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Species and Sex Differences in the Screams of Chimpanzees and Bonobos

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We examined screams of chimpanzees and bonobos to investigate interspecific and intraspecific variability in call structure. Measurement of 11 acoustic features of screams revealed differences between and within species. One-way analyses of variance and discriminant function analyses show that the calls of chimpanzees and bonobos differ primarily in spectral characteristics. Spectral features also account for acoustic differences between the sexes. These acoustic variations may be attributable to differences in body size and social dispersion between the two species and sexes. The effectiveness with which an acoustic feature could be used to discriminate the two species and female bonobos from male bonobos is negatively associated with its relative variability. These data are consistent with the hypothesis that optimal signals for group identification vary little within groups but differ widely between groups.

KEY WORDS: chimpanzees; bonobos; vocalizations.

INTRODUCTION

Recent research has revealed marked acoustic variability in the calls of nonhuman primates. Interspecific variability in call structure is employed increasingly to investigate problems in primate taxonomy and systematics (Struhsaker, 1970; Marshall and Marshall, 1976; Hodun *et al.*, 1981; Oates and Trocco, 1983; Macedonia and Taylor, 1985; Snowdon *et al.*, 1986; Mitani, 1987; Gautier, 1988; Zimmerman *et al.*, 1988). In addition, detailed examinations of intraspecific variability in vocalizations routinely show the important influences of age (Green, 1981; Seyfarth and Cheney, 1986;

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Gouzoules and Gouzoules, 1989; Inoue, 1988; Hohmann and Vogel, 1991; Elowson *et al.*, 1992) and sex (Marler and Hobbett, 1975; Snowdon and Cleveland, 1980; Green, 1981; Haimoff, 1984) on the acoustic morphology of calls.

Despite considerable evidence that calls differ within and between primate species, it is unclear why specific acoustic attributes are used to differentiate species and individuals. Traditional ethological studies emphasize the relative roles that acoustic differentiation and variability play in species discrimination. One hypothesis considers the discrimination task within the context of a community of multiple callers and proposes that those acoustic characteristics that differ significantly among species will provide the most reliable cues in specific recognition (Marler, 1960; Emlen, 1972; Dabelsteen and Pedersen, 1985; Nelson, 1989). In contrast, an alternate hypothesis suggests that individuals may use acoustic features that differ little within species to discriminate conspecific calls from those of heterospecifics (Marler, 1960; Falls, 1963; Emlen, 1972). Additional research combines the findings of species-recognition studies by predicting that individually distinctive signals should vary little within-individuals but differ markedly among individuals (Falls, 1982; Beecher and Stoddard, 1990).

Chimpanzees *(Pan troglodytes)* and bonobos *(Pan paniscus)* differ in their sexual behavior, feeding ecology, grouping patterns, and intergroup interactions (Kano, 1992), as well as in body size, tissue composition, and blood groups (Susman, 1984). Moreover, long-term research reveals important behavioral differences among animals living within the same population (Goodall, 1986). Despite these variations in behavior and morphology, few data (deWaal, 1988) exist regarding the degree to which the vocal repertoires of chimpanzees and bonobos differ between and within species. Here we address this problem by investigating acoustic variation in the screams of chimpanzees and bonobos. Specifically, we ask three questions. First, do calls differ between species and the sexes? Second, what is the acoustic basis of the observed species and sex differences? Third, how do acoustic differentiation and variability affect the discrimination process?

METHODS

Study Site and Subjects

We made tape recordings of chimpanzees and bonobos at the Mahale Mountains National Park, Tanzania, and the Scientific Reserve of the Luo, Zaire, respectively. Both areas have been the sites of long-term field investigations of chimpanzee and bonobo behavior (Nishida, 1990; Kano, 1992). We tape recorded calls from members of the M unit group or community at Mahale (Nishida, 1990) and from two unit groups of bonobos: E1 and P (Idani, 1990; Kano, 1992).

The Call

Chimpanzees and bonobos utter loud, distinctive screams in the context of aggression and social excitement (Marler and Tenaza, 1977; Goodall, 1986). Screams are typically emitted in bouts consisting of several calls (Fig. 1). Previous studies suggest that individuals of each species produce acoustically distinct screams in different behavioral contexts (Goodall, 1986; deWaal, 1988), but quantitative analyses have not been performed to validate the existence of these acoustic variants. Our sample of calls revealed considerable heterogeneity in the acoustic morphology of some screams given within the same bout (Fig. 1a). Other bouts comprised acoustically homogenous elements (Fig. 1c). Heterogeneity of screams within a single bout, coupled with the small samples of bouts recorded from each individual, precluded controlling for potential acoustic variation due to differing contexts of emission and caller identity.

