American Journal of Primatology 76:788–800 (2014)

RESEARCH ARTICLE

Vocal Behavior of Black-Fronted Titi Monkeys (*Callicebus nigrifrons*): Acoustic Properties and Behavioral Contexts of Loud Calls

CHRISTINI B. CASELLI[1]*, DANIEL J. MENNILL[2], JÚLIO CÉSAR BICCA-MARQUES[3], AND ELEONORE Z. F. SETZ[1]
[1]Departamento de Biologia Animal, Universidade Estadual de Campinas, Campinas, SP, Brazil
[2]Department of Biological Sciences, University of Windsor, Windsor, Ontario, Canada
[3]Laboratório de Primatologia, Pontifícia Universidade Católica do Rio Grande do Sul, Brazil

Loud calls can be heard over long distances due to their high amplitude and low frequency. These calls are commonly used for both within- and between-group communication in many bird and primate species. In the Neotropics, mated pairs of socially monogamous titi monkeys (genus *Callicebus*) emit conspicuous, coordinated loud calls. These vocalizations appear to play a role in territorial defense, a hypothesis derived from studies of only three of the 31 recognized *Callicebus* species. Here, we describe the acoustic properties and organization of the loud calls of black-fronted titi monkeys (*Callicebus nigrifrons*). We compare the behavioral and ecological contexts associated with these vocalizations to investigate their role in within- and between-group communication, resource defense, and mate defense. Black-fronted titi monkeys create loud calls by combining a finite number of syllables to form more complex phrases, which are assembled to compose long sequences of loud calls. Bioacoustic features distinguish the loud calls used in different contexts, involving communication within- and between-groups. We found support for the hypothesis that vocalizations used for between-group communication are cooperative displays used by the mated pair and other group members to regulate access to important food resources, such as fruits. On the other hand, we only found weak support for the mate defense hypothesis. Am. J. Primatol. 76:788–800, 2014. © 2014 Wiley Periodicals, Inc.

Key words: acoustic analysis; duet; mate defense; territorial defense; vocal communication

INTRODUCTION

The high amplitude and low frequency of loud calls allow them to be heard over long distances [Wich & Nunn, 2002] and their use for within- and between-group communication is widespread among birds and primates [Hall, 2004; Oliveira & Ades, 2004]. These calls can be emitted as solos or as jointly produced signals by two (duets) or more individuals (choruses) [Geissmann, 2002; Kitchen, 2004; Wilson et al., 2001].

Coordinated loud calling, especially as duets by mated pairs, are commonly observed in primates that form long-term pair bonds, and their function are usually associated with joint resource defense or mate guarding [Oliveira & Ades, 2004; Wich & Nunn, 2002]. As a joint resource defense signal, coordinated loud calls communicate to outsiders the callers' resource holding potential and willingness to defend territories [Hall, 2004]; as a mate guarding signal, these calls announce the callers' mated status and their intent to repel same-sex rivals [Levin, 1996; Robinson, 1981]. An individual also can join in calling to deter extragroup individuals who may be a threat to its partner's breeding position [Grafe & Bitz, 2004]. While in the first scenario of mate guarding the response reflects within-pair conflicting interests and is directed to same-sex outsiders, the response in the second scenario reflects within-pair cooperative interests and is directed to opposite-sex intruders [Hall, 2004].

In the Neotropics, the socially monogamous titi monkeys (genus *Callicebus*) emit loud calls in duets, which appear to play a role in territorial defense, a

---

Contract grant sponsor: FAPESP; contract grant number: 2008/05127-0; contract grant sponsor: CAPES; contract grant number: BEX 5637/11-2; contract grant sponsor: Natural Sciences and Engineering Research Council of Canada (NSERC) (partial support); contract grant sponsor: Canada Foundation for Innovation; contract grant sponsor: The Government of Ontario; contract grant sponsor: Brazilian National Research Council; contract grant number: CNPq #303154/2009-8.

*Correspondence to: Christini B. Caselli, Departamento de Biologia Animal, Universidade Estadual de Campinas, Caixa Postal 6109, CEP 13083-970, Campinas, SP, Brazil.
E-mail: ccaselli@gmail.com

Received 27 June 2013; revised 6 February 2014; revision accepted 7 February 2014

DOI: 10.1002/ajp.22270

hypothesis derived from studies of only three of the 31 currently recognized *Callicebus* species [Kinzey & Robinson, 1983; Mason, 1968; Price & Piedade, 2001; Robinson, 1979a, 1981]. In yellow-handed titis [*C. lucifer*, formerly *C. torquatus*; Kinzey & Robinson, 1983; for details of taxonomic revision see van Roosmalen et al., 2002] and masked titis [*C. personatus*; Kinzey & Becker, 1983; Price & Piedade, 2001] loud calls seem to be used to alert the group's location to neighbors and avoid encounters, while in ornate titis [*C. ornatus*, formerly *C. moloch*; Mason, 1968; Robinson, 1979a] loud calls appear to promote encounters at the boundary of territories, resulting in spatial demarcation. Loud calls may also play a role in mate defense, since mates usually initiate the duets in response to same-sex solo vocalizations [Robinson, 1979a, 1981].

The structure and organization of loud calls were comprehensively described only for red-crowned [*C. discolor*, formerly *C. moloch*; Moynihan, 1966], ornate [Robinson, 1979b] and coppery [*C. cupreus*; Müller & Anzenberger, 2002] titi monkeys. In these species, calls (composed of syllables) are assembled into phrases, which are then combined into longer sequences. A careful bioacoustic description of the structure of animal vocalizations is a critical first step in understanding their ecology and evolution. Yet the structure, organization, and function of loud calls in the remaining 26 species of titi monkeys have not been investigated. Furthermore, little attention has been given to the possible function of these calls in within-group communication [Kinzey et al., 1977] and between-group mate defense [Robinson, 1979a,b, 1981].

Mate defense has been proposed as a function for the loud calls of gibbons [Cowlishaw, 1992]. Gibbons represent a good comparative model to titi monkeys because the members of both groups are frugivorous territorial primates that form long-term pair bonds [Bartlett, 2007], occasionally engage in extra-pair copulations [gibbons: Palombit, 1994a,b; Reichard & Sommer, 1997; titis: Defler, 2004; Mason, 1966], and whose mated pairs may experience turnover [gibbons: Reichard & Sommer, 1997; titis: Caselli, unpublished data]. Therefore, it is worthwhile to test whether loud call coordination in titi monkeys is associated with situations compatible with mate guarding as a strategy to promote male reproductive success.

In this study, we describe the loud calling behavior of black-fronted titi monkeys (*Callicebus nigrifrons*). Like other titis, these monkeys are predominantly frugivorous and live in family groups composed of an adult breeding pair and one to three young offspring [Kinzey, 1997]. During preliminary field observations we recognized two types of loud vocalizations, which we distinguished as "type 1" and "type 2". Type 1 appeared to be used for intragroup communication, whereas type 2 appeared to function as an intergroup signal. Here we describe the acoustic properties of both types and analyze their associated behavioral and ecological contexts to test whether they are context-specific. Then, we test whether the joint resource defense hypothesis or the mate guarding hypothesis better explains the emission of vocalizations used for intergroup communication. If these vocalizations are important in joint resource defense, we predict that titis will emit loud calls at a higher frequency (1.a.) as coordinated choruses or duets when encountering outsiders (because all members of the group would have a common interest in defending their shared resources from other groups or individuals), and (1.b.) when defensible and valuable resources, such as fruits, are available. On the other hand, if these vocalizations are important in mate guarding, we predict that titis will loud call at a higher frequency (2.a.) as uncoordinated solos or duets with notable differences in participation aimed at repelling same-sex rivals and (2.b.) when valuable food resources are low and the female is fertile (i.e., the time when the risk of extra-pair copulation is higher).

