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Contextual variation in chimpanzee pant hoots and its implications for referential communication

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There have been several previous studies of the loud, long-distance call of chimpanzees, termed a 'pant hoot'. Some have explored the possibility that there are acoustically distinct subtypes of pant hoots that communicate to distant listeners different information about the caller's behaviour, or ecological and social circumstances. However, results to date have been either inconclusive or conflicting. To help resolve these issues, we undertook research on pant hoots produced by wild chimpanzees, *Pan troglodytes schwienfurthii*, living in the Budongo Forest, Uganda. In this paper, we report the results of acoustic analysis of 201 pant hoot series produced by seven adult males. Principal components analysis (PCA) was used to identify key dimensions of structural variation in the calls, which were then related to a large set of behavioural, social and ecological variables associated with call production. Although there was little evidence for distinctive pant hoot subtypes according to many of the social and ecological dimensions traditionally recognized, a number of significant patterns were identified. Specifically, pant hoots were produced with higher probability at abundant food sources, and they were more likely to contain a 'let-down' phase when produced in specific behavioural contexts, such as travelling and upon arrival at a food source. In addition, pant hoots produced while travelling along the ground in small parties prior to joining-up with other community members were consistently different from all other pant hoots, varying reliably in the fundamental frequency of their build-up elements, the tonal quality of climax elements and in the presence of a let-down phase. We discuss the possible mechanistic bases for these differences in the pattern of calling and detailed spectral structure of the calls and consider the implications for referential communication.

Loud, long-distance vocalizations are produced by many animal species, including birds, frogs and mammals (Clutton-Brock & Albon 1979; Ryan 1985; Leonard & Horn 1995). Although they can serve a variety of different functions depending on the details of species' ecology and social organization (Wich & Nunn 2002), the most frequently cited functions generally involve either attracting or repelling conspecifics, or both. For example, in many species of songbird, male songs can function both to attract potential female mates and to repel rival males in nearby territories. Among primates, loud calls can function similarly. In some species, they appear to play a role in regulating territorial relationships, repelling the members of neighbouring groups (Waser & Waser 1977; Mitani 1988). In others they can function to attract conspecifics, typically members of the same group (Gautier & Gautier-Hion 1977; McComb 1992; Mitani & Stuht 1998). In still others, they may serve both functions at the same time, promoting spatial cohesion among individuals within groups, while reinforcing the spatial boundaries that separate the members of different groups (Mitani 1985).

Pant hoots are the loud vocalizations typically used by chimpanzees to communicate over long distances. Like loud calls in many other species, pant hoots appear to function in spacing neighbouring groups (Wilson et al. 2001) and also in rallying and maintaining cohesion among individuals within groups (Goodall 1986; Mitani & Nishida 1993). That pant hoots can serve both functions

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suggests that, at the very least, the calls must be acoustically distinctive between the members of different groups, and several studies have confirmed marked individual differences in the structure of pant hoots (Goodall 1968; Marler & Hobbett 1975; Bauer & Philip 1983; Mitani 1996) as well as consistent interpopulation variation in the calls (Mitani et al. 1992, 1999; Crockford et al. 2004).

Research has also begun to explore the existence and potential communicative significance of within-individual variation in the structure of pant hoots produced in different contexts. Research on several other primate species, as well as some nonprimates, has described context-specific acoustic variants in broader call types (e.g. Seyfarth et al. 1980; Gouzoules et al. 1984; Gyger et al. 1987; Macedonia 1990; Rendall et al. 1999; Zuberbühler 2000). In several cases, these call variants appear to communicate different information about features of the environment, such as the presence of predators of different types, or the availability of food. Because the referential quality of such call variants appears to be at least crudely similar to the referential, or semantic, quality of human words, this research has inspired considerable productive theorizing about the animal foundations from which important properties of human language may have been elaborated (Marler 1977, 1984; Gouzoules et al. 1995).

Part of the significance of the search for context-specific pant hoot variants in chimpanzees, then, lies in exploring potential evolutionary precursors to the referential, or semantic, qualities of human language. Their very close phylogenetic affinity to humans by itself recommends chimpanzees as especially promising candidates for language precursors. Their demonstrated abilities in using and responding to symbolic contrasts in the artificial languages (and even speech) to which they are exposed in laboratory studies (Fouts 1973; Savage-Rumbaugh et al. 1998) further recommends the search for referential contrasts in their own natural communications in the wild.

Current formulations of 'functionally referential' communication systems require that acoustic variation within call types be specific to particular production contexts and also be salient to conspecific receivers such that receivers can make inferences about the eliciting context and select a response appropriate to it (Marler et al. 1992; Macedonia & Evans 1993; Evans 1997). Consistent with a referential communication function, pant hoots produced by wild chimpanzees are known to be highly variable in their structure (Marler 1969). Unfortunately, it has proved difficult to establish consistent variation in the calls associated with specific contexts of production (Table 1).

Table 1. Summary of proposed functions for pant hoots from selected studies

Study	Proposed pant hoot function
Wrangham 1977	Announce food location
Clark & Wrangham 1993	Announce food location
Clark & Wrangham 1994	Advertise social status
Mitani & Nishida 1993	Recruit social allies
Uhlenbroek 1996	Referential subtypes specific to travel, arrival and feeding contexts

For example, pioneering studies by Reynolds & Reynolds (1965), Goodall (1968) and Wrangham (1977) proposed that different types of pant hoots might well serve different communicative functions primarily related to ecological dimensions, such as the location, quality or quantity of a local food resource. Some additional support for this hypothesis has been obtained (Clark & Wrangham 1993; Hauser et al. 1993). However, the nonexclusive association of particular patterns of calling and specific eliciting contexts has led to other proposals. Thus, Clark & Wrangham (1994) proposed that pant hoots produced at food sources are used primarily to advertise a caller's social status rather than to indicate anything about food sources per se, and that the benefits to calling come from attracting other community members, including potentially sexually receptive females. Others have likewise emphasized the social functions of pant hoots, arguing that in the spatially fluid social organization of chimpanzees, pant hoots function primarily to maintain cohesion among dispersed group members and sometimes also to attract particular social partners by announcing the caller's identity, location, and possible movement (Boesch 1991; Mitani & Nishida 1993; Mitani 1994). Consistent with this proposal is the finding that males call more often when social alliance partners are nearby and are then frequently joined by them (Mitani & Nishida 1993) and that males that spend more time together begin to converge in the structure of their calls (Mitani & Brandt 1994). Not all studies have shown these effects, however (Clark & Wrangham (1994).

