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Long-Call Structure and Its Relation to Taxonomy in Lion Tamarins

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Recent evidence on craniodental morphology suggests the acceptance of three species of lion tamarins (*Leontopithecus*). Confirmatory evidence is presented here using the morphology of long-call vocalizations recorded from several individuals of each type of lion tamarin. Recordings were made of *Leontopicthecus rosalia*, *Leontopithecus chrysopygus*, and *Leontopithecus chrysomelas* at the Centro de Primatologia do Rio de Janeiro (FEEMA) and of *L. rosalia* at Monkey Jungle in Florida. Thirty separate parameters were measured, and 17 of them differed significantly between populations. In general, *L. chrysomelas* had higher pitched calls with shorter note duration, while *L. chrysopygus*, the larger of the animals, had lower pitched calls with longer note duration. *L. rosalia* was either intermediate to the other two populations or resembled *L. chrysopygus*. Thus, the results from the analysis of vocal structures closely paralleled the results obtained with more traditional taxonomic methods and suggests that the quantitative analysis of vocal strucures can be a useful adjunct in taxonomy.

Key words: ***Leontopithecus*, vocalizations**

INTRODUCTION

The lion tamarins are among the rarest and least known of New World primates. They survive today in three widely-separated remnant forests along the southeastern coast of Brasil and in the interior highlands of the state of São Paulo. Each of the populations differs considerably in coat coloration. The most familiar population is the golden lion tamarin (*Leontopithecus rosalia*), found in the state of Rio de Janeiro, which has been the subject of a major conservation effort and world-wide captive breeding program [Kleiman, 1981; Hoage, 1982]. The other two populations have rarely bred in captivity and are virtually unknown outside of Brasil. The golden rumped lion tamarin (*L. chrysopygus*) is found in the state of São Paulo, and the golden mantled lion tamarin (*L. chrysomelas*) is from the coastal region in the state of Bahia (see Rosenberger & Coimbra-Filho [1984] for distribution map).

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The taxonomic status of these populations has been in flux, the same authorities first classifying them as separate species and then as subspecies of a single species [Hershkovitz, 1949, 1977; Coimbra-Filho, 1970; Coimbra-Fillho & Mittermeier, 1972; Napier & Napier, 1967, 1976]. Most previous taxonomies have been based on geographical distribution and pelage; access to anatomical and behavioral data has been scant. Recently, Rosenberger and Coimbra-Filho [1984] have published the results of analyses of craniodental and morphological data obtained from adequate sample sizes of all three populations. Based on visually assessed characters and measurements, they concluded that the genus *Leontopithecus* probably includes three separate species rather than subspecies. They found clear differences among all populations, but *L. rosalia* and *L. chrysopygus* were more similar to one another in some characters than either was to *L. chrysomelas*. *L. chrysomelas* was the most distinctive. It had robust physique, relatively massive incisors, small cheek teeth, and a unique cranial shape in addition to its distinctive coloration of a black body with a golden mane. *L. rosalia* was the smallest and most gracile, with abbreviated premaxilla and reduced anterior dentition. *L. chrysopygus* was the largest in most dimensions, but was more similar to *L. rosalia* than to *L. chrysomelas* in anterior tooth size and proportions and in facial structure.

The long calls or loud calls (Type I calls [Gautier & Gautier, 1977]) are quite stereotyped in form and have frequently been used in taxonomic analyses in many species, especially song in birds [eg, Smith, 1966]. In primates Hodun et al [1981] found that there were subspecies differences in the structure of syllables in the long calls of the saddle back tamarin (*Saguinus fuscicollis ssp.*). Oates and Trocco [1983] have used the structure of loud-call vocalizations of several populations of the black and white colobus (*Colobus sp.*) to develop a putative taxonomy. Walek [1978] noted similarities between the vocalizations of *Colobus polykomos* and Marler's [1972] recordings of *Colobus guereza* and suggested that these might be the same species. Struhsaker [1970] analyzed the differences in vocalization in several species of *Cercopithecus* in order to determine their phylogenetic relations.. Wilson and Wilson [1975] used the vocalizations of banded leaf monkeys (*Presbytis melalophus*) to describe possible phylogenetic affinities.

