

Buttress Drumming by Wild Chimpanzees: Temporal Patterning, Phrase Integration into Loud Calls, and Preliminary Evidence for Individual Distinctiveness

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ABSTRACT. Wild chimpanzees (*Pan troglodytes*) generate low-frequency sounds that are audible to humans from a distance of at least 1 km away by hitting the buttresses of trees with their hands and feet. This buttress drumming occurs in discrete bouts of rapidly delivered beats that usually accompany "pant hoots," the species-specific long-distance vocalization. Individual differences in male chimpanzee (*Pt. verus*) drumming were investigated during a 6-month field study in the Taï National Park, Ivory Coast. Analysis of drumming bouts recorded from six adult males revealed significant differences between individuals in three acoustic features: (1) mean duration of inter-beat interval; (2) mean number of beats per bout; and (3) mean bout duration. Preliminary analysis indicated that individuals differ in their tendency to deliver drum beats in temporally close pairs separated by longer interbeat intervals. Qualitative examination also suggested that individuals may differ in the temporal integration of drumming into the pant hoot vocalization. These results suggest that there may be acoustic cues available for chimpanzees to recognize unseen males by their drumming performances alone. Drumming by Taï chimpanzees was also compared to drumming by chimpanzees (*Pt. schweinfurthii*) from the Kanyawara study group in Kibale National Park, Uganda. The Kanyawara chimpanzees appeared to drum more often without vocalizing than did the Taï chimpanzees. When they did drum and vocalize together, the Kanyawara chimpanzees appeared to integrate their drumming later into the associated pant hoots than did the Taï chimpanzees. These results suggest the possibility that interpopulation variation exists in chimpanzee buttress drumming.

Key Words: Chimpanzee; Drumming; Individual distinctiveness; Signatures; Dialects.

INTRODUCTION

Long-distance nonvocal acoustic signals are rare in primates. Many species incorporate branch-shaking into aggressive displays, but the acoustic aspect of this signal appears secondary to the visual component. The best-described non-vocal acoustic signal among primates is chest-beating in mountain gorillas (*Gorilla gorilla beringei*; SCHALLER, 1963). Like branch-shaking in this and other primate species, chest-beating is typically incorporated into aggressive display sequences that involve both locomotion and vocalization. Since these displays are generally performed near individuals that are in view, it is not clear what function chest-beating might serve as a long-distance acoustic signal. Nonetheless, SCHALLER (1963) reports several instances of gorillas responding with chest-beating to chest-beating from unseen individuals in other groups. He also reports that the sound may carry for up to a mile, apparently aided by inflatable laryngeal air sacs that act as resonators. It thus appears that chest-beating has evolved to serve at least some long-distance signaling functions, though these have yet to be accurately described.

Chimpanzees generate acoustic signals by hitting a variety of substrates with their hands and/or feet, including their chests, the ground, tree trunks, and the buttresses of trees. Any of these signals may be incorporated into visual displays performed near conspecifics (GOODALL,

1965, 1968, 1986) or, more rarely, individuals of other species (e.g. red colobus monkeys, *Colobus badius*: ACA, pers. obs.). The sound produced by drumming on buttresses is thought to carry the farthest of these signals, and is the subject of the present analysis. Buttress drumming is audible for at least 1 km (DR, pers. obs.; BOESCH, 1991a) and is typically done by adult males. The drummer may stand on the ground and hit on both sides of the end of the buttress, strike a single side in passing, or perch atop the crest at an intermediate point along its length and hit with hands and/or feet. Drumming may be integrated into "charging displays" (GOODALL, 1968, 1986) that include loud vocalizations.

Drumming on tree buttresses by chimpanzees has been noted since the earliest accounts of wild chimpanzee behavior (reviewed in REYNOLDS & REYNOLDS, 1965). MARLER (1976) and MARLER and TENAZA (1977) note the evident similarity in both mode and context of production of chimpanzee buttress drumming to gorilla chest-beating. In contrast to chest-beating, however, drumming on tree buttresses by chimpanzees occurs frequently during travel, as well as during long-distance acoustic exchanges between individuals that are not in visual contact (REYNOLDS & REYNOLDS, 1965; GOODALL, 1968). Buttress drumming therefore appears to be primarily a long-distance signal.

Long-distance acoustic signals seem to play an important communicative role within chimpanzee groups. Although chimpanzees live in semi-closed "unit-groups" or "communities" that have stable male memberships, the composition of foraging subgroups varies daily (NISHIDA, 1968; GOODALL, 1986; BOESCH, 1996; WRANGHAM et al., 1996). Auditory contact, involving a wide range of calls used by individuals of all ages and both sexes, is commonly maintained between dispersed unit-group members. Some authors have suggested that the species-specific loud call, or "pant hoot," which is predominantly given by adult males, is used in particular to coordinate intra-unit-group travel and spacing (GOODALL, 1965, 1986; REYNOLDS & REYNOLDS, 1965; MITANI & NISHIDA, 1993). Buttress drumming typically occurs in conjunction with pant hooting, often being integrated into the phrase sequence of the vocalization. It has consequently been hypothesized that drumming, like pant hooting, is used to coordinate group spacing and travel (REYNOLDS & REYNOLDS, 1965; MARLER, 1976; BOESCH, 1991a).