METHODS

Subjects and Study Site

We recorded the vocalizations of six groups of black-fronted titi monkeys at three Atlantic Forest sites in the state of São Paulo, southeastern Brazil: one habituated and three non-habituated groups at Serra do Japi (a 350-km^2 forest remnant; 23°11′S, 46° 52′W), municipality of Jundiaí; one habituated group at Cantareira State Park (a 79-km^2 forest remnant; 23°27′S, 46°37′W), municipality of São Paulo; and one habituated group at Ribeirão Cachoeira (a 2.45 km^2 forest remnant; 23°27′S, 46°37′W), municipality of Campinas. We complemented our dataset with recordings of three captive groups kept at Bauru Zoo (Bauru, state of São Paulo), Guarulhos Zoo (Guarulhos, state of São Paulo), and Scientific Breeding Center of Companhia Brasileira de Metalurgia e Mineração - CBMM (Araxá, state of Minas Gerais). Captive animals were born in the wild and, therefore, were capable of performing the species-typical calls when stimulated by playback.

The analysis of the context of loud calls was based on the observations of the habituated group at Serra do Japi (hereafter, group 1). This group was composed of five to six individuals. These observations were complemented with data from a habituated mated pair (hereafter, group 2) that inhabited an area adjacent to the territory of group 1.

Loud Call Recording

We recorded vocalizations in WAV format using a Sennheiser ME-67 directional microphone and a Marantz PMD-671 digital recorder at 48 kHz sampling rate and 16-bit resolution. We collected recordings between June 2010 and June 2011 at distances of up to 20 m (usually *ca*. 5 m) from the tree where the monkeys were calling. Whenever possible, we recorded all occurrences of loud calls emitted by group 1, both spontaneously and in response to neighbor groups or playback. For the other groups we only recorded those calls emitted in response to loud calls of neighbor groups or playback. Recordings of the Ribeirão Cachoeira group were used as playback for group 1, whereas the recordings of group 1 were used as playback for all the other groups. To record the calls of the captive groups we broadcasted a 1-min. stimulus from concealed locations at a distance of *ca*. 70 m (2-m high) from the focal group's cage using a T-120B CSR loudspeaker (audio output: 40 W; frequency response: 25 Hz to 15 kHz) connected to a Marantz PMD-671 portable digital recorder. This procedure simulated the calling of a neighboring group, as is commonly experienced by wild groups. The same procedure was adopted in the field. The researcher was hidden in the understory for recording the vocalizations of non-habituated groups to minimize the influence of her presence on the behavior of the study subjects. The success of this strategy was confirmed by the absence of the characteristic alarm calls emitted by non-habituated titis in the presence of human observers [Cäsar et al., 2012].

Despite the difficulty in individually identifying titi monkeys in the wild, we were able to distinguish between the male and female of the mated pair of habituated groups and between them and their offspring based on the size of the animals when they were close to each other. Males are slightly larger than females, and adults (>30 months of age) are larger than subadults (18–30 months) and juveniles (6–18 months). Infants (<6 months) are easily recognized based on their small size [de Luna et al., 2010; Kinzey, 1997; Valeggia et al., 1999]. Hereafter, we will refer to both subadults and juveniles as young.

Acoustical Analysis

For all acoustic analyses we used 66 recordings, 55 from spontaneous recordings and 11 from playback-induced recordings. We used different subsets of the recordings for different analyses: 20 were used for measuring and characterizing syllable types (10 from spontaneous and 10 from playback-induced recordings), 26 were used for measuring and characterizing vocalizations type 1 and 2 (13 of each; 22 from spontaneous and four from playback-induced recordings; all type 1 loud calls came from spontaneous recording); 50 were used for measuring the total duration of loud calls (25 of each type; 46 from spontaneous and four from playback-induced recordings).

We generated spectrograms of the recordings using Syrinx-PC software [John Burt, Seattle, WA; Blackman window type; 2,048 FFT] and identified the types of syllables (syllable categories) based on the visual inspection of the spectrograms of all groups. We defined syllables as uninterrupted spectrographic tracings separated by silent intervals [following Robinson, 1979b]. These units are rarely produced in isolation. They are often assembled to form phrases that are combined to form longer sequences.

Because recordings often consisted of overlapping vocalizations of at least two individuals, we selected a subset of 20 recordings (one or more recordings from each of the nine groups) in which we were able to select individual syllables with no overlap. We randomly selected up to 10 examples of each syllable type for each group (mean ± SD number of syllables per type per group = 6.4 ± 4.0) for measuring the following fine structural parameters: duration of the entire syllable, number of harmonics under 2 kHz; harmonic-to-noise ratio [a parameter for quantifying the noise within a signal; Gamba & Giacoma, 2005]; minimum and maximum frequency; and total number of harmonic peaks above −15 db at 5 milliseconds of the beginning and the end of the syllable. We obtained these measurements in Avisoft-SASLab Pro 5.2.05 [R. Specht, Berlin, Germany] using the automatic parameter measurement tool (settings: two thresholds of −16 and −20 dB, 23 ms hold time, 1,024 FFT size, 98.43% overlap, Blackman window, 1 ms time resolution and 22 Hz frequency resolution). Before measuring the sounds, we normalized each call to the same amplitude (−1 dB) and filtered all sounds above 20 kHz and below 80 Hz to standardize calls and eliminate background sounds that fell outside the frequency spectrum of the species' vocalizations. The use of automated parameter measurements minimized the influence of subjectivity in measuring the structural features of these calls.

We identified five qualitatively distinct phrases formed by the combination of one or two different syllables. Then, we quantified the following parameters to assess possible structural differences between the vocalizations type 1 and 2: relative proportion of each type of syllable and phrase in each type of vocalization, phrase type duration, rate of syllable and phrase emission, and probability of transition between two consecutive syllable and phrase types. We selected a subset of 26 recordings (13 of type 1 and 13 of type 2) that allowed us to analyze the sequence of these vocal units for at least one animal vocalizing in each recording (either because the vocalization of one of the individuals was louder in the recording and, consequently, more visible in the spectrogram, or because the other group members were silent during part of the recording) to carry out these measurements. For type 1 vocalizations this subset included recordings of four groups (three wild and one captive), whereas for type 2 we used only recordings of two wild groups. The analysis of the sequence of vocal units (syllables or phrases) was conducted by drawing boxes around them using Syrinx-PC's time cursors. For measuring the total duration of the vocalization types 1 and 2, we included 12 additional recordings of each, totaling 25 examples of each.

Vocal Behavior

We monitored group 1 from dawn to dusk (50 complete days) or from the moment it was found until it was lost (29 incomplete days) for 3 to 5 days each month over a period of 20 months (November 2009–June 2011). We documented all occurrences [Altmann, 1974] of loud calling by group 1, their context and time of day. Context description included: (i) occurrence of loud calling by neighbor groups before and after the events of vocalization of the focal group; (ii) number of animals vocalizing; and (iii) behavior of the animals during the vocalization session. When calls were emitted in response to other groups we also recorded: (iv) latency to the start of the response; and (v) physical response of the group (neutral, retreat, or approach) based on its estimated angle-of-turn after the call by setting the direction from which the neighbor group called as 0° [modified from da Cunha & Byrne, 2006]. We considered an approach when the group turned to within 60° relative to the direction of the calling neighbors (300°–60°) and moved towards them, and a retreat when it turned between 120° and 240° relative to the direction of the neighbors and moved away from them. We considered a neutral response when the focal group remained stationary or moved in other directions.

The animals were observed in the wild and no individual was captured or handled. This research adhered to Brazil's legal requirements and the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

Estimate of Fruit Availability

We monitored the fruit availability of 22 zoochoric species that are important food sources to titis according to Caselli and Setz [2011] at Serra do Japi to assess its relationship with the vocal behavior of group 1. We selected at least 15 individuals of each species or all mature individuals within group 1's territory of the less common species (mean ± SD of the number of individuals per species $= 9.8 \pm 3.5$; see supplementary material online). To estimate the monthly fruit production of each plant we assigned scores from 0 to 4 depending on the percentage of the crown bearing mature fruits [0: no fruit; 1: 1 to 25% of the crown bearing fruit; 2: 26 to 50%; 3: 51 to 75%; 4: 76 to 100%; following Sun et al., 1996]. We transformed these scores into percentages (using the midpoint percentage of each score) and calculated a monthly index of relative fruit availability [following Kinnaird, 1992] by summing up the percentages of all individuals of a given species and dividing it by the number of individuals. The overall monthly index of fruit availability was calculated as the mean of all species.

