

# Agonistic Screams in Wild Chimpanzees (*Pan troglodytes schweinfurthii*) Vary as a Function of Social Role

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Some nonhuman primates have demonstrated the capacity to communicate about external objects or events, suggesting primate vocalizations can function as referential signals. However, there is little convincing evidence for functionally referential communication in any great ape species. Here, the authors demonstrate that wild chimpanzees (*Pan troglodytes schweinfurthii*) of Budongo forest, Uganda, give acoustically distinct screams during agonistic interactions depending on the role they play in a conflict. The authors analyzed the acoustic structure of screams of 14 individuals, in the role of both aggressor and victim. The authors found consistent differences in the acoustic structure of the screams, across individuals, depending on the social role the individual played during the conflict. The authors propose that these 2 distinct scream variants, produced by victims and aggressors during agonistic interactions, may be promising candidates for functioning as referential signals.

Primates vocalize to one another most often during evolutionarily relevant events, such as predator avoidance, defense against aggressors, and food discovery. The relationship between the function of vocalizations and their acoustic structure has been the focus of much research, with relationships reported between the acoustic structure of calls and the caller's motivational state (Morton, 1977), physical attributes of the caller (Hauser, 1993; Morton, 1977), and the occurrence of discrete external events (reviewed in Cheney & Seyfarth, 1990). From a cognitive perspective, the most interesting studies are those showing that individuals produce calls in response to discrete external events, such as the appearance of a predator or the occurrence of a specific social context (e.g.,

Cheney & Seyfarth, 1988; Zuberbühler, Noë, & Seyfarth, 1997). In these circumstances, primate calls may function as referential signals. Functionally referential calls are defined as vocalizations with specific acoustic structures produced in narrowly defined contexts that elicit specific responses from recipients. The essential first step in determining whether a call functions referentially is to investigate the correspondence between acoustic characteristics of a call and external events (Marler, Evans, & Hauser, 1992). If calls are found to be structurally discrete and to have a degree of stimulus specificity, they are promising candidates for being functionally referential signals. Playback experiments are then required to establish if a call elicits particular responses from recipients, thus showing the call conveys information about external events to conspecifics in the absence of immediate contextual cues (Evans, 1997).

Evidence for nonhuman primates using functionally referential calls stems largely from studies of monkey alarm calls. The first report of primate alarm calls functioning referentially came from studies of the vervet monkey (*Ceropithecus aethiops*), in which individuals responded to acoustically distinct alarm calls with particular and adaptive antipredator responses (Seyfarth, Cheney, & Marler, 1980; Struhsaker, 1967). Comparable research into the alarm calls of Diana monkeys (*Ceropithecus diana*; Zuberbühler et al., 1997), Campbell's monkeys (*Ceropithecus campbelli*; Zuberbühler, 2001), and prosimians (*Lemur catta*; Macedonia, 1990) has yielded similar findings. However, it is not only primate alarm calls that can be functionally referential in nature. Certain vocalizations used in social contexts also appear to function referentially, with rhesus monkeys (*Macaca mulatta*) encoding various aspects of agonistic encounters in their scream vocalizations. These calls appear to convey information to recipients about the severity of the attack and the relative rank of the opponent (Gouzoules, Gouzoules, & Marler, 1984). Further evidence that monkeys are indeed responding to the reference of their own calls, rather than to their motivational or emotional intensity alone, comes from a series of playback experiments based on the

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habituation–dishabituation paradigm. These studies demonstrate that individuals, habituated to a particular call, show dishabituation only when the referent of the call is changed, independent of the call's acoustic structure (e.g., Cheney & Seyfarth, 1988; Hauser, 1998; Zuberbühler, 2000; Zuberbühler, Cheney, & Seyfarth, 1999).

Surprisingly, there are no convincing comparable observations of natural referential communication in any ape species, casting doubt on whether functionally referential communication is a universal feature of primate cognition. One study of a chimpanzee long call, the pant hoot, has provided limited evidence that these calls convey information about external events (Uhlenbroek, 1996), but another study failed to replicate these findings (Clark & Wrangham, 1993). The most promising evidence to date comes from a study of chimpanzees' differential use of grunts for different amounts of food (Hauser, Teixidor, Field, & Flaherty, 1993; Hauser & Wrangham, 1987) and, more recently, a study of their use of acoustically graded bark subtypes during hunting and when encountering a snake (Crockford & Boesch, 2003). This relative lack of strong evidence is particularly puzzling, given the phylogenetic proximity between humans and apes and their proven skill in using artificial communication systems (e.g., Premack, 1970). Additionally, this lack of evidence is problematic for theories concerning the evolution of cognitive capacities underlying speech and language. If some monkey species exhibit cognitive capacities related to those involved in speech processing, why is there no comparable evidence for these abilities in the natural communication of our closest living relatives?

Researchers initially thought that the graded nature of the chimpanzee call system might prohibit this species from encoding anything other than motivational and emotional information in their vocalizations (Smith, 1977). However, Marler (1976) argued that if calls in a graded system were perceived in a discrete manner, such systems had the potential to convey a considerable amount of information. From an evolutionary perspective, it would seem highly advantageous for chimpanzees to have evolved functionally referential signals, given the physical and social environment they inhabit. Chimpanzees live in a low visibility environment within a fission–fusion social system, suggesting that vocal signals would be the optimum way of alerting kin and recruiting aid when faced with predation threat, intercommunity encounters, or dangerous intracommunity aggression. In these circumstances, in which the benefits of transmitting unambiguous information to conspecifics are great, it is expected that functionally referential signals should have evolved (Bradbury & Vehrencamp, 1998).

