International Journal of Primatology, Vol. 17, No. 4, 1996

Selection for Acoustic Individuality Within the Vocal Repertoire of Wild Chimpanzees

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Received March 1, 1995; revised June 9, 1995; second revision received January 16, 1996; accepted April 1, 1996.

Individual primates typically produce acoustically distinct calls. To investigate the factors that facilitate the evolution of individual vocal signatures, we examined two components of the call repertoire of chimpanzees: the pant hoot and pant grunt. Pant hoots are long-distance signals whose recipients can be several hundred meters away, while pant grunts are short-range calls given to conspecifics within close visual range. Given their markedly different contexts of emission, we predicted that natural selection would favor the elaboration of individually distinctive acoustic features in pant hoots compared with pant grunts. Analyses of nine acoustic features revealed that pant hoots are more stereotyped within-individuals and variable between-individuals than pant grunts. These data are consistent with the hypothesis that selection may act to encode varying degrees of individuality in different components of the vocal repertoire of a single species.

KEY WORDS: primate vocal communication; vocal signatures; individual recognition.

INTRODUCTION

Many primates live within complex social groups and interact with multiple individuals, which vary in age, sex, kinship, and rank (Smuts *et al.*, 1987). Insofar as vocal behavior mediates these interactions, there must be strong selection for the ability to identify the calls of individuals. Selection for individual vocal recognition may act to sharpen characteristics related

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to the production or perception of calls, and field and laboratory evidence indicates that primates readily discriminate acoustic differences between the vocalizations produced by conspecifics (Snowdon, 1986; Cheney and Seyfarth, 1988).

While social life undoubtedly creates a strong selective pressure for vocal recognition of individuals, recent studies suggest that under certain conditions natural selection may favor the further elaboration of acoustic features that differentiate individuals. For example, large aggregations hamper individual recognition (Scherrer and Wilkinson, 1993), and the calls of animals living in such groups appear to contain more individually distinctive acoustic characteristics than those found within smaller groups (Beecher *et al.,* 1986; Medvin *et al.,* 1993). In a similar fashion, individual recognition by voice may be at a selective premium in situations in which animals are frequently separated versus those in which individuals are typically within visual range of each other (Insley, 1992).

Previous researchers have considered whether selection favors the evolution of individual vocal signatures in some species compared with others. We extend this line of inquiry by investigating the degree to which selection acts to encode individually distinctive acoustic features differentially within the signalizing system of a single species. Our investigation focuses on chimpanzees, which, like most primates, produce and use calls in a variety of situations. The two most frequently uttered calls by chimpanzees regulate spacing between widely separated individuals and dominance relationships among them. These vocalizations are the long-distance pant hoot and short-range pant grunt, respectively (Marler, 1976; Marler and Tenaza, 1977; Mitani, 1996). The recognition task involved during the perception of these two calls differs considerably. Pant hoots are long distance signals typically delivered to potential recipients that may be as far away as several hundred meters. In contrast, pant grunts are commonly uttered within close visual range of call recipients. Given their markedly different usage, we hypothesize that selection will act to encode a greater degree of individuality in the long-range pant hoot compared with the pant grunt. We expect selection for individuality in the short-range pant grunt to be relaxed given the ability of recipients to use other sensory modalities to identify signalers.

We explore the predictions outlined above by examining the degree of within- and between-individual acoustic variability in the calls of chimpanzees. Since signaling systems characterized by within-individual stereotypy facilitate individual recognition (Falls, 1982; Insley, 1992), we test the hypothesis that when compared with pant grunts, pant hoots vary little within individuals but differ markedly between individuals.