Long calls in some callitrichids have been well studied. They appear to be used in several contexts: defending a territory against intrusion by a new group, maintaining cohesion within the group or maintaining contact between separated animals, and possibly attracting a mate [Moynihan, 1970; Cleveland & Snowdon, 1982; McConnell & Snowdon, in press]. In the cotton top tamarin (*Saguinus oedipus*), there are two different forms of long calls, which are used in different contexts, and these forms elicit different responses in playback studies [Snowdon et al, 1983]. While there are individual differences in the structure of long calls [Snowdon et al, 1983; Snowdon & Hodun, 1985], these individual differences can be separated from the features common to a population [Hodun et al, 1981]. Although there are sex differences in the rate of long calling (with female cotton top tamarins calling twice as frequently as males [McConnell & Snowdon, in press]), no sex differences in long call structure have been found.

There is relatively little information on long calls in *Leontopithecus*. McLanahan and Green [1977] described long calls in *L. rosalia*, finding that they were intense, high arousal calls given by both males and females, often accompanied by locomotor displays, piloerection, visual scanning, and fixation. The calls were frequently given as duets in mated pairs, and the calling spread to animals in adjacent groups. Most calls were given early in the morning. McLanahan and Green [1977] suggested that the calls were used for pair formation and the maintenance of the pair bond, much as are the long calls of the cotton top tamarin described above.

We were interested in determining whether the structure of the long calls of lion tamarins could illuminate the affinities among *Leontopithecus* and contribute to a sound taxonomic scheme. Reported here are analyses of long calls recorded from each of the three types of lion tamarins at the Centro de Primatologia in Rio de Janeiro, as well as recordings of additional golden lion tamarins housed under similar conditions at Monkey Jungle in Florida, U.S.A.

METHODS

Subjects and Study Sites

The Centro de Primatologia do Rio de Janeiro (FEEMA), Brasil, is located approximately 100 km north of the city of Rio de Janeiro in the foothills of the Serra dos Orgãos mountains. Tamarins are housed in pairs or family groups in separate enclosures constructed of concrete, wood, and wire mesh (6 × 3 × 2.5 m). At the time of our study, there were two clusters of enclosures approximmately 70 m apart. The lower cluster contained five groups of *L. rosalia*, two groups of *L. chrysomelas*, and eight groups of *L. chrysopygus*. The upper cluster contained five additional groups of *L. chrysomelas*. Other marmoset and tamarin species were housed in each cluster. The adults of each group were wild-caught animals.

Monkey Jungle is located approximately 25 km southwest of Miami, FL, USA. Five pairs of captive-born *L. rosalia* were housed in a contiguous bank of wire mesh cages approximately 4 × 8 × 10 m. Live trees in each cage provided climbing surfaces and shade, and nest boxes provided shelter. Pairs of other tamarins (*S. oedipus* or *S. labiatus*) were in the cages between the different groups of lion tamarins. All lion tamarins at Monkey Jungle were captive-born.

Recordings

Recordings of spontaneous long calls were made using a Sony TCD-5M Cassette tape recorder and a Sennheiser MD-80 microphone with a KD-3U preamplifier. This provided a recording system with a flat frequency response up to 16 kHz. The microphone was highly directional, so that long calls made by animals in the cage at which the microphone was aimed could be discriminated in intensity from any long calls emanating from nontarget animals.

In Rio de Janeiro, recordings were made between 0900 and 1400 h. The microphone was aimed at a cage, and the observers retreated 20–30 m from the cage and recorder to avoid disturbing the animals. A stopwatch was used to calibrate the recordings, and notes were made whenever an animal in the target group was observed to open its mouth to emit a long call. Field notes were then interpolated with the location of long calls on the tape. The Monkey Jungle recordings were made between 0630 and 0830 h prior to the arrival of the public. These monkeys were more habituated to human observers than the mokeys in Rio, so it was possible to observe from a close distance and record the counter number of the tape recorder whenever a target animal emitted a long call.

Analysis

Because we could not identify individual animals within each group, we analyzed the vocalizations by cage group. Because we were recording spontaneous vocalizations, we obtained different numbers for each group. The parameter values from the calls from each cage were averaged to provide a single average value for each parameter for each cage. We were able to record from seven different cages of *L. rosalia*, six different cages of *L. chrysopygus*, and five different cages of *L. chrysomelas*. The number of calls per cage ranged from 2–23, with a mean number