As a result, there is reasonable consensus that pant hoots play a general role in regulating spatial relationships among individuals within and between chimpanzee communities. However, beyond this generalized function, there is considerable outstanding uncertainty about the presence of acoustically distinctive variants of pant hoots, whether or not they are reliably associated with specific behavioural activities or social and ecological circumstances, and what their communicative significance might ultimately be. To help clarify these issues, we undertook research on the vocalizations of chimpanzees, *Pan troglodytes schwienfurthii*, of the Budongo Forest, Uganda. In this paper, we report the results of acoustic analyses designed specifically to test whether or not the chimpanzees produce structurally distinct variants of pant hoots during different behavioural activities or in different social and ecological contexts.

METHODS

Study Site and Subjects

Research was conducted over a 12-month period (March 1999–March 2000) in the Sonso study area of the Budongo Forest Project, which is situated in the southwestern part of the Budongo Forest Reserve. The forest is located in western Uganda, along the western Rift Valley

(1°37′–2°00′N; 31°22′–31°46′E) at a mean altitude of 1050 m. The reserve covers 793 km^2 of tropical moist, semideciduous forest and grassland, of which 428 km^2 is in continuous forest cover. Details of the reserve's floral composition and management policies can be found in Eggeling (1947), Synnott (1985) and Plumptre et al. (1997). The Sonso community of chimpanzees numbered between 49 and 52 individuals during the study period. Individuals were previously habituated without food-provisioning and they tolerated human observers at close range (approximately 5 m). Additional details of the Sonso chimpanzee community are given in Reynolds (1998).

General Data Collection

Data collection by H.N. focused on recording pant hoots and collecting detailed information on the social, ecological and other behavioural concomitants of call production and responses to calls. Data were collected in 1-h focal animal samples (Altmann 1974) during which a specific target individual was followed by two observers, one keeping a continuous record of all behaviours and the other recording all long-distance vocalizations produced by the subject. Observations were made of both male and female adults and young adults. Additionally, ad libitum recordings were made of the vocalizations of any other identifiable chimpanzees within sight.

Behavioural activities associated with call production

Each time an animal called, its behavioural activity was noted using the following categories: travelling, feeding, arriving at a food patch, or resting either on the ground or in a food patch. The category, 'arriving at a food patch', was defined as the 5-min period that immediately followed a chimpanzee's first contact with the base of a food tree and its subsequent entry of the tree.

Social circumstances associated with call production

Several variables related to the social context surrounding call production were also recorded each time an animal called. First, the calls were classified into three categories according to whether they were produced spontaneously without receiving an audible response (labelled 'isolated' calls), produced spontaneously and received a response within 30 s ('answered'), or produced in response to the calls of another animal ('replies'). It is possible that the calls of distant animals were not always heard by human observers, which would lead to an overestimation of the number of 'isolated' calls by focal animals.

After each call, we also noted whether the caller joined, or was joined by, another individual or party within 15 min. This interval was chosen because in this forest pant hoots are audible over a distance of approximately 1 km, and 15-min is the approximate time it would take a chimpanzee that heard another's pant hoots to travel that distance (assuming an average rate of travel of 4 km/h, which is reasonable for the chimpanzees in most circumstances). To explore the additional potential effects of party size, we also noted whether or not the caller was in the company of other chimpanzees at the time it called and if so what the size of the party was: a pair, a small party (3–5 other individuals), or a large party (>5 other individuals). Individuals were counted as party members regardless of age or sex class (excluding unweaned infants) but only if they were within 100 m of the caller. This distance criterion was chosen for two reasons. First, it appeared to correspond to the natural distance over which individuals coordinated group activities such as travelling and vocal chorusing. Second, the forest at Sonso contained systematic transect paths at 100-m intervals that facilitated reliable estimates of chimpanzee dispersal over this distance.

Ecological circumstances associated with call production

For pant hoots produced in, or upon arrival at, a food patch, the quality and quantity of available food was estimated and the plant species and plant part consumed (leaves/flowers, seeds/pods, or ripe fruits) were recorded. Only plant species with appreciable sample sizes (i.e. >10 observations) were retained, and these were lumped into four broader groups: the genus *Ficus*, and the species *Maesopsis eminii, Celtis durandi* and *Cynometra alexandri*. An additional category, labelled 'other', was constructed by lumping plant species with smaller sample sizes. Food abundance was estimated in four (quartile) categories according to the percentage of the plants' canopy that contained flowers, ripe fruit or seed pods. Because the sample sizes for some categories proved small, the quartile estimates of food abundance were collapsed into just two categories for purposes of analysis: (1) ≤50%, or (2) >50% of the canopy contained flowers, fruit or seeds/pods.

Pant Hoot Vocalizations

Recording pant hoots

Pant hoot vocalizations were recorded on chromium-dioxide cassette tapes using a Marantz PMD 221 cassette recorder and a Sennheiser directional microphone with a K6 powering module covered by a Rycote softie windshield. From the database of recordings, we considered for analysis only those of the highest possible quality with minimum background noise. This screening yielded a total of 201 pant hoots from seven adult and young-adult males that were suitable for analysis. Table 2 provides a summary of the call sample sorted by individual and behavioural context. Females sometimes produced pant hoots that were often a truncated version of the four-phase pant hoot typical of males (Clark Arcadi 1996). However, the sample of female calls was small, particularly when spread across the various production contexts recorded. Hence, they were not included in the analyses. Analogue field recordings of male pant hoots were subsequently digitized using the Praat acoustics software (Version 4.1.9, Amsterdam) at

Table 2. Summary of call sample by individual, age class and context

Individual	Age class	Behavioural context Travel (ground)	Rest (ground)	Arrive at food	Feed	Rest (tree)	Total
Bk	Adult	4	2	13	7	7	33
Dn	Adult	10	5	6	8	1	30
Jm	Adult	8	9	8	5	1	31
Ma	Adult	2	3	6	4	1	16
Mu	Adult	7	6	10	10	3	36
Nk	Young adult	5	1	11	6	2	25
Zf	Young adult	11	6	5	6	2	30
Totals:		47	32	59	46	17	201

a sampling rate of 40 kHz and then downsampled to 20 kHz, yielding an effective analysis bandwidth of 10 kHz.