Assessment of Estrus

To estimate the period when the females of groups 1 and 2 were fertile, we recorded the timing of copulations or counted back from the dates of birth recorded in the field. We used values concernign the minimum [122 days; Valeggia et al., 1999] and maximum [167 days; Defler, 2004] gestation length known for titi monkeys to determine reproductive conduction. We obtained the data on group 2 between March and November of 2007 during a 253 hr study on its feeding ecology [Caselli & Setz, 2011].

Statistical Analyses

We conducted a discriminant function analysis (DFA) to test the validity of the syllable types that we categorized visually. We randomly selected one example of each of the six syllable types from each of the nine groups and constructed a DFA based on these 54 syllables. To test the significance of the discriminant model we performed a MANOVA. We cross-validated this analysis to determine whether it is possible to correctly predict the type of syllable on the basis of the measured fine structural parameters (independent variables) using a second example of each syllable type from each group. We performed the DFA with seven independent variables because three of the 10 independent variables were highly correlated with at least one of the other variables (Spearman's rank correlation coefficient ranging from -0.60 to 0.59, $P < 0.05$). We report the accuracy of the DFA as the proportion of these second syllables correctly assigned to the appropriate syllable type. These analyses were performed using the packages "MASS" version 7.3–18 [Venables & Ripley, 2002] and "stats" in R software version 2.15.0 [R Development Core Team, 2011].

To compare the structure of vocalizations type 1 and 2, we first analyzed the transition pattern between syllable and phrase types for each vocalization. We used the winnowing log-linear-based approach [Bakeman & Quera, 2011] to determine whether the transitions between any two consecutive syllables or phrases occur at rates significantly different than expected by chance given their observed frequencies. This analysis is based on the chi-square test of independence, where the events in the rows (lag 0) of contingency tables are preceded by the events in the columns (lag 1). The dimension of contingency tables is determined by the number of syllable and phrase types that labels both rows and columns. For phrase transition tables, for example, we included "start" and "end" as new categories, resulting in a 7×7 contingency table. These new categories were introduced to investigate which type of phrase is significantly associated with start and end of each type of vocalization. We performed the winnowing log-linear-based approach using ILOG 3 program [Bakeman et al., 2010] to analyze phrase transitions for both type 1 and 2 vocalizations and syllable transitions for vocalizations type 1. We could not use the log-linear approach to describe the pattern of syllable transition in vocalizations type 2 due to the reduced size of the contingency table, since one of the syllable types was rare in this type of vocalization. In this case we ran a lag sequential analysis using the GSEQ program 5.1 [Bakeman & Quera, 2011], producing a 3×3 table of p-values for the transition probabilities. We applied a Bonferroni correction, adjusting the alpha level of significance by the number of tests, to reduce the risk of type 1 error [Sokal & Rohlf, 1995].

Proceeding with the investigation of structural differences between the vocalizations type 1 and 2, we compared their mean duration, mean phrase duration and mean syllable and phrase rate using two sample *t*-tests. When the data did not fit parametric assumptions, even after log transformation, we performed Wilcoxon rank sum tests.

We used a 2×2 contingency table to test if the use of vocalizations type 1 or 2 was dependent of behavioral contexts (in intra- or intergroup communication). To test the joint resource defense hypothesis we used a Chi-square test to evaluate whether the frequency of vocalizations used for intergroup communication was higher when food availability was more abundant. To calculate the expected number of vocalizations in the lean and rich periods (represented by months with scores of fruit availability higher and lower than the mean), we considered the number of observation hours for each period. We used the same approach to test the mate guarding hypothesis, analyzing whether monkeys vocalize more frequently in periods of female estrus. These analyses were performed using the package "stats" in R software version 2.15.0 [R Development Core Team, 2011].

RESULTS

Loud Call Acoustic Properties and Structure

We identified six syllable categories, named *A* to *F*, varying in spectro-temporal properties (Fig. 1, Table I): *A* syllables are composed by high (range: 3–12 kHz) and low frequency components (near 1 kHz) with some faint or absent middle harmonics (see between the dashed lines in Fig. 1); *B* syllables are composed of many tight harmonics and sub-harmonics, with little frequency modulation, and most of the energy concentrated under 2 kHz; *C* syllables are composed by many loose harmonics and with greater frequency modulation than *B* syllables; *D* and *F* syllables are similar to *A*s, but with middle harmonics between the top and bottom components, where *D* syllables are short and *F* syllables are long (Table I), with more modulation that is especially notable in the higher components; *E* syllables are similar to *A* syllables, but entirely lack the low frequency components.

A discriminant analysis based on seven fine structural features (Table I) differentiated these six categories of syllable (Wilks Lambda $= 0.02$, $P < 0.0001$, $N = 54$). The cross-validation assigned syllables to the correct type with an accuracy of 67.0%, significantly higher than the 16.7% accuracy expected by chance (Binomial test: $P = 0.01$). This analysis correctly predicted most *B*s, *C*s, and *E*s, but showed a lower performance in distinguishing *A*s, *D*s, and *F*s. Therefore, *A*, *D*, and *F* syllables were lumped in all subsequent analyses and hereafter referred to as *A*s.

We recognized five types of phrases that the monkeys created from these syllable types (Fig. 1): *ab* and *bc* phrases are formed by alternated emissions of each syllable; *aa* and *bb* are formed by consecutive emissions of each syllable; and *ae* is formed by combined emissions of *A*s and *E*s with no particular order. Except for the phrase types *aa* and *ae*, which were also produced outside of loud calls sequences (such as in alarm contexts or when animals were foraging closer to the ground), all other phrase types were used only in the composition of loud calls sequences.

Although a few instances of syllable *E* were detected in type 2 vocalizations during preliminary inspections of sonograms, this syllable, and consequently the *ae* phrase, were not present in the subset of recordings we used for detailed analysis. Therefore, except for the *ae* phrase, all phrase types were used in the composition of both type 1 and 2 vocalizations. These phrases were combined to produce sequences of variable duration (Figs. 2 and 3). The mean duration of vocalizations (Wilcoxon rank sum test: $W = 42$, $P = 0.16$, $N = 50$; Fig. 3) and the duration of the *bb* phrase (two sample *t*-test with log transformed data: $t = -0.86$, df $= 57$, $P = 0.39$) did not differ between type 1 and 2 vocalizations, but the duration of the *aa*, *ab*, and *bc* phrases and the rate of syllable and phrase emission differed (two sample *t*-test with log transformed data: *aa* duration, $t = 3.37$, df $= 56$, $P < 0.01$; *ab* duration, $t = -13.18$, df $= 124$, $P < 0.001$; Wilcoxon rank sum test: *bc* duration, $W = 1{,}270$, $P < 0.001$, $N = 147$; syllable rate, $W = 42$, $P < 0.05$, $N = 26$; phrase rate, $W = 126$, $P < 0.05$, $N = 26$; Fig. 3).