In this study, we focus on the vocal communication of wild chimpanzees during agonistic encounters in the Budongo forest, Uganda. We were particularly interested in the most common vocal signal produced during agonistic interactions: screams. Little systematic investigation of these calls has been conducted. Goodall (1986) described screams being produced in a number of different behavioral contexts, suggesting that these calls might contain crucial acoustic variation that could enable nearby listeners to assess the nature of an ongoing event. Previous work on chimpanzee screams has provided some information on the acoustic structure of these calls, particularly in relation to the two sexes (Marler & Tenaza, 1977; Mitani & Gros-Louis, 1995), but to our knowledge no quantitative analysis has been conducted to relate call

structure to context. Some authors have suggested that screams produced during agonistic interactions may function to recruit help or elicit reassurance behaviors from third parties (Goodall, 1968; Marler & Tenaza, 1977). In particular, Goodall (1968) observed that individuals sometimes responded to screams by “hurrying toward the calling individual and threatening or charging the aggressor” (p. 308), giving support to the notion that these calls fulfilled an important function in the recruitment of allies during agonistic interactions. In accordance with these previous research efforts, two pilot studies (Zuberbühler & Slocombe, 2001, 2002) conducted on captive individuals strongly suggested that significant acoustic variation was present in this call type and that this variation was meaningful to recipients.

In the present study, we investigate whether there is consistent acoustic variation in screams produced in agonistic encounters, which could encode socially relevant information about the ongoing interaction. We focused on the two most basic roles that individuals could take during an agonistic interaction: the aggressor and the victim. Middle- and lower-ranking chimpanzees produce screams in both roles. We tested whether the acoustic structure of the screams differed depending on the role the individual played in the conflict.

## Method

### *Study Site*

Data were collected by KS for 5 months between February 2003 and January 2004 on a habituated study group in the Sonso region (Reynolds, 1992) of the Budongo Forest Reserve, Uganda. Budongo Forest covers an area of 428 km<sup>2</sup> of moist, semideciduous tropical forest between 1°35' and 1°55'N and between 31°08' and 31°42'E (Eggeling, 1947). The study site is located at an altitude of 1,100 m and has an annual rainfall of about 1,600 mm. There is a dry season between December and February in between two rainy seasons (Newton-Fisher, 1999). Habituation of these chimpanzees to humans began in 1990 and provisioning has never been used.

### *Selecting Study Animals*

At the time of the study, the Sonso community consisted of 53 wild chimpanzees (*Pan troglodytes schweinfurthii*), of which there were 9 adult males and 17 adult females, 4 subadult males and 2 subadult females, and 21 juveniles and infants. Due to the rare nature of agonistic encounters within this community of chimpanzees, all-occurrence sampling (Altmann, 1974) was used. Fourteen different chimpanzees contributed scream bouts to the data set as both victims and aggressors, and calls from these 28 bouts were used for the main acoustic analysis. In addition, 19 other chimpanzees contributed scream bouts, given only in the social role of victim, to a secondary analysis, in which these screams were compared with those used in the main analysis.

### *Observational Notes*

Recording started whenever two chimpanzees engaged in an aggressive interaction. The identity of the individuals involved and their respective roles during the conflict were determined. All variables were entered into a check sheet, or in some cases, spoken commentary was given and later transcribed.

We determined the role of the participant by noting the presence of specific behaviors performed by the caller. Individuals were classified as victims if they were running or climbing away from an approaching

aggressive chimpanzee that was pursuing them individually (directed aggression). Individuals were classified as aggressors if they engaged in one of the following behaviors: charging at another individual, shaking branches or saplings at another individual, or lunging at or pursuing another individual with or without subsequent physical contact (slapping, stamping, or beating). Agreement between KS and an experienced field assistant (RO) that one of these specific behaviors had occurred was required in order to classify the caller as either a victim or aggressor. If both KS and RO could not confirm that one of the key behaviors had been performed by the caller, the calls remained unclassified and were not used for analysis.

### Acoustic Analyses

Vocalizations were recorded with a Sennheiser K6/ME67 directional microphone (Sennheiser U.K. Ltd., Buckinghamshire, U.K.) and a Sony TCD-D8 portable digital audiotape (DAT) recorder. Recordings of vocalizations were transferred digitally from the DAT recorder onto a PC. Calls were digitized at a sampling rate of 44.1 kHz, 16 bits accuracy, with Cool Edit Pro LE (1999). Quantitative analysis of calls was carried out with Raven (2003) Version 1.0 with the following settings: Hanning window function; filter bandwidth: 159 Hz; frequency resolution: 86.1 Hz; and grid time resolution: 0.113 ms.