Acoustic analysis

Pant hoots are complex vocalizations, consisting of a series of different individual call units strung together in a sequence that can last between 3 and 23 s (Marler & Hobbett 1975). The sequence can include up to four distinct phases: an introduction, a build-up, a climax, and a let-down (Fig. 1). The introduction phase usually consists of a short series of unmodulated, tonal elements that resemble the low-pitched 'hoo' vocalization with a fundamental frequency (F_0, which translates perceptually as the pitch) ranging from 200 to 600 Hz (Marler & Tenaza 1977). The build-up phase consists of a series of shorter inhalation/exhalation, or 'panting', elements that are low-pitched and slightly modulated and may become increasingly high-pitched as the call proceeds. The climax phase includes one or a series of long, high-frequency elements that may be tonal and frequency-modulated signals ranging from 500 to 1800 Hz in frequency and sound 'wail-like', or they may be more broadband, 'noisy' signals that sound 'roar-like'. Finally, the let-down phase is similar in acoustic structure to the build-up phase except that it tends to decrease in both amplitude and frequency over time. Let-down phases are also typically much shorter than the build-up phase. Although the typical pant hoot sequence contains all four phases, one or two phases can be omitted. Phases within the pant hoot can also grade into one another so that the distinction between them is not always clear.

Given these general characteristics, acoustic analyses of the pant hoot sequence focused on features of the calls manifest at three different levels: (1) discrete features of the sequence that reflected its overall structure and patterning; (2) various measures of the temporal patterning of the entire sequence and of the duration of specific elements within it; and (3) quantitative measures of the frequency structure of specific elements within the sequence. Because the distance of subjects from the microphone varied across recordings, we made no measurements of the absolute intensity of call components.

Measures of the duration and frequency structure of specific call elements focused on the 'build-up' and 'climax' phases because these phases were almost always present whereas the 'introduction' and 'let-down' phases were often missing. We measured 37 features of pant hoots directly, many of which were suggested from

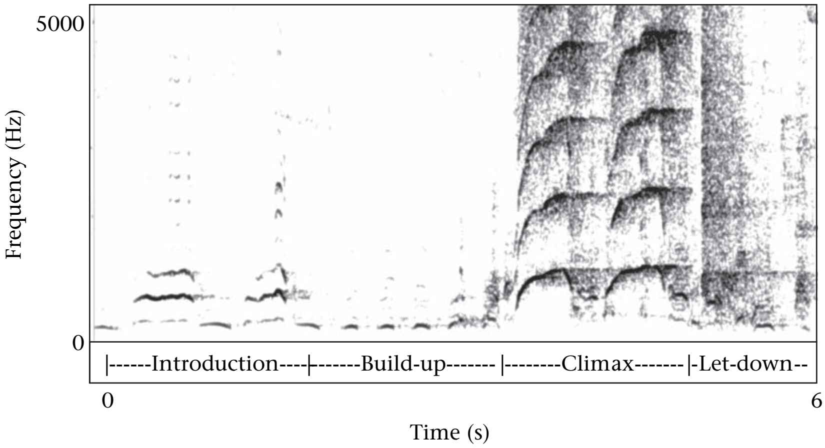

Figure 1. Spectrogram showing the four different phases of a typical pant hoot sequence. Spectrogram was created from a set of successive high-resolution (2000 point) fast Fourier transformations produced with a Hanning window and 50% frame overlap.

previous studies (e.g. Mitani et al. 1992; Clark & Wrangham 1993; Hohmann & Fruth 1994; Mitani & Brandt 1994; Notman 1996, 2003; Uhlenbroek 1996). An additional 17 features were derived as composites of some of these features. Thus, we used a total of 54 acoustic variables to characterize each pant hoot sequence (see Table A1, Appendix for a complete list of acoustic features measured).

Measurements of the detailed spectral structure of pant hoots focused on the fundamental frequency (F_0) of call components obtained from overlapping 1024-point fast Fourier transforms (FFT, frequency resolution = 19 Hz; temporal resolution = 25 ms). Because many calls consisted of a relatively tonal source with an associated clear harmonic structure, it was straightfoward to obtain accurate measurements of the F_0. In a few cases, the F_0 was selectively muted compared to higher harmonics. To capture this variation, we used an additional variable labelled 'emphasis' to identify the harmonic of highest amplitude (labelled the 'principal frequency'), which was typically the F_0 itself but was sometimes the second, or an even higher, harmonic.

Several additional measures were used to quantify variation in the relative tonality of the calls. Variation at this level was more prevalent in the climax elements, which are by far the loudest components of the pant hoot sequence. First, we counted the number of significant modulations (>100 Hz) to the F_0 contour of each climax element. Second, we calculated the bandwidth of the F_0 at the midpoint of each climax element from a high-resolution (1024 point) FFT. Finally, we used a set of discrete categories to capture additional qualitative distinctions in the F_0 contour that sometimes occurred. These included rapid bifurcations or 'jumps' in the F_0 contour, instances of biphonation (spontaneous period doubling), or amplitude side-bands, all of which contributed a 'rough' quality to the voice and probably reflected nonlinearities in the vocal production process yielding more complex source spectra (Fitch et al. 2002; Tokuda et al. 2002; Owren et al. 2003).

Statistical Analysis

Several statistical techniques were used to test for consistent differences in the structure of pant hoots that were correlated with differences in the behavioural activities, and social or ecological circumstances, associated with call production. The analysis proceeded in three steps. First, because individual differences in pant hoots might be misattributed as contextual differences, we used a discriminant function analysis to test for individual differences in call structure. Next, to examine the detailed structure of pant hoots for evidence specifically of contextual variation, we used a principal components analysis (PCA) to first reduce the large set of acoustic features measured to a smaller set of orthogonal factors that summarized the major dimensions of acoustic variation in the calls. We then used the general linear model to test for significant variation in these factors according to the behavioural, social and ecological circumstances surrounding calling.

To control for the effects of individual differences in call structure in this analysis, we undertook two separate precautions. To begin, the original raw data were standardized within individuals prior to the PCA. This step preserved potential differences across contexts within individuals but removed acoustic variation between individuals. As a further precaution, subsequent statistical tests on the factors derived from the PCA involved two-way analysis of variance (ANOVA) with individuals entered as a random factor and behavioural, social, or ecological circumstances entered as fixed factors. In this way, we could focus on only those factors that showed a significant context effect without also showing an individual effect, or an individual-by-context effect as could happen if some individuals were overrepresented in some contexts and underrepresented in others. For those factors showing only a context effect, Scheffe and Student-Newman-Keuls post hoc tests were used to identify the particular production contexts between which the calls showed significant acoustic variation. A Bonferroni correction for multiple comparisons was used to reduce the probability of type I error. The standard alpha level of 0.05 was divided by the number of PCA factors tested (nine) and conservatively rounded down to yield a revised alpha level for statistical testing of 0.005.