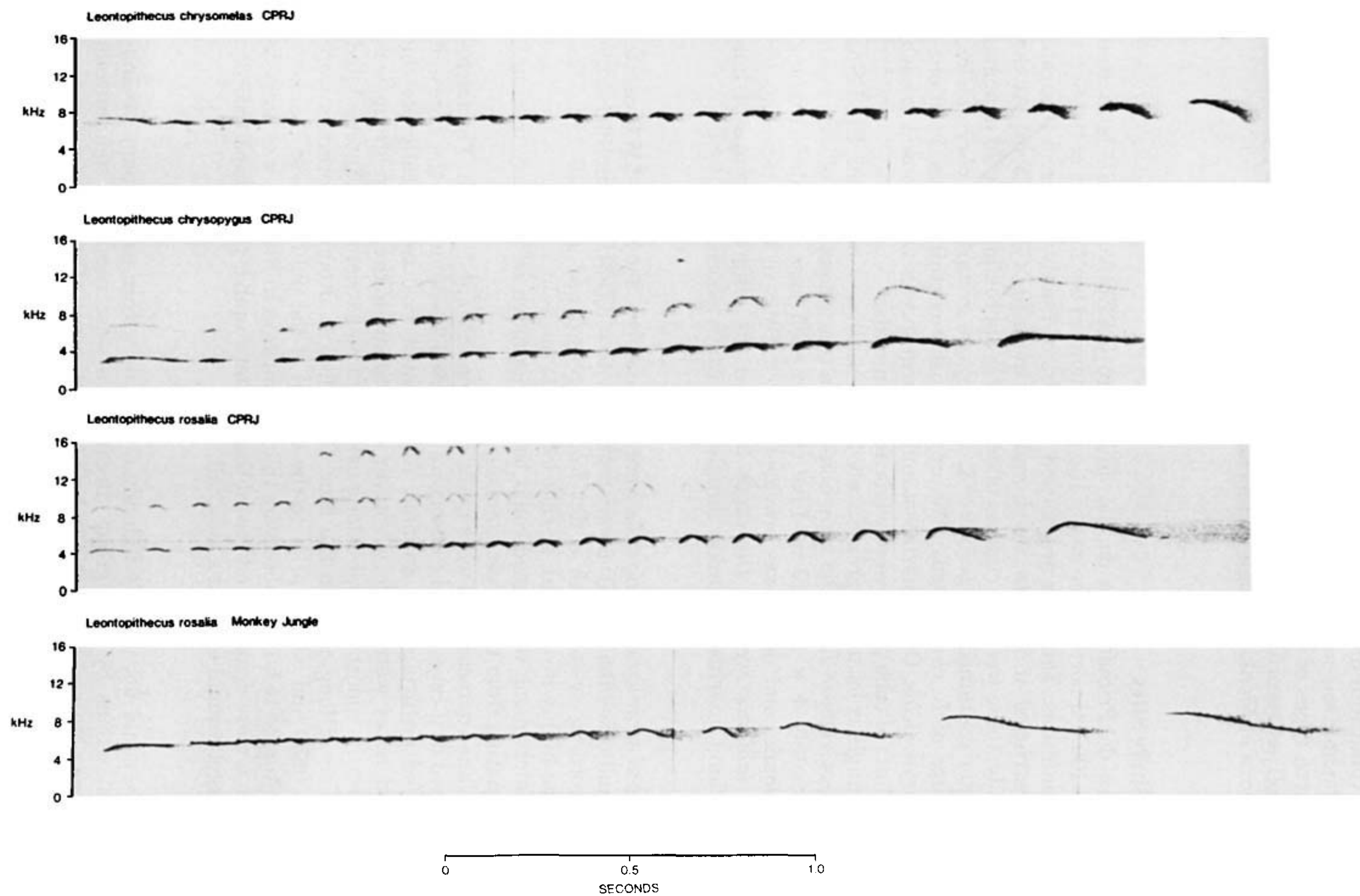

Fig. 1. Sound spectrogram of a long call typical of each population. An example of a long call from a golden lion tamarin at Monkey Jungle is also presented. CPRJ, Centro dos Primates do Rio de Janeiro.