METHODS

The Calls

Chimpanzees emit pant hoots and pant grunts in bouts containing multiple calls. Pant hoots are loud, species-typical signals that communicate over long distances (Marler and Hobbett, 1975; Mitani and Nishida, 1993). The calls comprise four acoustically and temporally distinct parts: an introduction, a build-up, a climax, and a let-down (Fig. 1a). We restricted our analyses to climax elements since they are uttered at relatively high amplitudes (Fig. 1a) and are the only part of the call that can be heard over long distances, situations in which senders and receivers are unlikely to be able to see each other (Mitani and Nishida, 1993). In contrast, pant grunts consist of a series of broad band acoustic elements (Fig. 1b). Pant grunts are given by low-ranking chimpanzees to high-ranking individuals in close proximity and within visual contact (Goodall, 1986; Hayaki *et al.*, 1989). Context-specific acoustic variation in calls similar to that found in other primate signaling systems (Seyfarth and Cheney, 1985) has not been documented in pant hoots (Clark and Wrangham, 1993; Mitani unpublished data). The high degree of within-individual, within-bout acoustic variability in pant grunts makes it unlikely that their acoustic structures differ as a function of their context of emission (Table IV).

Study Site and Subjects

Mitani observed chimpanzees of the Munit group and tape-recorded their vocalizations in January–June 1990, June–August 1992, and April–August 1994 at the Kasoje Research Station in the Mahale Mountains National Park, Tanzania. M-group chimpanzees have been observed during the past 27 years (Nishida and Kawanaka, 1972). By virtue of prior fieldwork, the demographic and social histories of most of the M-group chimpanzees are well-known (Nishida *et al.*, 1990).

Previous research indicates that an individual's age and sex affects the acoustic structure of chimpanzee calls (Marler and Hobbett, 1975; Mitani and Gros-Louis, 1995). To control for these potentially confounding factors, we restricted analyses to calls produced by adult males. We included only males from which we made a sufficient number of recordings of both call types. Our sample comprised seven males (Table I).

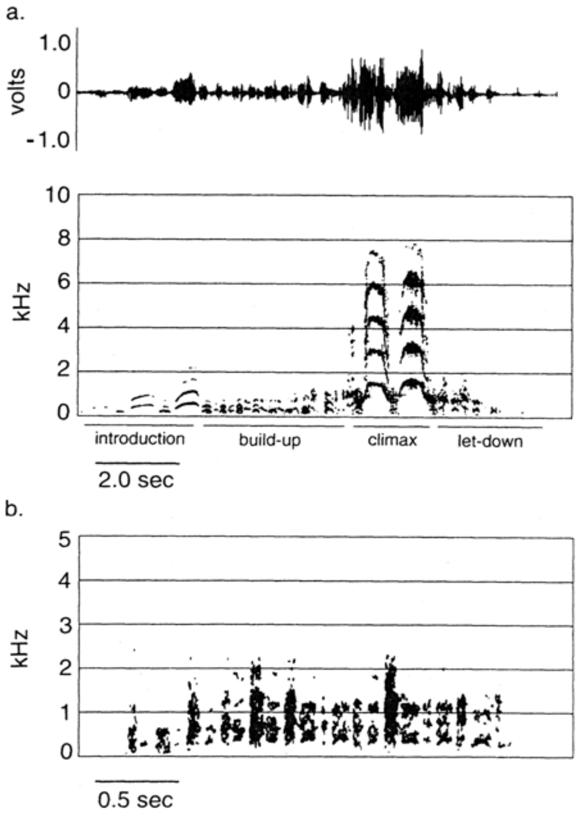

Fig. 1. Comparison of pant hoots and pant grunts. (a) Waveform and audiospectrogram of a representative pant hoot. Analysis range: 11 kHz. Frequency resolution = 43 Hz. (b) Spectrogram of pant grunts. Analysis range: 5.5 kHz. Frequency resolution = 43 Hz. Note that pant hoots and pant grunts are produced in bouts composed of multiple calls, depicted by continuous tracings on spectrograms; the relative amplitudes of pant hoot climaxes are considerably higher than other parts of the call. Spectrograms were produced via MacRecorder sound analysis software.

