fedurek et al., 2016). Acoustic measurements were done via visual inspection of a spectrogram whilst simultaneously listening to the pant hoot. Spectrogram settings were always set to a 50 to 8000 kHz viewing range using a window length of 0.01s. The pant hoots were visually separated into the introduction, build-up and climax phase that are well described and easily discernible (Marler & Hobbett, 1975; Mitani & Brandt, 1994; Crockford et al., 2004; Notman & Rendall, 2005) . Chimpanzees at Taï rarely include a let down phase (Arcadi, Robert & Boesch, 1998); therefore, it was not included in our analysis because it was not observed. The three remaining phases could include a variable number of inhaled and exhaled call elements with the exception of the climax phase which sometimes had no vocal elements but only buttress drumming (57/212 pant hoots in this analysis). Only the number of voiced call elements and/or drum beats in each phase was counted.

Durations were measured for the total pant hoot and for each of the three phases, excluding leaf clipping if it occurred, as well as the drumming bout (start of first voiced call or drum beat to end of last call or drum beat). The drumming bout was usually confined to the climax phase but was sometimes observed to overlap with the end of the build-up (126/212 pant hoots included drumming). We also measured duration and frequency parameters from a single call isolated from each phase. The build-up phase consisted largely of unmodulated calls therefore we chose the middle call of the build-up to be analyzed. If the build-up had an odd number of total voiced call elements, we considered the next element as the middle call of the build-up (i.e., for a build-up phase with seven calls we analyzed number four). For the introduction phase we selected the last call for analysis since sometimes the first calls of the pant hoot were missing or of poor recording quality (i.e., incomplete). For the climax, the call with the greatest peak frequency was selected (See Figure 1 for overview of pant hoot variables).

The fundamental frequency (F0) and peak frequency (pF) were measured for selected calls using the spectral slice tool which automatically calculates a power spectrum of a selected call. The first peak in the spectral slice corresponded to the F0 and the peak with the highest relative amplitude the pF. Values for fundamental and peak frequencies were also verified visually. In total we had 18 quantitative variables assessed for 212 pant hoots produced by 5 chimpanzee males (see Table S2 for full list of acoustic variables).

Statistical Analysis

All statistical analyses were conducted in R version 3.2.4 (R Core Team, 2017). We fitted linear mixed models (LMM) and Generalized Linear Mixed Models (Baayen, 2008; Bates et al., 2015) to test the effects of male rank, period of male instability, and leaf clipping on the 18 acoustic variables measured from a total of 212 pant hoots produced by five chimpanzee males of a single community, the South group. Not all pant hoots contained all applicable variables measured therefore sample size varied among models (Table S2). Before fitting models, the value for male rank was standardized to range from 0 to 1 to correct for the number of males in the group. All models were fitted using the functions 'lmer','glmer' or 'glmer.nb' of the package lme4 in R (Bates et al., 2016). The response variables were the acoustic variables, and the fixed effects always included three test predictors (period (before, during, after), leaf clipping (Y/N), and rank) and one control predictor of whether the recording included the complete pant hoot produced by the chimpanzee or not (Y/N). All models also included the random effect for caller ID and the random slopes of all fixed effects within caller ID as centered dummy variables (Schielzeth & Forstmeier, 2009; Barr et al., 2013).

All continuous response variables (durations and F0 and pF variables) were analysed using LMMs (i.e., with a Gaussian error structure and identity link function) with the argument REML set to false. The single Poisson model for the number of calls in the introduction was fitted using the function 'glmer' of the package lme4 with the argument family set to poisson and using a log link function (Bates et al., 2016). We fitted negative binomial models for three response variables using the function 'glmer.nb' with a log link function (Bates et al., 2016): number of voiced elements in the build-up, the number of elements in the climax and number of drum beats. None of the poisson and negative binomial models suffered from overdispersion (all disperison parameters < 1.13; (Dobson & Barnett, 2008)). Gaussian models were checked for normally distributed and homogeneity of residuals by visual inspections of QQ-plots and residuals plotted against fitted values which did not indicate any violation of these assumptions. Additionally, all models were assessed for stability by verifying that model estimates did not vary greatly when individuals were removed one at a time. We further checked for collinearity among predictors by determining Variance Inflation Factors (VIF; (Field, 2005)) using the function 'vif' of the package car on a linear model with no random effects included (Fox & Weisberg, 2011). All VIFs were between 1.01-1.06 and therefore were no cause for concern. Model significance was assessed using a likelihood ratio test comparing the full versus null model using the function 'anova' with a Chisq approximation (Forstmeier & Schielzeth, 2011). The null model lacked the fixed effects of period, rank and leaf clipping but was otherwise identical to the full model. If this was significant (P<0.05) we went on to assess the significance of the individual test predictors using a likelihood ratio test with the help of the 'drop1' function in R set to using a Chisq approximation (Dobson & Barnett, 2008; Barr et al., 2013).