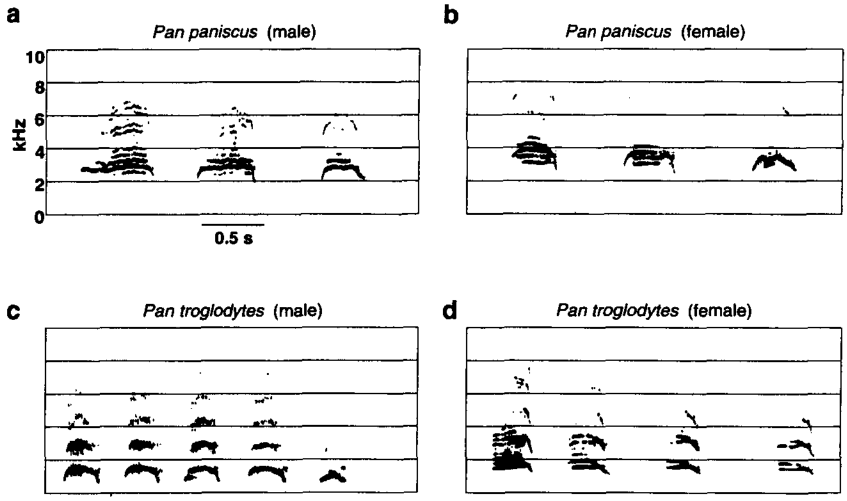

Fig. 1. Audiospectrogram of screams produced by bonobos and chimpanzees. Representative calls of both sexes are illustrated. Spectrograms via Sound Edit Pro sound analysis software. Analysis range, 11 kHz. Frequency resolution, 86 Hz.

Sample of Calls

We used screams from 26 bonobos and 29 chimpanzees in the following analyses. We analyzed only calls from adult individuals. Individuals of both species reach adulthood at approximately 15 years (Goodall, 1986; Kano, 1992); we included subjects whose known or estimated age exceeded this figure in the sample. Sixteen males and 10 females constitute the bonobo sample, while the chimpanzee sample contains 11 males and 18 females.

Calls emitted within the same bout cannot be regarded as independent given their observed acoustic homogeneity. Accordingly, we chose only one call from each bout of screaming for analysis. Our qualitative inspection of calls revealed no consistent and predictable differences in the acoustic structure of screams as a function of their location within a bout, and we selected calls via a random numbers table. This procedure ensured that calls from the start, middle, and end of bouts are equally represented in the entire sample ($\chi^2 = 2.33$, 2 df, $p > 0.10$). The number of calls analyzed from each bonobo ranged from 1 to 14 (mean = 3.6, SD = 3.4); individual chimpanzees contributed 1–9 exemplars (mean = 2.4, SD = 2.2). Within each species, the average number of calls contributed by males and females did not differ (chimpanzee females mean = 2.5, SD = 2.0; chimpanzee males mean = 3.1, SD = 2.7; bonobo females mean = 2.4, SD = 1.5; bonobo males mean = 4.4, SD = 3.9; Mann–Whitney *U* tests, $p > 0.25$ for both comparisons).

Field Methods

Between December 1989 and June 1990 and between June and August 1992, Mitani recorded vocalizations at Mahale (Mitani *et al.*, 1992; Mitani and Nishida, 1993; Mitani and Brandt, 1994). Mitani also tape recorded bonobos between March and June 1991. He made all recordings of chimpanzees while following them in their natural habitat. He recorded bonobos primarily around two provisioning stations (Kano, 1992). Tapes were recorded with Sony TC-D5M and WM-D6C recorders and Sennheiser ME 80 and ME 88 microphones.

Acoustic Analyses

We examined inter- and intraspecific acoustic variations in screams via 486 microcomputers and a digital signal processing program designed for the analysis of animal vocalizations (Engineering Design, 1992). We sampled screams at 40,000 points/sec, yielding an effective analysis bandwidth of 16 kHz.