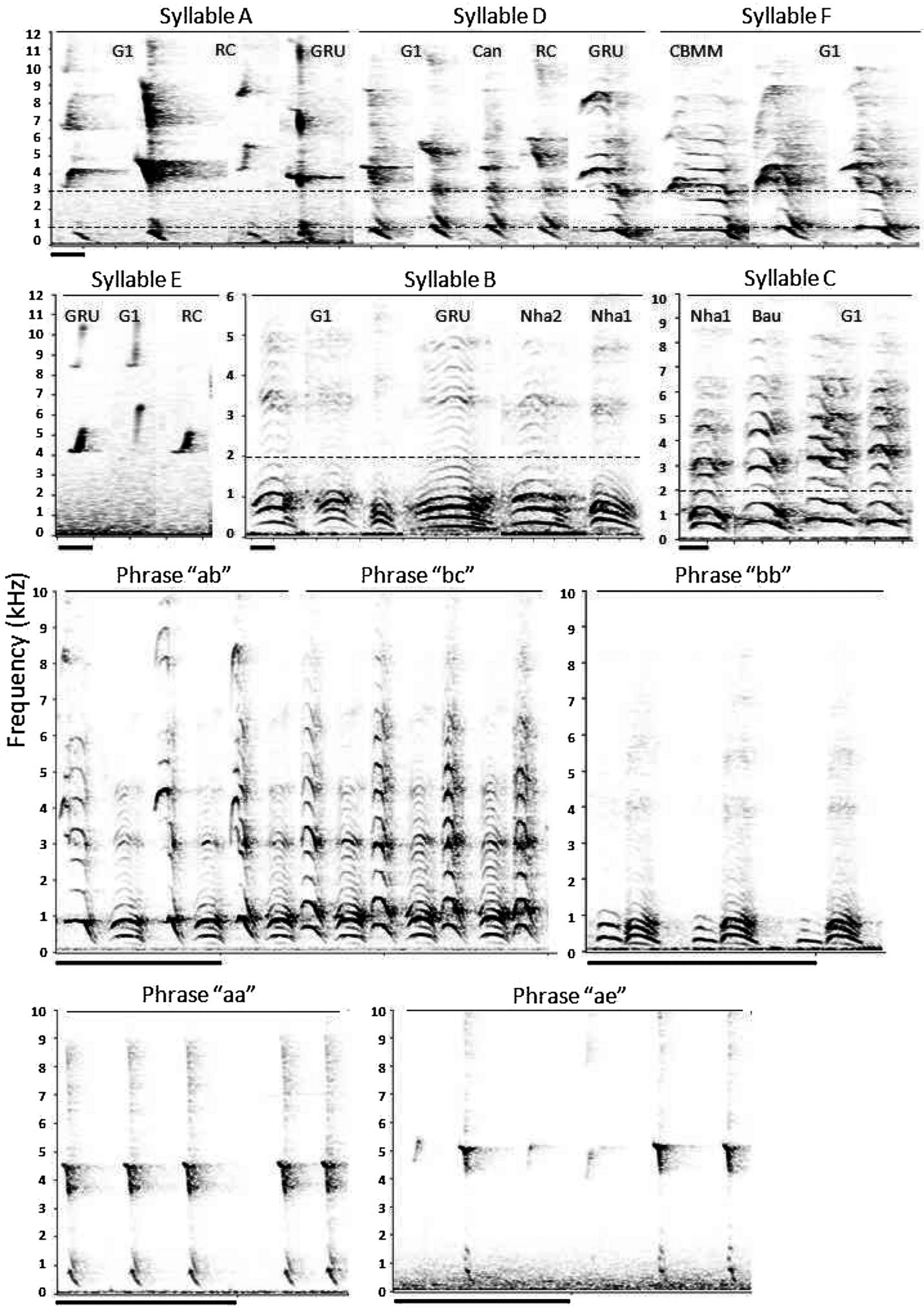

Fig. 1. Sound spectrograms of syllables and phrases used by *Callicebus nigrifrons* to compose loud calls. For syllable spectrograms, the scale bar along the horizontal axes corresponds to 0.1 sec; for phrases spectrograms the scale bar corresponds to 1 sec. Syllables recorded from different groups are shown (Wild groups: group 1(G1), Ribeirão Cachoeira (RC), non-habituated groups from Serra do Japi (Nha1 and Nha2), Cantareira (Can); Captive groups: Guarulhos (GRU), Araxá (CBMM) and Bauru (Bau)). The dashed lines at syllables *A*, *D*, and *F* panels draw attention to the middle harmonics and the dashed lines at syllables *B* and *C* panels draw attention to the number of harmonics under 2 kHz (see text for details). The phrase samples are from group 1.

TABLE I. Mean Values of Fine Structural Parameters Measured for Six Types of Syllables for Nine Groups of *Callicebus nigrifrons*

				Start				End			
Syllable	*N*	*N* harmonics (≤2 kHz)	Duration (sec)*	Min freq. (Hz)*	Max freq. (Hz)	HNR (dB)	N peaks	Min freq. (Hz)*	Max freq. (Hz)	HNR (dB)	*N* peaks
A	38	2 (1–3)	0.08 (±0.03)	3,313 (±949)	6,427 (±1,874)	39 (±9)	2 (1–3)	344 (±661)	1,117 (±1,440)	51 (±9)	1 (1–2)
B	75	6 (3–11)	0.14 (±0.05)	221 (±110)	1,812 (±985)	41 (±13)	2 (1–6)	170 (±83)	1,553 (±755)	43 (±13)	2 (1–4)
C	73	3 (1–4)	0.10 (±0.04)	463 (±208)	3,107 (±1,502)	40 (±14)	3 (1–6)	253 (±110)	2,008 (±1,364)	47 (±12)	2 (1–8)
D	42	2 (1–5)	0.10 (±0.04)	3,883 (±1,325)	6,196 (±1,765)	40 (±12)	1 (1–5)	272 (±95)	1,614 (±858)	46 (±12)	2 (1–3)
E	31	0 (–)	0.05 (±0.02)	3,830 (±917)	6,161 (±1,954)	40 (±6)	1 (1–3)	3917 (±866)	6,817 (±2,140)	46 (±6)	2 (1–5)
F	67	2 (1–5)	0.18 (±0.07)	2,851 (±1,235)	5,695 (±1,851)	41 (±10)	2 (1–5)	271 (±149)	1473 (±841)	48 (±13)	2 (1–5)

HNR, harmonic-to-noise ratio; N peaks, number of harmonic peaks above -15 dB. The asterisk indicates the parameters excluded from the DFA.
The values in brackets indicate the standard deviation, except for number of harmonics (≤2 kHz) and number of peaks, for which the numbers in brackets corresponds to maximum and minimal values.

The proportional contribution of syllable and phrase types and their transition patterns also differed between type 1 and 2 vocalizations (Fig. 4). The transitions between consecutive *A*s and *E*s and between *C*s and *B*s in type 1 vocalizations occurred at higher rates than expected, whereas the transitions between *A*s and *B*s and between *A*s and *C*s occurred at lower rates than expected (complete model before the removal of significant transitions between syllables: $G^2 = 3066.24$, df $= 9$, $N = 2{,}565$, $P < 0.001$; resulting model after the removal of the four significant transitions from the 16 possible: $G^2 = 14.83$, df $= 1$, $N = 297$, $P < 0.001$; Fig. 4). In type 2 vocalizations the transitions between *A*s and *B*s and between *C*s and *B*s also occurred at higher rates than expected, whereas the transitions between consecutives *B*s and *C*s and from *A*s to *C*s occurred at lower rates than expected (complete model before the removal of significant transitions: $G^2 = 2651.07$, df $= 4$, $N = 3{,}767$, $P < 0.0001$; the above mentioned transitions were significant at alpha $= 0.005$ Bonferroni corrected levels; Fig. 4).

Eight of all possible transitions between phrase types observed for vocalizations of type 1 occurred at rates either higher or lower than expected by chance (complete model before the removal of significant transitions: $G^2 = 357.60$, df $= 29$, $N = 265$, $P < 0.001$; resulting model after eight removals: $G^2 = 12.73$, df $= 1$, $N = 67$, $P < 0.001$; Fig. 4). Type 1 vocalizations often start with *aa* phrases, followed by repeated sequences of *ab*, *bc* and *bb*, generally in this order, followed by repeated sequences of *aa* that either ended the vocalization or were followed by sequences of *ab* (Figs. 2 and 4). No phrase type was significantly associated with the end of type 1 vocalizations.

On the other hand, the *aa* phrase was rare in type 2 vocalizations. When it was used, it also began the vocalization (Figs. 2 and 4). Only the presence of *aa* and *bb* phases at the start and *bb*s at the end of type 2 vocalizations occurred at rates greater than expected by chance (complete model before the removal of significant transitions: $G^2 = 83.18$, df $= 19$, $N = 215$, $P < 0.0001$; resulting model after three removals: $G^2 = 20.20$, df $= 1$, $N = 203$, $P < 0.001$). The remainder of this vocalization type comprised *ab* and *bc* phrases (and, near the end of the vocalization, some sequences of *bb*) which cycled by chance (Figs. 2 and 4). In sum, type 1 and 2 vocalizations differed in structure, phrase composition, and phrase organization.