Since we fitted a total of 18 models, one for each of the acoustic variables, a correction for multiple testing was required. We used the procedure proposed by Potter and Griffiths (Potter & Griffiths, 2006) which is a modification of Fisher's Omnibus test (Haccou & Meelis, 1994) accounting for non-independence of the tests ~~(which was given in our case since we determined the acoustic parameters for the same set of calls)~~ by deploying a permutation procedure (Adams & Anthony, 1996; Manly, 1997). In brief, this approach consists of repeatedly randomizing ('permuting') all response variables simultaneously (i.e., the correlations among the call parameters are retained) and then fitting the respective model for each of the permuted data sets. To further account for the non-independence of calls recorded from the same individuals we restricted the randomizations to take place only within individuals. We conducted 1,000 permutations into which we included the original data as one permutation. For each of the permuted data sets we fitted the same model and conducted a full null model comparison as for each of the 18 acoustic parameters as described above. We then combined the derived P-values into a single test statistic $ts=-2\times\Sigma\log(p)$. Finally, we determined the overall P-value as the proportion of permutations revealing a test statistic at least as large as that obtained from the original data set. This revealed an overall P value (accounting for multiple correlated tests) of 0.002.

We fitted two additional GLMMs to assess the effect of period, rank and leaf clipping on rates of male pant hoot production and aggression during all day focal follows. There were a total of 68 focal follow days for the five males (mean: 9.79 hours; range: 3 - 12.5 hours). Both GLMMs had a negative binomial error structure with a log link function and were fitted using the function ‘glmer.nb’ of the package lme4 (Bates et al., 2016) with the total number of pant hoots or total number of aggressive interactions as the response variables, respectively. Pant hoots included calls with or without buttress drumming components, and aggressive interactions included all male displays (directed or undirected at conspecifics), chasing and hitting (Muller & Mitani, 2005). The fixed effects included the three predictors: period, rank and leaf clipping as in the previous models. We also included an offset term for the number of hours (log transformed; (McCullagh & Nelder, 1989)) the individual was ~~focaled~~ during a given day (Dobson & Barnett, 2008). For the aggression rates model, rank was kept as a control fixed effect since we were not particularly interested in rank related effects on aggression and expected higher ~~ranked~~ individuals to be more aggressive, given the way in which chimpanzee dominance is exerted and maintained (Boesch & Boesch-Achermann, 2000; Muller & Mitani, 2005). A random effect for focal ID was included, along with all random slopes for the fixed effects within focal ID (Barr et al., 2013). Again, VIFs and dispersion parameters were calculated as explained above and indicated no issues (maximum dispersion parameter: 1.11; maximum VIF 1.37). Additionally, model stability was evaluated as described above, and significance of both models was assessed using a likelihood ratio test in comparison with a respective null model which consisted of only the offset, control predictor (if applicable) as well as random effects and random slopes (Forstmeier & Schielzeth, 2011).

Results

At the time of the study, the chimpanzees of this community had not been seen to leaf clip since December 2009 when the group had lost half of its members during a respiratory disease outbreak (unpublished data). None of the remaining adult males were observed to leaf clip following this outbreak despite frequent observations of leaf clipping in the neighbouring habituated community (pers. obs.). A physical fight was observed on the evening of October 16, 2011 between the alpha and beta male. ~~The then beta male~~, Kuba, was the first individual observed to leaf clip on October 17, 2011 and all other males of the community were present at the time. We subsequently observed the behaviour to dissipate among the males of the community, although not all individuals (Table 1). On October 23, 2011 the contested alpha male, Woodstock, also began to leaf clip and only the beta and alpha male were seen to leaf clip until January 18, 2012 when the ~~then 5th ranked male~~, Romario, began to leaf clip. After their first occurrences of leaf clipping all three males continued to occasionally leaf clip but no other male in the group was seen to start leaf clipping during the study period. The leaf clip gesture primarily occurred preceding a pant hoot vocalization, and was thus produced sequentially, not simultaneously. We observed a total of 36 leaf clips by the three males during the 11 month study period (Table S1), 33 of which directly preceded a pant hoot vocalization and of these, 27 pant hoots were recorded and therefore were part of this analysis (Table 1). The remaining 3 leaf clip observations occurred after a pant hoot had ended or accompanied a directed charge at a conspecific without a pant hoot. Of all 36 leaf clipping observations, 10 were accompanied by a direct charge at a conspecific, in 11 cases a female chimpanzee in estrus was present, and in 5 cases the caller was alone with no other conspecific in sight whilst leaf clipping. Therefore, an audience was visually present for 86% (31/36) of the leaf clipping observations.

