

RESEARCH ARTICLES

Sex Differences in Vocal Structure in a Callitrichid Primate, *Leontopithecus rosalia*

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Four types of calls (long calls, chirps, chucks, and trills) from Golden Lion Tamarins (*Leontopithecus rosalia*) were analyzed for sex differences in structure. Six or more acoustic variables were analyzed for each call type. One or more variables from each call category differed significantly between the sexes. In addition, discriminant function analyses were conducted on male vs. female data for each call type. Long calls, chirps, and chucks from males and females were quite discriminable, but trills were not. That these differences exist is surprising given that callitrichid primates are otherwise quite monomorphic in structure and behavior. Possible functions served by sex differences in call structure include group censusing or assessing the sex of transient individuals.

Key words: vocalizations, golden lion tamarins, acoustic variables

INTRODUCTION

In spite of the ubiquitous differences in the acoustic qualities of human male and female voices, surprisingly little work has addressed the topic of sex differences in nonhuman primate vocalizations. Sex differences in primate vocalizations occur in two ways. First, males and females may differ in the relative frequency of production of a vocal signal, including, as an extreme case, the complete absence of a call type from the repertoire of one sex. Second, there may be sex differences in the acoustic structure of vocal signals.

Sex differences in the relative frequency of call production is perhaps the most commonly reported dimorphic pattern. For example, Hohmann and Herzog [1985], studying lion-tailed macaques (*Macaca silenus*), reported that dominant males emit "loud calls" when separated from their troops. This call is not emitted by subordinate males nor by females in the same situation. Males and females do not differ in the frequency of production or in the structure of the other calls of their repertoire. Bornean gibbons (*Hylobates muelleri*) [Mitani 1985a,b,c] and orangutans (*Pongo pygmaeus*) [Mitani 1985d] also have sex-specific calls. Male orangutans emit "long calls" that apparently regulate territorial spacing; females do not use these calls. Male and female gibbons both participate in territory defense using different sex-specific calls in their duets [Mitani 1985a].

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Several primate species have calls that are not exclusive to one sex but which are emitted more often by one sex than the other. For example, McConnell and Snowdon [1986] report that, in simulated encounters among unfamiliar cotton-top tamarin (*Saguinus o. oedipus*) groups, females used more Normal Long Calls, but males used more F-chirps and F-trills. None of the call types was restricted to a single sex, and there were no sex differences in the acoustic structure of the calls.

Finally, there are a few reports of sex differences in acoustic morphology in primates. Robinson [1979] discovered four call types in titi monkeys (*Callicebus moloch*) that had significant sex differences in acoustic structure. In two of the four call types, females had a significantly higher dominant frequency at the midpoint of the call than did males. In the other two call types, females had a significantly lower dominant frequency at the midpoint than did males. Mitani [1986] reported that male Japanese macaques (*Macaca fuscata yakui*) had a lower fundamental frequency than females across most of their repertoire. Seyfarth et al. [1980] reported acoustic differences in the alarm calls of male and female vervet monkeys (*Cercopithecus aethiops*) to mammalian carnivores.

Most callitrichid species have large vocal repertoires, but a review of the Callitrichid literature from 1975 to 1987 revealed only two papers reporting sex differences in the acoustic morphology of their vocalizations. Heymann [1987] reported several sex differences in the long call of moustached tamarins (*Saguinus m. mystax*). Heymann's results are based on data taken from only two individuals (one male and one female), so it is possible that the differences represent individual variation rather than sex differences. Masataka [1987] reported that red-chested moustached tamarins (*Saguinus l. labiatus*) discriminate the sex of the caller on the basis of acoustical differences in the long calls of the animals. Subsequent analyses revealed that males have more syllables in their long calls and have shorter inter-syllable intervals than females.

McLanahan and Green [1977] characterized the vocal repertoire of the golden lion tamarin (*L. rosalia*) and placed 17 call types into five major categories. Although they did not evaluate sex differences in vocal structure, they showed that males trilled more often than females and that females emitted more nontonal calls than males.