Vocal Behavior

During 730 hr of observation of group 1 we registered a total of 289 loud vocalizations (80 of type 1 and 209 of type 2). Type 1 and 2 vocalizations were emitted in different contexts (2 × 2 contingency table: $\chi^2 = 91.19$, df $= 1$, $P < 0.001$); whereas most type 1 calls were spontaneously emitted when group

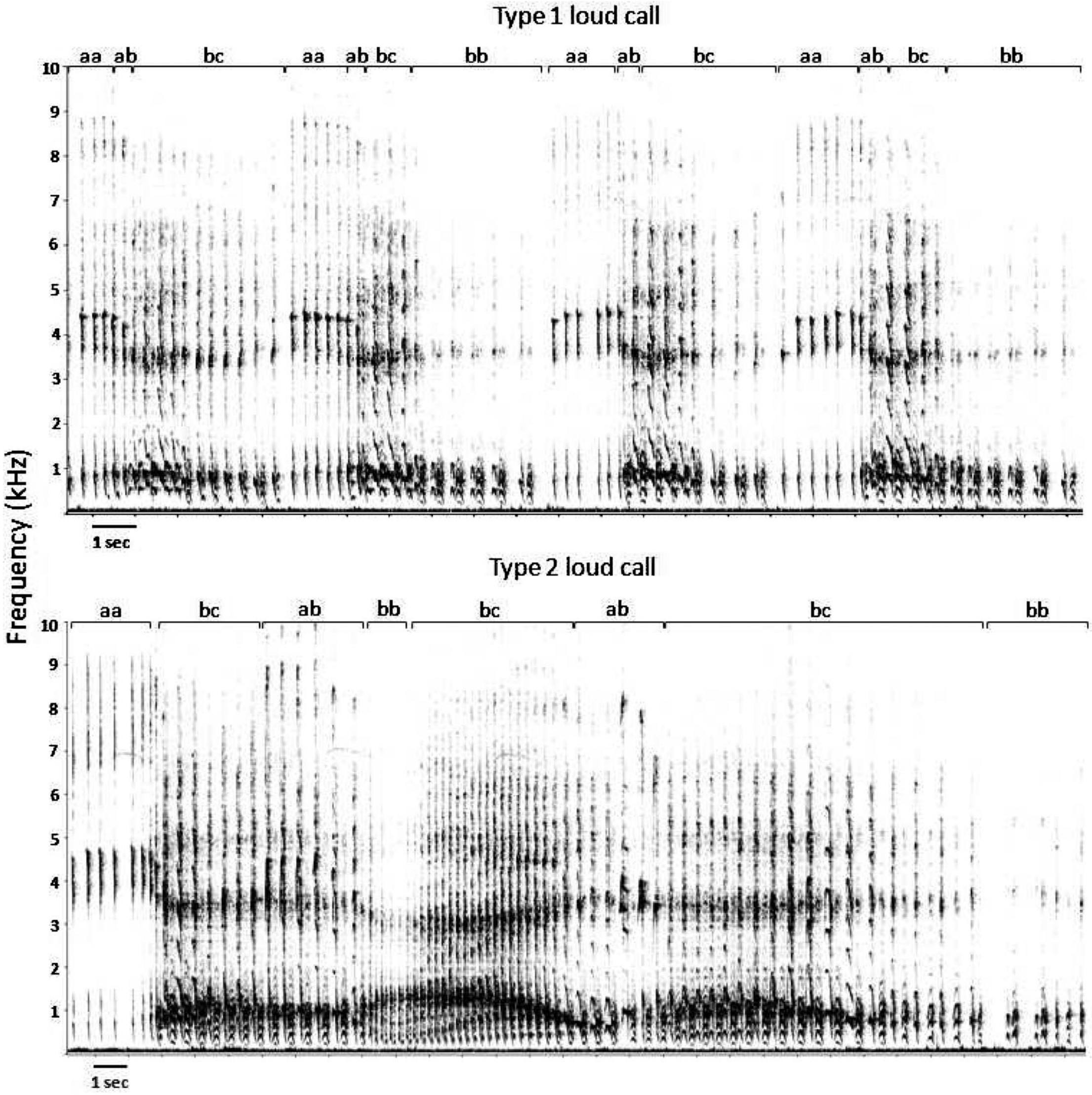

Fig. 2. Sound spectrograms of type 1 (intragroup) loud calls (top), and type 2 (intergroup) loud calls (bottom) showing the phrase sequence pattern for each call.

members were spread out (over ≥100 m) in the home range (74% vs. 23% emitted in reaction to other groups; $N = 80$), most type 2 calls were emitted in reaction to other groups (80% vs. 20% emitted spontaneously; $N = 209$), either during encounters (43%) or in response to the vocalizations of other groups (37%). Neighbor groups counter-called in 60% of the spontaneous emissions of type 2 vocalizations ($N = 41$). The focal group reacted and counter-called to neighbors' vocalizations after an average of 3 min (range: 0–29 min; $N = 209$), moving towards the call (55%), moving in the opposite direction (9%) or remaining in the same place (36%).

Type 1 calls were often performed in chorus by all group members (60%; $N = 80$). The remaining cases were performed by at least two individuals (36%) or as solos (4%). Type 1 vocalizations were usually followed by coordinated activities. Group members often came together again after being away from each other (61% of cases), emitted type 2 vocalizations in sequence (28%) and/or changed their travel direction (18%). We documented 25 events of type 1 calls of neighboring groups. When these calls were emitted from places near the territory of the focal group (15 of 25 events, or 60% of cases), group members reacted by producing type 2 or type 1 calls followed by type 2 calls. In the remaining 40% of the cases (10 of 25 events), the calls were ignored by the focal group. Therefore, type 1 calls were used mainly in a context of within-group communication, whereas type 2 calls appear to play a role in between-group communication.

In support to the joint resource defense hypothesis (prediction 1.a.), most type 2 calls ($N = 209$) were

