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A comparison of buttress drumming by male chimpanzees from two populations

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Abstract Wild chimpanzees (*Pan troglodytes*) produce low-frequency sounds by hitting the buttresses and/or trunks of trees. This “buttress drumming” occurs in discrete bouts that may be integrated into the phrase sequence of the chimpanzee’s long-distance vocalization, the “pant hoot.” The aim of this study was to investigate whether regional variation exists in the drumming behavior of male chimpanzees from Kibale National Park (Kanyawara community), Uganda, and Taï National Park, Ivory Coast. Recordings were made during a 6-month field season at Taï in 1990, and a 12-month field season at Kanyawara in 1996–1997. Acoustic analysis revealed the following: (1) Kanyawara males drummed significantly less frequently in conjunction with a pant hoot or hoot than did Taï males; (2) drumming bouts by Kanyawara males included significantly fewer beats, and were significantly shorter in duration, than those of Taï males; these differences disappeared when only those bouts produced in conjunction with a call were compared; (3) when Kanyawara chimpanzees did call and drum together, they tended to integrate drumming into the vocalization at a later point than did Taï males; and (4) individual differences in the temporal patterning of drumming bouts were not apparent for Kanyawara males, whereas a previous analysis revealed individual differences among Taï males.

Keywords Buttress drumming · Pant hoot · *Pan troglodytes*

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Introduction

Regional variation in animal vocalizations is of interest because it suggests the possibility that social learning is involved in the development of the signal repertoire (Marler 1990; Kroodsma 1996). In contrast to the vocalizations of many primate species, some chimpanzee vocalizations appear to exhibit such dialectal variation (Mitani et al. 1992, 1999; Arcadi 1996; Arcadi et al. 1998; Marshall et al. 1999). The aim of the study reported here was to determine whether a non-vocal acoustic signal produced by chimpanzees, “buttress drumming,” also exhibits regional variation and may therefore be modified through social learning. The possibility that buttress drumming is influenced by learning is intriguing for two reasons. First, buttress drumming is often integrated into the long-distance call of chimpanzees, the “pant hoot,” altering the phrase sequence of the call as well as the temporal patterning of the drum bout (Arcadi et al. 1998). Thus, regional differences in buttress drumming would involve a combination of signal channels, and by extension could be supported by more complex learning mechanism(s) (Janik and Slater 2000). Second, the evolution of the intimate connection between manual gestures and speech in humans remains unexplained (McNeill 1992). Examination of the nature and social transmission of buttress drumming and calling in wild chimpanzees may provide insights into the origins of the hand/mouth connection in the evolution of linguistic communication.

Methods

The field research reported here was conducted at the Kanyawara study area of the Makerere University Biological Field Station (MUBFS) in Kibale National Park, Uganda, from December 1996 to November 1997 (by A.C.A. and F.M.), and in Taï National Park, Ivory Coast, from March to August 1990 (by D.R.). Details concerning the study sites, animals, and data collection and analysis can be found in Arcadi et al. (1998), with the following additions. In 1996–1997 the Kanyawara unit-group included ten adult

males, eight central adult females, an additional nine peripheral mothers intermittently observed in the northern and southern parts of the community range, and two adolescent males. The community was fully habituated and could be observed at close range (<5 m) during all-day follows. The Kanyawara chimpanzees were located at their night nests before dawn, by following their loud calls or drumming, or by visiting known fruiting trees. Recordings at Kanyawara were made by A.C.A. from 1 December 1996 to 22 January 1997, and by F.M. from 23 January to 17 November 1997. Recordings at both sites were made using Sony WM-D6C stereo cassette recorders, Sennheiser directional microphones (K3U power module, ME80 recording head) with windscreens, and CrO₂ tapes.

Results

A total of 108 and 34 drumming bouts were recorded at Kanyawara and Taï, respectively (Table 1). Drumming by females was not observed at either site during this study. Drumming was performed with and without pant hoots at both sites. Spectrograms of drumming bouts with and without vocalizations are shown in Fig. 1.