The ability to communicate one's geographic position, age, sex, and, if possible, identity would have clear benefits for dispersed chimpanzees. Coalitions among specific males are used to establish rank and gain access to mates and resources (NISHIDA, 1983). It would therefore be advantageous for males to be identifiable acoustically to allies within the unit-group in order to coordinate travel and facilitate reunions (MITANI & NISHIDA, 1993). In addition, chimpanzees of all ages and both sexes are subject to lethal aggression from neighboring males in at least some unit-groups (Gombe: GOODALL et al., 1979; Mahale: NISHIDA et al., 1985; Kibale: R. WRANGHAM, pers. comm.). Acoustic exchanges, including both vocalizations and drumming, occur near range borders and appear to mediate intergroup spacing, with smaller groups avoiding larger groups (GOODALL, 1986; C. BOESCH, pers. obs.). It would consequently be advantageous for individuals to be recognizable to group members who could support them in intercommunity confrontations.

MARLER and HOBETT (1975) and MITANI and BRANDT (1994) found acoustic evidence of individual differences in pant hooting by male chimpanzees, though it remains to be demonstrated that individuals can in fact recognize each other by their calls only. Although field workers have found it difficult to recognize individuals by their drumming rhythms alone (BOESCH, 1991a), there are two reasons to suspect that drumming, like pant hooting, might be individually distinctive. First, individual chimpanzees differ physically (in strength, coordination, and possibly handedness: BOESCH, 1991b), and these differences could affect drumming patterns. Second, drumming is intimately associated with pant hooting: at Tai it occurs most

often simultaneously with pant hoots, like pant hooting it is predominantly an adult male behavior, and the sound produced by drumming on tree buttresses carries at least as far as the associated pant hoot vocalization. We might therefore predict that drumming has communicative significance in parallel with pant hooting, and that senders would benefit from individually recognizable drumming. Hence, the possibility that male chimpanzees have drumming signatures warrants investigation.

In this paper we describe buttress drumming by six adult male chimpanzees from Tai Forest, Ivory Coast. Six acoustic features are analyzed: number of beats per bout, duration of drum bouts, duration of interbeat intervals, alternation of longer and shorter interbeat intervals, percentage of drum beats made during the climax phrase of pant hoots, and the integration of drumming into the phrase sequence of the pant hoot vocalization. We show that there are systematic differences in the way individuals drum that could be used to identify a drummer out of visual contact. We also compare buttress drumming at Tai with drumming at Kanyawara (Kibale National Park), and with SCHALLER's (1963) data on gorilla chest-beating.

METHODS

STUDY AREAS AND ANIMALS

The field research reported here was carried at two study sites: in the Tai National Park, Ivory Coast, from March to August 1990 (by DR); and at the Kanyawara study area of the Makerere University Biological Field Station (MUBFS) in the Kibale National Park, Uganda, from May 1988 to December 1989 (by ACA, formerly A. CLARK). Descriptions of Tai Forest may be found in BOESCH and BOESCH (1983, 1989). Briefly, Tai Forest is a relatively flat (maximum altitude difference of 150 m), low-altitude evergreen rain forest (mean annual rainfall 1,800 mm, mean maximum temperature 24°C) located in western Ivory Coast (5°50' N, 7°20' E). It is the largest remaining forest block in West Africa (430,000 ha), and is home to a diverse flora and many large mammal species. Common tree species with large, buttressed trunks used by the chimpanzees for drumming include *Tarieta gracilis* and *Piptadeniastrum africanum*. There are 11 species of primates in the forest, including a chimpanzee (*P. t. verus*) population estimated at 4,500 individuals (MARCHESI et al., 1995).

One chimpanzee community at Tai was habituated to human observers without provisioning between 1979 and 1985 (BOESCH & BOESCH, 1989). At the time of the present study, there were 56 known individuals in this group: 7 adult males, 22 adult females, and 21 subadults, juveniles, and infants. We consider the chimpanzees at this time to have been almost fully habituated to human observers: most individuals, and all the adult males, could be approached without obvious disturbance to within 5 m. The chimpanzees were followed from dawn if their nesting area was known from the previous day of observation, or located by their loud calls or drumming, or by visiting fruiting trees. Observation sessions were usually terminated at dusk at the next nesting area. Due to the high degree of habituation of the Tai chimpanzees and the relative lack of thick, obstructive vegetation on the forest floor, observations and audio recordings were rarely interrupted when individuals being observed were traveling. Data were collected on 87 observation days, and complete dawn to dusk follows were made on 21 of these.