Of the 18 acoustic parameters tested in GLMMs for the influence of leaf clipping, period of instability, and rank, 12 had significant full versus null model comparisons (all $P<0.05$; Table S2). Of these 12 acoustic variables, five measured durations (s) of the whole loud call or parts of the pant hoot, three were the number of call and/or drum elements in the introduction, build-up, and climax phase, and one was the total number of drum beats. The other three significant acoustic variables were related to frequency parameters; namely, the fundamental frequency (F0) and peak frequency (pF) of the middle call of the build-up and the maximum pF recorded in the climax (Table 2). For 8 of the 12 models, the control variable complete or incomplete pant hoot recording had a significant impact in these models, controlling for the fact that incomplete recordings were more likely to be shorter or have fewer elements as expected. Therefore, all of our results controlled for the bias possible with an incomplete recording.

Only three acoustic parameters of the pant hoot were affected by the rank of the male chimpanzee caller: the introduction phase was shorter (est ± SE: -0.39 ± 0.10, $\chi^2=6.90$, df=1, N=173, P=0.0086; Fig. S1) and contained fewer call elements for higher ranking males (-0.58 ± 0.11, $\chi^2=9.31$, df=1, N=173, P=0.0023; Fig. S1) while the number of voiced calls in the build-up phase was larger for higher ranking males (0.55 ± 0.21, χ^2=8.07, df=1, N=189, P= 0.0045; Table 2).

Many acoustic parameters of the loud call were found to change when a male chimpanzee leaf clipped immediately before emitting a pant hoot. Leaf clipping was associated with longer pant hoots overall (est ± SE: 0.48 ± 0.09, χ^2=9.23, df=1, N=212, P=0.0024~~; Figure 2; Table 2; Table 3~~). Following leaf clipping the durations of the introduction (0.42 ± 0.11, χ^2=3.74, df=1, N=173, P=0.053) and climax phases (0.29 ± 0.09, χ^2=5.04, df=1, N=189, P=0.025) were longer although the duration of the middle call of the build-up was shorter (-0.34 ± 0.09, χ^2=7.74, df=1, N=189, P=0.0054). Additionally, when leaf clipping occurred there were more call elements in the build-up (0.21 ± 0.12, χ^2=4.33, df=1, N=189, P=0.037) and climax (0.81 ± 0.15, χ^2=7.89, df=1, N=189, P=0.0051). With respect to buttress drumming, the total duration of drumming was longer when leaf clipping occurred (0.60 ± 0.12, χ^2=8.84, df=1, N=210, P=0.0029) and there were also more drum beats produced by the caller (1.17 ± 0.28, χ^2=7.62, df=1, N=210, P=0.0058; Figure 2; Table 2; Table 3).

Many of the effects observed for leaf clipping on the acoustic properties of pant hoots differed with respect to the effects of instability period on those same acoustic parameters (Figure 2; Table 2; Table 3). In particular, the duration of the total pant hoot was shorter during and after the alpha takeover (χ^2=6.28, df=2, P=0.043; *during*: est. ± SE: -0.27 ± 0.12; *after*: -0.21 ± 0.09); the number of voiced calls in the build-up was also lower during the period of instability (χ^2=6.42, df=2, P=0.040; *during*: -0.31 ± 0.12; *after*: -0.09 ±0.12; Figure 2) while the duration of the middle call of the build-up phase tended to be longer (χ^2=5.19, df=2, P=0.075; *during*: 0.46 ± 0.17; *after*: 0.09 ± 0.08). The F0 of the middle call of the build-up was higher during the alpha takeover (χ^2=12.24, df=2, P=0.0022; *during*: 2.21 ± 0.67; *after*: 1.61 ± 0.48) and likewise with the pF of the middle call of the build-up (χ^2=10.37, df=2, P=0.0056; *during*: 0.26 ± 0.10; *after*: 0.20 ± 0.06; Figure 2; Table 2; Table 3).