Most drumming bouts were clearly discrete events, separated in time and space from other drumming events. In 13 of 108 cases from Kanyawara, more than one drumming bout was scored for the same long charging display since more than 2 s (range: 2.1–48.9 s) elapsed between clusters of closely spaced beats, and the clusters were produced on different substrates. The 108 bouts included a total of 212 interbeat intervals (IBIs), of which 205 IBIs (96.7%) from 101 bouts were less than 1 s in duration. The remaining seven IBIs (3.3%) from seven bouts were between 1 and 2 s in duration. In six of the seven bouts in which these longer IBIs were

recorded, the chimpanzees drummed on the same substrate throughout. In one case it was unclear if the chimpanzee hit a neighboring tree.

There were no instances in the Taï sample in which more than 2 s elapsed between IBIs, and in all cases the chimpanzees drummed on the same substrate. Of 163 IBIs in 34 bouts, 156 (95.7%) were less than 1 s in duration, and 7 (4.3%) were between 1 and 2 s in duration. In five of these seven cases, the longer interval occurred when the chimpanzee interrupted the drumming sequence to produce the climax phrase of his pant hoot. In the remaining two cases, the longer interval occurred immediately after the production of the climax phrase.

Do Kanyawara males have individual drumming signatures?

There was a significant difference between Kanyawara males in mean number of beats per bout (Kruskal-Wallis, $H=14.453$, $df=5$, $P<0.05$) (Fig. 2). However, elimination from the sample of either the individual with the highest number of beats per bout (MS) or the individual with the lowest number of beats per bout (AJ) rendered the difference non-significant (without MS: $H=2.73$, $df=4$, $P>0.5$; without AJ, $H=7.148$, $P>0.1$). There were no significant differences between individuals in mean duration of drumming bouts ($H=7.719$, $df=5$, $P>0.1$) or in mean duration of interbeat intervals ($H=7.322$, $df=5$, $P>0.1$). Comparable data for the Taï males are published in Arcadi et al. (1998).

Table 1 Number of recorded drumming bouts by male chimpanzees from Kanyawara (1996–1997) and Taï Forest (1990)

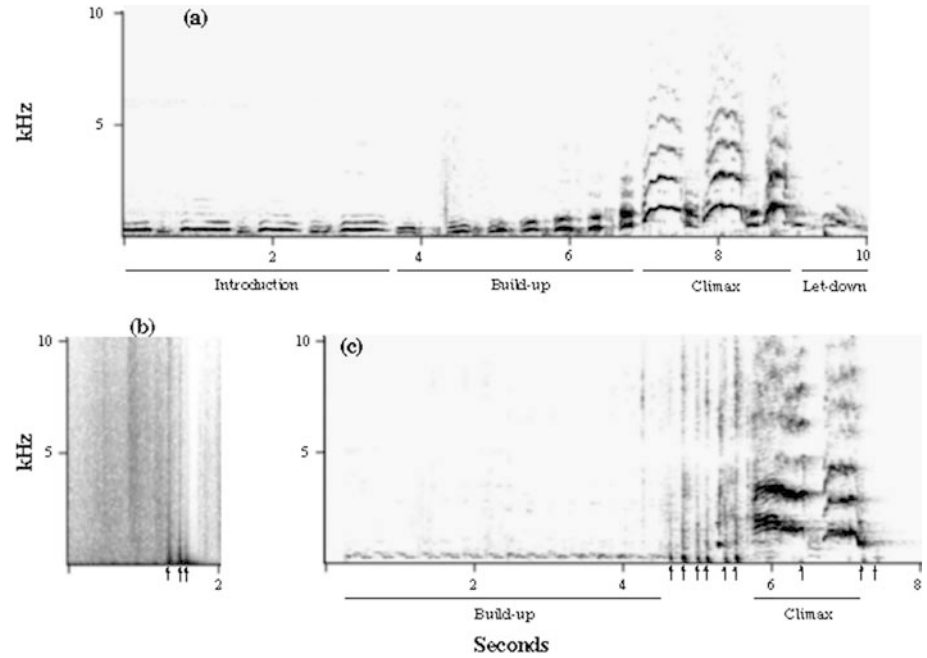
Individual	No. of bouts with hoots	No. of bouts with pant hoots	No. of bouts with no vocalization	Total no. of bouts	% Bouts with no vocalization
Kanyawara adult males					
AJ	0	3	8	12 ^a	0.67
BB	1	3	6	10	0.60
BF	0	2	3	5	0.60
LB	1	0	6	7	0.86
MS	3	16 ^b	19	39 ^a	0.50
SL	1	0	0	1	0
ST	1	1	1	3	0.33
TU	0	0	4	4	1.00
YB	1	5	16	22	0.73
Subtotal	8	30	63	103	0.61
Kanyawara subadult males					
KK	0	1	0	1	0
LK	0	2	2	4	0.50
Subtotal	0	3	2	5	0.40
Taï Forest adult males ^c					
BR	0	6	0	6	0
DA	0	3	0	3	0
KE	2	6	0	8	0
MA	0	2	1	3	0.33
RO	0	7	0	7	0
UL	1	5	1	7	0.14
Subtotal	3	29	2	34	0.06