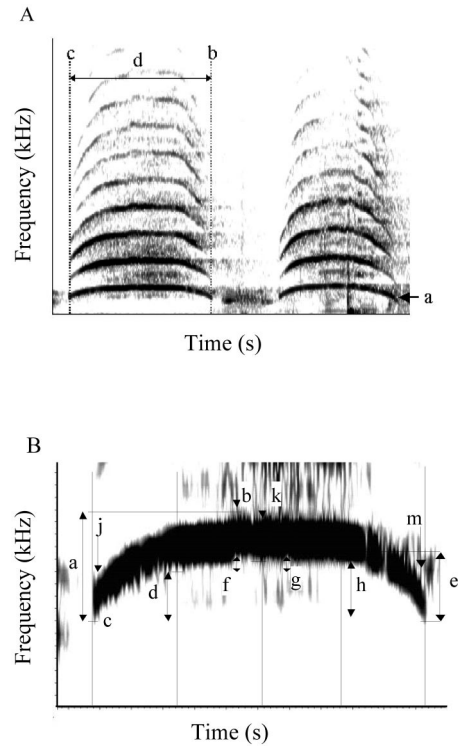
Chimpanzee screams consisted of a fundamental frequency band ( $F_0$ ) and a series of harmonic overtones. All measurements were taken from the  $F_0$ . To describe the overall acoustic structure, we determined that the following 10 parameters—2 temporal parameters (see Figure 1a) and 8 spectral parameters (Figure 1b)—were most suitable for describing the shape and acoustic structure of the screams:

#### Temporal Parameters

1. Bout length: Number of calls given successively in a single bout and separated from other bouts by at least 30 s of silence.
2. Duration of the call (s).

#### Spectral Parameters

3. Frequency modulation: Highest frequency minus the lowest frequency in the  $F_0$  (Hz).
4. Peak frequency: Frequency at which maximum acoustic energy occurs in the  $F_0$  (Hz).
5. Relative transition—first quarter: Relative change in frequency during first quarter of the call divided by the total change in frequency occurring along the bottom edge of the  $F_0$  band, over the entire call (%).
6. Relative transition—second quarter: Relative change in frequency during second quarter of the call divided by the total change in frequency occurring along the bottom edge of the  $F_0$  band, over the entire call (%).
7. Relative transition—third quarter: Relative change in frequency during third quarter of the call divided by the total change in frequency occurring along the bottom edge of the  $F_0$  band, over the entire call (%).
8. Relative transition—fourth quarter: Relative change in frequency in the last quarter of the call divided by total change in frequency occurring along the bottom edge of the  $F_0$  band, over the entire call (%).



*Figure 1.* A: Illustration of the fundamental frequency and how temporal acoustic parameters were measured. a = fundamental frequency ( $F_0$ ) upon which all spectral variables were measured; b–c = call duration; bout length is the number of calls, where one call = d. B: Illustration of how spectral acoustic parameters were measured. Frequency modulation (illustrated in figure by a) = high frequency (b) – low frequency (c). Relative transition—first quarter =  $\Delta$  frequency in 1st quarter (d)/ $\Delta$  frequency along the bottom of  $F_0$  band over entire call (e). Relative transition—second quarter =  $\Delta$  frequency in 2nd quarter (f)/ $\Delta$  frequency along the bottom of  $F_0$  band over entire call (e). Relative transition—third quarter =  $\Delta$  frequency in 3rd quarter (g)/ $\Delta$  frequency along the bottom of  $F_0$  band over entire call (e). Relative transition—fourth quarter =  $\Delta$  frequency in 4th quarter (h)/ $\Delta$  frequency along the bottom of  $F_0$  band over entire call (e). Absolute transition onset = frequency of maximum energy at call onset (j) – frequency of maximum energy at call middle (k). Absolute transition offset = frequency of maximum energy at call middle (k) – frequency of maximum energy at call offset (m). Peak frequency is not illustrated here.

9. Absolute transition onset: Frequency of maximum energy at call onset minus frequency of maximum energy at call middle (Hz).
10. Absolute transition offset: Frequency of maximum energy at call middle minus frequency of maximum energy at call offset (Hz).

Measurements of the frequencies at which maximum acoustic energy was present were obtained from creating spectrogram slices (amplitude plotted against frequency) at the relevant points indicated in Figure 1b.

In order to check for colinearity between the 10 acoustic parameters, we calculated variance inflation factors for each parameter. Variance inflation factors measure the degree to which the variance of one parameter is inflated by the existence of linear and higher order correlation among other parameters in the model. They are therefore a sensitive measure of colin-