The Makerere University Biological Field Station is located in the north-central part of the Kibale National Park, Toro district, western Uganda (0° 13' to 0° 41' N and 30° 19' to 30° 32' E). Detailed descriptions of the forest may be found in KINGSTON (1967), WING and BUSS (1970), STRUHSÄKER (1975), GHIGLIERI (1984), and SKORUPA (1988). Briefly, Kibale Forest is a

small, mid-altitude evergreen rain forest (766 km², maximum altitude 1,590 m, mean annual rainfall 1,570 mm, mean maximum and minimum temperatures 23° and 16°C: BUTYNSKI, 1990) comprised of a mosaic of mature high rain forest (60%), and various types of grassland, woodland-thicket, and colonizing forest (40%). Like Tai, Kibale has a diverse flora and is inhabited by many species of large mammals. It is home to 11 species of primates, including a chimpanzee (*P. t. schweinfurthii*) population of at least 1,100 individuals (estimated from CHAPMAN & WRANGHAM, 1993).

MUBFS maintains two study areas in the forest with gridded trail systems: Kanyawara, located on the edge of the park 12 km southeast of the town of Fort Portal; and Ngogo, located 10 km southeast of Kanyawara in the center of the forest (0° 29' to 0° 31' N and 30° 24' to 30° 26' E). The chimpanzees in the Kanyawara study area were habituated to human observers without provisioning by G. ISABIRYE-BASUTA between 1983 and 1985 (ISABIRYE-BASUTA, 1989), and again by R. WRANGHAM and assistants in 1987 after a 2-year break in observations. They have been under continuous observation from 1987 to the present.

Detailed descriptions of the sampling protocol at Kanyawara are published elsewhere (WRANGHAM et al., 1992; CLARK, 1993). Briefly, the chimpanzees were usually located by visiting large fruiting trees in the early morning (95 of 125 of all observation sessions). Most observation sessions were terminated when animals traveling on the ground were lost from view (89 of 125). We consider the animals to have been at this time "semi-habituated": in the presence of observers: all regularly seen individuals ($n=26$, including all of the prime adult males) were at ease when feeding arboreally, and could be followed without obvious disturbance on the ground at a distance of approximately 15 m. In addition, most males and some females would approach sitting observers to within 5 m.

RECORDING METHODS, BEHAVIORAL OBSERVATIONS, AND ACOUSTIC ANALYSIS

Tape recordings of pant hoots and drumming bouts at Tai Forest used for acoustic analysis ($n=34$ from 6 adult males) were made using a Sony WM DC-6 stereo cassette recorder, a Sennheiser directional microphone (K3U power module, ME80 recording head) with type MZW415 windscreen, and CrO₂ tapes. Recordings were made opportunistically at a distance of 5–100 m during all-day follows of target males, and used for analysis if the identity of the vocalizer was known. Drumming individuals were usually in direct view ($n=29$ bouts from 6 individuals) or their identities were inferred based on recent observation during close ground follows ($n=5$ bouts from 4 individuals). We noted the time of day of each event, as well as general behavioral context: *feeding*, if the drummer was actively processing food matter; *socializing/resting*, if no one was feeding, and the group had been in the same location for at least 5 min; and *traveling*, if the group was moving through the forest without feeding and without stopping for more than 5 min. The tape recordings used for our analysis of individual differences were made on nine different days in April, July, and August 1990.

Tape recordings of pant hoots and drumming bouts at Kanyawara were made using a Marantz PMD430 stereo cassette recorder, a Sennheiser directional microphone (K3U power module, ME80 recording head) with a windscreen, and CrO₂ tapes. In all cases ($n=30$) the drumming individuals were out of view and presumed traveling, at an estimated distance of 30–200 m. We consequently do not know the identities of the drummers or the types of trees used at Kanyawara.

We consider the variation in recording conditions to have had a minimal effect on our analyses. For the Tai calls, all recordings were made from distances at which there was no ambiguity about the presence or absence of call components, and error in temporal measurements would

be negligible. Similarly, variation in recording distances at Kanyawara was assumed to have had no effect on the analysis of the presence or absence of call components in these vocalizations. In part because the Kanyawara calls were recorded at greater distances, resulting in reduced time resolution, we did not conduct temporal analyses on them.

Acoustic analyses were performed digitally on a Macintosh Power PC using the sound analysis program "Canary" (CORNELL UNIVERSITY BIOACOUSTICS PROGRAM, 1995). The recordings were digitized at a sampling rate of 22,000 points per second with 8-bit precision. Spectrograms were produced by 1024-point Fourier transforms. This resulted in a filter bandwidth of 87 Hz, a grid time resolution of 23 ms, and a grid frequency resolution of 21 Hz. Frequency and temporal measurements were made using on-screen cursors.

All duration measurements were made on waveforms, accompanied by aural monitoring using high-isolation headphones. Duration measurements of drumming began and ended with the onset of energy in a beat. We defined the *interbeat interval* as the time elapsed from the beginning of one beat to the beginning of the next beat, and the *bout duration* as the time elapsed from the beginning of the first beat to the beginning of the last beat. From spectrograms we counted the number of beats per bout, and calculated the percentage of beats that occurred during the climax phrase of a given pant hoot, where the climax phrase was defined as starting at the beginning of the first and ending at the end of the last climax element (see Results for description of pant hoot phrasing). Because drumming typically began prior to the commencement of the climax, and the chimpanzees did not vocalize at the onset of drumming, build-up elements did not grade into climax elements. Hence there was never ambiguity about phrase onset and termination, as there has been previous analyses (CLARK & WRANGHAM, 1993; ARCADY, 1996).