Lastly, we used multiway frequency analysis (often termed log-linear modelling, LLM) to evaluate the two-way associations between behavioural, social and ecological circumstances and discrete variables of pant hoots such as the probability of calling and the likelihood that calls would include a let-down phase, while controlling for those associations that might be anchored by particular individuals as revealed through significant three-way associations between these dimensions and individual identity (Vokey 1997, 2003).

RESULTS

Individual Variation in the Acoustic Structure of Pant Hoots

Discriminant function analysis revealed clear individual differences in pant hoots. This was reflected in an extremely low value for the Wilk's lambda test statistic ($\lambda = 0.0039$), which is statistically significant when evaluated with the chi-square approximation ($\chi^2_{168} = 926$, $P < 0.001$). It is further evidenced by the high rate of successful classification of calls to the individual that produced them, which was 87.4% across all individuals when the calls to be classified were also used in generating the discriminating functions (Table 3). We subsequently undertook a more conservative split-sample analysis in order to test the generality of this result. In this analysis, we randomly selected approximately half of the cases from the data set to serve as the basis for generating the discriminant functions, which we then applied to

Table 3. Confusion matrix for discriminant function classification of calls based on caller identity

	Predicted ID							
Actual ID	Bk	Dn	Jm	Ma	Mu	Nk	Zf	Total
Bk	30	1	0	0	1	0	0	32 (94%)
Dn	2	24	0	1	0	1	0	28 (86%)
Jm	0	0	27	0	0	3	1	31 (87%)
Ma	0	1	0	14	1	0	0	16 (88%)
Mu	5	0	0	0	30	1	0	36 (83%)
Nk	0	0	1	0	1	23	0	25 (92%)
Zf	1	0	3	0	1	0	25	30 (83%)
Total	38	26	31	15	34	28	26	173 (87.4%)

classification of the remaining cases. We repeated this process 10 times, each time using a different set of randomly identified cases to generate the discriminant functions that were then applied to the remaining unused cases. The mean classification success across these 10 iterations was 72.7% (range 68.2–77.6%). As expected, classification success in this split-sample analysis dropped from that observed in the original analysis. However, it remained many times greater than chance (14% for this sample of 7 individuals), confirming the generality of the finding that the acoustic structure of pant hoots is individually distinctive.

Of the entire set of 54 acoustic features, 51 showed significant heterogeneity across individuals in univariate analyses. The only exceptions were the three bandwidth features BWF1C, BWF2C and BWF3C. Many of the acoustic features were strongly interrelated, however, and only eight acoustic features were identified as contributing uniquely to individual distinctiveness in pant hoot structure (see Table A1, Appendix for a list of acoustic features).

Major Dimensions of Within-individual Acoustic Variation in Pant Hoots

Principal components analysis generated a set of nine orthogonal components, or factors, each with an eigenvalue greater than one and associated with at least three original variables (Streiner 1994). These nine factors together accounted for 62% of the variation remaining in the entire data set, once the variation attributable to individual differences in call structure had been removed. Each of the factors represents an independent dimension of structural variation in the pant hoots consistent across all individuals. Table 4 lists these factors, the proportion of variance accounted for by each, their association with specific acoustic features, and thus the general acoustic dimensions that they capture. Acoustic features were associated with a particular factor if their loading on that factor exceeded 0.60.

Factor 1 was associated with 12 nonderived frequency variables that together captured the overall spectral structure of the climax elements. Factor 2 captured the temporal patterning of climax elements. Factor 3 was associated with frequency characteristics of build-up elements. Factors 4, 5 and 6 were associated with several measures of the frequency range, slope and contour of the F_0 of each climax element. Together, these three factors described the overall spectral ‘shape’ of climax elements. Factors 7 and 8 captured frequency modulations in climax elements and the frequency band that attained the highest amplitude in each element, respectively. Factor 9 was associated exclusively with the three measures of F_0 bandwidth in climax elements and thus captured their tonal quality.

Evidence for Pant Hoot Variants According to Behavioural Activity

ANOVA tests on the nine acoustic dimensions resulting from the PCA revealed a significant effect of the callers’ behaviour at the time of calling on only two acoustic dimensions: the F_0 of build-up elements ($F_{4,6} = 5.57$, $P < 0.001$) and the tonal quality of climax elements ($F_{4,6} = 6.38$, $P < 0.001$; Table 5). Post hoc comparisons revealed that build-ups produced by chimpanzees engaged in activities on the ground (i.e. travelling and resting on the ground) had lower F_0 values than those produced in any other context, and particularly relative to those produced upon arrival at a food source (Table 6). In addition, there was a significant difference in the clarity of climax elements produced while travelling compared to those produced during all other behavioural activities (Table 6). Climax elements produced by travelling chimpanzees had a greater bandwidth, which was manifest in a perceptibly ‘rough’, or atonal, quality of climax elements produced by travelling chimpanzees and is illustrated in the spectrograms in Fig. 2.

Log-linear modelling revealed that the behavioural activity of calling chimpanzees also significantly affected the probability that their pant hoots would contain a let-down phase (LLM partial chi-square: $\chi^2_4 = 93.1$, $N = 201$, $P < 0.001$). A let-down phase was significantly more likely in pant hoots produced while travelling and upon arrival at a food source and less likely in pant hoots produced while feeding or while resting in a food tree. This relationship was not driven by particular individuals but rather was robust across all of them, the log-linear modelling revealing no three-way association between caller identity, the inclusion of a let-down phase, and behavioural context ($G^2_{24} = 22.77$, $N = 201$, $P = 0.535$).

The inclusion of a let-down phase also significantly affected the detailed acoustic structure of other elements in the pant hoot series. Thus, the presence or absence of a let-down phase affected the tonal quality of climax elements ($F_{1,6} = 17.16$, $P < 0.001$). Pant hoots containing a let-down phase had climax elements whose F_0 showed a wider bandwidth (i.e. rougher quality) than pant hoots lacking a let-down phase (Table 5).