TABLE I. Parameters of Long-Call Vocalizations for Lion Tamarins (Mean ± SD)*

Parameter	Population		
	rosalia (n = 7)	chrysopygus (n = 6)	chrysomelas (n = 5)
Total call			
Total duration (ms)	3,158.6 ± 268.2	2,881.7 ± 615.3	3,316.0 ± 122.8
Number of syllables	17.1 ± 2.3[a]	15.0 ± 1.7[a]	24.8 ± 2.1[b]
Syllable duration (ms)	186.1 ± 21.7[a]	191.0 ± 24.8[a]	134.4 ± 12.3[b]
Long syllables (>100 ms)	4.2 ± 1.1	3.3 ± 1.2	3.3 ± 1.2
Total frequency range (kHz)	2.6 ± 0.4	2.2 ± 0.7[a]	3.4 ± 1.1[b]
Slope (kHz/s)	0.8 ± 0.1	0.8 ± 0.1	1.0 ± 0.3
First syllable			
Duration (ms)	63.9 ± 8.2[a]	64.7 ± 9.4[a]	49.4 ± 10.3[b]
Start to peak duration (ms)	4.7 ± 6.5	18.0 ± 9.2	8.0 ± 6.2
Peak position (%)	22.4 ± 13.1	29.0 ± 15.7	16.0 ± 13.7
Start frequency (kHz)	5.0 ± 0.4[a]	4.5 ± 0.2[a]	6.3 ± 0.9[b]
Peak frequency (kHz)	5.1 ± 0.4[a]	4.7 ± 0.2[a]	6.4 ± 0.9[b]
End frequency (kHz)	4.9 ± 0.4[a]	4.5 ± 0.2[a]	5.9 ± 0.7[b]
Frequency range (kHz)	0.2 ± 0.1	0.2 ± 0.1	0.5 ± 0.4
Peak to start frequency (kHz)	0.2 ± 0.2	0.2 ± 0.2	0.1 ± 0.1
Middle syllable			
Duration (ms)	67.4 ± 5.8[a]	59.0 ± 6.4[b]	47.2 ± 7.5[c]
Start to peak duration (ms)	21.9 ± 6.6	22.5 ± 6.3	14.4 ± 10.1
Peak position (%)	32.4 ± 9.0	37.7 ± 7.4	29.0 ± 18.5
Start frequency (kHz)	5.4 ± 0.4[a]	4.7 ± 0.3[a]	6.8 ± 0.7[b]
Peak frequency (kHz)	5.8 ± 0.4[a]	5.2 ± 0.3[b]	7.1 ± 0.7[c]
End frequency (kHz)	5.2 ± 0.4[a]	4.6 ± 0.3[a]	6.4 ± 0.6[b]
Frequency range (kHz)	0.6 ± 0.3	0.6 ± 0.2	0.7 ± 0.2
Peak to start frequency (kHz)	0.5 ± 0.3	0.5 ± 0.2	0.2 ± 0.2
Last syllable			
Duration (ms)	279.3 ± 73.6[a]	360.2 ± 92.0[a]	152.4 ± 13.0[b]
Start to peak duration (ms)	26.4 ± 10.4[a]	43.3 ± 14.7[b]	11.0 ± 12.3[a]
Peak postion (%)	10.4 ± 5.1	12.3 ± 3.7	7.0 ± 7.7
Start frequency (kHz)	7.3 ± 0.7[a]	6.4 ± 0.8[b]	9.1 ± 0.5[c]
Peak frequency (kHz)	7.7 ± 0.6[a]	6.9 ± 0.8[a]	9.1 ± 0.5[b]
End frequency (kHz)	6.2 ± 0.5	6.0 ± 0.6	6.5 ± 0.6
Frequency range (kHz)	1.5 ± 0.5[a]	0.9 ± 0.3[b]	2.7 ± 0.5[c]
Peak to start frequency (kHz)	0.5 ± 0.2[a]	0.5 ± 0.1[a]	0.2 ± 0.2[b]

*Means labeled with different superscripts are significant at $p < 0.05$.

of 6.6 calls per group. We did not have a large enough sample size of cages to analyze the results of *L. rosalia* from Monkey Jungle and from Rio de Janeiro separately.

Sound spectrograms of long calls were made with a Kay Model 6061B Sonagraph using a narrow band filter and a 160–16,000 Hz frequency range. A Krohn-Hite Model 3500 Band Pass Filter was used to eliminate all background noise below 4 kHz. All long calls that could be definitely attributed to cage of origin were considered for analysis. Since sex of caller could not be identified in our recording situation, and since no sex differences in call structure have been found in previous studies of callitrichid long calls, no analysis of sex differences was attempted.