STATISTICAL ANALYSIS

The data on interbeat intervals, bout duration, and number of beats per bout were not normally distributed, and we were unable to render them normal through arithmetic transformation. We consequently used nonparametric procedures to assess individual differences in these measures (SOKAL & ROHLF, 1981). To determine if there was a tendency for drum beats to occur in pairs, we used 2×2 contingency tables to test the following null hypothesis. Given an interbeat interval y , a preceding interbeat interval x , and a following interbeat interval z , H_0 = the duration of z is independent of the duration of x . That is, the null hypothesis is that there is no tendency for interbeat intervals to alternate between longer and shorter durations, which is what happens if beats occur in temporally close pairs; rejection of H_0 suggests that fast pairs are separated by longer pauses.

RESULTS

DESCRIPTION OF BUTTRESS DRUMMING

Buttress drumming in Taï Forest occurs most on *Tarieta utilis* and *Piptadeniastrum africanum*. Buttresses of *T. utilis* may attain lengths of 4–5 m (perpendicular distance from main trunk), beginning at a height of 2–3 m and tapering nearly exponentially to the ground. Buttresses may be 10–15 cm thick at the ground, and as narrow as 4–6 cm along their crests. Analysis of the acoustic properties of the wooden plate formed by one test buttress are in progress (ROBERT, in prep.). Tree species at Kanyawara with large buttresses that are used for drumming include *Aningeria altissima*, *Ficus exasperata*, *Ficus dawei*, and *Olea welwitschii*.

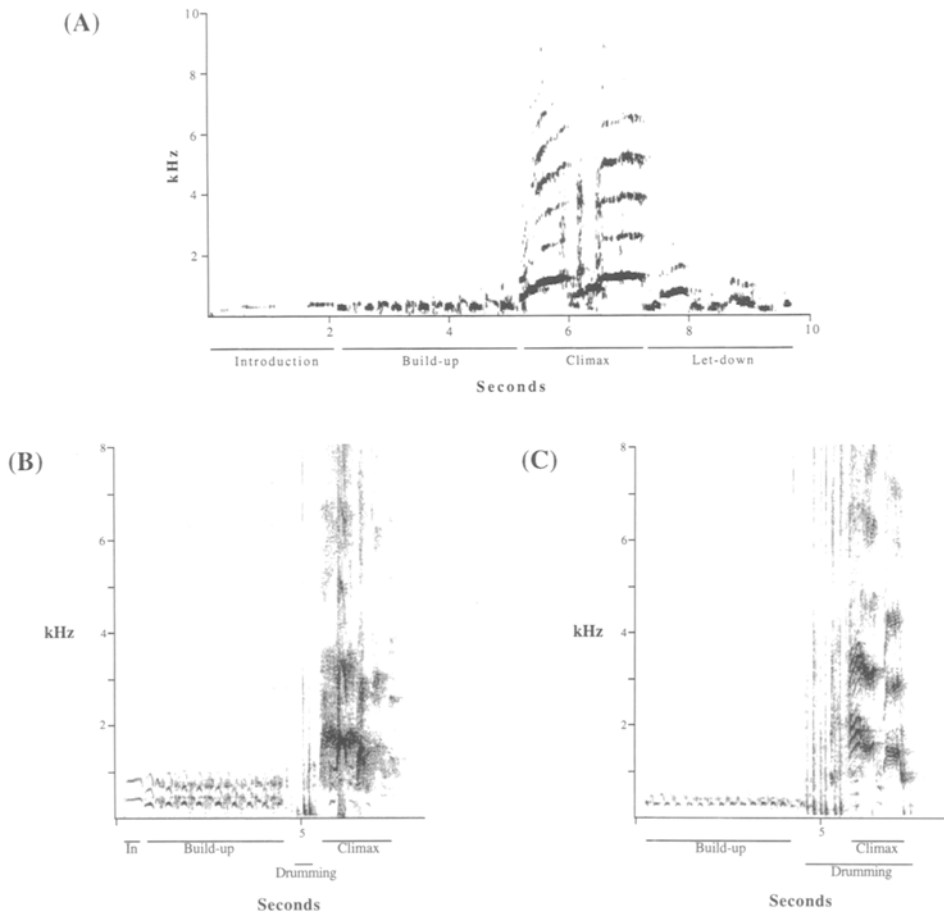


Fig. 1. Sound spectrograms of adult male pant hoots from Kanyawara and Tai chimpanzees. (A) Four-phrase pant hoot without drumming by Kanyawara adult male *BF*. Note lack of pause between build-up and climax. (B) Pant hoot and drumming by Tai adult male *DA* showing last element of introduction, build-up, and climax, with three drum beats inserted in the pause between the build-up and climax. (C) Pant hoot and drumming by Tai adult male *UL* with eight drum beats showing the “double beat” pattern: the first, third, fifth, and seventh interbeat intervals are shorter than the second, fourth, and sixth ones.