Table 4. Acoustic structural dimensions of pant hoots identified through principal components analysis

Factor	Eigenvalue	Variation explained (%)	Acoustic structural dimension	Associated acoustic features
1	7.66	14.18	Spectral structure climax	*begf1c, begf2c, begf3c, endf1c, endf2c, endf3c, maxf1c, maxf2c, maxf3c, midf1c, midf2c, midf3c*
2	5.47	10.14	Temporal pattern climax	*dur1c, dur2c, dur3c, avdurc, ratec*
3	3.83	7.09	Build-up F_0	*buF01, buF02, buF03, avbuF0*
4	3.72	6.88	Contour shape climax	*begslope1c, begslope3c, posmaxf1c, posmaxf3c, rpmax1c, rpmax2c*
5	2.67	4.94	Contour range climax	*frqdiff1c, frqdiff2c, frqdiff3c*
6	2.57	4.76	Contour end slope climax	*endslope1c, endslope2c, endslope3c*
7	2.47	4.57	Frequency modulation climax	*fm1c, fm2c, fm3c*
8	2.45	4.54	Peak frequency emphasis	*emphasis1c, emphasis2c, emphasis3c*
9	2.4	4.45	Tonal quality climax	*bwf1c, bwf2c, bwf3c*

Evidence for Pant Hoot Variants According to Social Circumstances

There were no significant differences in any of the acoustic dimensions of pant hoots that were categorized as 'isolated', 'answered', or 'replies'. However, there were differences as a function of both party size and the probability that callers would be joined by, or would join, others. Pant hoots produced in parties of different size varied specifically in the ending slope of the F_0 contour of their climax elements (factor 6; $F_{3,6} = 4.96$, $P = 0.003$). Post hoc comparisons revealed differences in calls produced by lone chimpanzees as compared to those produced by animals in any larger grouping, with lone chimpanzees producing climax elements with steeply descending end slopes. However, these differences were not significant (Table 7).

Variation in the tonal quality ($F_{2,6} = 7.62$, $P = 0.001$) of climax elements was also associated with variation in the probability of subsequent joining between the caller and another party. Post hoc comparisons showed significant differences in this acoustic dimension between calls produced by individuals who subsequently travelled and joined others as opposed to ones that 'attracted' others to the caller. The climax elements of pant hoots that attracted others were characterized by comparatively narrow bandwidths (i.e. a smooth, tonal quality), while those produced by callers who subsequently joined another party had comparatively wide bandwidths (Table 8). In addition, there was a nonsignificant tendency for the spectral structure of these same climax elements to differ ($F_{2,6} = 4.83$, $P = 0.009$). The climax elements of calls produced by chimpanzees who subsequently joined others had higher minimum and maximum frequencies than those produced in the other social contexts.

Log-linear analysis revealed that the inclusion of a let-down phase also varied as a function of several dimensions of the social context. Thus, pant hoots that were subsequently answered by others contained a let-down phase more often than expected, while those produced in answer to the calls of others were less likely to contain a let-down phase (LLM partial chi-square: $\chi^2_2 = 17.38$, $N = 195$, $P < 0.001$). Pant hoots produced by lone or paired individuals also contained a let-down phase more often than expected compared to those produced by individuals in larger parties ($\chi^2_3 = 13.34$, $N = 194$, $P < 0.01$). Finally, callers who subsequently joined-up with other community members were more likely to produce pant hoots containing a let-down phase, while callers who did not join others or who were not joined by others were less likely to include a let-down phase in their pant hoots ($\chi^2_2 = 19.84$, $N = 161$, $P < 0.001$). However, in all three cases, there was also a significant (or nearly significant) three-way association with caller identity, suggesting that the inclusion of a let-down phase in pant hoots in each of these situations depended at least in part on who was calling, whose calls were being answered, and who was joining-up with other community members (call sequence: $G^2_{12} = 37.55$, $N = 195$, $P < 0.001$; party size: $G^2_{18} = 27.09$, $N = 194$, $P = 0.077$; social joining: $G^2_{12} = 31.56$, $N = 161$, $P < 0.01$).

Evidence for Pant Hoot Variants According to Ecological Circumstances

There was a positive association between the abundance of food in a patch and the probability that pant hoots would be produced upon arrival at it ($\chi^2_1 = 5.79$, $N = 30$, $P = 0.016$; Table 9). There was no association between the inclusion of a let-down phase and any aspect of a food source (food species: $\chi^2_4 = 4.51$, $N = 112$, $P = 0.34$; food type: $\chi^2_2 = 1.74$, $N = 110$, $P = 0.42$; food abundance: $\chi^2_1 = 1.2$, $N = 64$, $P = 0.27$). Nor were there any significant differences in the detailed acoustic structure of pant hoot elements according to any aspect of a food source, including the abundance of food available, its type, or the plant part consumed.

DISCUSSION

In this study, we used a large number of features to characterize the pattern of calling and detailed acoustic structure of chimpanzee pant hoots. To begin with, we

Table 5. Results of two-way GLM ANOVA on principal component analysis factors showing F statistics for the effects of context (A), individual identity (B) and individual-by-context interactions (AB)

	Behavioural context		Social context		Party size		Let-down phase included	
Acoustic dimension (Factor)	F	P	F	P	F	P	F	P
Spectral Structure (climax)								
A	6.10	<0.001	4.83	0.009	1.24	0.300	34.5	<0.001
B	0.29	0.944	0.83	0.546	0.59	0.740	0.54	0.778
AB	2.90	<0.001	1.86	0.050	1.27	0.220	5.60	<0.001
Temporal pattern (climax)								
A	1.69	0.154	0.33	0.719	0.57	0.634	0.002	0.970
B	0.26	0.957	0.27	0.949	0.88	0.514	0.10	0.996
AB	2.70	<0.001	1.05	0.410	1.60	0.076	4.20	0.001
Build-up F_0								
A	**5.57**	**<0.001**	2.84	0.062	2.22	0.088	0.02	0.884
B	**0.79**	**0.576**	1.61	0.150	0.11	0.995	0.10	0.997
AB	**1.40**	**0.118**	2.50	0.007	1.35	0.180	2.06	0.060
Contour shape (climax)								
A	0.59	0.668	0.38	0.688	1.69	0.172	0.87	0.351
B	0.52	0.794	0.12	0.994	0.61	0.725	0.17	0.985
AB	1.72	0.030	0.47	0.920	1.47	0.120	2.19	0.050
Spectral range (climax)								
A	0.80	0.524	1.56	0.215	1.67	0.176	0.01	0.907
B	0.47	0.827	0.45	0.842	1.16	0.330	0.06	0.999
AB	1.38	0.120	0.99	0.460	1.95	0.020	1.50	0.190
Contour end slope (climax)								
A	1.94	0.106	0.61	0.545	**4.96**	**0.003**	0.09	0.762
B	0.91	0.488	0.33	0.918	**1.27**	**0.280**	0.10	0.997
AB	1.54	0.060	1.02	0.430	**1.44**	**0.130**	2.10	0.054
Frequency modulation (climax)								
A	0.51	0.729	0.62	0.540	0.66	0.580	2.14	0.145
B	0.21	0.972	0.37	0.890	0.19	0.980	0.07	0.999
AB	1.14	0.310	0.59	0.840	0.67	0.810	0.66	0.683
Peak frequency (climax)								
A	0.01	0.990	0.57	0.570	0.45	0.716	1.20	0.275
B	0.08	0.99	0.12	0.994	0.29	0.944	0.02	1.0
AB	1.40	0.101	1.12	0.350	0.86	0.610	1.04	0.400
Tonal quality (climax)								
A	**6.38**	**<0.001**	**7.62**	**0.001**	2.48	0.063	**17.2**	**<0.001**
B	**0.75**	**0.607**	**0.75**	**0.614**	1.16	0.330	**0.16**	**0.986**
AB	**1.54**	**0.060**	**1.13**	**0.350**	0.84	0.630	**0.63**	**0.709**