The spectrograms were measured using a calibrated transparent graticule. Frequency was measured to within 250 Hz and duration to within 15 ms. Total call duration, number of syllables, number of syllables longer than 100 ms, and the difference in frequency from the beginning to the end of the call were measured, and from these measurements we derived the mean syllable duration and the slope of the call (kHz/s). In order to determine the structure of individual syllables and whether those structures changed across the call, a sample of three syllables was measured for each call: the first, middle, and last syllable. In calls with an even number of syllables, the syllable immediately following the midpoint was chosen. For each syllable we measured duration, start to peak duration (the time from the start of the call until the peak frequency was reached), and start, peak, and end frequencies. From these measurements we derived peak position (start to peak frequency duration divided by total duration), frequency range (peak frequency minus end frequency, which was always the lowest frequency), and start to peak frequency change (peak minus start frequency). The same person made all measurements.

The values of each of these parameters for each long call were averaged for each group. The group means of each parameter were analyzed using the one-way ANOVA program of UNIX/STATS. For each variable that produced a significant F-ratio ($p < 0.05$; d.f. = 2,15), Tukey HSD tests were performed to determine the differences between means. A significant F-ratio indicated that population differences of a given parameter were significantly greater than individual differences within that population.

RESULTS

Representative sound spectrograms for each of the different populations are shown in Figure 1. The long calls of each population were similar to the long calls of other callitrichids (*Saguinus fuscicolis* [Hodun et al, 1981; Moody & Menzel 1976]; *Saguinus mystax* [Snowdon & Hodun, 1985]; *Cebuella pygmaea* [Pola & Snowdon, 1975]; but with the exception of *Saguinus oedipus* [Cleveland & Snowdon, 1982]). The calls were approximately 3 s long and consisted of several short frequency modulated syllables. The frequency range of the calls was relatively high—from 4.5 to 9 kHz. In each of the populations, the long calls rose in frequency from the beginning to the end.

Table I presents the mean and standard deviation for each of the parameters for each of the three populations. Seventeen of the 30 parameters were significant in analyses of variance. Means that differed significantly on the basis of Tukey tests are marked with different superscripts in the table.

Table II presents a summary of the significant differences. The greatest differences occurred in the comparison between *L. chrysomelas* and the other two populations, *L. rosalia* and *L. chrysopygus*. In general the calls of *L. chrysomelas* had more notes or syllables with shorter mean note duration, and a higher pitch was found for almost all frequency parameters. There was a greater frequency range for the last syllable but a lower start to peak frequency range of the last syllable for *L. chrysomelas* than for the other populations.

L. chrysomelas differed from *L. chrysopygus*, but not from *L. rosalia*, by having a shorter start to peak duration in the last syllable and by having a greater frequency change over the entire long call.

L. rosalia differed from the other two populations by having a longer duration for the middle syllable. It was intermediate to the other two populations on middle syllable peak, end frequency, last syllable start frequency, and last syllable frequency range. On several other frequency parameters, *L. rosalia* had mean values intermediate to the other two populations, although these were not significantly different from the values for *L. chrysopygus*.

DISCUSSION

The analyses of vocal parameters of the long calls of the existing three populations of lion tamarins has shown that there are consistent differences in long-call structure that are greater than any individual differences within each population. Of the thirty parameters measured, 17 indicated significant differences between populations. *L. chrysomelas* differed from *L. rosalia* and *L. chrysopygus* in 15 parameters and from *L. chrysopygus* alone in two parameters. The golden maned lion tamarin (*L. chrysomelas* had higher frequency parameters and shorter, more frequent syllables within the long call compared to the other two populations.

The golden lion tamarin (*L. rosalia*) differed from the other two populations by having intermediate frequency values in some parameters. In many other parameters, the mean values for the golden lion tamarin were intermediate between the other two but did not differ significantly from the means of the golden rumped lion tamarin (*L. chrysopygus*).

These results show interesting parallels to the morphological findings which indicated that *L. chrysomelas* was more distinct from *L. rosalia* and *L. chrysopygus* than either was from each other [Rosenberger & Coimbra-Filho, 1984]. In this independent study we found that 15 of 17 parameters differentiated *L. chrysomelas* from both of the other populations, while only five parameters differentiated *L. rosalia* from *L. chrysopygus*.