Figure 1 shows spectrograms of pant hoot vocalizations and associated drum beats from Kanyawara (Fig. 1A) and Tai (Fig. 1B, 1C). MARLER and HOBETT (1975) described four phrases in the compound pant hoot vocalizations they recorded at Gombe: (1) an “introduction,” consisting of one or more long, unmodulated, low-pitched elements, similar to the “hoo” vocalization; (2) a “build-up,” consisting of a variable number of low-pitched, frequency-modulated elements that are shorter in duration but louder than introduction elements, and voiced on both inhalation and exhalation; (3) a “climax,” characterized by one or more long, high-pitched, frequency-modulated elements, similar to “screams”; and (4) a variably present “let-down,” similar to the build-up, but decreasing in intensity. Kanyawara chimpanzees also produce pant hoots containing these four phrases, as shown in Figure 1A. Tai pant hoots, by contrast, frequently incorporate drumming, but lack let-down phrases. Drum beats appear as short-duration, broad frequency band spikes on the spectrogram, with most of the sound energy

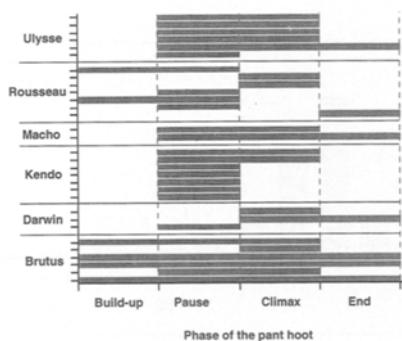


Fig. 2. Schematic representation of integration of drumming bouts into 29 pant hoots and 2 other vocalizations by adult male Tai chimpanzees. Vertical dotted lines indicate divisions between four sections of the calls: the build-up, the pause between the build-up and the climax, the climax, and following the climax (“end”). Horizontal bars indicate section in which drumming began and ended. For example, the first drumming bout by *UL* begins in the pause and ends in the climax; the first drumming bout by *RO* begins in the build-up and ends in the pause; and the first drumming bout by *DA* begins and ends in the climax. Two calls, one by *KE* and one by *UL*, began and ended after a build-up, but no climax followed.

concentrated at very low frequencies, i.e. in hundreds of Hz. Three beats are visible in Figure 1B, all occurring in the pause between the build-up and climax; eight beats are visible in Figure 1C, six between build-up and climax and two following the climax.

We defined a *drumming bout* as including all those drum beats that occurred during and closely following a pant hoot vocalization, a build-up-like vocalization (climax not present), or a silent charging display. Thirty-four (34) bouts were recorded from six adult males: *Ulysse* (*UL*, $n=7$), *Rousseau* (*RO*, $n=7$), *Macho* (*MA*, $n=2$), *Kendo* (*KE*, $n=9$), *Darwin* (*DA*, $n=3$), and *Brutus* (*BR*, $n=6$). Most drumming occurred in conjunction with a pant hoot vocalization ($n=29$ of 34 recorded drumming bouts, or 85%), and less frequently followed a build-up-like vocalization without climax ($n=3$) or a silent charging display ($n=2$). Drumming bouts that accompanied a pant hoot vocalization began and ended during or between either of three pant hoot phrases, as shown schematically in Figure 2. The majority of drumming bouts with pant hoots ($n=19$ of 29, or 66%) began in the pause between the build-up and climax. The drumming bouts with build-up only were performed by *KE* ($n=2$) and *UL* ($n=1$). One of these (from *KE*) could not be analyzed for phrasing, and is not included in Figure 2. The remaining two are diagrammed as bars beginning and ending in the pause after the build-up. The drumming bouts unaccompanied by a vocalization were performed by *KE* ($n=1$) and *UL* ($n=1$), and are not shown in Figure 2.

In contrast to Tai, only about half of the recorded drumming bouts at Kanyawara occurred with a pant hoot (vs 85% at Tai; Table 1). Of these 16 bouts, 9 included enough of the vocalization to determine phrasing: only 1 began and ended in the pause between build-up and climax (vs 66% at Tai), 4 began and ended in the climax, and 4 began and ended after the climax. One

Table 1. Association of drumming with vocalizations in Tai Forest and Kanyawara chimpanzees.

	No. of drumming bouts	No. of bouts with pant hoot	No. of bouts with build-up only	No. of bouts given without vocalization
Tai Forest	34	29 (85%)	3 (9%)	2 (6%)
Kanyawara	30	16 (53%)	1 (4%)	13 (43%)