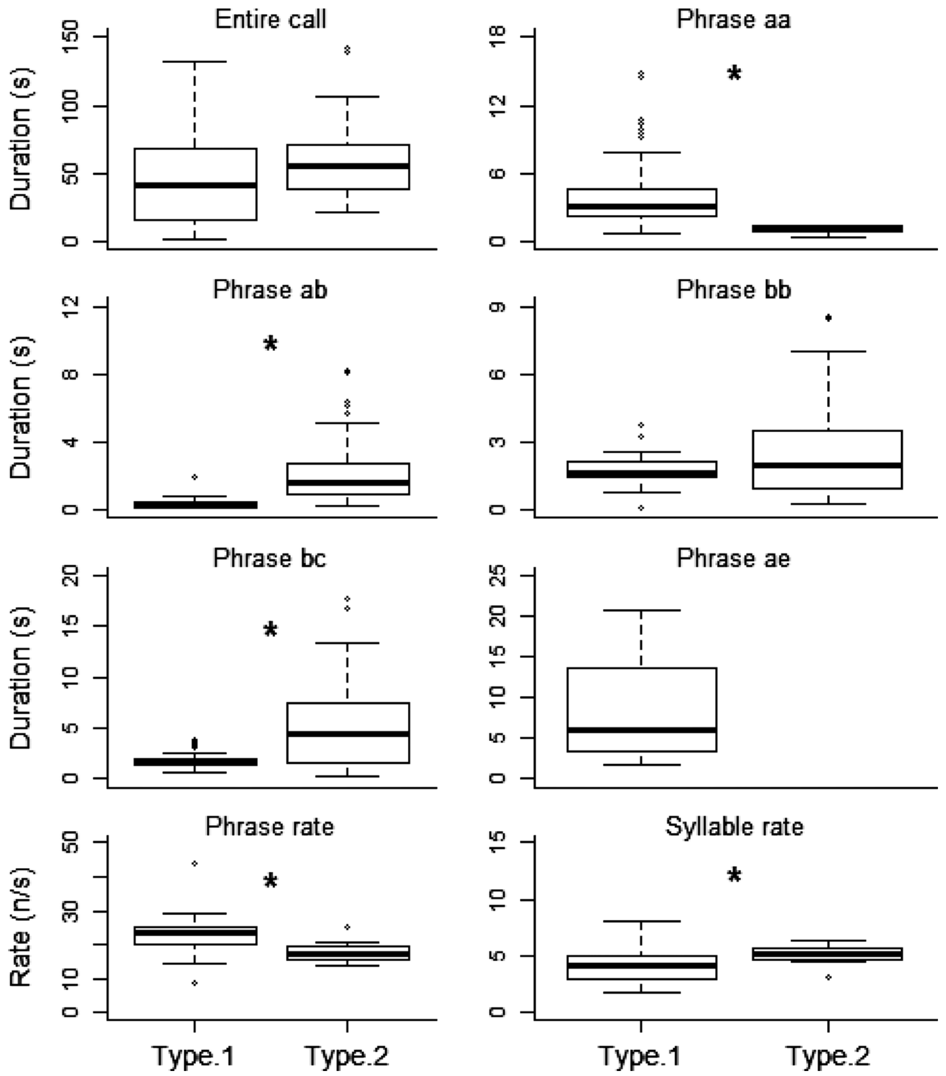

Fig. 3. Comparisons between type 1 and 2 loud calls regarding total duration (top), the duration of the phrase types (top and middle), and syllable and phrase emission rate (bottom). The horizontal line shows the median, the bottom and top of each box show the 25th and 75th percentiles (or the first and third quartiles), respectively, and vertical dashed lines shows 1.5 times the interquartile range of the data (approximately 2 standard deviations). The dots beyond the vertical bars represent the outliers and the asterisks indicate the significant differences between type 1 and 2 loud calls according to the *t*-test and Wilcoxon rank sum test (see text for details).

performed in duets by the mated pair (52%) or in choruses (46%) with the participation of young group members. Type 2 solos (2%) were emitted only by young individuals that continued calling alone after calling in chorus. The mated pair always stayed together during calling, either in physical contact, sometimes with intertwined tails, or separated by <0.5 m. As far as we are aware, this is the first observation of pair-members performing duets with inter-twined tails. It was not possible to identify the individual that started duetting, but the spectrogram inspection of 25 recordings shows that individuals often started calling together or with a short time difference (mean ± SE latency between individuals = 1.1 ± 0.4 sec, $N = 17$). This pattern support the mate defense hypothesis (prediction 2.a.).

Loud Calling and Fruit Availability

In support of the joint resource defense hypothesis (prediction 1.b.), type 2 calls were more common than expected by chance in months with higher fruit availability (61% emitted in months with higher fruit availability vs. 39% in months with low fruit availability, $N = 209$; Chi-squared test: $\chi^2 = 12.82$; df = 1, $P < 0.001$).

Loud Calling and Female Estrus

The female of group 1 gave birth between the end of July and the beginning of August in three consecutive years (2009–2011). In 2010 and 2011 the female gave birth at the beginning of August and, although copulations were not observed in this group,

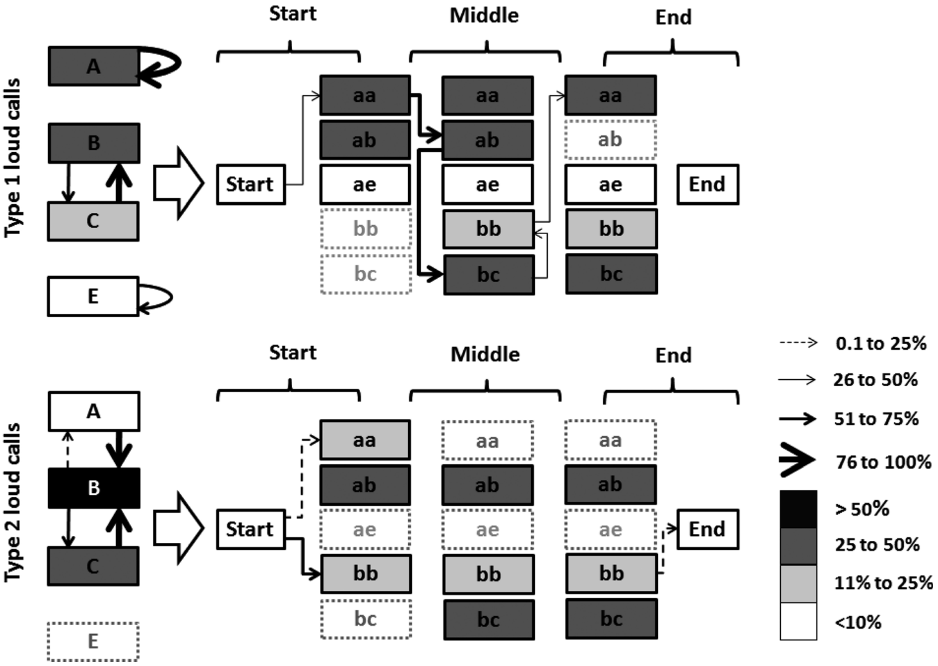

Fig. 4. Flow diagrams showing the probabilities at which syllable (left) and phrase (center) types follow from one type to another for each type of loud calls (group 1). The arrows represent the path between consecutive vocal units and the different arrows type indicates the probability of each transition as shown in the scale on the right. We only represented the transitions that happened more than expected by chance. The shading in the boxes shows the proportional contribution of each type of vocal unit to each type of loud call as shown in the scale at right. The boxes with the dashed lines indicate that a particular vocal unit did not occur in loud calls composition or at a particular position within loud calls. In the center panel the first column shows the phrases that can be used in the beginning of each type of loud vocalization; the second column shows the ones used in the middle, which often involves cyclical call emission; and the third column shows the phrases that can be used in the end of the calls. The phrases showed in the third column can finalize the call or can lead to another phrase (as shown in the middle column). Intra-group loud calls: N of syllables = 2,578, N of phrases = 252, N of calls = 13; intergroup loud calls: N of syllables = 3,767, N of phrases = 228, N of calls = 13.

the female was considered to be fertile between March and April of each year based on the estimates of gestation length. This estimate is supported by the observation of frequent copulation events in group 2 in March and April 2007. Contrary to the prediction (2.b.) based on the mate defense hypothesis, groups 1 and 2 did not vocalize more in periods when females were estimated to be fertile (Chi-square test, group 1: 90% emitted during the non-fertile period, $N = 16$ months, vs. 10% during the fertile period, N = 4 months, $\chi^2 = 11.97$, df = 1, $N = 209$, $P < 0.01$; group 2: 88% non-fertile, $N = 7$ months, vs. 12% fertile, $N = 2$ months, $\chi^2 = 6.16$, df = 1, $N = 43$, $P < 0.05$).

DISCUSSION

Here we show that black-fronted titi monkeys combine different small units (syllables) to form higher hierarchical structures (phrases) that are assembled to compose the long sequences of loud calls. This pattern is very similar to that described for red-crowned [Moynihan, 1966], ornate [Robinson, 1979b] and coppery titis [Müller & Anzenberger, 2001]. We based our analysis on lower hierarchical structures, the syllables, instead of on the calls (a subset of syllables) as performed in previous studies. Despite adopting a distinct terminology derived from this methodological difference, we were able to identify similarities between our phrase types and the calls of other species based on their descriptions and sonograms: (a) *aa* phrases are similar to "chirrups", (b) *ab* phrases are similar to "bellows", (c) *bc* phrases are similar to "pants" and "pumps", and (d) *bb* phrases are similar to "bellows" and "honks" [Moynihan, 1966; Müller & Anzenberger, 2001; Robinson, 1979b]. The fact that some phrase types were similar to more than one call type described by Robinson [1979b] and Müller & Anzenberger [2002] may derive from differences in the interval between syllables and their duration, variables believed to be also influenced by the motivation of the singing individual [Bradbury & Vehrencamp, 1998]. For instance, "pants" and "pumps" appear to be alternations of *B*s and *C*s. Therefore, the approach adopted in the present study reduces the subjectivity of the classification of vocal units. No correlates on the vocal repertoire of other species were found for *ae* phrases. This phrase type (that can be produced alone in contexts of alarm or during foraging near the ground) was rarely used by black-fronted titis during sequences of loud calls. It is possible that *ae* phrases are mainly used as a simple call in other circumstances, as the "cheep" alarm calls described for this species [Cäsar et al., 2012].