Cells highlighted in bold indicate factors for which there was a significant context effect but no individual effect or individual-by-context effect ($P = 0.005$).

found that pant hoots were highly individually distinctive. Although we did not find evidence for additional differentiation in pant hoots according to many of the behavioural, social and ecological dimensions considered, our analyses did reveal several statistically significant patterns. Thus, we found that pant hoots were more likely to be produced upon arrival at an abundant food source. We also found that pant hoots produced while travelling along the ground in small parties prior to joining-up with other community members were consistently different from all other pant hoots, varying reliably in the tonal quality and slope of the F_0 contour of climax elements, the F_0 of build-up elements, and in the presence of a let-down phase. Pant hoots that contained a let-down phase were also more likely to elicit pant hoots from others.

These patterns are generally consistent with and extend the results of previous studies of chimpanzee pant hoots. Several authors have described individual differences in pant hoots (Mitani & Brandt 1994; Mitani et al. 1996) and many have also noted the variety of contexts in which pant hoots are produced, including while feeding, travelling and joining-up with other community members (Goodall 1986; Clark & Wrangham 1993; Mitani & Nishida 1993; Mitani 1994). The association between pant hoots and food sources, in particular, has also been emphasized previously, and some studies have documented an increased rate and likelihood of calling when food is especially abundant or of high quality (Wrangham 1977; Hauser et al. 1993). The variable inclusion of a let-down phase has also been reported previously and, as here, has been associated with details

Table 6. Differences in the fundamental frequency (F_0) of build-up elements and the bandwidth of climax elements according to behavioural activity

Behaviour	Build-up F_0*	Bandwidth* (climax)
Rest (on ground)	230 Hz^{a}	72 Hz
Travel (on ground)	236 Hz^{b}	88 Hz^{a,b}
Feed	257 Hz	62 Hz^{b}
Rest (in tree)	275 Hz	60 Hz^{a}
Arrive at food	283 Hz^{a,b}	69 Hz

*Superscripted letters (a, b) denote the specific behavioural contexts between which acoustic differences were statistically significant in Scheffe post hoc tests.

of food sources (Wrangham 1977; Clark & Wrangham 1993).

Several of the differences identified here in the more detailed spectral features of pant hoots are novel but some have been observed previously. Thus, like us, Uhlenbroek (1996) noted that the climax elements of pant hoots produced by travelling chimpanzees were noisy and rough, lacking a clear harmonic structure that made them ‘roar-like’, whereas those produced while resting or feeding were more tonal and ‘wail-like’.

The overall pattern of our and others’ results for pant hoots is also generally consistent with that of a recent study on chimpanzee ‘bark’ vocalizations (Crockford & Boesch 2003). Although barks are distinct from pant hoots in being short, abrupt, noisy (i.e. broadband) calls, they are like pant hoots in being given in a variety of different behavioural, social and ecological contexts. Paralleling our results, Crockford & Boesch found differences in the structure of barks produced in only two of the six contexts studied, namely while hunting and when encountering a snake.

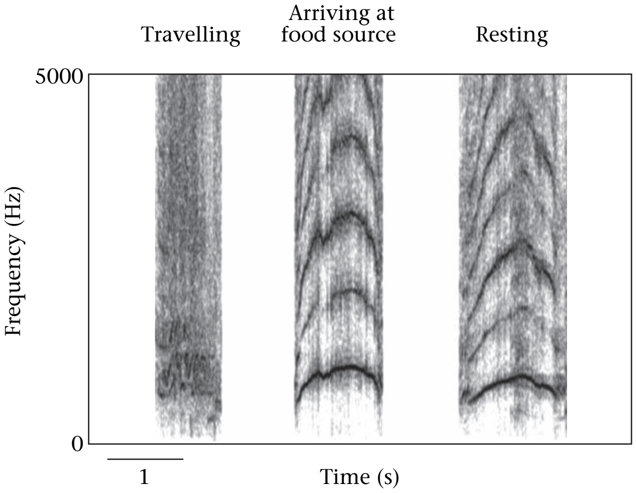

Figure 2. Spectrograms of three climax elements, each taken from a pant hoot series produced while, travelling, arriving at a food tree, and resting in a tree. Spectrogram settings as in Fig. 1.

Implications for Referential Communication

One interpretation of these patterns, both for pant hoots and for barks, is that they reveal significant call variants or subtypes that reflect selective diversification in the structure of chimpanzee calls to support a system of referential communication about important features of the environment. Of course, the perceptual salience to listeners of structural differences in either pant hoots or barks has not been confirmed or even tested yet, and this is a very important step in demonstrating the referential quality of structural call variants (Macedonia & Evans 1993). Nevertheless, it seems at least a reasonable working hypothesis that the animals themselves are sensitive to the structural variation identified in the calls, and that they can use the variation to make at least probabilistic inferences about the activities of other animals that they hear calling (Premack 1972; Owren & Rendall 2001; Seyfarth & Cheney 2003).

Another interpretation involves questioning why the acoustic differences are not more obvious and more pervasive. For both pant hoots and barks, analyses using a large number of acoustic features and a similarly large number of potentially relevant behavioural, social and ecological dimensions have revealed only a handful of significant effects. For pant hoots, in particular, several studies by different researchers have failed to identify many consistent and obvious subtypes of the call that are associated with specific production contexts, and what few effects have been documented have been acoustically quite subtle. For example, one of the principal dimensions of acoustic variation in pant hoots (the tonal quality of climax elements) identified in this study as varying consistently between a few of the contexts studied nevertheless accounted for only a small fraction ($<5\%$) of the overall variation in these calls.