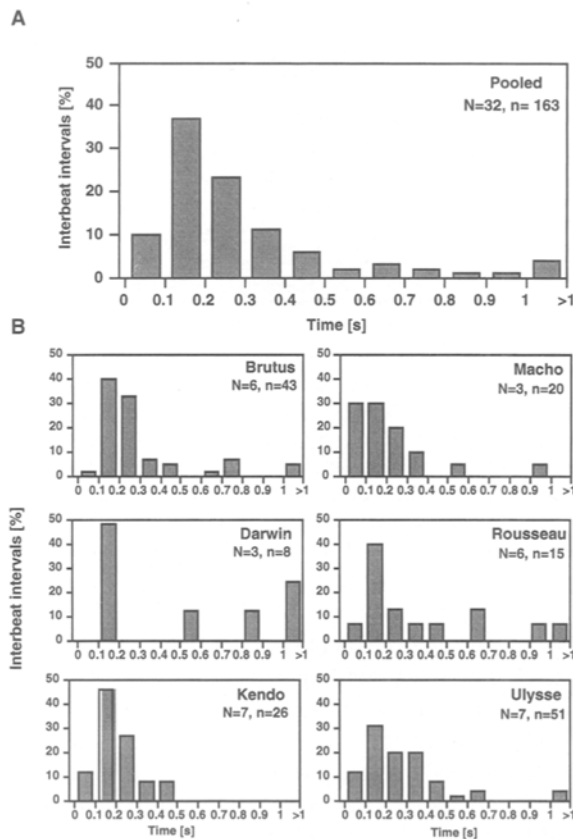


Fig. 3. Percentage of all interbeat intervals that were of specified durations, with the data grouped in .1 s intervals. (A) Interbeat intervals for all Tāi adult males pooled; (B) interbeat intervals for each male. *N*: Total number of drumming bouts; *n*: total number of interbeat intervals.

drumming bout followed a build-up without climax (4%). The remainder (43%) apparently occurred in the absence of vocalization, whereas drumming rarely occurred without vocalization at Tāi (2 of 34 bouts, or 6%).

None of the pant hoots in the Tāi sample contained a final “let-down” phrase, as described in pant hoots from other populations (Gombe, Tanzania: MARLER & HOBETT, 1975; Mahale, Tanzania: MITANI et al., 1992; Kibale, Uganda: CLARK & WRANGHAM, 1993). Drumming at Tāi was therefore always integrated into the first three pant hoot phrases defined by MARLER and HOBETT (1975).

Tāi chimpanzees drummed most during travel (22 of 32 bouts for which behavior was noted, or 69%), less often while socializing/resting (6 of 32 bouts, or 19%), and rarely during feeding (4 of 32 bouts, or 12%).

Figure 3 shows the frequency distribution of interbeat intervals for all recorded drumming bouts combined, and for each individual. The duration of interbeat intervals ranged from 0.045 to 1.4 s. Most interbeat intervals were less than 0.4 s ($x=0.30$ s, $SD=0.29$).

INDIVIDUAL DIFFERENCES IN TĀI FOREST DRUMMING

Figure 4 shows the results of analyses of individual differences in four acoustic measures of drumming performances from Tāi Forest chimpanzees. Significant differences were found

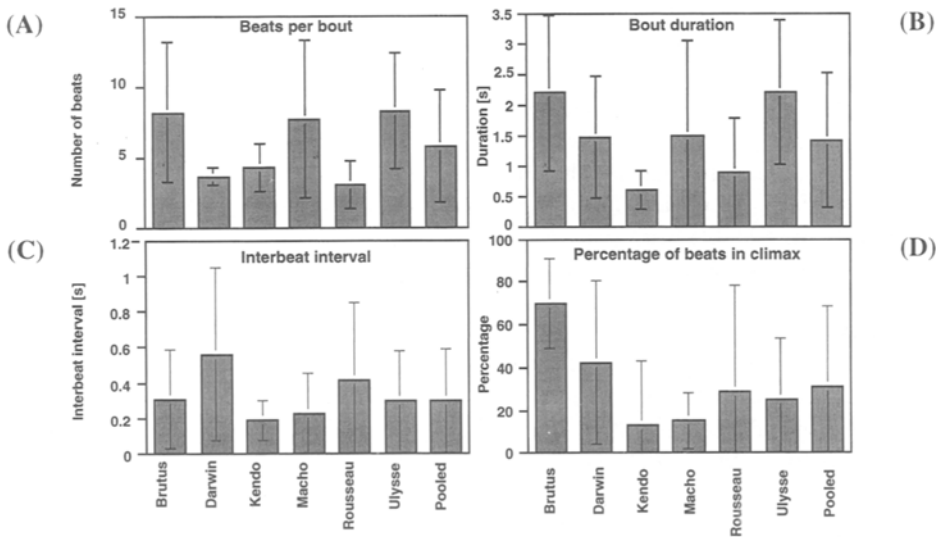


Fig. 4. Means and standard deviations for each Tai adult male of (A) number of beats per drumming bout (see text for number of bouts for each individual); (B) bout durations; (C) durations of interbeat intervals; (D) percentage of all drum beats in a drumming bout that were given after the beginning of the first and before the end of the last climax element. Significant differences were found between individuals for (A), (B), and (C). Note similarity of (A) and (B).

between individuals in mean number of beats per bout (Kruskal-Wallis $H=16.197$, $p<.01$, $df=5$), mean bout duration ($H=11.77$, $p<.05$, $df=5$), and mean duration of interbeat intervals (Kruskal-Wallis $H=12.343$, $p<.05$, $df=5$). That is, the null hypothesis that the true “location” of the several populations is the same is rejected. The number of beats per bout ranged from 1 to 18. Individuals did not differ in the percentage of drum beats given during the climax phrase (Kruskal-Wallis $H=9.548$, $p>.05$, $df=5$).