Although nonreproductive anatomical and physiological sex differences are practically nonexistent in golden lion tamarins [e.g., Rosenberger & Coimbra-Filho, 1984], Hershkovitz [1977] reports that the medial ventral laryngeal sac is enlarged in males and reduced or absent in females. This difference in the vocal apparatus might influence some acoustic features of the vocalizations of these animals. Thus, the following study was conducted to determine whether sex differences exist in the morphology of golden lion tamarin vocalizations.

METHODS

Animals and Their Maintenance

The Callitrichid Research Center at the University of Nebraska at Omaha (UNO) consisted of 20 animals in six cages at the time of this study. Fifteen animals in three family groups were studied. Each group consisted of a breeding pair and their juvenile, subadult, or adult offspring. The family groups were housed in separate rooms in 2.0 × 2.0 × 2.0 m cages. Cages were arranged so that adjacent family groups were visually isolated, although acoustic and olfactory contact between groups was possible. French and Stribley [1985, 1987] provide additional details of maintenance and husbandry protocols.

Materials and Procedure

Vocal behavior was continuously recorded, using a Sennheiser ME-40 microphone, onto one channel of a Uher 4200 Report Monitor tape recorder at 19 cm/sec tape speed. Vocalizations were recorded while the researcher sat outside the cage in the room containing the focal group. A running commentary, indicating the identity of the vocalizer, and the behavioral context in which the call occurred (e.g., moving, grooming, or eating) was recorded by the observer on the other channel. Each family group was recorded for 24 minutes once per day, but never on consecutive days. Each was recorded nine times for a total of 3.6 hours. Thus, 10.8 hours of recordings comprised the sample vocal library.

Analysis

The calls were analyzed in two ways. First, a Voice Identification, Inc. Model 700 sound spectrograph was used to create sonograms. A narrow band (60 Hz) filter and a range of 0–12,500 Hz were employed. All measurements were taken from the fundamental frequency (F_0), using a clear metric ruler, and were accurate to within 200 Hz and 5 msec. Second, a Personal Acoustics Laboratory system [Davis 1986a,b] was used to digitize the recordings for subsequent measurement of peak frequency, low frequency, and duration. These measurements were accurate to within 100 Hz and 5 msec. One of us (JJB) was responsible for all measurements.

We measured vocalizations from four of the five vocal categories identified by McLanahan and Green [1977]. The categories were chuck, chirp, trill, and long call. Nontonal calls were not evaluated due to their rarity. The four calls chosen were all extremely common in the animals' repertoires. Exemplars of each category are displayed in Figure 1.

We measured at least six variables from the F_0 on each call. For chirps and chucks, these variables were Total Duration, Peak Frequency, Low Frequency, Sweep (= Peak Frequency - Low Frequency), Fall (= duration of falling part of call), Slope (= Sweep / Fall; i.e., how quickly the call went from its highest frequency to its lowest frequency), and Ratio (= Total Duration / Fall; i.e., the percentage of the call that is falling in frequency). For trills, we measured Total Duration, Peak Frequency, Low Frequency, and Sweep as defined above, as well as the Number of Elements and Mean Element Length. For long calls we measured Total Duration, Peak Frequency (= the highest frequency over the entire call), Low Frequency (= the lowest frequency over the entire call), Sweep, Slope, Number of Syllables, Number of Syllables Longer Than 100 msec, and Mean Syllable Length (see Table 1 for a listing of all the variables measured for each call type). These variables were chosen to conform with work done by other researchers [see, e.g., Masataka, 1988]. We analyzed these data with univariate ANOVAs and with discriminant function analyses, using SPSS-X, Version 3 [SPSS, Inc., 1988].