With respect to the climax phase of the pant hoot, the duration of the climax was shorter during the instability period (χ^2=16.72, df=2, P=0.00023; *during*: -0.44 ± 0.10; *after*: -0.31 ± 0.09) and drumming duration was also shorter (χ^2=24.29, df=2, P=0.000053; *during*: -0.75 ± 0.13; *after*: -0.46 ± 0.12). There were also fewer call elements associated with the climax during the alpha takeover (χ^2=20.37, df=2, P=0.000038; *during*: -1.05 ± 0.17; *after*: -0.57 ± 0.15) and fewer drum beats (χ^2=17.38, df=2, P=0.00017, *during*: -1.54 ± 0.31; *after*: -0.66 ± 0.28). One additional variable of the climax was also influenced by the period of instability which was the pF of the call with the highest energy in the climax phase (χ^2=11.05, df=2, P=0.0040; during: -0.34 ±0.13; after: -0.53 ± 0.13) where the pF was lower relative to before the dominance hierarchy was disrupted (Figure 2; Table 2; Table 3).

With respect to the rate of daily pant hoot production by males, this was significantly affected by the predictors (full versus null model: χ^2=14.24, df=4, P<0.01, N=68). In particular, individual pant hoot rates were highest during the alpha takeover (χ^2=6.29, df=2, P=0.043; Figure 3), and also on days when the focal male was seen to leaf clip (est.±SE=0.46±0.19, χ^2=5.18, df=1, P=0.023). Rank did not significantly influence pant hoot rates (χ^2=1.61, df=1, P=0.20). Individual aggression rates were also affected by the predictors (full vs. null model: χ^2=10.14, df=3, P=0.017, N=68) where they were elevated during and after the alpha male takeover relative to before (χ^2=9.98, df=2, P<0.01; Figure 3) but leaf clipping had no significant effect on aggression rates (est.±SE=-0.07±0.31, χ^2=0.053, df=1, P=0.82).

Discussion

We found strong support for pant hoots associated with leaf clipping being modified in both spectral and temporal acoustic properties. Pant hoots preceded by leaf clipping had longer phases and call durations, contained a greater number of call elements and drum beats, and had lower fundamental and peak frequencies in the build-up phase. We also found that increased ~~male-male competition via~~ dominance hierarchy instability, affected the acoustic properties of male pant hoots. Pant hoots produced by males during and after an alpha male takeover had shorter durations, fewer calls and drum beats, and higher fundamental and peak frequencies in the build-up phase relative to before. Additionally, we also found male pant hoot rates to be higher when the male hierarchy was unstable and on days when males leaf clipped. Therefore, in line with our predictions, the re-emergence of leaf clipping in this chimpanzee community was associated with measurable acoustic variation in male loud calls, which was also affected by social instability via male-male competition. Male rank did not influence pant hoot rates and we were generally surprised to find only a few acoustic parameters varying according to male rank albeit we only had five males in this community. However, for the majority of our study period the male dominance hierarchy remained highly unstable due to the third ranked male disappearing soon after the alpha male takeover, ~~therefore~~ rank may have had a relatively inconsequential effect in our dataset. Nevertheless, the results of Fedurek and colleagues (Fedurek, Zuberbühler & Dahl, 2016) who found rank related information encoded in pant hoots of another chimpanzee subspecies, strengthens our findings that pant hoots may contain some information relevant for male-male competition.

The contrasting direction of the effects of leaf clipping and social hierarchy instability on pant hoot parameters (Table 2) suggests that leaf clipping could help to alleviate vocal exhaustion caused by an increased pant hoot rate and increased aggression during the alpha takeover period in this study. Vocal exhaustion is characterized by calls becoming shorter with fewer call elements (Fischer et al., 2004) similar to the pant hoots produced by males during the period of instability in this study (Figure 2; Table 2; Table 3). It has also been reported that chimpanzees are energetically stressed during periods of elevated male-male competition which could further contribute to poorly produced pant hoots at this time (Georgiev, 2012). However, it is difficult to assess what, if any, physiological benefits leaf clipping could have on pant hoots with respect to sound production or respiration therefore detailed knowledge about chimpanzee vocal production and anatomy is needed to elucidate any potential mechanism at work here. However, it is clear that leaf clipping before a pant hoot usually necessitates individuals to stop moving for a few seconds up to a minute (pers. obs.) before vocalizing which in itself could help to conserve some energy and rest the respiratory system right before producing the loud call and buttress drumming.