Screams given by both species consist of a set of frequencies that appear to be harmonically related (Fig. 1). We refer to these as frequency bands in the absence of precise information regarding the manner in which animals produce calls. We made acoustic measurements on spectrograms created by 512-point Fourier transforms (time resolution, 13 msec; frequency resolution, 78 Hz). We selected the single lowest-frequency band that reached the highest amplitude for analysis from each scream. We measured 11 acoustic features of these bands. Initially, we measured five features: duration, starting frequency, ending frequency, minimum frequency, and maximum frequency. We calculated three derived acoustic variables based on these original five acoustic measures: frequency range = maximum frequency - minimum frequency; position of minimum frequency = time of minimum frequency/duration; and position of maximum frequency = time of maximum frequency/duration.

We included three additional variables, bandwidth, the number of bands, and average frequency in our analyses. We computed bandwidths by conducting a 1024-point Fourier transform over the midpoint of each signal (frequency resolution, 39 Hz). We assigned the lowest-frequency band from the resulting amplitude spectrum a value of 0 dB, and defined bandwidths as the range of frequencies spanned between these reference values and the highest frequency bands within -12 dB of the lowest-frequency bands. We ascertained the number of frequency bands by counting the number of distinct energy peaks spanned by our measure of bandwidth.

We computed average frequencies after performing a series of measurements across each scream. We attempted to base our calculations on a set of nonoverlapping time intervals that yielded acceptable frequency resolutions. Our measures of call duration show that bonobos emit screams between 229 and 771 msec (95% confidence interval), while screams of chimpanzees typically span 180–723 msec. As a result, we averaged 10 frequency values computed by performing 10 successive 1024-point Fourier transforms over the length of each signal (frequency resolution, 39 Hz). We made the first measurement at the start of the signal, with successive measurements made at intervals equal to 0.105 (≈1/10) of the duration of the element. Previous analyses indicated that use of an interval equal to one-tenth of calls typically yielded spurious frequency measures of the terminal portions of the longest elements due to low amplitudes at those points (Mitani and Brandt, 1994). Accordingly, we employed an interval marginally longer than one-tenth of the signal.

Statistical Methods

We performed two analyses to investigate inter- and intraspecific variability in the screams of chimpanzees and bonobos. First, we conducted nonparametric univariate statistical analyses using the 11 original acoustic variables. To correct for the increased probability of making type I error in these 11 statistical comparisons, we adjusted our criterion of significance to 0.005 (Sokal and Rohlf, 1981). Second, we conducted discriminant analyses to investigate within- and between-species acoustic variability in a multivariate fashion. Before preceding with these analyses, we used principal components analyses (PCA) to reduce the original set of 11 acoustic variables to a smaller set of uncorrelated variables (Dunteman, 1989). We conducted one PCA using the entire data set to examine interspecific variation in screams. We computed two additional PCAs via measured variables for bonobos and chimpanzees separately to investigate intraspecific sex differences. For subsequent discriminant analyses, we retained those principal component scores whose eigenvalues (λ) exceed 0.10 and differentiated species or the sexes in an analysis of variance at $p < 0.05$ (Jolliffe, 1986). We used discriminant functions to classify calls according to species and sex. We withheld calls from the Mahale chimpanzees in 1992 from calculations of discriminant functions and used them to conduct cross-validation analyses of the species and chimpanzee sex-difference classificatory results (Klecka, 1980). We subdivided the bonobo sample by randomly selecting half of the calls to generate discriminant functions and retaining the other half for cross-validation. We employed the canonical loadings of discriminant functions to identify those principal components and acoustic variables that play the most important roles in differentiating the two species and sexes.

Results of discriminant analyses revealed that one species or sex was correctly assigned consistently more often than the other. To examine whether the relative variability of acoustic features affected the discrimination task, we computed multivariate coefficients of variation (mcv) for the acoustic variables that were used to generate the classification functions and employed an extension of Levene's mean ratio test to compare mcv's between members of the two species and sexes (van Valen, 1978). Finally, we used each acoustic variable singly in a discriminant analysis to estimate its effectiveness in classifying screams. We compared classification success rates for acoustic variables with their coefficients of variation to assess whether a feature's relative variability affectes its ability to differentiate species and the sexes. We performed all analyses using Systat statistical software for the MacIntosh, Version 5.2 (Wilkinson *et al.*, 1992).