A second finding of Rosenberger and Coimbra-Filho [1984] was that *L. rosalia* was smaller and more gracile. One might expect the vocal equivalent of this body type to be manifest in a higher pitched call. However, it was *L. chrysomelas* that had higher pitch measurements on virtually all frequency parameters. The distribution of *L. rosalia* is geographically intermediate between those of the other two populations. This is mirrored by the tendency for significant *L. rosalia* parameter values to differ from the other two populations in being intermediate between them. Thus, there is a similarity of pattern between geography, the morphological and craniodental analyses, and the results of our analysis of long-call structure, demonstrating that long-call vocalizations can supplement more traditional taxonomic techniques.

TABLE II. Significant Differences Between Populations

L. chrysomelas compared to *L. rosalia* and *L. chrysopygus*	*L. chrysomelas* compared to *L. chrysopygus*
More syllables	Shorter last syllable start to peak duration
Shorter mean syllable duration	Greater frequency change over total call
Shorter first syllable duration	*L. rosalia* compared to *L. chrysopygus* and *L. chrysomelas*
Higher first syllable start frequency	Longer middle syllable duration
Higher first syllable peak frequency	Intermediate middle syllable peak frequency
Higher first syllable end frequency	Intermediate middle syllable end frequency
Shorter middle syllable duration	Intermediate last syllable start frequency
Higher middle syllable start frequency	Intermediate last syllable frequency range
Higher middle syllable peak frequency	
Higher middle syllable end frequency	
Shorter last syllable duration	
Higher last syllable start frequency	
Higher last syllable peak frequency	
Greater last syllable frequency range	
Lower last syllable start to peak frequency range	

This study illustrates the value of using quantitative analyses of vocalizations. Although a variety of reports have used vocalizations as an aid in primate taxonomy, only Symmes et al [1979] and Hodun et al [1981] have used measurements of vocal parameters coupled with statistical decision technques to evaluate calls from different populations. Quantitative measurements and statistical decision techniques are necessary to assure the reliability of any differences reported. Many of the differences we have reported are subtle and were not apparent in initial visual inspection of sound spectrograms.

In summary, the analysis of vocal parameters of the long-call vocalizations of lion tamarins supports, in general, the results of a study on the anatomy and measurement of craniodental fetaures. These two lines of evidence, taken together, suggest that the three forms of *Leontopithecus* should be regarded as separate species. Since each population is currently restricted to tiny bits of remnant forest, each is currently on the endangered species list. We must now consider the conservation of three species of lion tamarins rather than one species.

CONCLUSIONS

1. The long calls of the three types of lion tamarins were recorded, and 30 parameters were measured from each call.
2. There were 17 parameters that differentiated between populations. The golden maned lion tamarin (*L. chrysomelas*) was more distinct from the golden lion tamarin (*L. rosalia*) and the golden rumped lion tamarin (*L. chrysopygus*) than either of these populations was from each other.
3. The pattern of results from the analysis of long-call parameters closely parallels the pattern reported in a recent analysis of craniodental and other anatomical data from specimens of the same populations. This suggests the value and compatibility of analyzing vocal features, especially those of a stereotyped call like the long call, when combined with more traditional taxonomic methods.
4. The data support the division of lion tamarins into three separate species. Since each population is seriously endangered in the wild, conservation efforts must focus on all three populations.

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REFERENCES

Cleveland, J.; Snowdon, C.T. The complex vocal repertoire of the adult cotton top tamarin, *Saguinus o. oedipus*. ZEITSCHRIFT FÜR TIERPSYCHOLOGIE 58:231–270, 1982.

Coimbra-Filho, A.F. Mico-leão, *Leontideus rosalia* (Linneaus, 1766), situação actual de especie no Brasil (Callitrichidae, Primates) REVISTA BRASILEIRA DE BIOLOGIA 30:609–618, 1970.

Coimbra-Filho, A.F.; Mittermeier, R.A. Taxonomy of the genus *Leontopithecus*, Lesson, 1840, pp. 7–22 in SAVING THE LION MARMOSET, Bridgewater, ed. Wheeling, WV, Wild Animal Preservation Trust, 1972.

Gautier, J.-P.; Gautier, A. Communication in Old World Monkeys, pp. 890–964 in HOW ANIMALS COMMUNICATE. T.A. Sebeok, ed. Bloomington, Indiana, Indiana University Press, 1977.

Hershkovitz, P. Mammals of Northern Colombia. Preliminary Report No. 4 Monkeys (Primates) with taxonomic revision of some forms. PROCEEDINGS OF THE UNITED STATES NATIONAL MUSEUM 98:323–427, 1949.