Although the exact mechanism remains unclear, at the very least the leaf clipping behaviour does lengthen the male loud call display by combining the gesture and pant hoot into a more complex multimodal signal, Additionally, leaf clipping has been described as an attention grabbing gesture (Watts, 2007); therefore the behaviour could serve to draw the attention of nearby conspecifics to the signaler and the subsequent pant hoot vocalization. Attention-altering signals are common to multimodal displays of animals, particularly in noisy environments where individuals can benefit from first cueing their targeted audience by drawing their attention to the signaler (Hebets & Papaj, 2005). Indeed, audible gestures often form key components of the multimodal signals present in the communicative repertoire of chimpanzees, both in the wild (Wilke et al., 2017; Hobaiter, Byrne & Zuberbühler, 2017) and in captivity (Leavens, Russell & Hopkins, 2010). Hence, male chimpanzees may increase the perceived effect of their pant hoots by first capturing the attention of nearby conspecifics using leaf clipping. Indeed, 86% of the leaf clipping observations observed occurred in the presence of an audience. In the remaining 5 cases pant hoots could be heard from nearby parties in the distance, often resulting in chorusing back and forth between the lone, leaf clipping male and another party; therefore, signalers at least remained in auditory contact with conspecifics.

With regards to the motivation for leaf clipping, it is likely not a coincidence that the behaviour re-appeared in this community during a time of intense male-male competition. Although leaf clipping was not directly correlated with daily rates of male aggression the association may be one of a more general context of social frustration as has been described for leaf clipping in other chimpanzee communities (Sugiyama, 1981; Boesch, 1995). Leaf clipping itself is a conspicuous tool-use gesture to receivers in close proximity (Watts, 2007) which may signal a threat of aggression to nearby conspecifics (Boesch, 1995). Indeed, when males begin to leaf clip, nearby conspecifics were often observed to move away from the signaler as if giving him space (pers. obs.). Although not all males in this study were observed to leaf clip (Table 1) those that did were often observed to be piloerect and swaying back and forth while leaf clipping, behavioural indications of high arousal (Muller & Mitani, 2005; Clutton-Brock, 2016). In mammals, individuals in an elevated state of arousal often call at higher rates and produce longer calls with higher peak frequencies; however, this is often true in both positive and negative affective contexts (Briefer, 2012). It is therefore difficult to assess how much of the acoustic variation observed in pant hoots preceded by leaf clipping can be attributed to greater arousal alone. However, according to Morton's motivation structural rules (Morton, 1977) we do expect lower fundamental frequencies when animals signal aggressive intent which is supported by our results.

Conclusion

Based on our findings, we show that the leaf clipping gesture combined with the pant hoot vocalization at Taï is associated with an overall conspicuousness of the male chimpanzee loud call. Specifically, pant hoots accompanied by leaf clipping were longer, had more call units and drum beats, and modified fundamental and peak frequencies. Since all males of this chimpanzee community have now been observed to leaf clip, including those that were too young at the time of this study (Taï Chimpanzee Project, unpublished data), the leaf clipping behaviour continues to maintain itself as a socio-cultural trait in this community. Further research is needed to assess whether the results reported here are indicative of a general phenomenon whenever leaf clipping and pant hooting co-occur, or if it is limited to this chimpanzee group, and which proximate mechanisms are responsible for the observed acoustic variation. It is also worth highlighting that some scholars have suggested that the emergence of rhythmic orofacial movements combined with vocal utterances was key to the evolution of human language (Bergman, 2013; Ghazanfar & Takahashi, 2014; Wacewicz & Zywiczynski, 2017). As there may be some degree of coordination between the orofacial praxis with call production when leaf clipping is combined with pant hoots, similar to the lip-smacking behaviour in non-human primates, including chimpanzees (Fedurek et al., 2004; Bergman, 2013; Micheletta et al., 2013), this could be a promising new area for future research in language evolution studies.

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Table 1(on next page)

Names of each male chimpanzee and rank(s) held during the eleven month study period (1 = alpha).

The number of aggressive interactions, leaf clipping observations and high-quality pant hoots recorded and used for analysis before, during and after the alpha takeover are also given.

	Rank(s)	# of leaf clipping observations*			# of aggressive interactions[‡]			# of pant hoots recorded*		
		before	during	after	before	during	after	before	during	after
Jacobo	4, 3	0	0	0	NA	3	18	0	3	19
Kuba	2, 1	0	8	6	1	13	42	9	37	46
Romario	5, 4	0	0	9	NA	NA	8	0	2	46
Utan	3	0	0	0	4	21	9	10	9	2
Woodstock	1, 2	0	1	3	18	7	13	10	9	10

*data were collected opportunistically and ad libitum whenever individuals were present

[‡]based on focal follow data; NA means individuals were not focalled

Table 2(on next page)

Summary of the direction of significant effects (P<0.05) of the three predictors on the twelve acoustic pant hoot variables which revealed significant full null model comparisons.