Recording Methods and Acoustic Analyses

During following episodes of individual chimpanzees (Mitani and Nishida, 1993), Mitani made tape recordings ad libitum using a Sony WM-D6C cassette recorder and a Sennheiser ME-80 cardiod microphone. The frequency response of this system spans 50–15,000 Hz and covered the range shown by calls (Fig. 1). Gros-Louis subsequently examined recordings in the

Table I. Subjects and Samples of Calls

	Pant grunts		Pant hoots	
Individual	Bouts	Calls	Bouts	Calls
AJ	12	78	21	54
BE	28	203	33	81
FN	13	65	25	58
JI	13	79	18	38
MA	19	113	12	31
NS	12	51	51	125
TB	15	118	17	45

laboratory with a digital signal processing program designed for the analysis of animal calls (Beeman, 1992). We sampled calls at 20,000 points/sec with 12-bit precision, resulting in an effective analysis bandwidth of 8 kHz.

Pant hoots and pant grunts show considerable differences in call structure (Fig. 1), and for the following analyses, we searched for a set of acoustic variables that are common to both but could still be used to characterize calls adequately. Using these criteria, we selected nine variables (Table II). We measured durations from waveforms and associated spectrograms after calculating 256-point Fourier transforms across each call (time resolution = 13 ms). We calculated six frequency variables from the lowest-frequency bands visible on spectrograms. We computed minimum and maximum frequencies after performing 512-point Fourier transforms (frequency resolution = 39 Hz) over the midpoint of each call. We set the peak amplitude of the lowest-frequency band to 0 dB and then went –3 dB down either side of the spectral peak to locate minimum and maximum values (Fig. 2a). We computed bandwidths by subtracting minimum from maximum frequencies (Dunn, 1961). We determined average frequencies from a series of 512-point spectral sections made at successive, equally spaced intervals across each call. A preliminary analysis indicated that pant hoot climax elements are considerably longer ($X = 636$ msec, SE = 25 sec; $N = 120$) than pant grunt elements ($X = 78$ msec, SE = 3 sec; $N = 129$). We therefore matched sample sizes and maintained a constant frequency/time resolution (39 Hz, 26 msec) by averaging three spectral sections over both call types. We determined starting and ending frequencies from the first and last of these three measurements. Both call types show multiple frequency bands (Fig. 1). To assess part of the acoustic variability contained in these bands, we performed a 512-point Fourier transform over the midpoint of each call and ascertained the frequency values of the first and second bands. We used the difference of these two bands and the value of the second band as two additional acoustic variables (Fig. 2b).

Table II. Acoustic Variables

Acoustic variable	Description
Duration (dur)	Call length (msec)
Minimum frequency (mnf)	Minimum frequency of call midpoint (kHz)
Maximum frequency (mxf)	Maximum frequency of call midpoint (kHz)
Bandwidth (bw)	Maximum–minimum frequency (kHz)
Average frequency (af)	Average of a call's starting, ending, and midpoint frequencies (kHz)
Starting frequency (sf)	Frequency of first 26 msec of call (kHz)
Ending frequency (ef)	Frequency of last 26 msec of call (kHz)
Frequency of band 2 (F2)	Frequency of second frequency band's midpoint (kHz)
Frequency difference of bands 2 & 1 (F2–F1)	Frequency of band 2–frequency of lowest band's midpoint (kHz)

Statistical Analyses

To investigate within-individual variability in calls, we calculated coefficients of variation for each acoustic variable. We computed mean values