The “double beat” pattern occurs when shorter interbeat intervals alternate with longer interbeat intervals, so that pairs of beats delivered in close temporal proximity are separated by somewhat longer pauses. There was some variation between individuals in the tendency for this to occur, although individual sample sizes were too small for a complete interindividual

Table 2. Two by two (2x2) contingency tables to test for the tendency to alternate shorter and longer interbeat intervals for six males.

ID	Preceding interval was	Following interval was			ID	Preceding interval was	Following interval was		
		Shorter	Longer	Same			Shorter	Longer	Same
<i>Brutus</i> (BR)	Shorter	9	4	0	<i>Macho</i> (MA)	Shorter	3	4	
	Longer	5	9	1		Longer	3	3	
	Same	0	2	0		Same			
<i>Darwin</i> (DA)	Shorter	1	1		<i>Rousseau</i> (RO)	Shorter	4	0	
	Longer					Longer	0	0	
	Same					Same			
<i>Kendo</i> (KE)	Shorter	3	2		<i>Ulysse</i> *** (UL)	Shorter	15	3	1
	Longer	3	4			Longer	4	13	0
	Same					Same	1	0	0

comparison. Table 2 shows 2×2 contingency tables for each individual. Where sample sizes were large enough, a chi-square test of independence was performed to test the null hypothesis that for interval y , the duration of the interval following (z) was independent of the duration of the interval preceding (x). The chi-square was not significant for *BR* ($\chi^2=3.0$, $p>.05$, $n=27$), *KE* ($\chi^2=.3$, $p\gg.05$, $n=12$), or *MA* ($\chi^2=.07$, $p\gg.05$, $n=13$), but was significant for *UL* ($\chi^2=12.6$, $P<.001$, $n=37$), rejecting the null hypothesis in his case. For *UL*, that is, if the interval preceding was short, the interval following was also short more often than expected by chance, thus producing the "double beat" pattern.

Finally, individuals appeared to differ in the manner in which they integrated their drumming into associated pant hoot vocalizations (Fig. 2). All of *KE*'s and *UL*'s bouts began in the pause between build-up and climax. Five (5) of *KE*'s seven ended in the pause between build-up and climax, while the remaining two ended in the climax. Similarly, four of *UL*'s six bouts ended in the climax, while one ended in the pause and one ended post-climax. The drumming bouts of these two individuals consequently appear tightly clustered around the pause and climax (Fig. 2). By contrast, *BR* and *RO*'s bouts were more variable with respect to the phrases of their pant hoots. *BR*'s bouts began in the build-up, pause, or climax, and ended either during or after the climax. *RO*'s bouts began in the build-up, pause, climax, or post-climax, and ended in the pause, climax, or post-climax. Sample sizes for *DA* and *MA* were too small to interpret.

DISCUSSION

Although various behavioral aspects of drumming on tree buttresses by wild chimpanzees have been described by field observers (GOODALL, 1965, 1968, 1986; REYNOLDS & REYNOLDS, 1965; GHIGLIERI, 1984; BOESCH, 1991a), no account has thus far included acoustic analyses of tape recorded events. Speculation about the possible functions of buttress drumming has consequently been limited by our ignorance of basic features of the signal, such as whether it is individually distinctive and how it is associated with the better-studied long-distance vocal signal, the pant hoot (MARLER & HOBETT, 1975; MITANI et al., 1992; MITANI & NISHIDA, 1993; MITANI & BRANDT, 1994; CLARK & WRANGHAM, 1993, 1994; ARCADI, 1996). In the present study we have attempted to fill this gap by providing quantitative data on individual differences in temporal measures of drumming, as well as on general aspects of drumming as a long-distance acoustic signal. Our results provide the first evidence of systematic differences between individuals in patterns of drumming, and corroborate earlier behavioral descriptions of drumming by GOODALL (1965). These findings lay the groundwork for future research into the functional significance of buttress drumming by chimpanzees.

GENERAL ASPECTS OF BUTTRESS DRUMMING

Previous observers have noted that chimpanzees drum on tree buttresses while traveling through the forest, and that buttress drumming is frequently associated with the pant hoot vocalization (GOODALL, 1965, 1968, 1986; REYNOLDS & REYNOLDS, 1965; BOESCH, 1991a). We found that Taï chimpanzees also drummed most during travel (69% of observed bouts at Taï), and usually while pant hooting (Table 1). Chimpanzees typically feed on many different food types throughout each day (WRANGHAM, 1977; BOESCH & BOESCH, 1989), and frequently must travel to find them. In addition, chimpanzees travel to find other group members and to patrol the borders of their territory. Thus buttress drumming occurs throughout the day corresponding to periods of travel and calling by male chimpanzees in search of food or conspecifics.