RESULTS

Approximately 2,400 calls, which were identifiable with regard to caller, were recorded. To analyze the calls for sex differences in acoustic morphology, we obtained a random sample of 19 or 20 calls of each type from each sex, with the only criterion for selection being that each animal was represented approximately equally. Because our sample contained nine males (all adult) and six females (four adults, two juveniles 5 months old), there was an average of 2.2 calls per male and 3.3 calls per female in each vocal category. No male contributed fewer than two or more than three calls to any category, and no female contributed fewer than three or more than four to any category. The means, standard deviations, and coeffi-

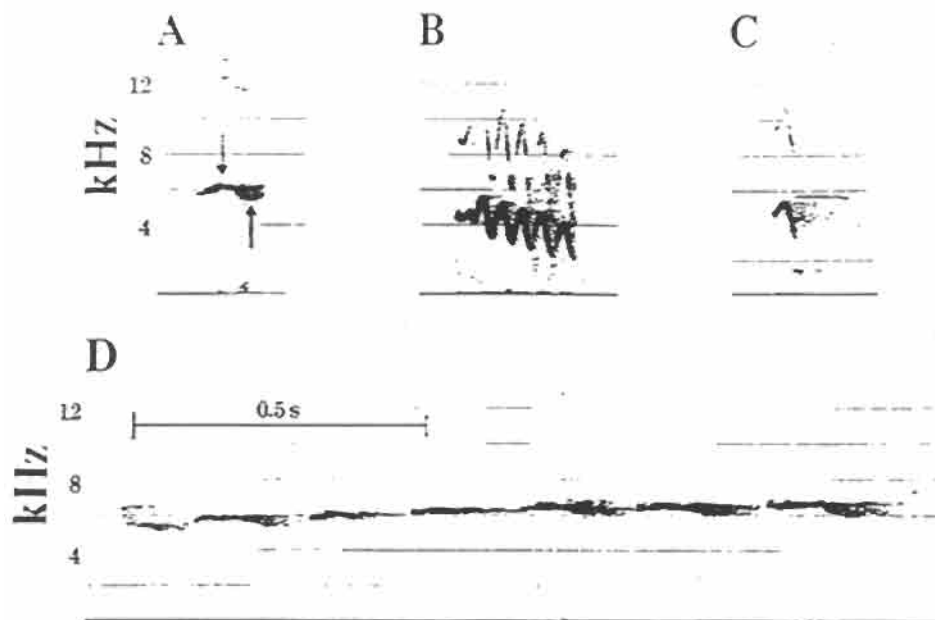


Fig. 1. Sonograms of the four types of *Leontopithecus rosalia* vocalizations that were analyzed in this study. A) Chirp. The variable Fall is the duration from Peak Frequency (top arrow) to Low Frequency (bottom arrow). Sweep is the frequency change between these two points. See text for further definition. (B) Trill. (C) Chuck. D) Long Call.

coefficients of variation of the acoustic variables for the four call categories for both sexes are provided in Table I.

Sex differences in each of the variables were tested using univariate ANOVAs. The results are summarized in Table I. In brief, female chucks had a significantly larger Ratio (of fall to total duration) than did male chucks. Female chirps had a shorter Total Duration and shorter Falls than did male chirps. Female trills had a higher Peak Frequency and a greater Sweep than did male trills. Finally, female long calls had a higher Peak Frequency and a higher Low Frequency than did male long calls.

Discriminant function analyses were computed to determine whether tamarin calls contained sufficient acoustical variation to make accurate statistical predictions as to the sex of the caller. For each call, one discriminant function was computed, using all but one of the variables measured for each call. Sweep was discarded due to collinearity in each case.

For every discriminant function, a chi-square test for sphericity was calculated to determine whether, based on the canonical correlation, any significant relationships existed to be extracted. The canonical correlations and sphericity chi-square values (with degrees of freedom and *P* values) are presented in the first four columns in Table II. The discriminant functions that were generated were then used to classify the calls. The results of the reclassification, and its chi-square value and probability, are presented in the last columns in Table II.

For all calls except trills, the reclassification was significantly better than could be expected by chance. That is, the discriminant function did well in predicting the sex of the caller based only on the acoustic parameters of the call.