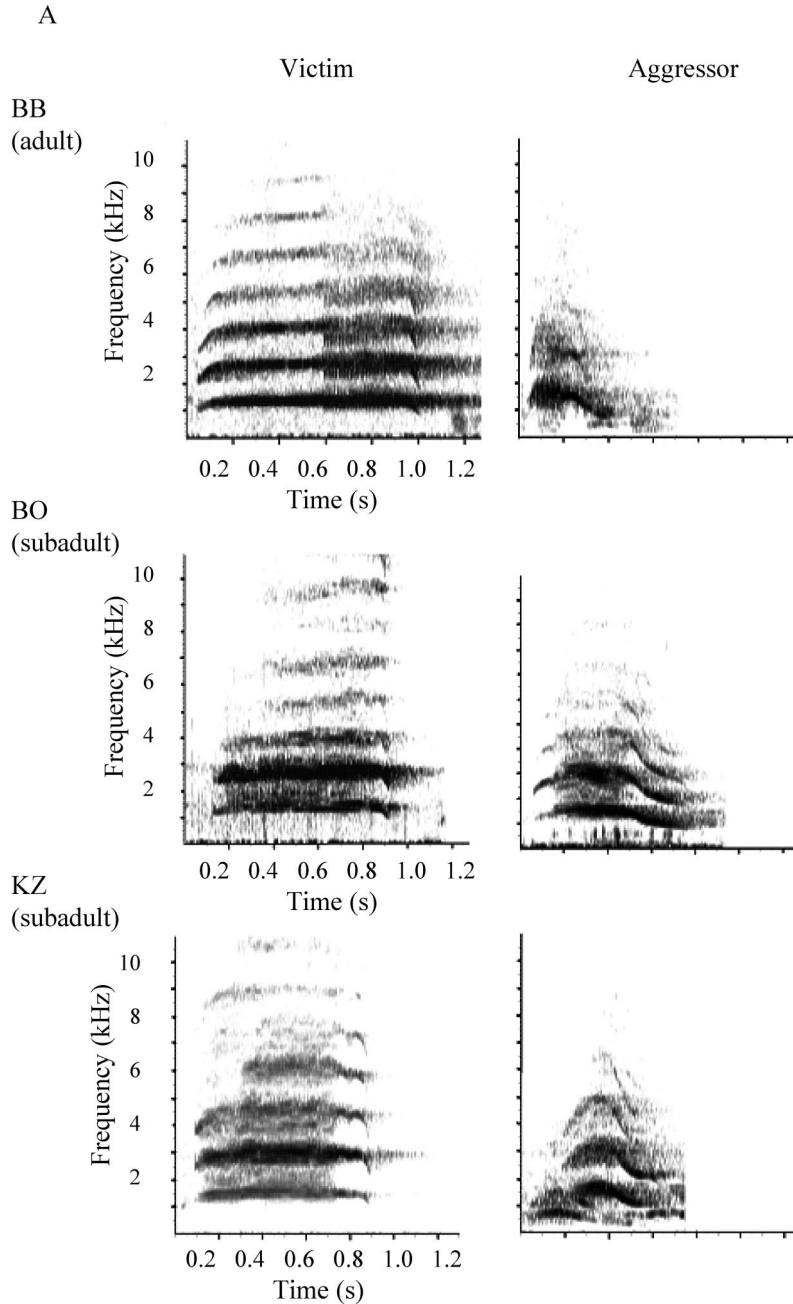


Figure 2. A: Spectrograms of scream vocalizations given by 3 randomly chosen males during agonistic interactions in which they acted as victims and aggressors. B: Spectrograms of scream vocalizations given by 3 randomly chosen females during agonistic interactions in which they acted as victims and aggressors.

earity, and they highlight potential problems of instability in a model (Howell, 1997). All 10 of the acoustic parameters had acceptable variance inflation factors ( $VIF < 8.0$ ).

Most calling bouts consisted of three or more screams. In order to get a good estimate of the typical acoustic structure of an individual's screams, we measured the first three recorded calls per bout sequence and calculated the median values for each of the 10 acoustic parameters.

## Results

### *Behavioral Observations During Social Conflicts*

Individuals targeted by an aggressor during a social conflict commonly produced screams. These victim screams were given in response to all kinds of aggressive behaviors ranging from

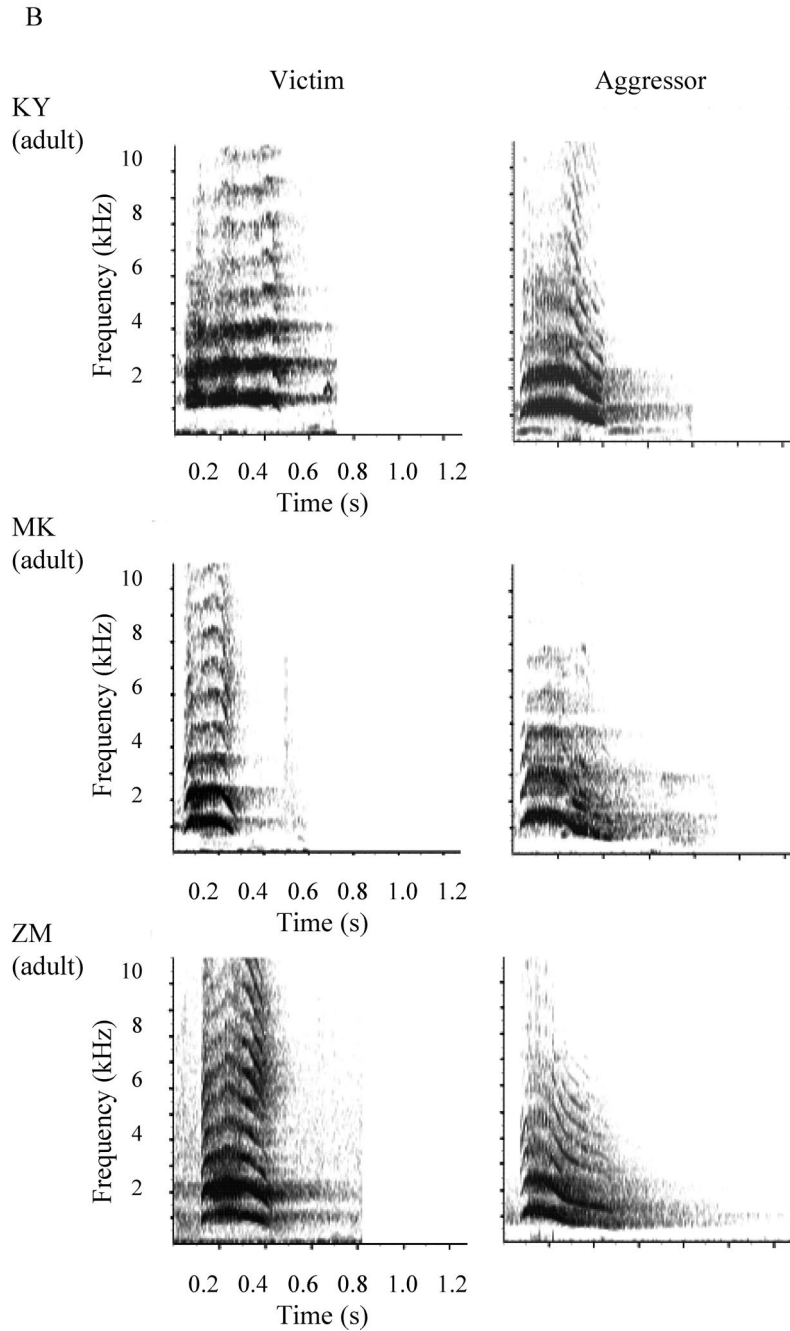


Figure 2 (continued).