Table I. Comparison of Screams Produced by Chimpanzees and Bonobos[a]

(a)

Acoustic variable	Chimpanzees	Bonobos	% correct
Start frequency (Hz)*	956 ± 30 (0.28)	2192 ± 86 (0.38)	88
End frequency (Hz)*	798 ± 27 (0.29)	2057 ± 63 (0.30)	88
Minimum frequency (Hz)*	758 ± 23 (0.27)	1898 ± 77 (0.39)	87
Maximum frequency (Hz)*	1757 ± 37 (0.18)	3315 ± 52 (0.15)	95
Average frequency (Hz)*	1275 ± 24 (0.17)	2846 ± 57 (0.19)	94
Frequency range (Hz)*	998 ± 33 (0.29)	1416 ± 67 (0.46)	67
Bandwidth (Hz)*	2897 ± 184 (0.56)	2027 ± 187 (0.89)	55
Number of bands*	3.19 ± 0.17 (0.46)	1.75 ± 0.09 (0.49)	76
Duration (msec)	402 ± 27 (0.59)	501 ± 28 (0.54)	56
Position of minimum frequency	0.729 ± 0.048 (0.59)	0.679 ± 0.048 (0.69)	51
Position of maximum frequency	0.445 ± 0.025 (0.49)	0.517 ± 0.030 (0.57)	56

(b)

Acoustic variable	Principal component		
	1	2	4
Average frequency	0.97	-0.02	0.18
End frequency	0.96	0.09	0.06
Minimum frequency	0.94	0.31	-0.03
Maximum frequency	0.92	-0.20	0.31
Start frequency	0.91	0.37	0.01
Number of bands	-0.59	0.51	0.38
Frequency range	0.12	-0.77	0.53
Position of minimum frequency	0.10	0.61	-0.13
Duration	0.25	0.04	-0.36
Postion of maximum frequency	0.08	-0.32	-0.35
Bandwidth	-0.37	0.42	0.61

(c)

Actual membership	Predicted membership		% correct assignments
	Bonobos	Chimpanzees	
Bonobos	45	2	96
Chimpanzees	0	40	100
Total			98

(d)

Actual membership	Predicted membership		% correct assignments
	Bonobos	Chimpanzees	
Bonobos	43	4	92
Chimpanzees	0	38	100
Total			95

Table I. Continued

(e)

Principal component	Canonical loading
1	0.86
2	-0.11
4	0.05

[a](a) Acoustic differences and variability between the calls of chimpanzees and bonobos. Means ± SE and coefficients of variation (in parentheses) for 11 acoustic variables are shown. Asterisks denote those variables that differed between species at $P < 0.005$. "% correct" indicates the accuracy with which each variable classified calls according to species in a discriminant analysis. (b) Principal component loadings. Only those components that significantly discriminated between species are shown. (c) Classification results of a discriminant function analysis. (d) Cross-validation results of the discriminant function using subsamples of screams of chimpanzees and bonobos. (e) Canonical loadings of principal components based on a discriminant analysis.

RESULTS

Species Differences

Univariate statistical analyses revealed differences between the screams of chimpanzees and bonobos in all eight spectral features (Table Ia; Mann-Whitney U tests, $p < 0.005$ for all comparisons). Chimpanzees gave calls that are lower in pitch than those uttered by bonobos. The three temporal measures—duration and the positions of minimum and maximum frequencies—do not differ significantly between species ($p > 0.005$ for all three comparisons).

A principal components analysis produced 11 statistically independent components. The first seven components, with eigenvalues exceeding 0.10, account for nearly all of the variation in the data set (>99%). One-way ANOVAs revealed that principal components 1, 2, and 4 differ between the two species ($p < 0.05$ for all three comparisons). Component 1 represents the overall spectral structure of calls; average frequencies along with the four nonderived frequency variables are strongly correlated with this component (Table Ib). Frequency range contributes maximally to component 2, while bandwidth is highly correlated with component 4 (Table Ib).

The three principal components that differ between species produce a discriminant function that explains a significant amount of the variation between screams produced by chimpanzees and bonobos (Wilks' λ $F = 99.32$, df = 3,83, $p < 0.001$). This function was successful in classifying 98% of the sample of screams by species (Table Ic). We used subsamples of chimpanzee and bonobo screams to cross-validate the species classification results. The discriminant function created from the original data set correctly classified 95% of these calls (Table Id). Inspection of the canonical loadings of the discriminant function reveals that component 1—a measure of spectral structure—is the most important variable used to discriminate species (Table Ie). The calls of chimpanzees are assigned correctly slightly more often than those of bonobos, and this higher success rate is associated with low relative variation in those acoustic features used to generate the classification function; chimpanzees (mcv = 21.57) show less variability than bonobos do (mcv = 26.22; Levene's mean ratio test, $t = 1.84$, $n_1 = 78$, $n_2 = 94$, $p = 0.06$).