TABLE I. Summary of Means and Standard Deviations for Four Call Types in *Leontopithecus rosalia*

Call Variable	Male			Female			P
	Mean	SD	COV ^a	Mean	SD	COV	
Chirp	n = 21			n = 20			
Total duration (ms)	43.90	13.89	31.64	30.00	12.67	42.23	< .005
Peak frequency (kHz)	6.35	1.04	16.33	6.45	0.74	11.47	NS
Low frequency (kHz)	5.25	0.67	12.76	5.25	0.78	14.86	NS
Sweep (kHz)	1.10	0.74	69.09	1.20	0.57	47.50	NS
Fall (ms)	37.90	12.56	33.13	25.90	9.10	35.14	< .005
Slope (kHz.ms)	0.04	0.04	100.00	0.05	0.03	60.00	NS
Ratio	1.27	0.51	40.16	1.19	0.47	39.50	NS
Chuck	n = 21			n = 19			
Total duration (ms)	36.40	14.11	38.76	37.60	18.91	50.29	NS
Peak frequency (kHz)	6.51	1.11	17.06	6.05	1.06	17.52	NS
Low frequency (kHz)	4.77	0.77	16.36	4.66	1.01	21.67	NS
Sweep (kHz)	1.73	0.85	49.13	1.38	0.50	36.23	NS
Fall (ms)	29.10	13.81	47.42	23.30	13.65	58.58	NS
Slope (kHz.ms)	0.07	0.14	57.14	0.07	0.03	42.86	NS
Ratio	1.31	0.53	26.73	1.76	0.84	47.73	< .05
Trill	n = 21			n = 20			
Total duration (ms)	177.50	59.51	33.49	227.20	97.52	42.92	NS
Peak frequency (kHz)	5.77	1.14	20.10	6.97	2.12	30.42	< .05
Low frequency (kHz)	3.06	1.14	37.91	3.69	1.29	34.96	NS
Sweep (kHz)	2.70	0.71	26.67	3.29	1.08	32.83	< .05
Mean element length (ms)	35.50	9.57	24.66	45.60	19.29	42.50	NS
Number of elements	4.50	1.56	39.17	5.20	1.99	38.27	NS
Long call	n = 20			n = 20			
Total duration (ms)	2.05	0.53	25.85	2.01	0.85	42.29	NS
Peak frequency (kHz)	7.03	0.71	10.35	7.79	1.21	15.53	< .05
Low frequency (kHz)	4.32	0.59	18.52	5.28	0.53	10.04	< .001
Sweep (kHz)	2.71	1.06	39.11	2.51	1.02	40.64	NS
Slope (kHz.s)	1.31	0.25	19.05	1.30	0.34	26.15	NS
Mean syllable length (ms)	195.00	55.54	18.39	196.50	46.90	23.87	NS
Number of syllables	10.50	3.80	30.56	10.45	4.52	43.25	NS
Number of syllables > 100 ms	5.30	1.73	52.12	3.95	1.91	48.35	NS

^aCOV, coefficient of variation [= 100 × (SD/Mean)].

Because Sweep had a significant univariate *F*-value for Trills, we decided not to drop it from the discriminant analysis to decrease colinearity. Instead, Mean Syllable Length (MSL) and Low Frequency (LF) were dropped. The results for dropping only Sweep and for dropping MSL and LF are reported under the Trill heading in Table II. In neither situation (dropping only Sweep, or dropping MSL and LF instead) was the reclassification significant.

DISCUSSION

We found statistically significant univariate sex differences in vocal variables for each of the four call types. Moreover, for chirps, chucks, and long calls, combinations of these variables proved to be reliable predictors of the sex of the vocalizing animal. Although the acoustic variables of Peak Frequency and Sweep differed significantly between males and females with regards to trills, the resulting

TABLE II. Summary Table of Significant Canonical Correlations and Chi-Square Values for Discriminant Functions of Call Types Using all Variables (Except Those Noted Beneath Each Call) in *Leontopithecus rosalia* (n's as in Table I)*

Call Variable(s)	CC	χ^2	df	P	Reclassification							
					MM	MF	FM	FF	χ^2	Percent	P	
Chuck												
(without Sweep)	.56	12.66	6	.05	14	6	3	16	9.55	77	<.005	
Chirp												
(without Sweep)	.53	11.65	6	.07	12	8	4	16	5.10	70	<.05	
Long call												
(without Sweep)	.63	17.36	7	.02	16	4	3	17	14.43	83	<.0005	
Trill												
(without Sweep)	.40	6.00	5	.30	16	4	11	9	2.85	63	NS	
Trill												
(w/out MEL, LF)	.39	5.53	4	.21	15	5	9	11	2.60	65	NS	

*CC, canonical correlation coefficient; MM, males classified as males; MF, males classified as females; FM, females classified as males; FF, females classified as females; Percent, percent correct reclassification.