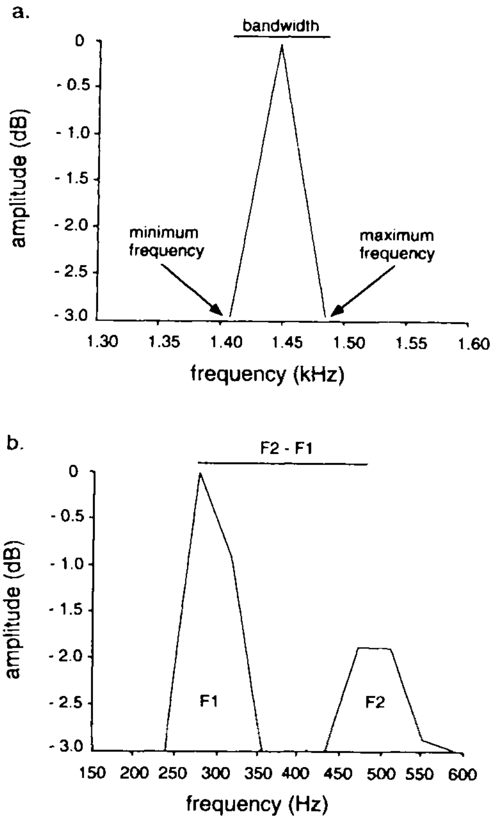

Fig. 2. Acoustic measurements. (a) Amplitude spectrum of pant hoot climax call. Displayed is a 512-point fast Fourier transform (FFT; 26 msec) over the midpoint of the first climax element illustrated in Fig. 1a. Minimum and maximum frequencies are shown along with their difference (= bandwidth). (b) Amplitude spectrum of the first pant grunt shown in Fig. 1b. A 512-point FFT over the midpoint of the call displays the values of the first frequency band (F1), the second frequency band (F2), and their difference (F2–F1).

based on the coefficients of the seven subjects and used them to construct variability profiles (Sokal and Braumann, 1980), which graphically illustrate within-individual variability in calls through plots of mean coefficients for each acoustic variable. We compared the two profiles via a Wilcoxon matched-pairs, signed-ranks test (Siegel and Castellan, 1988), employing a one-tailed test given our explicit, a priori prediction that pant hoots should exhibit more stereotypy than pant grunts. Variability of measured features typically decreases as a function of increasing sample size, and the number of recorded pant grunts exceeded those of pant hoots (Table I). Given these circumstances, we computed coefficients of variation using equal numbers of pant hoots and pant grunts. We conducted two comparisons. First, we computed coefficients using samples comprised of the minimum number of calls recorded from all individuals ($N = 31$; Table I). For individuals from which we recorded more than this minimum number, we selected a subsample using a random numbers table. Calls produced within a single bout may be acoustically homogeneous (Fig. 1b) and, for this reason, may not be independent for statistical purposes. We therefore conducted a second analysis using a sample of calls whose size equaled the minimum number of bouts produced by individuals ($N = 12$; Table I). For each individual, we constructed random samples consisting of a single call from each bout.

We examined between-individual acoustic variation in calls via a nested analysis of variance. This design controls for measuring multiple calls from the same bout and estimates variance components due to individuals, bouts within individuals, and calls within bouts (Sokal and Rohlf, 1995). Preliminary data analysis revealed that the nine acoustic variables are correlated and nonnormally distributed in one or both types of calls. We therefore conducted a principal-components analysis (PCA) using the entire data set of pant hoots and pant grunts. We used the component scores from the PCAs as dependent variables in a two-level nested ANOVA, retaining those components that exceeded Jolliffe's criterion with eigenvalues >0.70 (Jolliffe, 1986).

RESULTS

Within-Individual Acoustic Variation

Variability profiles graphically illustrate that pant hoots are less variable within individuals than pant grunts are in all but one of the nine acoustic measures (Wilcoxon $Z = 2.56$; $N = 9$; one-tailed $P = 0.005$; Fig. 3a). An additional comparison employing randomly selected subsets of calls from independent bouts (Fig. 3b) produced similar results, with pant hoots

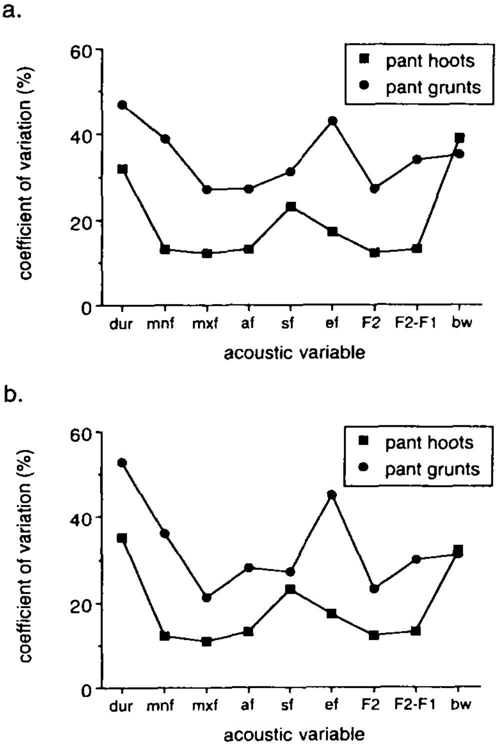

Fig. 3. Variability profile of nine acoustic variables for pant hoots and pant grunts. The mean coefficients of variation for seven individuals are plotted. Pant hoots show consistently lower within-individual variability than pant grunts in all but one variable. Abbreviations for acoustic variables are in Table II. (a) N calls per individual = 31. (b) N calls per individual = 12.