Previous observers noted that buttress drumming frequently occurred in conjunction with loud calling (GOODALL, 1965, 1968, 1986; REYNOLDS & REYNOLDS, 1965; BOESCH, 1991a). We similarly found that most drumming bouts were integrated into pant hoots, the species-specific long-distance call, although the percentage of instances was higher at Taï (85% of bouts) than at Kanyawara (53% of bouts). It is unclear whether these percentages represent a real difference between the two populations, however, since the lower incidence at Kanyawara may be an artifact resulting from poorer observation conditions. Drumming at Kanyawara was never directly observed, and frequently recorded from distances of greater than 50 m. It is therefore possible that associated vocalizations were missed. Similarly, we have too few recorded drumming events from Kanyawara to definitively assess possible population differences in the phrase integration of drumming into pant hoots, although available evidence suggests a tendency for drumming to be integrated later into the pant hoot phrase sequence at Kanyawara than at Taï.

GOODALL (1968, p. 42) observed that buttress drumming at Gombe tended to occur in rapid "double beats" separated by longer pauses. We also noted the frequent, but not universal, occurrence of rapidly delivered pairs of beats in our recordings (Fig. 1C). Analysis of durations of interbeat intervals supported this impression: there was a tendency for interbeat intervals to be both preceded and followed by either longer or shorter intervals in at least one individual. It is interesting to note that a similar "double beat" pattern is clearly evident in the several spectrograms of gorilla chest-beating provided by SCHALLER (1963). SCHALLER (1963, p. 348) also provided data for right-hand preference in initiating chest-beating displays, which prompts the speculation that the "double beat" pattern may be a consequence of handedness. In a comprehensive review and analysis of studies of handedness in the great apes, HOPKINS and MORRIS (1993) concluded that functional motor asymmetries are present in the great apes. Although we were unable to obtain data on hand use in buttress drumming, we speculate that the "double beat" pattern is a consequence of motor asymmetry in this behavior as well.

MARLER (1976) and MARLER and TENAZA (1977) noted the similarity in both mode and context of production of gorilla chest-beating and chimpanzee buttress drumming. Our analysis, in comparison with data from SCHALLER (1963), confirms the acoustic similarity of the two signals: (1) both can be delivered in "double beats"; (2) the number of beats per bout is similar in both (in the Taï chimpanzee sample, individual means ranged from 3.1 to 8.3, with a total range of 1–18 beats per bout: Fig. 4; SCHALLER reported that chest-beating bouts typically were comprised of less than 10 beats, but ranged up to 20); and (3) the duration of interbeat intervals is similar (\bar{x} =300 ms, SD =290 ms in the Taï chimpanzee sample, Figs. 3 & 4; SCHALLER reported a typical chest-beating interbeat interval of 100 ms, but ranging up to 200 ms).

INDIVIDUALITY IN BUTTRESS DRUMMING

Several observers have reported individual differences in chimpanzee pant hooting, based either on field observations (GOODALL, 1986; BOESCH, 1991b) or acoustic analyses (MARLER & HOBETT, 1975; MITANI & BRANDT, 1994). Our results suggest that acoustic cues also may be available for individuals to identify specific males by the pattern of their drumming. Significant differences between individuals were found in three acoustic measures: mean beats/bout, mean bout duration, and mean duration of interbeat intervals, with individual differences for bout duration closely paralleling those for beats per bout (Fig. 4). Patterns of phrase integration into pant hoots and the use of "double beats" may also differ between individuals, but more field data will be necessary to draw firm conclusions.

We were unable to evaluate the possibility that variation in drumming bouts was correlated with variation in drumming substrates. For example, chimpanzees might deliver more beats on

larger buttresses, or at trees with more buttresses, and temporal features of bouts might be associated with the geometry of buttresses on a given tree. Additionally, individual preferences could exist for larger or smaller trees, or for larger or smaller buttresses, and these preferences could then translate into acoustic differences in drumming bouts. One of us (ACA) is currently collecting quantitative data on specific trees used for drumming by known individuals to assess these possibilities for Kanyawara chimpanzees.

BOESCH (1991b, p. 82) noted that drumming by one Tai chimpanzee (*Snoopy*) differed from drumming by other males by being delivered after the pant hoot climax. Analysis of our tape recordings has revealed wide variation between and in some cases within individuals in the integration of drumming into the pant hoot phrase sequence (Fig. 2). Two individuals, *KE* and *UL*, consistently restricted their drumming to the pause between the build-up and climax and the climax. By contrast, *BR* and *RO* were more variable. Further observations will be necessary to determine if real individual differences exist in phrase integration, or if such differences may be related to social or environmental variables. This is an important issue, since phrase differences would be readily discernible at moderate distances (e.g. 100–200 m), at which both drumming and pant hooting are clearly audible. As with integration into the pant hoot phrase sequence, it was not clear from our sample whether individuals differed with respect to the tendency to deliver beats in closely spaced pairs (Table 2). Such differences would be discernible at longer distances, at which only drumming is audible to the receiver, and could possibly provide a basis for inter-individual drumming signatures.

FUTURE DIRECTIONS

We consider the data presented on individual patterns of drumming to be preliminary. Larger sample sizes will be necessary to confirm the existence of individual differences in drumming behavior. In addition, comparative data, which are currently being collected from Kanyawara chimpanzees, will be critical for determining if systematic differences in drumming behavior exist between different populations. Such differences would add to our understanding of cultural differences in communicative behavior between chimpanzee communities.

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