	Period of Instability	**Leaf Clipping**	**Rank**
total duration	⬇	⬆	–
# of calls in introduction phase	–	–	⬇
duration of introduction phase	–	⇧	⬇
# of voiced calls in build-up phase	⬇	⬆	⬆
F0 of the middle call of build-up phase	⬆	⬇	–
duration of the middle call of the build-up	⇧	⬇	–
pF of the middle call of build-up phase	⬆	⬇	–
# of elements in climax phase	⬇	⬆	–
duration of climax phase	⬇	⬆	–
the maximum pF of a climax call	⬇	–	–
duration of total drumming	⬇	⬆	–
# of drum beats	⬇	⬆	–

(Period of Instability: during and/or after the alpha takeover occurred relative to before; Leaf clipping: when leaf clipping preceded the pant hoot; Rank: as rank increases in dominance; unfilled arrows P<0.1).

Table 3(on next page)

Mean and associated standard error for all 18 acoustic variables measured from male chimpanzee pant hoots before, during and after the alpha male takeover and when leaf clipping did and did not occur.

	Period of Instability			Leaf clipping	
	Before	During	After	NO	YES
total duration (s)	7.71 ± 0.49	6.39 ± 0.37	7.19 ± 0.24	6.66 ± 0.17	9.58 ± 0.74
# calls in the introduction	3.04 ± 0.38	3.65 ± 0.44	4.03 ± 0.26	3.48 ± 0.21	5.42 ± 0.51
introduction duration (s)	1.92 ± 0.3	2.82 ± 0.36	3.02 ± 0.24	2.49 ± 0.16	4.56 ± 0.65
F0 of last call of the introduction (Hz)	401 ± 32.0	383 ± 11.3	404 ± 8.44	393 ± 8.17	422 ± 17.0
duration of the last call of the introduction (s)	0.30 ± 0.03	0.43 ± 0.04	0.42 ± 0.02	0.39 ± 0.02	0.46 ± 0.03
pF of the last call of the introduction (Hz)	577 ± 92.6	466 ± 32.4	506 ± 26.0	486 ± 23.4	610 ± 60.3
# of voiced calls in the build-up	10.4 ± 0.82	7.51± 0.66	7.99 ± 0.39	8.18 ± 0.33	8.46 ± 1.00
Duration of the build-up (s)	3.46 ± 0.25	3.10 ± 0.26	3.09 ± 0.13	3.17 ± 0.12	2.98 ± 0.27
F0 of the middle call of the build-up (Hz)	296 ± 11.8	369 ± 15.9	355 ± 7.78	355 ± 7.41	314 ± 8.55
Duration of the middle call of the build-up (s)	0.141± 0.004	0.214 ± 0.022	0.156 ± 0.007	0.176 ± 0.008	0.122 ± 0.007
pF of the middle call of the build-up (Hz)	316 ± 31.2	389 ± 23.5	379 ± 16.4	381 ± 14.1	314 ± 8.55
# of elements in the climax	9.43 ± 1.03	4.09 ± 0.51	5.92 ± 0.44	5.52 ± 0.37	8.96 ± 0.96
Duration of the climax (s)	2.44 ± 0.26	1.35 ± 0.13	1.62 ± 0.09	1.62 ± 0.08	2.05 ± 0.24
F0 of the highest call of the climax (Hz)	1221 ± 95.1	1097 ± 67.1	1114 ± 40.6	1109 ± 35.6	1271 ± 82.6
Duration of the highest call of the climax (s)	0.49 ± 0.04	0.57 ± 0.04	0.55 ± 0.02	0.55 ± 0.02	0.51 ± 0.06
pF of the highest call of the climax (Hz)	1848 ± 232	1532 ± 153	1447 ± 104	1546 ± 90.2	1474 ± 174
Duration of drumming (s)	1.55 ± 0.23	0.46 ± 0.10	0.85 ± 0.09	0.77 ± 0.08	1.28 ± 0.21
# of drum beats	7.07 ± 0.92	2.23 ± 0.40	4.42 ± 0.42	3.75 ± 0.33	6.93 ± 0.71

Figure 1

A spectrogram of a male chimpanzee pant hoot vocalization preceded by leaf clipping.

Curved lines identify the three main phases: introduction, build-up and climax while boxes denote the call targeted for further analyses within each phase. Both leaf clipping and buttress drumming also occur in this pant hoot and are indicated with arrows.