If an acoustic feature's ability to differentiate species were due in part to its low relative variability, then we would expect its discriminant-function classificatory success rate to be negatively correlated with its coefficient of variation. Table Ia shows classificatory accuracies and coefficients of variation for each of the 11 acoustic variables and reveals that the two measures are negatively related within each species (chimpanzees Spearman's $r = -0.91$, $p < 0.001$, $n = 11$; bonobos Spearman's $r = -0.98$, $p < 0.001$, $n = 11$).

Sex Differences: Chimpanzees

The screams of female and male chimpanzees differ significantly in only two spectral features: start frequency and end frequency (Table IIa; Mann-Whitney U tests, $p < 0.005$ for both comparisons). The calls of males show lower frequency values than those of females. Principal components analysis resulted in eight components with variances exceeding our predetermined cutoff ($\lambda > 0.10$). One-way ANOVAs indicate that four of these components—1, 2, 7, and 8—differ between the sexes ($p < 0.05$ for all four comparisons). The five nonderived frequency variables are highly correlated with the first principal component, while component 2 is related to three additional spectral features: bandwidth, number of bands, and frequency range (Table IIb). Two frequency variables—start frequency and average frequency—contribute strongly to the formation of components 7 and 8, respectively (Table IIb).

A discriminant function using the scores of the four principal components generated a function that significantly differentiated the sexes (Wilks' λ $F = 5.40$, df = 1,38, $p < 0.03$). The resulting discriminant function correctly classified 80% of the screams by sex (Table IIc), a significantly greater proportion than the 50% expected on the basis of chance (χ^2 test, 1 df, $p < 0.01$). The set of calls recorded in 1992 provided a means to

Table II. Comparison of Screams Produced by Female and Male Chimpanzees[a]

(a)

Acoustic variable	Females	Males	% correct
Start frequency (Hz)*	1036 ± 32 (0.21)	841 ± 52 (0.35)	64
End frequency (Hz)*	859 ± 35 (0.27)	710 ± 37 (0.29)	62
Minimum frequency (Hz)	811 ± 28 (0.23)	682 ± 37 (0.30)	62
Maximum frequency (Hz)	1771 ± 48 (0.18)	1737 ± 58 (0.19)	53
Average frequency (Hz)	1285 ± 32 (0.17)	1259 ± 37 (0.17)	51
Frequency range (Hz)	959 ± 38.4 (0.27)	1055 ± 57 (0.30)	54
Bandwidth (Hz)	2881 ± 242 (0.57)	2921 ± 289 (0.56)	54
Number of bands	3.22 ± 0.21 (0.45)	3.16 ± 0.27 (0.48)	47
Duration (msec)	416 ± 37 (0.61)	380 ± 37 (0.55)	50
Position of minimum frequency	0.761 ± 0.059 (0.53)	0.683 ± 0.082 (0.68)	58
Position of maximum frequency	0.487 ± 0.034 (0.47)	0.384 ± 0.033 (0.49)	63

(b)

Acoustic variable	Principal component			
	1	2	7	8
Minimum frequency	0.91	0.27	0.06	0.07
Average frequency	0.90	−0.16	0.16	−0.21
End frequency	0.88	0.22	0.08	0.12
Start frequency	0.76	0.41	−0.33	−0.06
Maximum frequency	0.75	−0.41	−0.02	0.10
Number of bands	−0.32	0.70	0.01	0.13
Bandwidth	−0.15	0.68	0.04	−0.12
Frequency range	0.19	−0.64	−0.07	0.06
Position of minimum frequency	0.18	0.28	0.15	0.07
Duration	0.44	0.24	−0.01	−0.03
Position of maximum frequency	0.25	0.03	−0.02	0.01

(c)

Actual membership	Predicted membership		% correct assignments
	Females	Males	
Females	20	6	77
Males	2	12	86
Total			80

(d)