showing greater stereotypy than pant grunts (Wilcoxon $Z = 2.55$; $N = 9$; one-tailed $P < 0.005$).

Between Individual Acoustic Variation

A PCA generated nine statistically independent components. The first two components exceeded Jolliffe's criterion, with eigenvalues >0.70 (Table III). These components accounted for virtually all of the variation in the data set (94%; Table III). Table III shows the component loadings or correlations between the original acoustic variables and the first two

Table III. Principal-Component Loadings and Their Percentage Variance Explained[a]

Acoustic variable	Principal component 1	Principal component 2
Average frequency	0.99	0.02
Maximum frequency	0.99	−0.01
Minimum frequency	0.99	0.06
Frequency of band 2	0.99	0.03
F2–F1	0.99	0.03
Ending frequency	0.98	0.01
Starting frequency	0.94	0.01
Duration	0.77	0.07
Bandwidth	0.21	−0.97
Eigenvalue	7.45	0.96
% variance explained	83	11

[a] Only those components that exceeded Joliffe's criterion with eigenvalues >0.70 are shown.

components produced by the PCA. The first component showed a strong correlation with seven frequency measures and reflected the overall spectral structure of calls. The eighth frequency measure—bandwidth—loaded highest on the second component.

We employed the first two components retained by the PCA in a nested analysis of variance to examine between- and within-individual acoustic variability in pant hoots and pant grunts. Both components were normally distributed (Kolmogorov–Smirnov tests, $P > 0.05$) and homoscedastic (Bartlett's tests, $P > 0.05$). Nested analyses of variance revealed that the acoustic structure of pant hoots varies between and within individuals (Table IV). The between-individual component of variation ranges from 12 to 39% in the two retained variables. Both principal components show significant heterogeneity among individuals ($P << 0.001$ for both comparisons; Table IV). Bouts produced within individuals were also highly variable as measured by the two principal components ($P < 0.01$ for both comparisons; Table IV). Pant grunts do not appear to be individually distinctive. Interindividual differences explained only a small fraction of the variation in each of the two components retained by the PCA, ranging up to only 3% in the first component (Table IV). Neither component shows significant differences among individuals (Table IV). In contrast, both components show significant heterogeneity between bouts produced within individuals ($P < 0.01$ for both comparisons; Table IV).

Table IV. Variance Components Attributable to Individuals, Bouts Within Individuals, and Calls Within Bouts for Each of Two Principal Components: (a) Pant Hoots; (b) Pant Grunts

Principal component	% variance due to		
	Individuals	Bouts	Calls
	a		
1	39**	42**	19
2	12**	11*	76
	b		
1	3	27**	69
2	1	10*	89

*$P < 0.01$.
**$P << 0.001$.

DISCUSSION

Marler and Hobbett (1975) were the first to document acoustic differences in the calls of chimpanzees. Their acoustic analyses revealed that the frequency and temporal structure of pant hoots differ among individuals. More recent analyses have confirmed that acoustic differences commonly exist between the vocalizations produced by individual primates (Snowdon, 1986). The widespread occurrence of individual vocal signatures should come as no surprise. Variation, after all, is a fundamental feature of life (Mayr, 1963), and more compelling biological lines of inquiry include investigating why and under what conditions calls differ acoustically between individuals.