Type 1 and 2 vocalizations are composed of loud, modulated, and broadband elements (Figs. 1 and 2) with a high amplitude that likely facilitate long range transmission, and may also provide information about the location and distance of the signaler [McComb & Reby, 2005]. According to Boinski [2000], the acoustic properties of loud calls encode information that is important to monitor both neighbors and dispersed group members. As expected, type 1 and 2 vocalizations differ in structure and organization. While type 1 vocalizations show a stereotyped organization with a cyclical pattern of phrase emission, type 2 show a more complex pattern. The pooling of male and female contributions in these analyses ignored possible sex-related arrangements and may have precluded the detection of a more consistent pattern for this vocalization. Data from other primates that vocalize in duets, such as gibbons, indris, and tarsiers [Geissmann, 2002; Heimoff, 1986; Nietsch, 1999], do not support this hypothesis. Mate contribution to duetting in these species is usually associated with more conspicuous differences, such as the type of notes [Geissmann, 2002; Giacoma et al., 2010] and/or sequences [Geissmann, 2002] that are only produced by individuals of one sex. The inspection of spectrograms of black-fronted titi duets revealed that both male and female contribute similarly by emitting the same syllable and phrase types, as observed in coppery and ornate titis [Müller & Anzenberger, 2001; Robinson, 1979b].

Type 2 vocalizations were emitted mostly in complex behavioral contexts, such as during intergroup interactions. The diversity of contexts and reactions may reflect motivational differences and be associated to signals with particular structures [Bradbury & Vehrencamp, 1998]. Therefore, it is not possible to rule out the hypothesis that type 2 vocalizations represent a set of distinct signals with different meanings. Alternatively, these calls may also represent signals whose meaning depends on what neighbors are singing [Vehrencamp, 2001]. The behavior of producing a similar signal type in response to a rival's signal is termed "matching" [Krebs et al., 1981] and is a mechanism commonly used for directing signals to a particular rival in birds. The extent of vocal matching can reveal the signaler's intention or motivational level and has been shown to function in territorial defense [Beecher et al., 2000; Krebs et al., 1981; Vehrencamp, 2001]. The fact that type 2 vocalizations were used in more complex contexts may explain their less stereotyped organization. Matching behavior has never been evaluated in primates, as far as we are aware. Such an investigation could provide new insights on the complexity of black-fronted titi monkey vocalizations used for between-group communication.

The contexts of the structurally distinct type 1 and 2 vocalizations are compatible with their respective roles in intra- and intergroup communication. Type 1 vocalizations resemble the "short sequences" used by ornate titi groups while approaching territory boundaries, during and after intergroup encounters [Robinson, 1979b, 1981]. Robinson [1979b, 1981] associated these vocalizations with contexts of intergroup communication because the short sequences emitted by one group often elicited the response of nearby groups. However, the use of these calls during the approach to, and departure from, territory boundaries suggests that they also may serve to coordinate group movement as we observed at Serra do Japi. Because these vocalizations can be heard over long distances, they can reveal the group's location and, thereby, be overheard by neighbors and elicit interactions between nearby groups [McComb et al., 2000]. Group 1, for example, used type 1 vocalizations to coordinate its activity and reunite with dispersed group members. Typically, this group usually reacted to this type of vocalization when the calling neighbor group was nearby. Although the use of long-range vocalizations for intragroup communication is often superfluous, it is useful when group members are foraging spread over the home range and out of each other's sight.

The type 2 loud calls described in this study resemble the "long sequences" of coppery and ornate titis [Müller & Anzenberger, 2002; Robinson, 1979b] usually associated with joint territorial advertisement, especially as duets [Kinzey & Robinson, 1983; Mason, 1968; Robinson, 1979b, 1981]. In black-fronted titis it also seems to play the same role. They were commonly emitted as duets or choruses during intergroup interactions, suggesting a common interest of group members in defending their shared resources and thereby giving support to the joint resource defense hypothesis. A similar pattern was found in indris (*Indri indri*), a species where the male, female and juveniles produce choruses as a mechanism of territorial advertisement when a group approaches or enters another's territory [Pollock, 1986].

This study produced only weak support for the hypothesis that loud calls used for intergroup communication plays a role in mate defense [Hall, 2004; Levin, 1996; Robinson, 1981]. Unfortunately, our small sample size (a single group plus some additional information from another) does not allow us to make more definitive interpretations. Therefore, future studies based on larger sample sizes will help to identify the behavioral contexts of this species' vocalizations. Although black-fronted titi duets are sometimes initiated by only one of the participants in accordance with prediction 2.a., contrary to prediction 2.b. the frequency of type 2 vocalizations was lower in months of likely female fertility. On the other hand, they were more frequent in periods of higher availability of defensible critical resources, such as fruits, lending support to the joint resource defense hypothesis [Maher & Lott, 1995]. In territorial gibbons the highest calling rate also coincided with periods of food abundance [Bartlett, 2007]. The coincidence in the period of female fertility with the season of low fruit availability (mean = 1.7 < overall monthly mean = 2.3) compromises the analysis of the contribution of each factor to the pattern of call frequency. Apparently, fruit availability overcomes any effect of mate defense on the vocal behavior of black-fronted titi monkeys at Serra do Japi. Comparative studies on sites where female fertility and fruit availability exhibit a different temporal relationship might help to disentangle the effects of social and ecological factors. Controlled playback experiments simulating invasions by solitary individuals and mated pairs would also be useful for evaluating this hypothesis. No interaction of study groups with solitary individuals was observed during this study to evaluate the reactions of males and females to same-sex rivals.

In sum, this is the first description and analysis of the functions of loud calls of black-fronted titi monkeys. We showed that titi's use structurally distinct vocalizations for within- and between-group communication and that the calls used with the latter role are cooperative displays emitted by the mated pair and other group members to regulate the access of neighbor groups to important seasonal food resources, such as fruits. On the other hand, we found only weak support to the mate defense hypothesis.

ACKNOWLEDGMENTS

We thank the Municipal Secretariat of Planning and Environment of Jundiaí and the Forest Institute of the State of Sao Paulo Environment Department for the permission to conduct the this research at Serra do Japi Municipal Reserve and to record the monkeys at Cantareira State Park, respectively. We also thank the Scientific Breeding Center of Companhia Brasileira de Metalurgia e Mineração (CBMM) and the Municipal Zoos of Bauru and Guarulhos for allowing us to record the vocalizations of captive monkeys. We thank P.E.C. Peixoto, R.G.T. Cunha, C.B. Araújo, P.I. Mauro, L.F.T.R. Pereira, L.R. Jorge and two anonymous reviewers for valuable comments and suggestions on earlier versions of this paper. We are also grateful to C. Gestich and M. Nagy-Reis for their assistance in the field and suggestions, and to M. Corbo for the instructions on recording techniques. This research was funded by FAPESP and CAPES. We also received field equipment from Idea Wild. Bioacoustic analyses were supported in part by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Canada Foundation for Innovation, and the Government of Ontario to DJM. JCBM also thanks the support of the Brazilian National Research Council (CNPq #303154/2009-8).

REFERENCES

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 40:227–267.

Bakeman R, Quera V. 2011. Sequential analysis and observational methods for the behavioral sciences. Cambridge, UK: Cambridge University Press. p 212.