Actual membership	Predicted membership		% correct assignments
	Females	Males	
Females	11	9	55
Males	3	15	83
Total			68

Table II. Continued

(e)

Principal component	Canonical loading
1	0.57
2	0.33
7	−0.58
8	0.35

[a](a) Acoustic differences and variability between the calls of females and males. Means ± SE and coefficients of variation (in parentheses) for 11 acoustic variables are shown. Asterisks denote those variables that differed between sexes at $P < 0.005$. "% correct" indicates the accuracy with which each variable classified calls according to sex in a discriminant analysis. (b) Principal component loadings. Only those components that significantly discriminated between sexes are shown. (c) Classification results of a discriminant function analysis. (d) Cross-validation results of the discriminant function using screams recorded in 1992. (e) Canonical loadings of principal components based on a discriminant analysis.

cross-validate the classification results of the discriminant function. The original function correctly classified 68% of these screams (Table IId), significantly more than that expected on the basis of random assignment (χ^2 test, 1 df, $p < 0.05$). Table IIe shows the canonical loadings of the discriminant function and reveals that components 1 and 7, two measures of spectral structure, are the most important variables to differentiate the screams produced by female and male chimpanzees.

A closer inspection of the cross-validation results indicated that the screams of male chimpanzees were correctly assigned more frequently than those of females (Table IId); the screams of females were attributed to males as often as they were to themselves. The sample of females used to produce the discriminant function was not identical to that employed in the cross-validation analysis, and the low classification success rate for females may have been due to a relatively high turnover of individuals contributing to samples. Forty-two percent of the females whose calls were used in the cross-validation analysis also contributed to the 1990 sample that generated the discriminant function. A similar proportion of shared individuals (44%) was employed to achieve the much higher cross-validation success rate for males, however. Alternatively, the low classification success rate for females may have been associated with relatively low variability in those acoustic features that were used to generate the discriminant function. A comparison of the multivariate coefficients of variation of those frequency measures that correlated strongly with principal components 1 and 7 did not support this prediction; males (mcv = 22.60) are more variable than females are (mcv = 19.99; Levene's test, $t = 1.80$, $n_1 = 32$, $n_2 = 46$, $0.10 < p < 0.05$).

Relative variability did not appear to affect an acoustic feature's ability to discriminate the sexes. For each sex, the classificatory accuracy of each variable is not correlated with its coefficient of variation (Table IIa; females Spearman's $r = -0.13$, $p > 0.50$, $n = 11$; males Spearman's $r = 0.26$, $p > 0.20$, $n = 11$).

Sex Differences: Bonobos

The screams of female and male bonobos showed significant acoustic differences in two frequency measures: minimum and maximum (Table IIIa; Mann–Whitney U tests, $p < 0.005$ for both comparisons). Both measures show higher values for females than males. A PCA resulted in seven components whose eigenvalues exceed 0.10 (Table IIIb). A series of one-way ANOVAs indicate that components 1 and 5 differ between the sexes ($p < 0.05$ for both comparisons). The first component reflects the spectral structure of calls; four frequency variables are strongly correlated with this component (Table IIIb). A single measure of the temporal structure of calls, the position of maximum frequency, is the primary variable contributing to component 5 (Table IIIb).

A discriminant function generated via the scores of the two principal components is successful in classifying 68% of screams by sex (Table IIIc); this classification success rate is significantly higher than the 50% expected on the basis of random assignment (χ^2 test, 1 df, $p < 0.02$). Cross-validation of the discriminant function using a subsample of screams resulted in a classification success rate of 72%, a significantly greater proportion than that expected by chance (Table IIId, χ^2 test, 1 df, $p < 0.05$). Principal component 1, comprised principally of four measures reflecting the spectral structure of calls, is the single most important variable to discriminate screams produced by female and male bonobos (Table IIIe).