^a Because of chorused vocalizations, it was unclear for one of the bouts whether or not the individual gave a call. Thus the total does not equal the sum of the columns.

^b One of MS's drumming bouts scored as "with pant hoots" followed a pant hoot by 2.8 s

^c We note that the number of drumming bouts reported in the text of Arcadi et al. (1998, p. 511) for two Taï males was incorrect (MA: $n=2$; KE: $n=9$). In addition, it was MA, not KE, that produced a drumming bout without vocalization. The graphic associated with these results (see Fig. 2 of Arcadi et al. 1998, p. 511), therefore, was accurate, as were the subsequent analyses

Fig. 1 Audiospectrograms of: **a** a 4-phase pant hoot vocalization without drumming, **b** a drumming bout produced without vocalization, and **c** a drumming bout inserted into a pant hoot. Drum beats appear as energy spikes and are marked with *arrows*: there are 3 and 9 beats in **b** and **c**, respectively. Part **c** shows the common Tai pattern, with drumming initiated after completion of the build-up phrase, prolonging the pause between the build-up and climax of the pant hoot



Are there differences between Kanyawara and Tai males in the temporal patterning of drumming bouts?

Tai males produced significantly more beats per bout (Mann-Whitney $U=35$, $n_1=6$, $n_2=6$, $P<0.01$) and their bouts were significantly longer in duration ($U=34$, $n_1=6$, $n_2=6$, $P<0.05$) (Fig. 3). In addition, Kanyawara males drummed without an accompanying vocalization significantly more often than Tai males did ($U=36$, $n_1=6$, $n_2=6$, $P<0.01$). We found no difference between Kanyawara and Tai males in the mean duration of interbeat intervals ($U=25$, $n_1=6$, $n_2=6$, $P>0.1$).

The above analyses suggested the possibility that drumming bouts by Tai males were longer because they drummed in conjunction with calling. To address this possibility, we compared only those Kanyawara and Tai drumming bouts that were accompanied by a pant hoot. In contrast to the above result, we found that neither the mean number of beats per bout, nor the mean bout duration, differed significantly between the two groups of males when only drumming bouts accompanied by a vocalization were included (for mean beats/bout: $U=17$, $n_1=6$, $n_2=4$, $P>0.1$; for mean bout duration: $U=26$, $n_1=6$, $n_2=6$, $P>0.1$).

Are there differences between Kanyawara and Tai males in the integration of drumming bouts into vocalizations?