*All chi-square values for reclassification data use Yates' correction for 1 degree of freedom [Hayes, 1981].

discriminant analyses did not reveal a significant discriminant function for classifying trill vocalizations.

It is theoretically possible that the differences in ages of the females (four adults, two juveniles) may potentially confound the reported sex differences. This seems unlikely, however. Lieblisch et al. [1980] reported no clear trend in the relationship of frequency with age in squirrel monkeys (*Saimiri sciureus*). In callitrichids, Snowdon [1987] reported that in pygmy marmosets (*Cebuella pygmaea*) trills given at very young ages (3 weeks) were much higher in pitch than adult trills but had reached adult levels by 5 weeks of age. There is circumstantial evidence, then, that a difference in pitch between the juvenile and adult females did not exist and would not have affected the results.

McLanahan and Green [1977] reported that golden lion tamarins tend to use long calls in high arousal situations, often as antiphonal calls in a duet by the mated pair. They suggested that long calls are used in pair formation and pair-bond maintenance, as they are in the cotton-top tamarin (*S. o. oedipus*; Snowdon et al., 1986). Thus, it may be possible for transient or unattached tamarins to monitor the status of a group without visual contact, using the long calls that they hear to determine, for example, whether both members of the breeding pair are present. In our data, correct classification was greater for long calls than for any other category; long calls would seem to be especially well suited for use as an indicator of the sexual composition of golden lion tamarin groups.

The demonstration of sex differences in vocal structure is surprising in light of the absence of sexual dimorphism in lion tamarins. Like other callitrichid primates, male and female lion tamarins are strikingly monomorphic in gross morphological features. There are no sex differences in pelage color or pattern, crown-to-rump measures, weight, or skeletal characteristics [Rosenberger & Coimbra-Filho, 1984; Hershkovitz 1977]. Although subtle sex differences in patterns of behavior have been noted [Kleiman, 1977a; French & Inglett, 1989; Rathbun, 1979; Stribley et al., 1987], lion tamarins are also conspicuous for their lack of dimorphism in behavioral characteristics, a trait they share with other marmosets and tamarins [Kleiman, 1977b]. However, Hershkovitz [1977, p. 852] reports that one of the few morphological differences between adult male and female lion tamarins is the elaboration

of the median ventral laryngeal sac in males, and its reduction or absence in females. Although this anatomical difference could potentially account for our reported sex differences in the frequency characteristics of trills and long calls, it is unlikely to affect the temporal variables for chirps, chucks, and trills. Hershkovitz's [1977] observation of morphological differences between male and female tamarins would appear to be worthy of further study.

We do not know whether the acoustic differences we have documented are perceived differently by tamarins, or whether tamarins respond differentially to male and female vocalizations. Masataka [1987] has shown that red-chested moustached tamarins (*Saguinus l. leoiatus*) are capable of discriminating the sex of a long-calling conspecific on the basis of auditory cues alone (syllable number and mean intersyllable interval) and that the tamarins respond to synthetic long calls in the same manner as they do to natural long calls. Lion tamarins are capable of identifying the sex of unfamiliar individuals within 15 seconds after presentation [French & Inglett, 1989], and this discrimination occurs in the absence of obvious olfactory investigation. It is possible that vocal cues, in combination with subtle behavioral differences between the sexes, allow for a rapid discrimination of the sex of an unfamiliar tamarin.

CONCLUSIONS

1. Golden lion tamarins have calls that are discriminably different between the sexes.

2. Using three of these calls (long calls, chirps, and chucks), the sex of the calling animal can be reliably discriminated.

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