One explanation for these failings is that we are simply missing a larger set of consistent structural differences in the calls. Despite attempts to characterize the calls exhaustively, our acoustic analyses are just not capturing many of their important structural features. Another explanation is that the contextual dimensions we recognize and use in analyses are tangential, or even largely orthogonal, to those that are important to the animals themselves. That is, we are effectively mischaracterizing the contexts. A third possibility is that we are not missing critical variation in the calls nor mischaracterizing the contexts per se but rather mischaracterizing the probable function of the calls.

What seems to be clear, not only in chimpanzees but also in many other nonhuman primates, is that certain general call types are often used in a variety of contexts that appear to us quite different. This observation has often prompted a detailed search for subtle call variants associated with the different production contexts on the assumption that the calls serve different informing functions in each of them. However, perhaps the broad contextual usage of some calls reflects the fact that they serve a generalized function that transcends the different contexts. In the case of pant hoots, it is possible that across the various contexts in which they occur, the calls

Table 7. Differences in the ending slope of the fundamental frequency contour of climax elements according to party size

Party size	F_0 end slope* (climax)
Alone	3283 Hz
Pair	1896 Hz
3–5	2067 Hz
>5	1978 Hz

*Acoustic differences were not statistically significant in Scheffe post hoc tests.

serve a generalized social function associated with monitoring and coordinating the activities and movements of dispersed social companions.

On the surface of it, this seems at least plausible given the decidedly dispersed and fragmented but intensely social quality of chimpanzee society in which individual and kin identity, social status, and flexible alliance networks are paramount. This combination of social-organization characteristics may create a vexing problem in coordinating a variety of critically important social relationships while often physically separated from one another. Under these circumstances, the primary function of pant hoots might be to clearly signal identity (and all the subsidiary social dimensions that flow from it, such as status, alliance relationships, etc.) in order to coordinate social activities and relationships at a distance. This proposal is, of course, very similar to some others offered for pant hoots (cf. Wrangham 1977; Mitani & Nishida 1993; Clark & Wrangham 1994; Mitani 1994). It is also supported by the fact that the most consistent finding from studies of pant hoots is that their structure is highly individually distinctive (Marler & Hobbett 1975; Clark & Wrangham 1994; Mitani et al. 1996).

Social factors might thus be of overriding importance across the various contexts in which pant hoots are produced, and this may limit our identification of clearly discrete subtypes of the call according to the many other contextual categories we ourselves recognize and define. The few subtle contextual differences that nevertheless emerge might then reflect rough correspondences that arise naturally from the way different contexts or associated behavioural activities affect vocal production. These could include effects on the pattern of calling or detailed acoustic features of the calls introduced by variation in caller arousal or motivation, variation in the caller's concurrent locomotor or other physical activities, or variation in the effort or exertion callers invest in vocalizing, or some combination of these factors. The pattern of contextual differences observed and the specific features of the calls that varied are both consistent with this possibility.

Table 8. Differences in the bandwidth of the fundamental frequency of climax elements according to social context

Social context	Bandwidth* (climax)
Alone	68 Hz^{a}
Others join	67 Hz^{b}
Joins others	86 Hz^{a,b}

*Superscripted letters (a, b) denote the specific behavioural contexts between which acoustic differences were statistically significant in Scheffe post hoc tests.

The Mechanistic Basis of Contextual Variation in Pant Hoots

Thus, the primary contextual differences we found in pant hoots involved animals arriving at an abundant food source, or travelling alone or with one other individual and attempting to locate and subsequently join other community members. Increased calling at bonanza food resources is commonly associated with elevated arousal. Differences in the calls of lone chimpanzees also plausibly reflect elevated arousal associated with social separation and a desire to reunite with others. Indeed, Uhlenbroek (1996) reported that pant hoots produced by travelling chimpanzees were frequently accompanied by piloerection and displaying, both common indexes of increased arousal.

Differences in the calls of travelling chimpanzees might in part also reflect effects due to the accompanying locomotor activity itself, or to increased vocal exertion related to the callers' efforts to broadcast calls widely. The latter possibility is suggested by the fact that we also found consistent differences in the detailed structure of climax elements produced when either travelling, arriving at a food source, or resting on the ground compared to when feeding or resting in a tree. One factor that unites the first group of three disparate activities as well as the latter two and that also distinguishes between the two groups is the position of the callers: the first three activities all involve animals calling from positions on the ground, while the latter involve animals calling from an elevated position in a tree. In forest habitats, sound propagation is particularly influenced by the position of the sound source, favouring propagation of sounds produced from elevated positions over those produced on the forest floor. This effect is underscored by the additional finding that the F_0 of build-up elements produced on the ground were significantly lower than those produced in a tree, which is consistent with efforts to maximize propagation of the calls (Waser & Brown 1984, 1986).

Not only are the patterns of contextual differences observed consistent with mechanisms rooted in variable caller arousal, physical activity profiles, or vocal exertion, but the specific acoustic features that varied in these different contexts and the direction in which they varied in each case are also consistent with such mechanisms. Thus, most of the differences were related to the probability of calling, the tonal quality of calls, and the variable inclusion of a let-down phase. The first two features are ones widely connected with variable arousal or vocal exertion in other primate species, including humans (reviewed in Hauser & Marler 1993; Murray & Arnot 1993; Hauser 2000; Traunmüller & Eriksson 2000; Rendall 2003), and they varied in predictable directions with increases in the probability of calling and degradation in the tonal quality of calls in contexts portending either increased arousal or increased exertion (i.e. encountering more as compared to less abundant food; when alone and joining others versus when with others and being joined; and when travelling as compared to feeding or resting). The variable inclusion of a let-down phase is also consistent with such mechanisms. It is a repeated inhalation/exhalation sequence that seems to represent the voiced, respiratory 'spill-over' from the preceding loud, exaggerated climax elements and it was more common in contexts associated with increased arousal, locomotor activity, or vocal exertion (when travelling alone or in pairs and subsequently joining others, or when arriving at a food tree). The fact that the immediately preceding climax elements in pant hoots containing a let-down phase were also harsh and atonal further supports this possibility.