Screams of female bonobos were correctly classified more often than those of males were (Table IIId). The lower classification success rate for males could not be attributed to a greater turnover of individuals between the modeling and the validation samples. Sixty-four percent of the males in the validation sample contributed to the modeling set used to generate the discriminant function. In contrast, a lower proportion of shared individuals between samples (43%) was employed to obtain the higher cross-validation success rate for females. While sampling error did not affect the accuracy with which calls are assigned to males and females, correct assignment appears to be inversely related to variation in the acoustic fea-

Table III. Comparison of Screams Produced by Female and Male Bonobos[a]

(a)

Acoustic variable	Females	Males	% correct
Start frequency (Hz)	2591 ± 95 (0.18)	2055 ± 106 (0.43)	60
End frequency (Hz)	2355 ± 113 (0.23)	1955 ± 72 (0.31)	61
Minimum frequency (Hz)*	2301 ± 104 (0.22)	1760 ± 92 (0.44)	57
Maximum frequency (Hz)*	3576 ± 96 (0.13)	3225 ± 57 (0.15)	63
Average frequency (Hz)	3113 ± 114 (0.18)	2755 ± 62 (0.19)	56
Frequency range (Hz)	1274 ± 106 (0.41)	1465 ± 81 (0.46)	47
Bandwidth (Hz)	1994 ± 376 (0.92)	2038 ± 217 (0.89)	49
Number of bands	1.79 ± 0.18 (0.49)	1.73 ± 0.10 (0.49)	49
Duration (msec)	428 ± 39 (0.45)	526 ± 35 (0.55)	56
Position of minimum frequency	0.875 ± 0.069 (0.39)	0.612 ± 0.058 (0.79)	52
Position of maximum frequency	0.532 ± 0.059 (0.54)	0.512 ± 0.036 (0.58)	51

(b)

Acoustic variable	Principal component	
	1	5
Minimum frequency	0.98	0.02
Start frequency	0.95	0.05
End frequency	0.90	0.01
Average frequency	0.90	0.01
Frequency range	−0.65	−0.02
Maximum frequency	0.63	−0.01
Number of bands	0.04	0.04
Duration	0.06	−0.38
Bandwidth	−0.08	−0.11
Position of minimum frequency	0.46	0.26
Position of maximum frequency	−0.27	0.73

(c)

Actual membership	Predicted membership		% correct assignments
	Females	Males	
Females	9	3	75
Males	12	23	66
Total			68

(d)

Actual membership	Predicted membership		% correct assignments
	Females	Males	
Females	11	1	92
Males	12	23	66
Total			72

Table III. Continued

(e)	
Principal component	Canonical loading
1	0.78
5	0.51

[a](a) Acoustic differences and variability between the calls of females and males. Means ± SE and coefficients of variation (in parentheses) for 11 acoustic variables are shown. Asterisks denote those variables that differed between sexes at $P < 0.005$. "% correct" indicates the accuracy with which each variable classified calls according to sex in a discriminant analysis. (b) Principal component loadings. Only those components that significantly discriminated between sexes are shown. (c) Classification results of a discriminant function analysis. (d) Cross-validation results of the discriminant function using a subsample of screams. (e) Canonical loadings of principal components based on a discriminant analysis.

tures used to generate the classificatory function. Males (mcv = 32.80) are significantly more variable in their frequency measures than females (mcv = 20.00; Levene's test, $t = 4.58$, $n_1 = 70$, $n_2 = 24$, $p << 0.001$).

Acoustic measures that differentiated the sexes show relatively low variability within both females and males; the discriminant function classification success rates of variables are negatively associated with their coefficients of variation (Table IIIa; females Spearman's $r = -0.78$, $p < 0.01$, $n = 11$; males Spearman's $r = -0.70$, $p < 0.05$, $n = 11$).

DISCUSSION

The preceding results indicate that the screams of bonobos and chimpanzees differ between species and members of the opposite sex. Five frequency variables—minimum frequency, maximum frequency, start frequency, end frequency, and average frequency—are the primary acoustic features that differentiated the screams of the two species. The calls given by chimpanzees—with relatively low frequency values—are readily distinguishable from those produced by bonobos. Spectral characteristics also provide the primary means to identify female screams versus male calls. The precise frequency variables contributing to sex differences in chimpanzees are not identical to those that differentiate the screams given by male and female bonobos. The calls of males could be discerned from those of females in both species, however, given their uniformly lower frequencies.