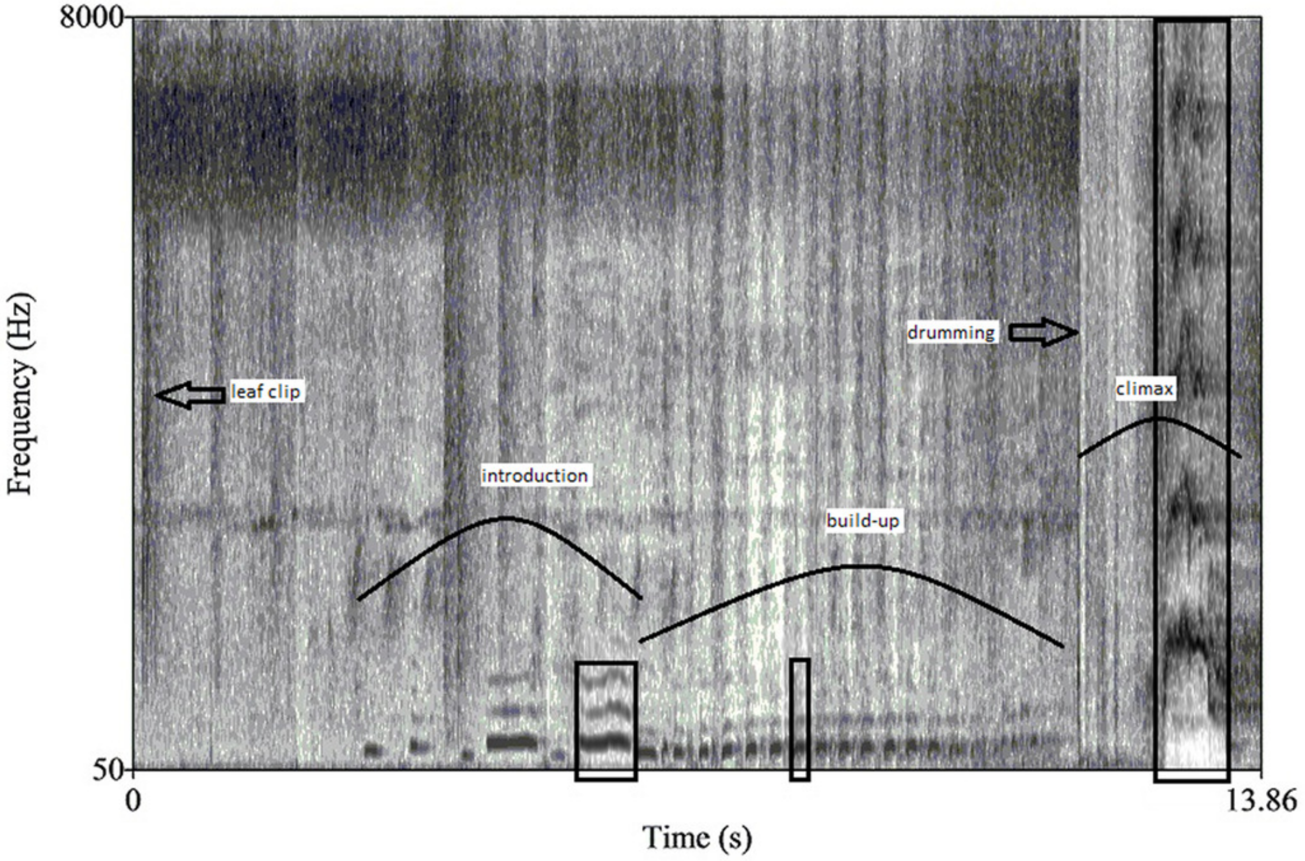

Figure 2

Variation in eight acoustic parameters of male chimpanzee pant hoots that were significantly affected by both leaf clipping and the period of instability.

Plots show the median (solid horizontal line) for each acoustic parameter. The boxes represent quartiles and the vertical lines show percentiles (2.5 and 97.5%). The y-axis is the acoustic parameter and the x-axis shows the levels of the two factors: leaf clipping and period of instability (before, during and after the alpha takeover). The dashed horizontal line shows the model prediction given all other fixed effects being at their average value.