simple postural threats to physical beatings. During this study, aggression levels varied considerably with the season and the number of females in estrus, with the number of conflicts observed in a day ranging from 0 to 30. For this study, we only analyzed victim screams given in response to directed aggression, when aggressors pursued the victim individually along the ground or through the trees, but without physical contact. Aggressors also produced screams during social conflicts, although less often. For example, high-ranking males were typi-

cally silent when engaging in aggressive acts. Aggressor screams were predominantly produced by low-ranking males, females, or juveniles. Aggressors produced screams as they were chasing, beating, or threatening an individual. Aggressor screams were often followed by “waa barks” once the interaction was terminated. Sometimes individuals engaged in both roles during a social conflict, for example, when retaliating against an individual that initially displayed aggression toward them. On a number of occasions, we observed that out-of-sight

third-party individuals approached and became involved in the ongoing social conflicts, presumably in response to hearing the individuals' screams.

### *Acoustic Analyses of Screams Recorded During Social Conflicts*

A total of 207 screams were recorded from 37 different chimpanzees during a wide range of agonistic encounters of varying severity. Thirty-three of these could be classified as being in the role of either aggressors or victims of directed aggression.

*Main analysis.* Only 14 chimpanzees gave one or more scream bouts in the roles of both aggressor and victim. Calls from these chimpanzees were taken for the main analysis. These 14 chimpanzees gave 51 scream bouts in total (range: 1–5 per individual in each social role). In order to prevent pseudoreplication, we only included one screaming bout in the sample of victim screams and one screaming bout in the sample of aggressor screams from each of these individuals; thus, calls from 28 bouts in total were analyzed in the main analysis. When more than one scream bout from an individual in a particular social role was recorded, the bout with the least overlap with other callers and minimum background noise was chosen. The 14 individuals included 8 adult females, 1 adult male, and 5 subadult males. Figure 2a and 2b illustrates examples of screams given by 3 randomly chosen males and 3 randomly chosen females, in both social roles.

*Secondary analysis.* In addition to the 14 chimpanzees who contributed screaming bouts to the main analysis, 19 additional chimpanzees gave screams only in the role of victim of directed aggression (3 adult males, 8 adult females, 3 subadult males, and 5 subadult females). These 19 individuals gave a total of 38 screams (range: 1–6 per individual). In order to prevent pseudoreplication, we included only one screaming bout for each individual in this data set. For individuals with more than one screaming bout, the bout with the least overlap with other callers and minimum background noise was chosen. The calls from these 19 additional screaming bouts were then compared with the set of screams used in the main analysis.

### *Main Analysis: The Effect of Social Role, Sex, and Age-Class on the Acoustic Structure of Agonistic Screams*

When we compared the spectrograms of screams given in both social roles, similar acoustic structures became apparent, with all screams consisting of an arched tonal signal of varying duration with a variable number of harmonic overtones. Differences in the acoustic structure between the two contexts predominately arose from the calls' acoustic fine structure, particularly the shape of the calls' down-sweep. Whereas victim screams displayed a relatively simple down-sweep, resembling the shape of the up-sweep, this was not the case for the aggressor screams. Here, calls ended with a more elaborate inverted S-shaped structure that was consistently present in all aggressor screams (Figure 2a and 2b). Our acoustic analyses adequately captured these visually conspicuous differences. Victim and aggressor screams differed significantly in most spectral parameters, particularly those describing the shape of the second half of the call (see Table 1 and Figure 3). The independent

variable *social role* explained the largest amount of variation for most shape-related acoustic parameters.

Mixed design analyses of variance (ANOVAs) were conducted, with social role as the within-subjects independent variable and sex and age as the between-subjects independent variables. These analyses revealed that 6 of the 10 acoustic parameters showed significant differences as a function of the social role the caller played during the conflict (see Table 1). Victims produced longer calls than did aggressors,  $F(1, 11) = 9.508, p < .05$ . Victim and aggressor screams also differed significantly in the spectral structure: Aggressor screams had larger frequency modulation,  $F(1, 11) = 28.069, p < .005$ ; greater absolute frequency transition offset,  $F(1, 11) = 107.084, p < .005$ ; and more specifically, a larger relative frequency transition in the third quarter of the call compared with victim screams,  $F(1, 11) = 52.511, p < .005$ . Victim screams, however, had greater relative frequency transitions in the second quarter of the call,  $F(1, 11) = 5.816, p < .05$ , and the fourth quarter of the call,  $F(1, 11) = 18.613, p < .005$ , compared with aggressor screams. The peak frequency of screams was affected by both sex,  $F(1, 11) = 30.202, p < .005$ , and age,  $F(1, 11) = 6.180, p < .05$ , with subadult and male callers tending to produce higher pitched screams than did adult and female callers. The independent variables age class and sex did not affect any other acoustic parameters (see Table 1). There were no interactions between any of the three independent variables for any of the acoustic parameters. In addition, individuals did not differ in the number of calls they produced in a single bout as a function of social role, nor did individual calls differ in three of the spectral parameters as a function of social role: peak frequency, relative transition in the first quarter of the call, and the absolute transition onset (see Table 1).