Several factors may play a role in producing interindividual acoustic differences. For example, individuals typically vary in body size (Uehara and Nishida, 1987), and size differences may correlate with variations in laryngeal production mechanisms leading to predictable differences in the spectral features of calls (Inoue, 1988; Gouzoules and Gouzoules, 1990). Moreover, vocal signatures may result through animals actively modifying their vocal tract filters during call production (Hauser, 1992). While these anatomical and behavioral factors provide some of the causal bases underlying interindividual acoustic differences, whether vocal individuality is favored in some social and ecological situations remains relatively unexplored (Beecher *et al.*, 1986; Insley, 1992; Medvin *et al.*, 1993).

Given their markedly different patterns of usage, we hypothesized that natural selection would favor the evolution of individual vocal signatures more strongly in pant hoots than in pant grunts. Specifically, we predicted that pant hoots would show greater within-individual stereotypy and between-individual variability than pant grunts. Results of our analyses confirmed both predictions and provide the first empirical demonstration that selection may act to encode varying degrees of individuality in different components of the vocal repertoire of a single species. Selection for individual distinctiveness in pant hoots may be intensified given the hypothesized function of these calls. Recent field observations suggest that calls are used selectively to recruit the company and support of preferred associates and allies (Mitani and Nishida, 1993). An important requirement of the selective recruitment hypothesis is that calls are individually distinctive.

Our failure to uncover a significant between-individual component of variation in pant grunts does not imply an absence of interindividual acoustic variation in these calls. We examined only a small number of acoustic features that pant grunts share with pant hoots, and it is possible that pant grunts will be shown to be individually distinctive through additional investigation. The typical contexts of call emission, however, may have created a situation in which selection for individual vocal signatures has been relaxed. Further study will be required to determine whether natural selection acts differentially on other components of the chimpanzee call repertoire under varying social and ecological conditions.

While our results are consistent with the hypothesis that selection for individual recognition may have led to readily discriminable interindividual differences in pant hoots, factors other than selection for individuality per se may account for the high degree of within-individual stereotypy shown by them. For example, long-distance communication is inherently noisy (Wiley, 1983, 1994). This high level of noise may be due to the effects of signal attenuation and degradation over distance (Wiley and Richards, 1982) or species-rich acoustic environments (Marler, 1957). Given a noisy channel, increased stereotypy may facilitate the detection and recognition of pant hoots broadcast over long distances (Marler, 1973; Wiley, 1983, 1994). In contrast, stereotypy is not required to aid the detection of sounds employed in short-range communication, and the high levels of within-bout variability shown by pant grunts (Table IVb) may reflect information regarding the internal state of the signaler (Wiley, 1983). Finally, we note that the long-distance communication channel places a selective premium on individual identification and may be the primary factor leading to the high degree of between-individual acoustic variation in pant hoots.

We conclude with two cautionary notes. First, our analyses are restricted to a limited sample of individuals, and whether our results can be generalized to a larger population remains an open empirical question. Second, it is important to note that although the existence of significant interindividual acoustic variation is a necessary condition for individual recognition, it is not in itself sufficient. The extent to which interindividual acoustic variability is perceptually salient and therefore biologically meaningful is presently unclear. Psychophysical (Zoloth *et al.*, 1979) or field playback (Mitani, 1987) studies that empirically evaluate the subjects' perception of calls will be required to investigate this problem.

ACKNOWLEDGMENTS

Fieldwork was sponsored by the Tanzania Commission for Science and Technology, the Serengeti Wildlife Research Institute, and the Tanzanian National Parks. We thank E. Massawe, A. Seki, H. Hayaki, T. Nishida, R. Purcell, S. Uehara, and the staffs of the Mahale Mountains National Park and Mahale Mountains Wildlife Research Centre for logistic support. We are especially indebted to M. Bunengwa, H. Bunengwa, M. Hamai, M. Hawazi, R. Hawazi, R. Kitopeni, H. Hayaki, T. Nishida, and S. Uehara for field assistance and J. Pepper, D. Rendall, C. Sims-Parr, A. B. Sorin, H. Wiley, and three anonymous reviewers for comments on the manuscript and discussion. Research was supported by a NSF Presidential Faculty Fellows Award to Mitani and by grants from the NSF (BNS-9021682), the Harry Frank Guggenheim Foundation, and the National Geographic Society to Mitani and from the Japanese Ministry of Education, Science, and Culture to Professor T. Nishida.

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