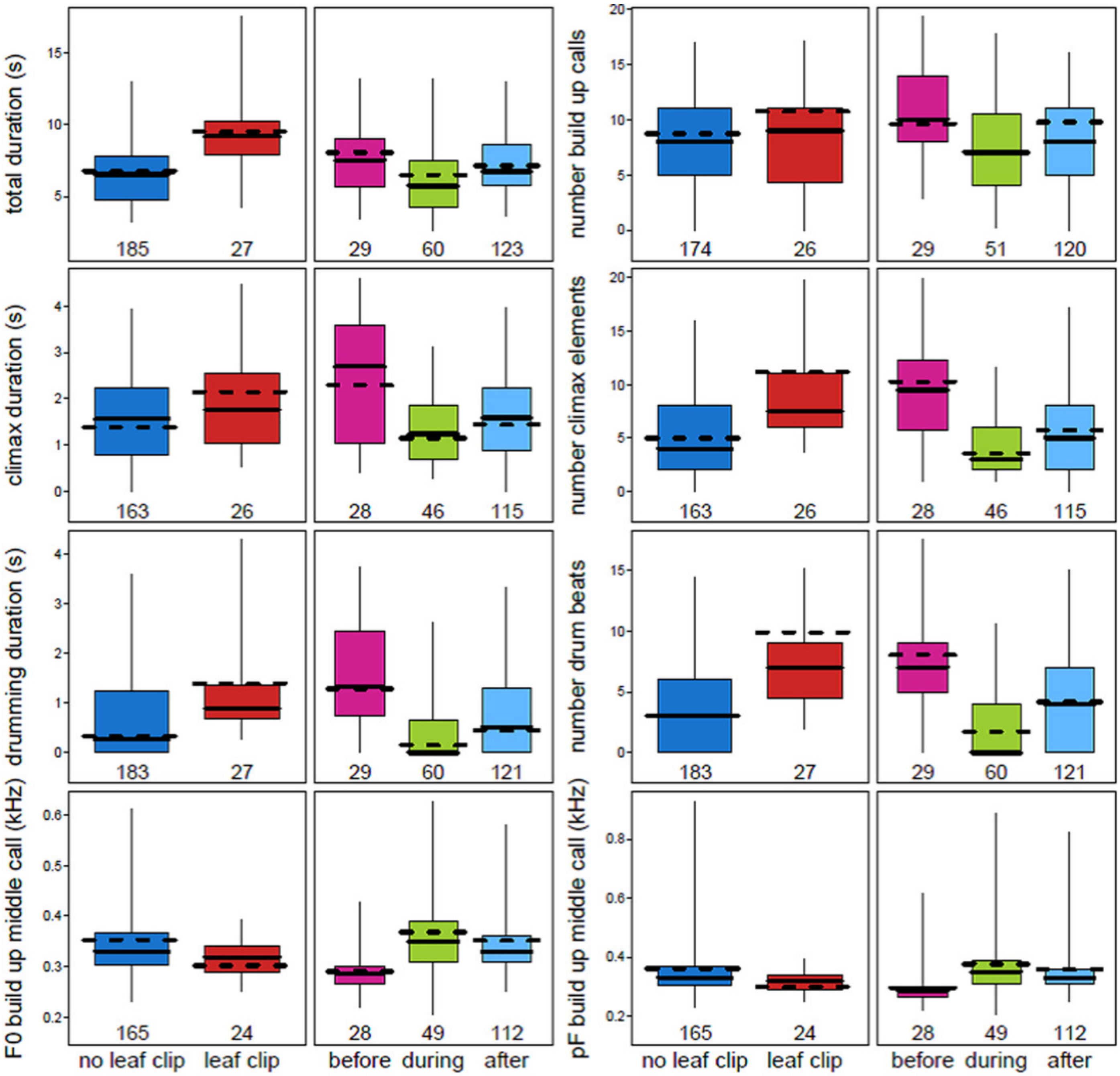
total duration (s)
15
10
5
185
27
29
60
123
number build up calls
20
15
10
5
0
174
26
29
51
120
climax duration (s)
4
3
2
1
0
163
26
28
46
115
number climax elements
20
15
10
5
0
163
26
28
46
115
drumming duration (s)
4
3
2
1
0
183
27
29
60
121
number drum beats
15
10
5
0
183
27
29
60
121
F0 build up middle call (kHz)
0.6
0.5
0.4
0.3
0.2
165
24
28
49
112
pF build up middle call (kHz)
0.8
0.6
0.4
0.2
165
24
28
49
112
no leaf clip
leaf clip
before
during
after
no leaf clip
leaf clip
before
during
after

Figure 3

Median rates of pant hooting (a) and aggression (b) per hour for each focal chimpanzee male before, during and after the alpha takeover.

Lines connect points of the same respective individual where applicable.