We used discriminant function analysis as a second method to investigate the quantitative acoustic differences between the screams produced by individuals in the two different social roles. All 10 acoustic parameters were used to generate the discriminant function. This function was able to explain a significant amount of variation between calls given in victim and aggressor roles, Wilks's  $\lambda = .104, F(10, 17) = 14.71, p < .001$ . In the cross-validation discriminant analysis, this function correctly classified 92.9% of calls according to social role. In addition, this discriminant function was able to explain a significant amount of variation between calls given by males and females, Wilks's  $\lambda = .344, F(10, 17) = 3.247, p < .05$ . In the cross-validation discriminant analysis, this function correctly classified 78.6% of calls according to the sex of the caller. Discriminant function analysis failed to find any significant effects for age class, with cross-validation discriminant analysis only correctly classifying 60.7% of cases.

### *Secondary Analysis: Comparison of Additional Victim Screams With the Main Analysis Data Set*

Screams from 19 different individuals in the role of victims were compared with the victim and aggressor screams from the 14 individuals used in the main analysis. As mentioned previously, each of the 33 individuals involved contributed only one screaming bout to each analysis. We analyzed the additional 19 victim screaming bouts in the same way as the bouts used in the main analysis.

Table 1  
*F Values From Mixed-Design Analyses of Variance Conducted on Each of the 10 Acoustic Parameters, as a Function of the Callers' Sex, Age, Class, and Social Role During a Conflict*

Acoustic parameters	Individual variables		
	Social role (victim–aggressor)	Age–class (adult–subadult)	Sex (male–female)
Temporal			
Bout length	0.011	2.498	0.588
Call duration	9.508*	1.368	3.557
Spectral			
Modulation frequency	28.069***	2.537	4.322
Peak frequency	2.082	6.180*	30.202***
Relative transition—1st quarter	3.667	3.193	0.204
Relative transition—2nd quarter	5.816*	0.933	1.244
Relative transition—3rd quarter	52.511***	2.245	0.206
Relative transition—4th quarter	18.613***	2.375	0.815
Absolute transition onset	3.046	0.321	0.050
Absolute transition offset	107.084***	0.072	1.104

*Note.* Social role was the within-subjects independent variable, and sex and age were the between-subjects independent variables. *d**f*s = 1, 11.

\*  $p < .05$ . \*\*\*  $p < .005$ .

One-way between-subjects ANOVAs revealed no significant differences between the 19 additional victim scream bouts and the victim screams from the main analysis in any of the 10 acoustic parameters (see Table 2). In contrast, one-way between-subjects ANOVAs revealed that the 19 additional victim screams were significantly different from aggressor screams used in the main analysis in 5 of the 10 acoustic parameters (see Table 2).

## Discussion

The results of this study demonstrate that chimpanzees produce scream calls during agonistic interactions that have different acoustic structures according to the role the individual plays in the interaction. To our knowledge, this field study is the first to quantitatively distinguish an aggressor scream from a victim scream, with acoustic analysis confirming that 6 of the 10 acoustic parameters differed significantly as a function of the social role. These calls are discernibly different to the human ear, and this audible difference is apparent in acoustic structures of the screams (see Figure 2). Aggressor screams were characterized by a distinctive down-sweep after midcall and a larger frequency range compared with the flatter and more symmetrically curved victim screams. Interestingly, bout length and peak fundamental frequency did not differ with social role, indicating that the overall shape of the call encoded the socially relevant information. Our findings were further supported by the results of a discriminant function analysis, which after cross-validation correctly classified 92.9% of the calls into the two categories of social role: victim and aggressor. This high level of accuracy from only 10 measures of the call indicated that nearby individuals should be able to discern between the two screams and the roles they represented. Although individual variation is visually apparent in these calls (see Figure 2a and 2b), consistent structural differences, as a function of social role, were found throughout the sample over a wide variety of ages and across sexes. The highly significant nature of the

statistical tests performed on the acoustic analysis, despite a relatively small sample size, illustrates the differences between these two call variants: victim and aggressor screams.

The distinction between these call variants was further supported by the analysis of the additional victim screams. These screams, taken from individuals of all four age–sex classes, were not different from the victim screams in the main analysis, indicating that screams given in the role of victim of directed aggression are relatively homogenous. Furthermore, these additional victim screams varied from aggressor screams in the same way as the main analysis victim screams. Four of the six acoustic parameters that differed significantly between the main analysis victim and aggressor screams also differed significantly between the additional victim screams and the aggressor screams (see Tables 1 and 2). Although the main and secondary analyses produced different results on whether 3 acoustic parameters differed significantly between victims and aggressors, all 10 acoustic parameters varied between victims and aggressors in the same direction in both analyses. The replication of the trends and differences in acoustic structure between victim and aggressor screams, with these additional victim screams from 19 different chimpanzees, greatly increased the validity and strength of our finding.