Figure 4 shows the phrase of the pant hoot during which drumming bouts by Kanyawara and Tai males both started and ended, for all bouts accompanied by this vocalization. Visual inspection of this schematic representation suggested the possibility that Kanyawara males tended to begin their drumming bouts later in the pant hoot phrase sequence, with, in particular, more

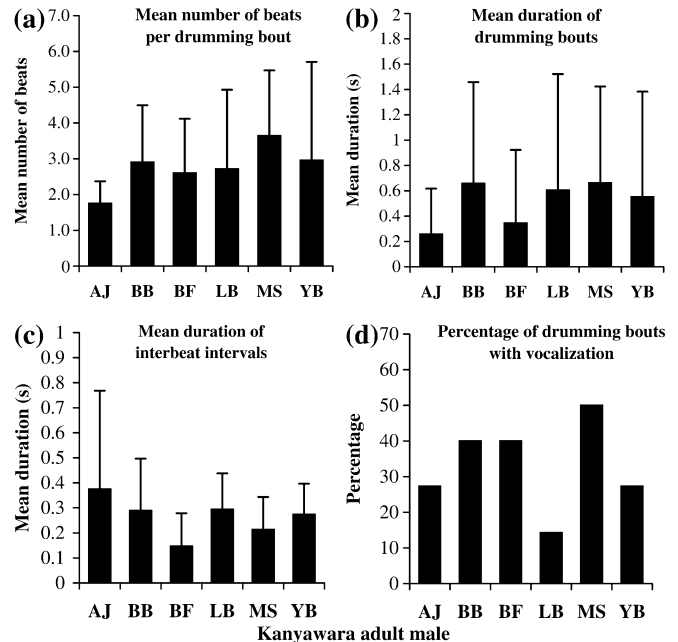


Fig. 2a–d Individual differences (not significant) in drumming for Kanyawara males

bouts begun after the completion of the call. In an effort to quantify this perception, we assigned two numbers to each drumming bout, one for the phrase during which it started, and one for the phrase during which it ended, where build-up=1, pause between build-up and climax=2, climax=3, and after climax=4.

Figure 5 shows the means of individual means for the start and end of drumming bouts for each population. Tai males began their pant hoots significantly earlier than Kanyawara males (Mann-Whitney $U=42$, $n_1=8$, $n_2=6$, $P<0.05$). There was not a significant difference

between populations in when drumming bouts ended ($U = 31, n_1 = 8, n_2 = 6, P > 0.1$).

Discussion

In a previous study we examined the acoustic patterning of buttress drumming by male chimpanzees from Tai

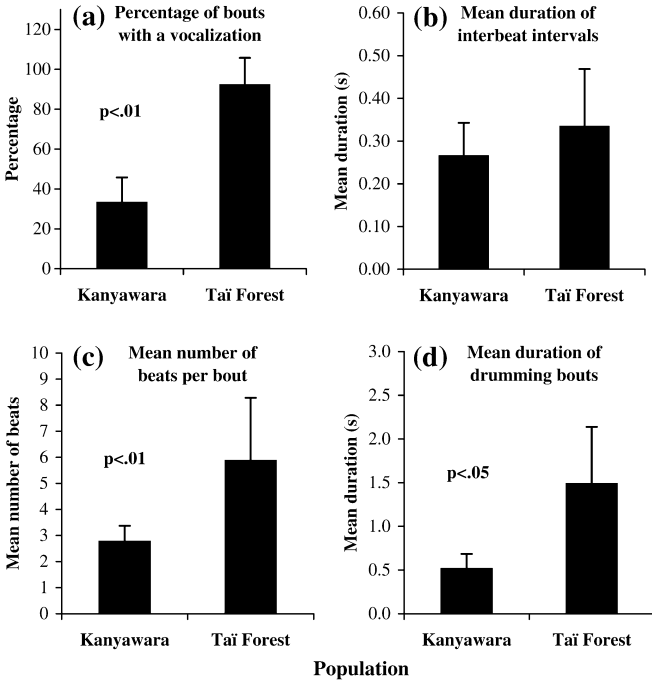
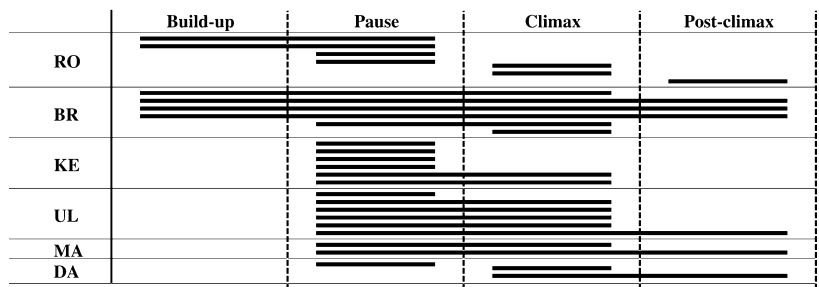