Anatomical and social factors may account for acoustic variability within and between species. First, acoustic variability may be related to differences in body size. Bonobos display neotenous characteristics especially in their craniofacial morphology (Cramer, 1977) and regions surrounding the basicranium (Laitman and Heimbuch, 1984). Consequently, they probably possess smaller vocal tracts than chimpanzees do. Likewise, males of both species are significantly larger than female conspecifics (Jungers and Susman, 1984; Uehara and Nishida, 1987). These size differences presumably give rise to related variations in laryngeal mechanisms, leading chimpanzees and males of both species to emit calls that are lower in frequency than those of bonobos and females, respectively (Inoue, 1988; Gouzoules and Gouzoules, 1990; Hauser 1993). Second, bonobos typically travel in more cohesive groups than chimpanzees do (Nishida and Hiraiwa-Hasegawa, 1987). Since higher frequency sounds attenuate more rapidly than those of lower frequencies (Wiley and Richards, 1978), the characteristic social dispersion of chimpanzees may have favored individuals that emit low-pitched screams for efficient transmission.

While anatomical and social factors may account for specific and sexual differences in screams, variations in body size possibly explain the observed distributions of frequency measures between and within species. Bonobos appear to be more sexually dimorphic in body size than chimpanzees are (Table IV), and this interspecific variation in dimorphism may account for the reported differences in frequency measures, with bonobos showing more variability (mcv's and Table Ia) and absolutely larger intersexual differences than chimpanzees do (Tables IIa and IIIa). In addition to interspecific differences in size dimorphism, intersexual differences in the distributions of weights exist as well (Table IV). Male chimpanzees adopt alternative mating tactics (Tutin, 1979), and disruptive or frequency-dependent selection may result in the greater variance in body size observed among males relative to females. Alternatively, sex differences in size variability may be due to intersexual differences in feeding competition. Irrespective of its causes, the observed pattern of variability leads us to predict that males will display greater relative variation in the frequency structures of their calls than females will. Results of the preceding analyses provide empirical support for this prediction in both species (mcv's and Tables IIa and IIIa).

Additional analyses are consistent with the hypothesis that an acoustic feature's effectiveness in discriminating the two species and sexes may have depended in part on its relative acoustic variability. An acoustic variable's ability to differentiate species, as revealed by discriminant function analysis, is inversely correlated with its coefficient of variation (Table Ia). A similar negative relationship between an acoustic feature's relative variability and its success rate in classifying the sexes exists among bonobos (Table IIIa). These data accord with the observation that chimpanzees show less acoustic variation in their frequency measures (mcv's and Table Ia) and a higher

Table IV. Body Weights and Sexual Dimorphism in Size of Chimpanzees and Bonobos[a]

Species	Body weight (kg) Females	Body weight (kg) Males	Dimorphism, Male/female	Source
Chimpanzee	35.2 ± 3.9 (8)	42.0 ± 5.4 (6)	1.19	Uehara and Nishida (1987)
Bonobo	33.2 ± 4.2 (6)	45.0 ± 8.4 (7)	1.36	Jungers and Susman (1984)

[a] Means ± SD with sample sizes in parentheses.

classification success rate than bonobos (Tables Ic and Id). In similar fashion, female bonobos are relatively acoustically invariant compared with males (mcv's and Table IIIa), and are the more easily discriminated sex (Tables IIIc and IIId). Although theory predicts and the preceding empirical examples support the hypothesis that ideal signals for group identification will vary little within each group and differ markedly between groups, our acoustic analyses suggest that the screams of chimpanzees may not be optimally designed for discriminating the sexes. Male chimpanzees are more readily classified according to sex (Tables IIc and IId), but show greater variability in the frequency structure of their calls than females do (mcv's and Table IIa). These results suggest that relatively invariant acoustic features are not used as a primary means to discriminate the sexes among chimpanzees; acoustic characteristics that vary widely between females and males are more likely to serve as reliable cues for sexual differentiation.

We conclude with two caveats. First, the biological significance of our findings is entirely dependent on the degree to which the perceptual processes of the subjects mimic the statistical discriminant classificatory procedure. The statistical technique that we employ assumes that screams are perceived and classified according to species and sex only after comparing them to generalized templates of calls. Results of experimental playbacks are consistent with the assumption that such stored representations exist for different species; behavioral responsiveness to calls appears to depend on the specific identity of the vocalizer (Mitani, 1987). Whether primates possess similar representations of the vocalizations uttered by females and males remains a question for future empirical research. Second, screams are probably individually distinctive (Marler and Hobbett, 1975; Mitani and Brandt, 1994), and nonhuman animals may employ this additional source of variability to classify calls with respect to species and sex. Analysis of variance using a larger sample of calls will provide the means to assess components of acoustic variability attributable to the species, sex, and individual identity of callers (Mitani and Brandt, 1994).

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