The variables sex and age had an effect on the peak frequency of the screams, which was probably a result of differences in body size. Previous studies have found a negative correlation between body size and frequency of vocalizations (Hauser, 1993), and a similar relationship was present in the current study: Subadult chimpanzee screams had higher peak frequencies compared with adults' screams. Although it seems counterintuitive, male screams also recorded a higher peak frequency than did female screams. This contrasted with Mitani and Gros-Louis's (1995) study, which found that males produced lower frequency screams compared with females. However, Mitani and Gros-Louis (1995) also concluded that this difference was likely to be a product of differences

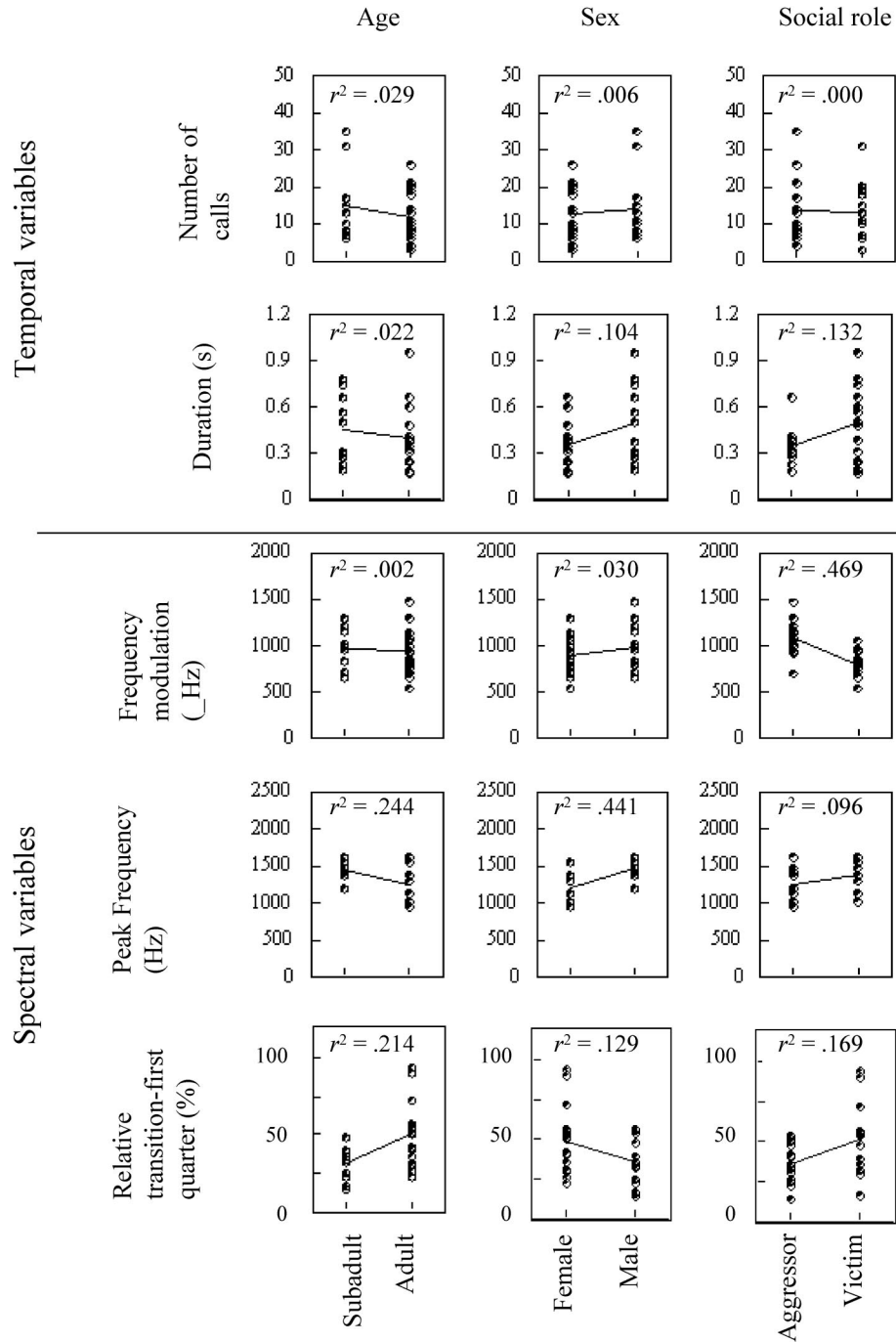


Figure 3. Scatter plots showing the values obtained for each of the 10 acoustic parameters measuring the temporal and spectral structure of the screams of 14 different chimpanzees given during agonistic interactions, plotted as a function of age class, sex, and social role. Each data point represents the median value for three successive calls measured at the beginning of a scream bout from a single individual ( $r^2$  refers to the relative amount of variance explained by the respective variable).

in body size; given that 5 out of the 6 males in this study were subadults, with smaller body sizes than most females, a similar explanation is applicable to this result. The large difference between the peak frequencies of the two sexes was sufficient for the

discriminant function analysis to successfully discriminate between the calls of male and females.