Bakeman R, Robinson BF, Gnisci A. 2010. Interactive log-linear analysis and contingency table manipulation with ILOG 3.0. Available online at: http://www2.gsu.edu/~psyrab/gseq/Download.html

Bartlett TQ. 2007. The Hylobatidae: small apes of Asia. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. Primates in perspective. New York, NY: Oxford University Press. p 274–289.

Beecher MD, Campbell SE, Burt JM, Hill CE, Nordby JC. 2000. Song-type matching between neighbouring song sparrows. Animal Behaviour 59:21–27.

Boinski S. 2000. Social manipulation within and between troops mediates primates group movement. In: Boinski S, Garber PA, editors. On the move: how and why animals travel in groups. Chicago, IL: The University of Chicago Press. p 421–469.

Bradbury JW, Vehrencamp SL. 1998. The principles of animal communication. Sunderland, MA: Sinauer. p 882.

Cäsar C, Byrne RW, Young RJ, Zuberbühler K. 2012. The alarm call system of wild black-fronted titi monkeys, *Callicebus nigrifrons*. Behavioral Ecology and Sociobiology 66:653–667.

Caselli CB, Setz EZF. 2011. Feeding ecology and activity pattern of black-fronted titi monkeys (*Callicebus nigrifrons*) in a semideciduous tropical forest of southern Brazil. Primates 52:351–359.

Cowlishaw G. 1992. Song function in gibbons. Behaviour 121:131–153.

da Cunha RGT, Byrne RW. 2006. Roars of black howler monkeys (*Alouatta caraya*): evidence for a function in inter-group spacing. Behaviour 143:1169–1199.

Defler TR. 2004. Primates of Colombia. Bogotá, CO: Conservación Internacional.

Gamba M, Giacoma G. 2005. Key issues in the study of primate acoustic signals. Journal of Anthropological Science 83:61–87.

Geissmann T. 2002. Duet-splitting and the evolution of gibbon songs. Biological Reviews 77:57–76.

Giacoma C, Sorrentino V, Gamba M. 2010. Sex differences in the song of *Indri indri*. International Journal of Primatology 31:539–551.

Grafe TU, Bitz JH. 2004. Functions of duetting in the tropical boubou, *Laniarius aethiopicus*: territorial defense and mutual mate guarding. Animal Behaviour 68:193–201.

Hall ML. 2004. A review of hypotheses for the functions of avian duetting. Behavioral Ecology and Sociobiology 55:415–430.

Heimoff EH. 1986. Convergence in the duetting of monogamous Old World primates. Journal of Human Evolution 15:51–59.

de Luna AG, Sanmiguel R, Di Fiore A, Fernandez-Duque E. 2010. Predation and predation attempts on red titi monkeys (*Callicebus discolor*) and equatorial sakis (*Pithecia aequatorialis*) in Amazonian Ecuador. Folia Primatologica 81:86–95.

Kinnaird M. 1992. Phenology of flowering and fruiting of an East African riverine forest ecosystem. Biotropica 24:187–194.

Kinzey WG. 1997. *Callicebus*. In: Kinzey WG, editor. New World primates. Ecology, evolution and behaviour. Hawthorne, NY, USA: Aldine de Gruyter. p 213–221.

Kinzey WG, Becker M. 1983. Activity pattern of the masked titi monkey, *Callicebus personatus*. Primates 24:337–343.

Kinzey WG, Robinson JG. 1983. Intergroup loud calls, range size, and spacing in *Callicebus torquatus*. American Journal of Physical Anthropology 60:539–544.

Kinzey WG, Rosenberger AL, Heisler PS, Prowse DL, Trilling JS. 1977. A preliminary field investigation of the yellow handed titi monkey, *Callicebus torquatus torquatus*, in northern Peru. Primates 18:159–181.

Kitchen DM. 2004. Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Animal Behaviour 67:125–139.

Krebs JR, Ashcroft R, Vanorsdol K. 1981. Song matching in the great tit *Parus major*. Animal Behaviour 29:918–923.

Levin RN. 1996. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. II. Playback experiments. Animal Behaviour 52:1107–1117.

Maher CR, Lott DF. 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. Animal Behaviour 49:1581–1597.

Mason WA. 1966. Social organization of the South American monkey, *Callicebus moloch*: A preliminary report. Tulane Studies in Zoology 13:23–28.

Mason WA. 1968. Use of space by *Callicebus*. In: Jay PC, editor. Primates: studies in adaptation and variability. New York, NY: Holt, Rinehart and Winston. p 200–216.

McComb K, Reby D. 2005. Vocal communication networks in large terrestrial mammals. In: McGregor PK, editor. Animal communication networks. Cambridge, UK: Cambridge University Press. p 372–389.

McComb K, Moss C, Sayialel S, Baker L. 2000. Unusually extensive networks of vocal recognition in African elephants. Animal Behaviour 59:1103–1109.

Moynihan M. 1966. Communication in the titi monkey, *Callicebus*. Journal of Zoology 150:77–127.

Müller AE, Anzenberger G. 2002. Duetting in the titi monkey *Callicebus cupreus*: structure, pair specificity and development of duets. Folia Primatologica 73:104–115.

Nietsch A. 1999. Duet vocalizations among different populations of Sulawesi tarsiers. International Journal of Primatology 20:567–583.

Oliveira DA, Ades C. 2004. Long-distance calls in Neotropical primates. Anais da Academia Brasileira de Ciências 76: 393–398.

Palombit RA. 1994a. Dynamic pair bonds in Hylobatids: implications regarding monogamous social systems. Behaviour 128:65–101.

Palombit RA. 1994b. Extra-pair copulations in a monogamous ape. Animal Behaviour 47:721–723.

Pollock JI. 1986. The song of the indris (*Indri indri*; Primates: Lemuroidea): natural history, form and function. International Journal of Primatology 7:225–264.

Price EC, Piedade HM. 2001. Ranging behavior and intraspecific relationships of masked titi monkeys (*Callicebus personatus personatus*). American Journal of Primatology 53:87–92.

R Development Core Team. 2011. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051- 07-0. Available online at: http://www.R-project.org/

Reichard U, Sommer V. 1997. Group encounters in wild gibbons (*Hylobates lar*): agonism, affiliation, and the concept of infanticide. Behaviour 134:1135–1174.

Robinson JG. 1979a. Vocal regulation of use of space by groups of titi monkeys *Callicebus moloch*. Behavioral Ecology and Sociobiology 5:1–15.

Robinson JG. 1979b. An analysis of the organization of vocal communication in the titi monkey *Callicebus moloch*. Zeitschrift fur Tierpsychologie 49:381–405.

Robinson JG. 1981. Vocal regulation of inter- and intra-group spacing during boundary encounters in the titi monkey, *Callicebus moloch*. Primates 22:161–172.

Sokal RR, Rohlf FJ. 1995. Biometry. New York, Ny: W.H. Freeman and company. p 887.

Sun C, Kaplin BA, Kristensen KA, et al. 1996. Tree phenology in a tropical montane forest in Rwanda. Biotropica 28: 668–681.

Valeggia CR, Mendoza SP, Fernandez-Duque E, Mason WA, Lasley B. 1999. Reproductive biology of female titi monkeys (*Callicebus moloch*) in captivity. American Journal of Primatology 47:183–195.

van Roosmalen MGM, van Roosmalen T, Mittermeier RA. 2002. A taxonomic review of the titi monkeys, genus *Callicebus* Thomas, 1903, with the description of two new species, *Callicebus bernhardi* and *Callicebus stephennashi*, from Brazilian Amazonia. Neotropical Primates 10:1–52.

Vehrencamp SL. 2001. Is song-type matching a conventional signal of aggressive intentions? Proceedings of the Royal Society of London, Series B: Biological Sciences 268: 1637–1642.

Venables WN, Ripley BD. 2002. Modern applied statistics with S. Fourth Edition. New York, NY: Springer. ISBN 0-387-95457-0.

Wich SA, Nunn CL. 2002. Do male long-distance calls function in mate defense? A comparative study of long-distance calls in primates. Behavioral Ecology and Sociobiology 52:474–484.

Wilson ML, Hauser MD, Wrangham RW. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Animal Behaviour 61:1203–1216.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.