Hershkovitz, P. LIVING NEW WORLD PRIMATES (Platyrrhini) WITH AN INTRODUCTION TO PRIMATES, Vol. 1. Chicago, University of Chicago Press, 1977.

Hoage, R.J. Social and physical maturation in captive lion tamarins *Leontopithecus rosalia rosalia* (Primates, Callitrichidae). SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY 354:1–56, 1982.

Hodun, A.; Snowdon, C.T.; Soini, P. Subspecific variation in the long calls of the tamarin, *Saguinus fuscicollis*. ZEITSCHRIFT FÜR TIERPSYCHOLOGIE 57:97–110, 1981.

Kleiman,, D.G. *Leontopithecus rosalia*. MAMMALIAN SPECIES 148:1–7, 1981.

Marler, P. Vocalizations of East African monkeys. II. Black and white colubus. BEHAVIOUR 42:175–197, 1972.

McConnell, P.B.; Snowdon, C.T. Vocal interactions between unfamiliar groups of captive, cotton top tamarins. BEHAVIOUR (in press).

McLanahan, E.B.; Green, K.M. The vocal repertoire and an analysis of the contexts of vocalizations in *Leontopithecus rosalia*, pp. 251–269 in THE BIOLOGY AND CONSERVATION OF THE CALLITRICHIDAE. D.G. Kleiman, ed. Washington D.C, Smithsonian Institution Press, 1977.

Moody, M.L.; Menzel, E.W. Vocalizations and their behavioral contexts in the tamarin, *Saguinus fuscicollis*. FOLIA PRIMATOLOGICA 25:73–94, 1976.

Moynihan, M. Some behavior patterns of Platyrrhine monkeys. II. *Saguinus geoffroyi* and some other tamarins. SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY 28:1–77, 1970.

Napier, P.H. CATALOGUE OF PRIMATES IN THE BRITISH MUSEUM (NATURAL HISTORY) PART 1: FAMILIES CALLITRICHIDAE AND CEBIDAE. London: British Museum of Natural History, 1976.

Napier, J.R.; Napier, P.H. A HANDBOOK OF LIVING PRIMATES. New York: Academic Press, 1967.

Oates, J.F.; Troco, T.F. Taxonomy and phylogeny of black and white colobus monkeys: Inferences from an analysis of loud call vocalizations. FOLIA PRIMATOLOGICA 40:83–113, 1983.

Pola, Y.V.; Snowdon, C.T. Vocalizations of pygmy marmosets (*Cebuella pygmaea*). ANIMAL BEHAVIOUR 23:826–842, 1975.

Rosenberger, A.L.; Coimbra-Filho, A.F. Morphology, taxonomic status, and affinities of the lion tamarins, Genus *Leontopithecus* (Callitrichinae; Cebidae). FOLIA PRIMATOLOGICA 42:149–179. 1984.

Smith, W.J. Communication and relationships in the genus *Tyrannis*. MONOGRAPHS OF THE NUTTALL ORNITHOLOGICAL CLUB 6:1–250, 1966.

Snowdon, C.T.; Hodun, A. Troop specific responses to long calls of isolated tamarins (*Saguinus mystax*). AMERICAN JOURNAL OF PRIMATOLOGY 8:205–213, 1985.

Snowdon, C.T.; Cleveland, J.; French, J.A. Responses to context- and individual-specific cues in cotton-top tamarin long calls. ANIMAL BEHAVIOUR 31:92–101, 1983.

Struhsaker, T.T. Phylogenetic implications of some vocalizations of Cercopithecus monkeys, pp. 365–444 in OLD WORLD MONKEYS: EVOLUTION, SYSTEMATICS, AND BEHAVIOR. J.R. Napier; P.H. Napier, eds. New York, Academic Press, 1970.

Symmes, D.; Newman, J.D.; Talmage-Riggs, G.; Lieblich, A.K. Individuality and stability of isolation peeps in squirrel monkeys. ANIMAL BEHAVIOUR 27:1142–1152, 1979.

Walek, M.L. Vocalizations of the black and white colobus monkey (*Colobus polykomos*, Zimmerman, 1780). AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 49:227–240, 1978.

Wilson, W.L.; Wilson, C.C. Species-specific vocalizations and the determination of phylogenetic affinities of the *Presbytis aygula-melalophus* group in Sumatra, pp. 459–463 in CONTEMPORARY PRIMATOLOGY. S. Kondo; M. Kawai; A. Ehara, eds. Basel, Karger, 1975.