From a production perspective, the chimpanzee agonistic scream system seems to be consistent with certain aspects of

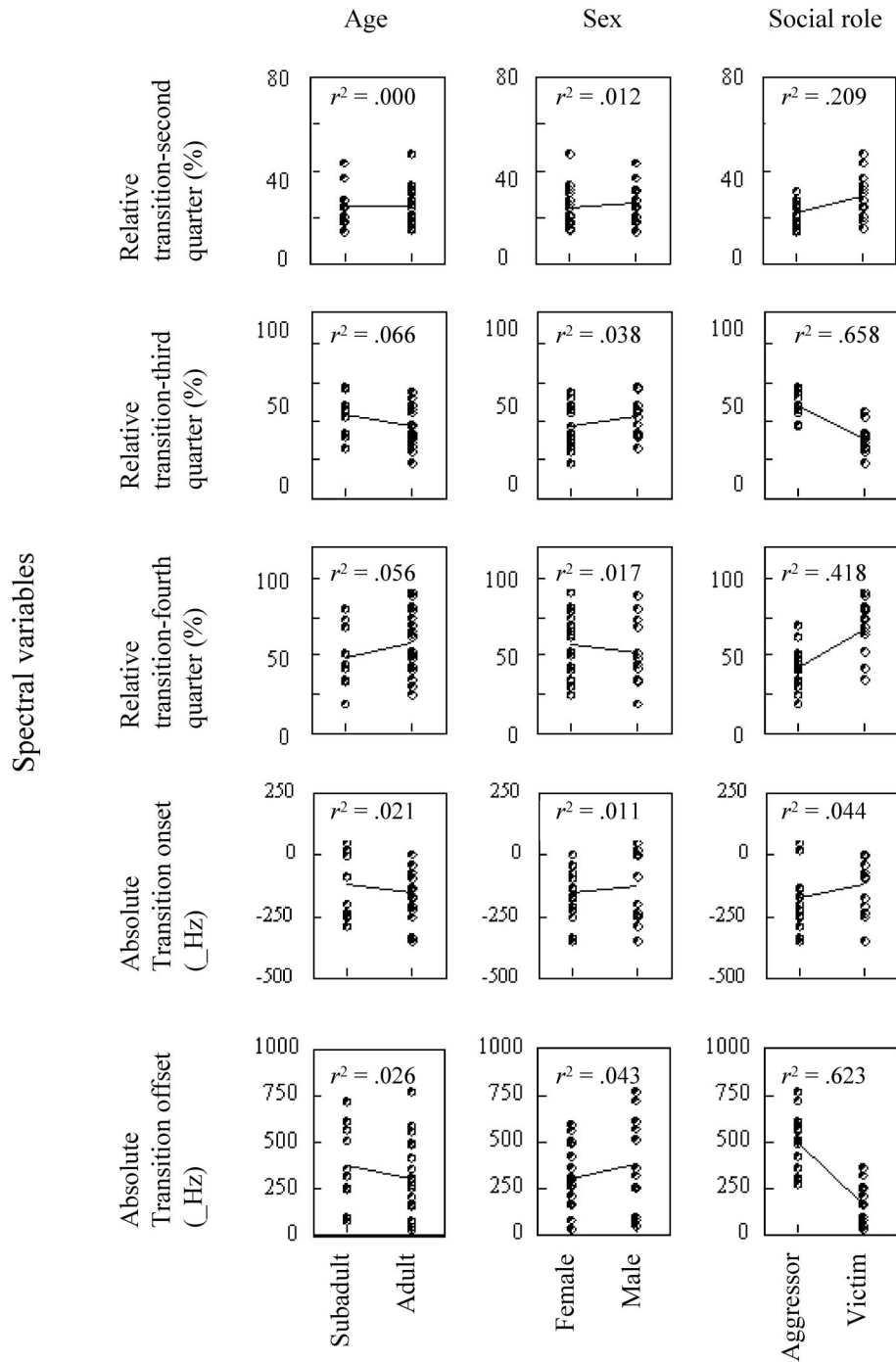


Figure 3 (continued).

Morton's (1977) idea of motivational–structural rules, which provide useful clues as to the possible evolutionary mechanisms underlying the diversification of these two scream types. In line with these rules, the screams of aggressive chimpanzees are shorter and contain larger elements of decreasing frequency patterns than do the screams of attacked chimpanzees. In addition, there is a

trend for aggressive individuals to produce lower frequency screams than victims.

Recipients could well use these acoustic differences as a basis for important behavioral decisions. Not only is it likely that the recipients draw inferences about the identity of the individuals involved in a conflict (Bauer & Philip, 1983), but our data also

Table 2

*F Values From One-Way Between-Subjects Analyses of Variance Conducted on Each of the 10 Acoustic Parameters Comparing Additional Victim Screams With Victim and Aggressor Screams From the Main Analysis*

Acoustic parameters	Additional victims compared with main analysis victims	Additional victims compared with main analysis aggressors
Temporal		
Bout length	0.878	1.839
Call duration	1.013	0.420
Spectral		
Modulation frequency	0.007	33.051***
Peak frequency	0.622	3.451
Relative transition—1st quarter	0.091	7.519**
Relative transition—2nd quarter	0.909	3.859
Relative transition—3rd quarter	4.125	118.388***
Relative transition—4th quarter	0.561	42.673***
Absolute transition onset	0.597	0.269
Absolute transition offset	1.202	26.917***

Note.  $dfs = 1, 31$ .

\*\*  $p < .01$ . \*\*\*  $p < .005$ .

suggest that chimpanzees could principally be able to infer the role each individual plays in the conflict. Goodall's (1968) observations of screams being used to recruit help, along with our own behavioral observations of approaches of out-of-sight third-party individuals rushing to aid one of the screaming protagonists, indicate that nearby individuals may be using acoustic signals to make important decisions as to whether it is appropriate to intervene in a conflict. However, this hypothesis that recipients are taking advantage of the socially relevant acoustic information contained in the scream vocalizations needs to be tested with playback experiments. If recipients do use these acoustic signals to mediate their behavioral responses, then chimpanzee victim and aggressor screams could qualify as functionally referential signals.

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