Fig. 3a-d Comparison of Kanyawara and Tai drumming. When only bouts produced together with a pant hoot were compared in the two populations, the differences in mean beats per bout and in mean duration of drumming bouts were not significant

Fig. 4 Schematic representation of the integration of drumming bouts into pant hoots at Tai and Kanyawara. Each horizontal bar depicts one drumming bout. The bar begins in the phrase that the first drum beat of the bout occurred in, and ends in the phrase that the last beat of the bout was given in. Drumming was never initiated during the introduction phrase, so this phrase is not shown in the schematic. Since Tai males did not include let-down phrases in their pant hoots, all beats delivered after the climax are represented as “post-climax.”

Tai Forest males



Kanyawara males



National Park (Arcadi et al., 1998), providing the first quantitative data on this long-distance acoustic signal. The results of a follow-up study reported here suggest that the temporal patterning of buttress drumming by these males differed from that of males in Kibale National Park.

Kanyawara males tended to drum in the absence of an accompanying pant hoot vocalization, whereas Tai chimpanzees usually combined the two signals. In addition, drumming bouts by Kanyawara chimpanzees were on average shorter in duration than those of Tai chimpanzees. Since this difference disappeared when only those bouts delivered in conjunction with a call were compared, it appears that the integration of calling and drumming prolonged Tai drumming bouts. When

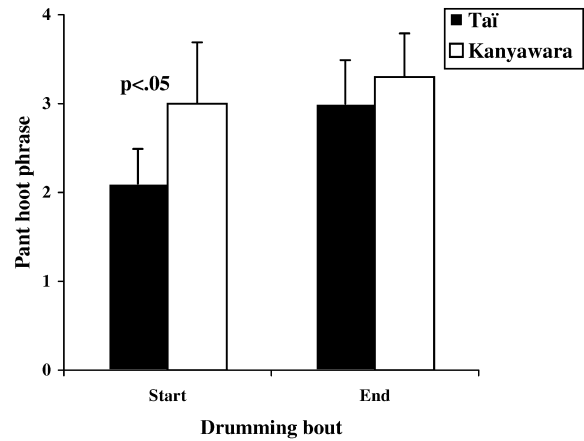


Fig. 5 Comparison of the timing of insertion of drumming bouts into pant hoot vocalizations by Tai and Kanyawara males. Each drumming bout was assigned a start and an end number: build-up = 1, pause = 2, climax = 3, and post-climax = 4. Individual means were computed and compared

they did combine the two signals, Kanyawara males began their drumming later in the call than did Taï chimpanzees. Moreover, four of the eight Kanyawara males initiated drumming immediately after the completion of the pant hoot, and for three of these males they did so the majority of the time. By contrast, drumming after the pant hoot was observed just once among the six Taï males. And finally, whereas in our previous analysis we found significant differences in the temporal patterning of drumming by individual Taï males, no such differences were found in the present analysis for Kanyawara males, possibly because their bouts were too brief for temporal variation to be expressed or easily detected.

Further study will be needed to examine the extent and significance of intra-individual variation in buttress drumming, and to explore the possible ways in which individual experience might affect the acquisition of buttress drumming as a manually produced acoustic signal that is variably combined with loud vocalizations in adult male chimpanzees.

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