In summary, we follow others in proposing a general social function for pant hoots (e.g. Mitani & Nishida 1993; Clark & Wrangham 1994; Mitani & Brandt 1994). We further suggest that the subtle structural differences observed in some contexts reflect the different effects on vocal production introduced by the variable arousal and motivation, physical demands, or vocal effort associated with calling in those contexts. We hope that future research can be designed to explore this possibility more systematically using generally accepted indexes of internal state (e.g. piloerection and respiration rate).

Importantly, this account of the mechanistic basis of the differences in pant hoots does not preclude a potential referential function for such differences as well; that is, it does not preclude the possibility that listeners might use the differences in the calls to make inferences about the caller's behaviour or the ecological and social circumstances surrounding call production, what has come to be termed 'functional reference' (Macedonia & Evans 1993; Evans 1997). However, the outstanding issues in this research area are no longer about whether listeners can glean information about their environments from the behaviour, including vocal signals, of companions. This is well established for many animal taxa (Shettleworth 1998). Rather, the key issues now concern the mechanisms underlying instances of functional reference, and, for those specifically interested in tracing the evolutionary trajectory of these mechanisms in humans, the extent to which they parallel those subserving linguistic reference. While this remains an open and debated issue generally, the data presented here for chimpanzee pant hoots suggest that any referential function of the calls may involve similar inferential abilities on the part of listeners but probably not similar mechanisms underlying the production of the referential contrasts in callers. Rather than reflecting intentional modification of call structure for purposes of conveying discrete messages, as typifies language, the contrasts seem more likely to reflect variation in the physical or physiological influences on vocal production introduced by arousal, locomotor activity, or calling effort. Although this account proposes somewhat different routes to reference in chimpanzee communication and human language, it is quite consistent with a broad phenomenal theme in evolutionary biology wherein functionally similar outcomes in different species can often arise from different mechanistic processes.

Table 9. Summary of tests of the effects of behavioural activity and associated social or ecological circumstances at the time of calling on the likelihood that pant hoots would be produced and that they would contain a let-down phase

	Likelihood of pant hoots	Let-down phase included
Behavioural activity		
Travel, arrive at food, or rest on ground vs feed or rest in tree		Yes–No
Ecological context		
Food abundance: <50% vs >50% of tree canopy contains food	Low–High	
Social context		
Party size: caller is alone or in pair vs a larger party		Yes–No*
Social joining: caller joins vs is joined by others or no change in social partners		Yes–No*
Call sequence: caller receives response vs caller is responding to distant call		Yes–No*

Only those comparisons showing significant effects are shown. For each of these, the direction of the effect is indicated. Asteritsks (*) indicate cases where there was also a significant (three-way) effect of caller identity on the effect observed, indicating that the two-way relationship was influenced by the patterns of particular callers rather than being common to all callers.

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Appendix

Table A1. Acoustic features measured or derived for each pant hoot showing P values from univariate ANOVAs and discriminant function analysis for each variable

Phase	Code	Description of parameter†
Build-up	NUMBU*,**	Number of elements in build-up phase
	DURBU*	Total duration of build-up
	BUF01*	Duration of 1st element in build-up
	BUF02*	Duration of 2nd element in build-up
	BUF03*	Duration of 3rd element in build-up
Climax	NUMC*,**	Number of elements in climax phase
	DURC*	Total duration of climax phase
	DUR1C*	Duration of 1st climax element
	DUR2C*	Duration of 2nd climax element
	DUR3C*	Duration of 3rd climax element
	BEGF1C*,**	Start F_0 of 1st climax element
	BEGF2C*	Start F_0 of 2nd climax element
	BEGF3C*,**	Start F_0 of 3rd climax element
	ENDF1C*	End F_0 of 1st climax element
	ENDF2C*	End F_0 of 2nd climax element
	ENDF3C*	End F_0 of 3rd climax element
	MAXF1C*	Maximum F_0 of 1st climax element
	MAXF2C*	Maximum F_0 of 2nd climax element
	MAXF3C*	Maximum F_0 of 3rd climax element
	MIDF1C*	F_0 frequency at midpoint of 1st climax
	MIDF2C*	F_0 frequency at midpoint of 2nd climax
	MIDF3C*	F_0 frequency at midpoint of 3rd climax
	POSMAXF1C*	Temporal position of maxf1c
	POSMAXF2C*	Temporal position of maxf2c
	POSMAXF3C*	Temporal position of maxf3c
	BWFIC	Bandwidth F_0 of 1st climax element
	BWF2C	Bandwidth F_0 of 2nd climax element
	BWF3C	Bandwidth F_0 of 3rd climax element
	FM1*	Number of frequency modulations in 1st climax element
	FM2*	Number of frequency modulations in 2nd climax element
	FM3*	Number of frequency modulations in 3rd climax element
	QLTY1C*	Spectral quality of 1st climax element
	QLTY2C*	Spectral quality of 2nd climax element
	QLTY3C	Spectral quality of 3rd climax element
	EMPHASIS1C*	Principal frequency of 1st climax element
	EMPHASIS2C*	Principal frequency of 2nd climax element
	EMPHASIS3C*	Principal frequency of 3rd climax element
Derived measures	RATEBU*,**	Rate of delivery of build-up elements
	AVDURBU*,**	Average duration of 1st three build-up elements
	AVBUF0*	Average F_0 of 1st three build-up elements
	RATEC*,**	Rate of delivery of climax elements
	AVDURC*	Average duration of all climax elements
	FRQDIFF1C*	Difference between F_0 minima and maxima of 1st, 2nd and 3rd climax elements
	FRQDIFF2C*	
	FRQDIFF3C*	
	RPMAX1C*	Relative position of the maximum F_0 of 1st, 2nd and 3rd climax elements
	RPMAX2C	
	RPMAX3C**	
	BEGSLOPE1C*	Frequency difference/duration from start of element to maximum frequency for 1st, 2nd and 3rd climax elements
	BEGSLOPE2C*	
	BEGSLOPE3C*	
	ENDSLOPE1C*	Frequency difference/duration from maximum frequency to end of element for 1st, 2nd and 3rd climax elements
	ENDSLOPE2C*	
	ENDSLOPE3C*	

*Variables showing significant individual heterogeneity under univariate ANOVA ($P < 0.001$).

**Variables contributing uniquely to individual differentiation of calls under discriminant analysis according to significant removed F probability statistics, $P < 0.001$.

†In cases where a particular call element was missing from a specific pant hoot series, the acoustic features for this call element were assigned a value equal to their grand mean calculated from all other cases across all individuals and contexts. This operation allowed these pant hoot series to be included in analyses (rather than dropped entirely) but ensured that their missing elements would not affect tests for individual or context differences in the calls.